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Morphological and morphometric variations in Middle and Late Pleistocene *Microtus arvalis* and *Microtus agrestis* populations:

chronological insight, evolutionary trends and palaeoclimatic and palaeoenvironmental inferences

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FAIG CONSTAR que aquest treball, titulat "Morphological and morphometric variations in Middle and Late Pleistocene *Microtus arvalis* and *Microtus agrestis* populations: chronological insight, evolutionary trends and palaeoclimatic and palaeoenvironmental inferences", que presenta Elisa Luzi per a l'obtenció del títol de Doctor, ha estat realitzat sota la meva direcció al Departament d'Història i Història de l'Art d'aquesta universitat.

Aquesta tesis doctoral opta a la menció de Doctorat Internacional

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Tarragona, 06/02/2018

El director de la tesi doctoral

Dr. Juan Manuel López-García

> “A famous palaeontologist once remarked that mammalian history,
> as known from fossils, featured little more than the mating of teeth
> to produce slightly modified descendant teeth.”
> S. J. Gould

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ABSTRACT

For this PhD thesis, Middle and Late Pleistocene populations of *M. arvalis* and *M. agrestis* coming from 13 sites of the Iberian Peninsula,14 sites of the Italian Peninsula, nine of the Carpathian Basin, three of Croatia and two of Belgium were analysed from a morphological and morphometric point of view, in order to underlie similarities and differences among them, possible common patterns of evolution and the influence of climatic and environmental conditions on their variations. Comparing samples from different chronologies and different geographic provenance, it was possible to refine the chronological attributions of palaeontological and archaeological sites of the Mediterranean region and to identify divergent lineages, early signs of speciation, immigration events and displacement of populations. Furthermore, we propose the use of a new index, L_{agr}/L_{arv}, to quantify the variations in size of *M. agrestis* and *M. arvalis* in relation to each other. This index proved to be an excellent indicator of the general humidity level and allow to detect oscillations and variations in the environmental conditions in the surroundings of a given sites.

RESUMEN

Para esta tesis doctoral, las poblaciones de *M. arvalis* y *M. agrestis* del Pleistoceno Medio y Superior procedentes de 13 yacimientos de la Península Ibérica, 14 de la Península Italiana, nueve de la Cuenca de los Cárpatos, tres de Croacia y dos de Bélgica han sido analizadas desde una perspectiva morfológica y desde un punto de vista morfométrico. Este estudio se ha llevado a cabo con la finalidad de destacar las similitudes y diferencias entre las diferentes poblaciones de ambas especies, posibles patrones comunes de evolución y la influencia de las condiciones climáticas y ambientales en sus variaciones poblacionales. Comparando material de diferentes cronologías y diferente procedencia geográfica, ha sido posible refinar las atribuciones cronológicas de los yacimientos paleontológicos y arqueológicos de la región mediterránea e identificar linajes divergentes, muestras tempranas de especiación, eventos de migración y desplazamiento de poblaciones. Además, proponemos el uso de un nuevo índice, Lagr / Larv, para cuantificar las variaciones entre sí del tamaño de *M. agrestis* y *M. arvalis*. Este índice ha demostrado ser un excelente indicador del nivel general de humedad y, permite detectar oscilaciones y variaciones en las condiciones ambientales en los alrededores de un yacimiento determinado.

RESUM

Per aquesta tesi doctoral, les poblacions de *M. arvalis* i *M. agrestis* procedents de 13 jaciments de la Península Ibèrica, 14 de la Península italiana, nou de la Conca dels Càrpats, tres de Croàcia i dos de Bèlgica han estat analitzats des d'un punt de vista morfològic i morfomètric. Aquest estudi s'ha realitzat per tal d' accentuar similituds i diferències entre les poblacions d'ambdós especies, possibles patrons d'evolució comuns i la influència de les condicions climàtiques i ambientals sobre les seves variacions poblacionals. Comparant material de diferents cronologies i diferents procedències geogràfiques, s'han pogut refinar les atribucions cronològiques dels jaciments paleontològics i arqueològics de la regió mediterrània i identificar llinatges divergents, signes inicials d'especiació, esdeveniments de migració i desplaçament de poblacions. A més, es proposa l'ús d'un nou índex, Lagr / Larv, per quantificar les variacions entre si en la talla de *M. agrestis* i *M. arvalis*. Aquest índex ha demostrat ser un excel·lent indicador del nivell general d'humitat i permet detectar oscil·lacions i variacions en les condicions ambientals en l'entorn d'un jaciment determinat.

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Luzi, E., López-García, J.M., Blasco, R., Rivals, F. and Rosell, J. 2017: 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). Journal of Mammalian Evolution 24, 495–503.

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Berto, C., **Luzi, E.**, Canini, G.M., Guerreschi, A. and Fontana, F. 2017: Climate and landscape in Italy during Late Epigravettian. The Late Glacial small mammal sequence of Riparo Tagliente (Stallavena di Grezzana, Verona, Italy). Quaternary Science Reviews.

López-García, J.M., **Luzi, E.** and Peresani, M. 2017: Middle to Late Pleistocene environmental and climatic reconstruction of the human occurrence at Grotta Maggiore di San Bernardino (Vicenza, Italy) through the small-mammal assemblage. Quaternary Science Reviews 168, 42–54.

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Berto, C., Bertè, D., **Luzi, E.**, López-García, J.M., Pereswiet-Soltan, A. and Arzarello, M. 2016: Small and large mammals from the Ciota Ciara cave (Borgosesia, Vercelli, Italy): An Isotope Stage 5 assemblage. Comptes Rendus Palevol 15, 669–680.

López-García, J.M., **Luzi, E.**, Furió, M., Susanna, I., Llenas, M. and Madurell-Malapeira, J. 2016: Biochronological data for the Middle pleistocene site of Grotte de la Carrière (Lachambre karstic complex, Corneilla-de-Conflent, Eastern Pyrenees, Southern France) inferred from the small-mammal assemblage. Quaternaire 27(2), 133-138.

SUMMARY

This PhD thesis is composed by 6 main chapters and 3 appendixes:

- Chapter 1: INTRODUCTION

In this chapter, the two species that are the focus of this work, *Microtus arvalis* and *Microtus agrestis*, are presented with the description of the distribution range, a brief phylogenetic history, the principal morphological and morphometric diagnostic characters and the ecological requirements of each species. The main objectives of this study are also listed.

- Chapter 2: MANUSCRIPTS

In this chapter, four papers already published, accepted or submitted for publication in international peer-review journal with IF are presented. The first one has been published on-line by *Historical Biology* and concerns populations of *M. arvalis* and *M. agrestis* of late Middle and Late Pleistocene of south-western Europe; the second, a case study on populations from the Late Pleistocene site of Teixoneres, was published in the *Journal of Mammalian Evolution*; the third and fourth, regarding populations from Italy and Hungary respectively, are currently under review at *PALAIOS* and *Lethaia* journals.

- Chapter 3: OTHER STUDIED SITES

In this chapter, data that have not been submitted for publication from Croatian, Italian and Belgian sites are presented, together with a brief discussion and conclusions.

- Chapter 4: GENERAL DISCUSSION

This section is divided in three parts: one regarding the morphological and morphometric variations undergone by *M. agrestis* during late Middle and Late Pleistocene in the different geographic regions, another one regarding the variations undergone by *M. arvalis* and the last one linking the relative oscillations of size of the two species to the climatic and environmental conditions that characterized the sites of provenance of the samples.

- Chapter 5: GENERAL CONCLUSIONS

The most important conclusions obtained from this study are presented.

- Chapter 6: FUTURE PROSPECTIVES

Short- and long-term objectives to expand this study are described.

- Chapter 7: REFERENCES

List of bibliographic references.

APPENDIX 1 - presents the tables with geographic, chronological and climatic information about the sites and complete measurements taken on the first lower molars of *Microtus arvalis* and *Microtus agrestis* for each site.

APPENDIX 2 – presents the papers in their published format:

Luzi, E. and López-García, J.M. 2017: Patterns of variation in *Microtus arvalis* and *Microtus agrestis* populations from Middle to Late Pleistocene in southwestern Europe. *Historical Biology*, 1–9.
doi: 10.1080/08912963.2017.1375490.

Luzi, E., López-García, J.M., Blasco, R., Rivals, F. and Rosell, J. 2017: 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). *Journal of Mammalian Evolution 24*, 495–503.
doi: 10.1007/s10914-016-9355-8.

APPENDIX 3 – present the papers not included in the dissertation but that contributed to the collection of the data.

Berto, C., Boscato, P., Boschin, F., **Luzi, E**. and Ronchitelli, A. 2017: Paleoenvironmental and paleoclimatic context during the Upper Palaeolithic (late Upper Pleistocene) in the Italian Peninsula. The small mammal record from Grotta Paglicci (Rignano Garganico, Foggia, Southern Italy). *Quaternary Science Reviews 168*, 30–41.
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Berto, C., **Luzi, E**., Canini, G.M., Guerreschi, A. and Fontana, F. 2017: Climate and landscape in Italy during Late Epigravettian. The Late Glacial small mammal sequence of Riparo Tagliente (Stallavena di Grezzana, Verona, Italy). *Quaternary Science Reviews*.
doi: 10.1016/j.quascirev.2017.07.022.

López-García, J.M., **Luzi, E**. and Peresani, M. 2017: Middle to Late Pleistocene environmental and climatic reconstruction of the human occurrence at Grotta Maggiore di San Bernardino (Vicenza, Italy) through the small-mammal assemblage. *Quaternary Science Reviews 168*, 42–54.
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López-García, J.M., Blain, H.-A., Lozano-Fernández, I., **Luzi, E**. and Folie, A. 2017: Environmental and climatic reconstruction of MIS 3 in northwestern Europe using the small-mammal assemblage from Caverne Marie-Jeanne (Hastière-Lavaux, Belgium). *Palaeogeography, Palaeoclimatology, Palaeoecology 485*, 622–631.
doi:10.1016/j.palaeo.2017.07.017

Berto, C., Bertè, D., **Luzi, E**., López-García, J.M., Pereswiet-Soltan, A. and Arzarello, M. 2016: Small and large mammals from the Ciota Ciara cave (Borgosesia, Vercelli, Italy): An Isotope Stage 5 assemblage. *Comptes Rendus Palevol 15*, 669–680.
doi:10.1016/j.palaeo.2017.07.017

López-García, J.M., **Luzi, E**., Furió, M., Susanna, I., Llenas, M. and Madurell-Malapeira, J. 2016: Biochronological data for the Middle pleistocene site of Grotte de la Carrière (Lachambre karstic complex, Corneilla-de-Conflent, Eastern Pyrenees, Southern France) inferred from the small-mammal assemblage. *Quaternaire 27(2)*, 133-138.
doi: 10.4000/quaternaire.7601.

1. INTRODUCTION

The arvicoline rodents (Arvicolinae, Rodentia) are very abundant in the European Pleistocene (ca. 2.58 -0.0117 Ma) fossil record: due to their wide Holartic geographic distribution, their rapid evolution, and their well-documented dental patterns, they function as chronological and biochronological markers (Heinrich 1990; Cuenca-Bescós & Laplana 1995; Maul 2001; López-García *et al.* 2015, among others), allowing the construction of biostratigraphic sequences and the correlations of faunas from different regions of the continent (Kretzoi 1953; Chaline 1972; Jánossy 1986; Horácev & Lozek 1988; Fejfar *et al.* 1997; Maul *et al.* 1998; Maul & Markova 2007; Sala & Masini 2007; Cuenca-Bescós *et al.* 2016, among others).

Furthermore, small mammals in general (including insectivores and bats), and rodents in particular, have been used as proxy for palaeoclimatic and palaeoenvironmental reconstructions, especially in studies concerning Middle and Late Pleistocene (Horácev & Lozek 1988; Gasparik 1993; Pazonyi 2006; Royer *et al.* 2016; Bañuls-Cardona *et al.* 2017; Berto *et al.* 2017; López-García *et al.* 2017, among others). Small mammals have a really close relationship with the local climatic and environmental conditions of the ecosystem they live in (Graham *et al.* 1996; Hernández Fernández 2001) and, because their accumulation in archaeological and palaeontological sites is often the results of opportunistic birds of prey hunting, they reflect local conditions in the surrounding of a given site without larger bias (Andrews 1990; Fernández-Jalvo *et al.* 2016).

This PhD thesis is focused specifically on the study of the common vole *Microtus arvalis* and the field vole *Microtus agrestis*. These two species were chosen because they are widespread and consistently present in the fossil record of late Middle and Late Pleistocene (ca. 420 – 11 ka) in Europe (Chaline 1972; Jánossy 1986; Kowalski 2001; Maul & Markova 2007; Sala & Masini 2007; Cuenca-Bescós *et al.* 2010; Markova & Puzachenko 2016, among others), therefore providing excellent samples for comparison between different chronologies and different geographic areas. Previous in-depth studies on morphology and morphometry of *M. arvalis* and *M. agrestis* have been conducted on fossil material from Late Pleistocene of Poland (Nadachowski 1982) and Croatia (Mauch Lenardić 2007) and from Middle and Late Pleistocene of France (Chaline 1972) and Ukraine (Rekovets & Nadachowski 1995). Applying these methodologies to our study, we analysed morphologies and morphometrics of fossil populations of common and field voles, taking as starting point the information available about living populations.

1.1. The common vole *Microtus arvalis* (Pallas, 1778): phylogeny, distribution range and habitat preferences

The common vole *Microtus arvalis* has a wide range, extending from Spain to Central Russia. The *arvalis*-group represent a well-supported sub-lineage in the *Microtus* genus (Jaarola *et al.* 2004; Martínková & Moravec 2012). In Europe, the *M. arvalis* is currently divided in six lineages that have probably separated after the Last Glacial Maximum (LGM) and that start showing signs of reproductive isolation (Heckel *et al.* 2005; Beysard & Heckel 2014; Beysard *et al.* 2015; Stojak *et al.* 2015, 2016).

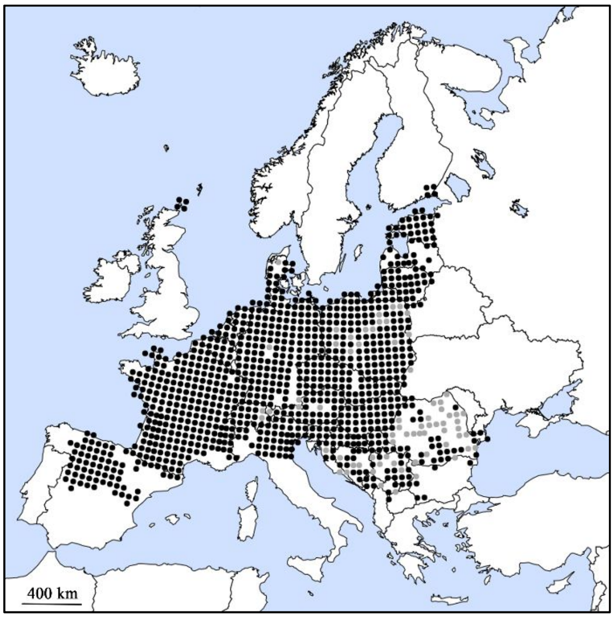


Figure 1.1.1. Distribution range of *Microtus* arvalis in Europe. Black dots: post-1970. Grey dots: pre-1970. Data from the EMMA database maintained by the Societas Europaea Mammalogica.

It occurs across western, central and eastern Europe (Fig.1.1.1) in Andorra, Austria, Belarus, Belgium, Bosnia and Herzegovina; Bulgaria; Croatia; Czech Republic; Denmark; Estonia; Finland; France; Germany; Hungary; northern Italy including the Po Plain; Latvia; Liechtenstein; Lithuania; Luxembourg; Macedonia, Moldova; Montenegro; Netherlands; Poland; Portugal; Romania; Russian Federation; Serbia; Slovakia; Slovenia; northern and central Spain; Switzerland; Ukraine. Isolated populations are present in the Guernsey Island and Orkney Islands (United Kingdom) while it is absent from most of southern Europe, Fennoscandia, northern Russia and Great Britain (Niethammer & Krapp 1982; Haynes *et al.* 2003; Wilson & Reeder 2005*a*; Martinkova *et al.* 2013; Cucchi *et al.* 2014; Hernández *et al.* 2017; IUCN 2017).

It is commonly found in open habitats, up to 2600 m a.s.l. It occurs in grassland, steppe, open woodland and forest edges, pastures, and meadows with short coverage. Due to its borrowing habits, *M. arvalis* tends to avoid areas with high groundwater level (Mitchell-Jones *et al.* 1999; IUCN 2017).

It does not avoid high-anthropogenic habitats, such as agricultural areas and cereals crops, where it often represents a pest (Luque-Larena *et al.* 2013). Laboratory experiments show that growing larger, the common vole develops a mechanism that reduce its need for water and that this need does not increase with increased temperature, making it better adapted to dry open environment with direct insolation and scarce groundwater supply. Furthermore, its burrowing habits make it avoid wet soil. Finally, its size, its aggressive behaviour toward other species and its high territoriality make it a strong competitor for other rodents, such as *M. arvalis*, the root vole *M. oeconomus* or the bank vole *Clethrionomys glareolus*, that can be led to local disappearance (Grant 1972; Dienske 1979; De Jonge 1983; Ligtvoet & Wijngaarden 1994).

1.2. The field vole *Microtus agrestis* (Linnaeus, 1761): phylogeny, distribution range, and habitat preferences

The field vole *Microtus agrestis* is a widespread Palaearctic species, ranging from western Europe to the Baikal Lake in south-east Siberia. Its position in the genus *Microtus* (Arvicolinae, Rodentia) tree is problematic, since it does not always cluster with Palaearctic groups, but with Nearctic ones, and it has been alternatively related to the genus *Microtus*, *Agricola*, *Lasiopodomys* or *Neodon* (Jaarola *et al.* 2004; Robovský *et al.* 2008; Martínková & Moravec 2012). This instability, also shown by the Iberian vole *Iberomys cabrerae* and the narrow-headed vole *M. gregalis* suggest that *M. agrestis*, like the two species cited previously, might have split early from the other *Microtus* species and had a long independent evolutionary history. Phylogenetic and phylogeographic studies show that in Europe the species is currently composed by at least three different lineages, highly divergent, one of which can be considered as a cryptic species (Jaarola & Searle 2004; Giménez *et al.* 2012; Paupério *et al.* 2012).

The field vole is widely distributed in temperate and boreal regions of Europe (Fig. 1.2.1) and it is present in Andorra, Austria, Belarus, Belgium, Bosnia and Herzegovina, Croatia, Czech Republic, Denmark, Estonia, Finland, France, Germany, Hungary, northern Italy, Latvia, Liechtenstein, Lithuania, Luxembourg, Moldova, Montenegro, Netherlands, Norway, Poland, northern and central Portugal, Romania, Russian Federation, northern Serbia, Slovakia, Slovenia, Pyrenees and north-western Spain, Sweden, Switzerland, Ukraine, and United Kingdom, but absent from Ireland, Iceland and southernmost areas of the continent (Niethammer & Krapp 1982; Wilson & Reeder 2005*b*; IUCN 2017; Mathias *et al.* 2017).

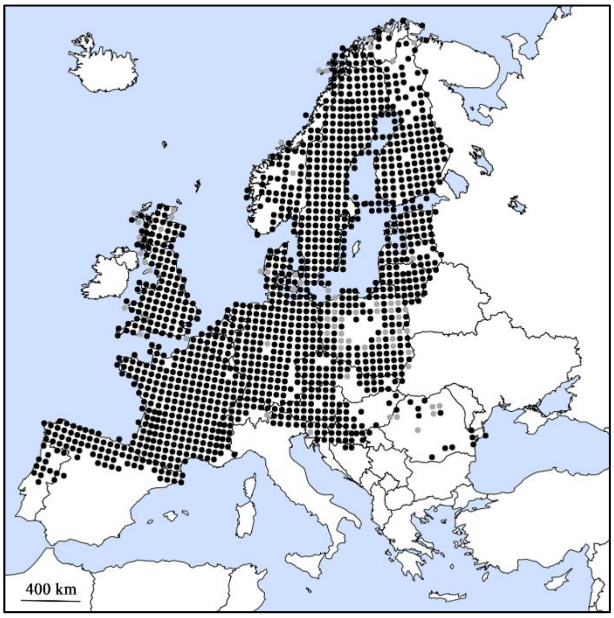


Figure 1.2.1. Distribution range of *Microtus agrestis* in Europe. Black dots: post-1970. Grey dots: pre-1970. Data from the EMMA database maintained by the Societas Europaea Mammalogica.

It is commonly found in moist habitats, with dense ground cover, up to an elevation of 2100 m a.s.l. It occurs in grasslands, upland heaths, marshes, peat-bogs and river-banks and to a lesser extent also in woodlands, dunes and hedgerows, tending to prefer damp areas while avoiding high-anthropogenic habitats and heavily grazed areas (Mitchell-Jones *et al.* 1999; IUCN 2017). Laboratory studies show that the need of water in *M. agrestis* is directly related to the size of individuals and that this need also increase with temperature. Furthermore, it tends to spend more time exploring its territory than *M. arvalis* (Hansson 1971; Dienske 1979; De Jonge 1983). The preference for moist habitats with dense and tall ground cover respond to these needs, because it provides a sheltered environment, protected from predators, shadowed from direct sun and where superficial water would dry slower.

1.3. Morphological criteria for the identification of *Microtus arvalis* and *Microtus agrestis* in the fossil record

The main instrument for the identification of fossil material of *Microtus arvalis* and *Microtus agrestis* is the comparison with morphological and morphometric characters of living individuals of these species. It is very rare to find in the fossil record complete mandibles, palates or skulls, therefore the most commonly found elements that bear diagnostic features are teeth.

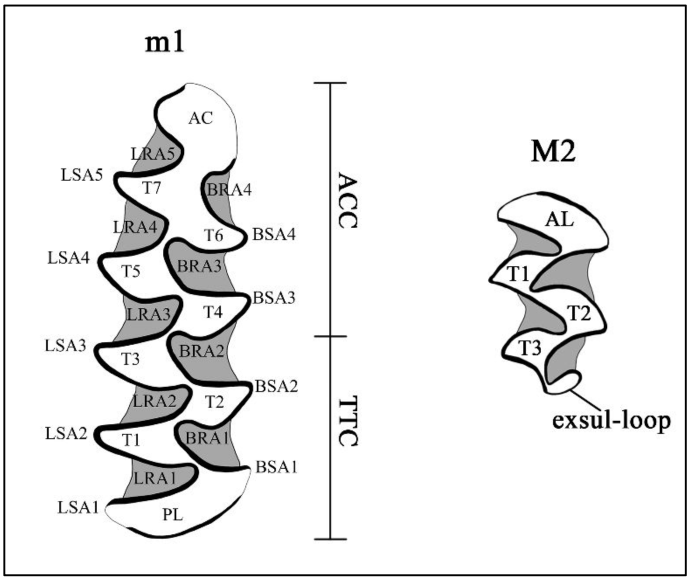


Figure 1.3.1. Nomenclature for the description of the first lower molar (m1) and second upper molar (M2). AL: anterior lobe; PL: posterior lobe; T: triangle; AC: anterior cap; LSA: lingual salient angle; LRA: lingual reentrant angle; BSA: buccal salient angle; BRA: buccal reentrant angle. ACC: anteroconid complex; TTC: talonid-trigonid complex. After Van der Meulen (1973) and Nadachowski (1982).

M. arvalis and *M. agrestis* have prismatic molars, that lack of roots and continue to grow through the entire life of the animal. On the grinding surface, the molars present dentine fields surrounded by enamel strips. This dentine fields usually assume a triangle shape (T) and are separated by synclines filled by cementum. These synclines are called re-entrant angles (RA), while the anticlines are called salient angles (SA). The first lower molar (m1) is usually the best diagnostic element. Its dentine fields are closed and separated from each other, except for the fields at the anterior part of the tooth, called the anterior cap (AC), that is small, somewhat rounded and usually open and connected with the other elements of the anteroconid complex (ACC). The ACC is the part of the m1 that present the highest variability, while the talonid-trigonid complex (TTC), composed by the posterior lobe (PL), the T1, T2 and T3 is normally very conservative in shape (Fig.1.3.1).

Based on the number of triangles of the m1s, (numbered consecutively from PL to AC), their relative shapes and proportions, their degree of confluence or separation, and the shape of the ACC, it is possible to assign the m1 to the appropriate species (Dienske 1969; Chaline 1974; Nadachowski 1982; Borodin & Markova 2015). *M. arvalis* presents a more symmetric and parallel disposition of both triangles and re-entrant angles: parallel BRA3- LRA 4 and BRA4-LRA5, opposite and confluent 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 BRA3- LRA 4 and BRA4-LRA5 which reduce the confluence between T6 and T7, giving a more angular shape to the ACC, sometimes with a well-developed LRA6 and T9. Furthermore, in *M. agrestis* the second upper molar presents a so-called “exsul-loop”, an additional closed field at the posterior end of the tooth that is absent in *M. arvalis* (Zimmerman 1956) (Table 1.3.1; Fig.1.3.2).

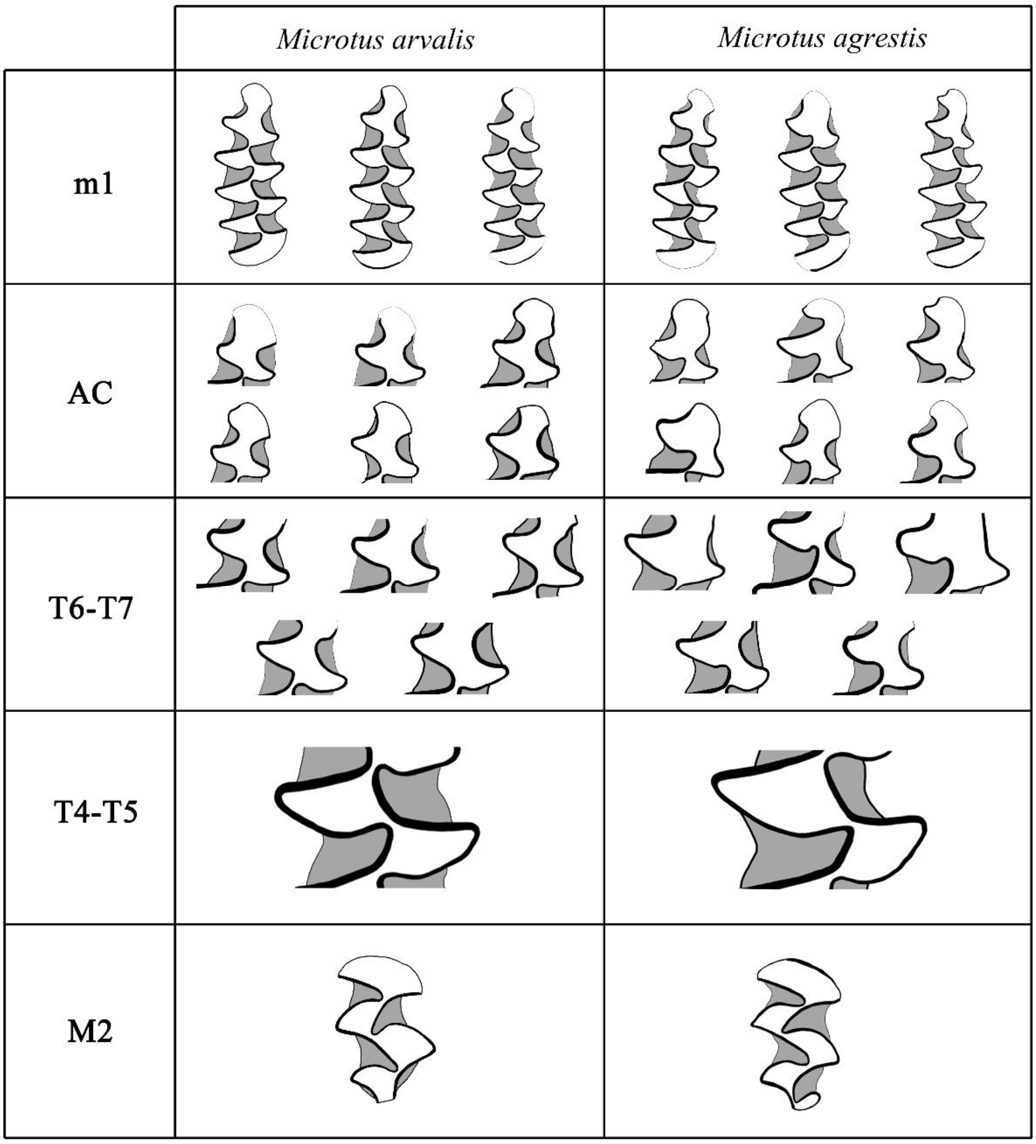


Figure 1.3.2. Morphological differences between *Microtus arvalis* and *Microtus agrestis* in the first lower molar (m1): anterior cap (AC), position and angles of the sixth and seventh triangle (T6-T7), asymmetry between the fourth and fifth triangle (T4-T5); and in the second upper molar (M2).

	Microtus arvalis	*Microtus agrestis*
AC	more rounded and symmetrical	more angular and asymmetrical
T6-T7	opposed and confluent	alternated and less/no confluent
T4-T5	T4 and T5 similar dimension	T5 larger than T4
M2	simple	exsul-loop

Table 1.3.1. List of morphological differences between *Microtus arvalis* and *Microtus agrestis.*

In this PhD thesis, the morphological traits of the m1s and M2 are going to be used to identify and separate the two species and to point out similarities and differences between coeval populations from different regions and between populations belonging to different chronologies (i.e. Middle, late Middle and Late Pleistocene).

1.4. Taxonomical, chronological and phylogeographic value of morphometric traits in the first lower molar of *Microtus arvalis* and *Microtus agrestis*

Measurements of the occlusal surface of m1s in Arvicolinae had been systemized by Van der Meulen (1973) and have been used ever since to quantify intraspecific and interspecific differences within and between species (Alcalde *et al.* 1981; Nadachowski 1991; Maul *et al.* 1998; Maul & Parfitt 2010; Petruso *et al.* 2011, among others). Since the ACC tends to be the area of the m1 that present the highest variability, most of the measurements of this tooth are taken in the anterior part (Fig. 1.4.1): L represents the total length of the tooth; a, the length of the ACC; W, the width of the ACC at T4-T5; e the width of the ACC at T6-T7; d the degree of constriction of the AC. Two measurements were added to quantify the degree of symmetry between the labial (or buccal) and lingual side of the tooth: La represents the width of T4 and Li the width of T5 (Nadachowski 1984; Cuenca-Bescós & Laplana 1995). These measurements have been combined in order to describe the relative proportions between the various parts of the m1.

One of the most important of these combinations is the a/L index, that measures the relative elongation of the ACC with respect to the total length of the tooth. This index have been widely used as indicator of different evolutionary stages within and between lineages of *Microtus* species since in this genus a progressive trend toward more developed and complex ACC has been observed in the fossil records (Rekovets & Nadachowski 1995; Maul & Markova 2007; Maul *et al.* 2007; Klimowicz *et al.* 2016; Rekovets & Kovalchuk 2017, among others). This trend has proved to be less regular than previously thought, but proved still to be and informative and useful tool (Maul *et al.* 2014).

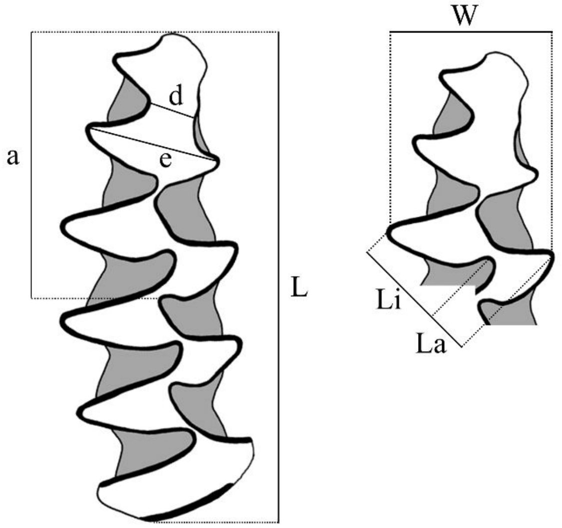


Figure 1.4.1. Measurements taken on first lower molar of *Microtus arvalis* and *Microtus agrestis*. L: total length of the tooth; a: length of the anteroconid complex (ACC); W: width of the ACC measured at T4-T5; e: width of ACC measured at T6-T7; d: closure of the anterior cap; La: width of T4; Li: width of T5, following Van der Meulen (1973) and Cuenca-Bescós & Laplana (1995).

In this PhD thesis, the values of the a/L index are going to be used to investigate the variations in *M. arvalis* and *M. agrestis* populations during Middle and Late Pleistocene and the differences between populations belonging to Mediterranean regions (i.e. northern Spain, Italy, south-western France, and Croatia) and continental Europe (i.e. Hungary and Belgium).

In order to quantify the asymmetry between the buccal (or labial) and the lingual side of the m1s of *M. arvalis* and *M. agrestis*, Nadachowski (1984) proposed to measure the ratio between the width of T4 and T5 (LT4/LT5 x100, or La/Li index, according to Cuenca-Bescós & Laplana 1995) and observed that 88% of *M. arvalis* show values > 65, while the 81% of *M. agrestis* show values < 65. Combined with the measure of the total length of the m1, the index allowed to totally separate 2 out of 3 paired living populations from Poland, while the third set of populations shows a small degree of overlapping, largely due to juvenile specimens.

In this thesis, the taxonomic value of the La/Li index combined with the total length (L) of the m1 is going to be tested in paired populations of *M. arvalis* and *M. agrestis*.

1.5. *Microtus arvalis* and *Microtus agrestis* role in palaeoclimatic and palaeoenvironmental reconstruction

Microtus arvalis and *Microtus agrestis* are widely present in the fossil record in Middle and Late Pleistocene Europe, therefore they have been included in the analysis of small mammal assemblages aiming to palaeoclimatic and palaeoenvironmental reconstructions. While in northern and eastern Europe during Late Pleistocene, strong occurrence of *M. arvalis* and *M. agrestis* signalled relatively temperate oscillations (Nadachowski 1982; Rekovets & Nadachowski 1995), in southern Europe it is a proxy for relatively cold and dry periods.

According to the method described by Sans-Fuentes & Ventura (2000) and Real *et al.* (2003), *M. arvalis* is classified as chorotype 1, where *M. agrestis* is classified as chorotype 2. A chorotype can be defined as a group of species whose distributions in space overlap more than expected at random. Chorotype 1 refers to species with mid-European requirements; with mean summer temperature lower than 20 ºC, a mean annual temperature between 10 ºC and 12 ºC, and a mean annual precipitation higher than 800 mm. Chorotype 2 refers to species with mid-European requirement but tolerant to Mediterranean conditions, with annual precipitation higher that 600 mm.

Both species are proxy for open landscape, the common vole indicating more arid environments with discontinuous ground coverture, while the field vole indicates more humid conditions. According to the Habitat Weighting method (Evans *et al.* 1981; Andrews 2006, modified by Blain *et al.* 2008; López-García *et al.* 2010, 2014), that distributes each small-vertebrate taxon in the habitat(s) preferentially occupied by each one, *M. arvalis* has a quotient of 0.75 for Open Dry and 0.25 for Open Woodland, while *M. agrestis* has a 0.5 for Open Humid and 0.5 for Open Woodland. "Open Dry" corresponds to meadowland subject to seasonal climate change; "Open Humid" indicates evergreen meadowland with pastures and dense topsoil; "Open Woodland" represent woodland margins and forest patches, with moderate ground cover.

Since *M. agrestis* reaches as north as the Scandinavian Peninsula (Chapter 1.2), the bioclimatic model elaborated by Hernández Fernández (2001), Hernández Fernández & Peláez-Campomanes (2005) and Hernández Fernández *et al.* (2007), assigns to *M. agrestis* a quotient 0.5 for climatic type VI (typical temperate with nemoral broadleaf–deciduous forest) and 0.5 for climatic type VIII (cold temperate coniferous forest) where *M. arvalis* has a quotient of 1.00 for type VI. This is probably an overestimation of the temperate and forest attribute of the common vole, given its preferences for dry and open environments.

In this PhD thesis, the morphometric characters of *M. arvalis* and *M. agrestis* are going to be related to the different climatic and environmental conditions detected from each site through the analysis of palaeoclimatic and palaeoenvironmental proxies (i.e. palynological and geomorphological sequence, small vertebrate assemblages, large mammal assemblages, malacological assemblages). To do so, also current habitat preferences and distribution range will be taken into account.

1.6. Objectives of this PhD thesis

In this PhD thesis, we are going to analyse populations of *Microtus arvalis* and *Microtus agrestis* from Middle and Late Pleistocene sites (ca. 478 – 11 ka) of northern Spain, south-western France, Italy, Belgium, Croatia and Hungary from a morphological and morphometric point of view. Then we will compare our data with those available in literature, with studies on palaeoclimatic and palaeoenvironmental reconstructions, with recent studies on phylogenetics, and with studies on ecology and ethology of these two species.

The data collected are going to be used:

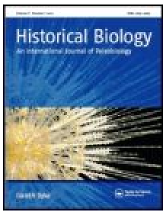
- to point out similarities and differences between synchronous populations of *Microtus arvalis* and *Microtus agrestis* from different geographic and environmental settings;
- to point out similarities and differences between populations of *Microtus arvalis* and *Microtus agrestis* belonging to different chronologies;
- to understand the effects of environmental and climatic conditions on morphology and morphometry of first lower molars of *M. arvalis* and *M. agrestis*;
- to possibly recognize patterns of interspecific interactions, movement and migration, intraspecific evolution and cryptic speciation.

This will allow:

- to better determine the relative chronological position of archaeological and palaeontological sites;
- to obtain new tools to refine palaeoclimatic and palaeoenvironmental reconstruction;
- to better understand the evolutionary history of the two species.

2. MANUSCRIPTS

Luzi, E. and López-García, J.M. 2017: Patterns of variation in *Microtus arvalis* and *Microtus agrestis* populations from Middle to Late Pleistocene in southwestern Europe. *Historical Biology*, 1–9. doi: 10.1080/08912963.2017.1375490.



Luzi, E., López-García, J.M., Blasco, R., Rivals, F. and Rosell, J. 2017: 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). *Journal of Mammalian Evolution 24*, 495–503. doi: 10.1007/s10914-016-9355-8.

Luzi E., Berto C., López-García, J.M., Middle to Late Pleistocene *Microtus arva*lis and *Microtus agrestis* from the Italian Peninsula: chronological insight and evolutionary trends. Under review - PALAIOS.

Luzi E., Pazonyi P., López-García J.M., The influence of climate on morphometric traits of fossil populations of *Microtus arvalis* and *M. agrestis* from the Carpathian Basin (northern Hungary). Under review - LETHAIA.

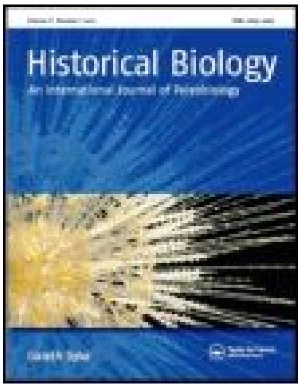
2.1. Patterns of variation in *Microtus arvalis* and *Microtus agrestis* populations from Middle to Late Pleistocene in southwestern Europe

Elisa Luzi, Juan Manuel López-García

Abstract

Fifteen paired fossil populations of *Microtus arvalis* and *Microtus agrestis* from southwestern Europe have been analysed from a morphological and morphometric point of view. The sites under consideration are located in the northern Iberian Peninsula and southern France, from the Middle Pleistocene to the end of the Late Pleistocene. The aim of this study is to stress once again the importance of keeping these two species separated in the fossil record in order to recognize specific trends of evolution and divergence and to obtain more precise information on palaeoclimatic and palaeoenvironmental conditions. It was possible to observe remarkable intraspecific differences between Middle and Late Pleistocene populations of both species. Furthermore, in synchronic co-specific populations from the Late Pleistocene, climatic and geographic conditions seem to exert a major influence in shaping intraspecific changes in dental pattern.

Key-words: morphology, morphometric, dental variation, *Microtus*, France and Spain.



2.1.1. Introduction

The common vole *Microtus arvalis* (Pallas, 1778) and the field vole *Microtus agrestis* (Linnaeus, 1761) are commonly found in Middle and Late Pleistocene palaeontological and archaeological sites of France (Chaline 1972), Italy (Sala & Masini 2007) and Spain (Cuenca-Bescós et al. 2016).

Their first occurrence in Spain is dated to the Holstein Interglacial, corresponding to Marine Isotopic Stage (MIS) 11 at roughly 424-374 thousand years (ka) ago (Lisiecki & Raymo 2005), in the sites of Sierra de Atapuerca (Kowalski 2001), and they are constantly present in the northern Iberian Peninsula throughout the Saalian glaciation (MIS 10 to 6) (López-García et al. 2014a; Cuenca-Bescós et al. 2016) and the Late Pleistocene (MIS 5 to 2) (López-García et al., 2014b; Rofes et al., 2015; Bañuls-Cardona et al., 2017, among many others).

The taxonomic identification of fossils belonging to the genus *Microtus* is based on the recognition of dental patterns, particularly the features of the first lower molars (m1s), the most abundant and best diagnostic element. *M. arvalis* and *M. agrestis* have similar m1 morphology, and the distinction between the two species can present some difficulties due to the considerable intraspecific variations and the partial superposition of the shapes and measurements of their m1s. Nevertheless, morphological and morphometric characters inferred from living populations (Chaline 1974; Nadachowski 1984; Niethammer & Krapp 1987; Gromov & Polyakov 1992) provide useful references in order to achieve reliable identification. In numerous studies of small-mammal assemblages (Lebreton et al., 2016; Popov & Marinska 2007; Bogićević et al., 2017 among others), they appear under the denomination "*Microtus arvalis-agrestis*", which is enough to account for the presence/absence of the taxa but leaves important issues unaddressed.

Even though they are both grassland species, the field vole and the common vole differ slightly in their ecological preferences, the latter inhabiting open dry terrain with discontinuous herbaceous cover such as crop fields and steppe, while the former favours dump areas such as marshes, peat-bogs and river-banks (IUCN, 2015). Hence, it is important to keep them separated in the fossil record, particularly in order to obtain more precise palaeoclimatic and palaeoenvironmental reconstructions.

Furthermore, recent molecular studies of their mitochondrial DNA (mtDNA) have revealed that after the Last Glacial Maximum (27-19 ka BP) (Clark et al., 2009) *M. arvalis* and *M. agrestis* underwent two very different evolutionary histories (Jaarola et al. 2004; Heckel et al. 2005; Braaker & Heckel 2009; Bužan et al. 2010; Herman et al. 2014) leading to the current intraspecific genetic diversity and the geographical distribution of the extant lineages (Jaarola & Searle 2002; Haynes et al. 2003; Paupério et al. 2012; Beysard & Heckel 2014; Stojak et al. 2016a; 2016b). It may thus be useful to analyse also the fossil record to try and recognize early patterns of isolation and divergence.

In this paper, *M. arvalis* and *M. agrestis* populations will be studied in order to underline the different patterns of change undergone by these two species during the Middle and Late Pleistocene in northern Spain and southwestern France.

2.1.2. Material and Methods

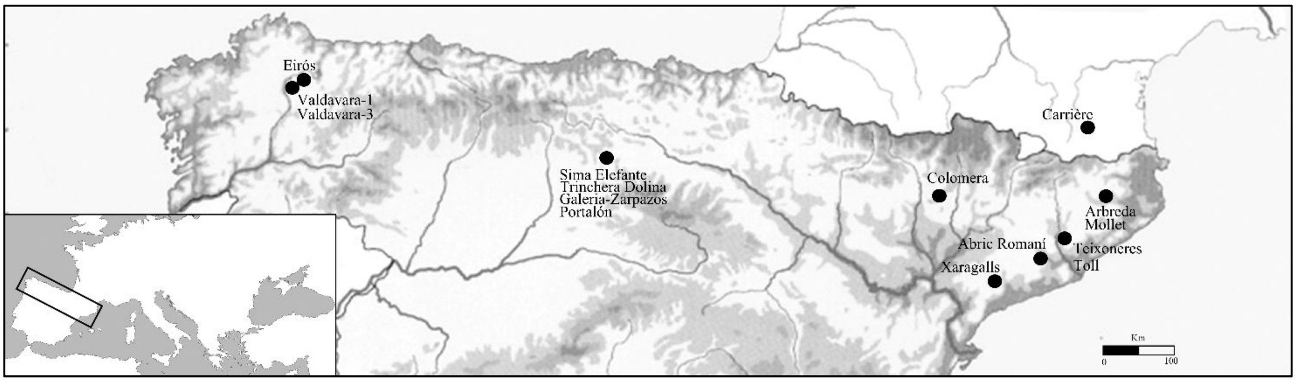


Figure 1. Geographical location of the sites.

The samples analysed in this study come from 14 archaeological and palaeontological sites located in the northern Iberian Peninsula. Valdavara-1, Valdavara-3 (Vaquero Rodríguez et al. 2009; López-García et al. 2011a) and Eirós Cave (Rey-Rodríguez et al. 2016) are located in Galicia, in the NW Atlantic region of the Iberian Peninsula. Mollet Cave (Maroto et al. 2012; López-García et al. 2014a), Teixoneres (Rosell et al. 2008; López-García et al. 2012a; Luzi et al. 2016; Talamo et al. 2016), Xaragalls (López-García et al. 2012b), Abric Romaní (López-García 2008), Arbreda (Soler Masferrer & Maroto Genover 1987; López-García et al. 2014c), Toll (Fernández-García & López-García 2013) and Colomera Cave (López-García et al. 2010a) are located in the NE of Iberia, facing the Mediterranean Sea. Sima del Elefante (López-García et al. 2011b), Trinchera Dolina (Cuenca-Bescós et al. 2010; Falguères et al. 2013), Trinchera Galería-Zarpazos (Galindo-Pellicena et al. 2011; Demuro et al. 2014) and Portalón (López-García et al. 2010b; Bañuls-Cardona et al. 2014) belong to the Sierra de Atapuerca complex, in the Bureba Corridor, connecting these two geographical regions. One last site, Grotte de la Carrière (López-García et al. 2016), is located in the French Eastern Pyrenees region, approximately 20 km from the Spanish border (Fig. 1). These sites cover a chronological range spanning from the Middle Pleistocene to the end of the Late Pleistocene (Table 1).

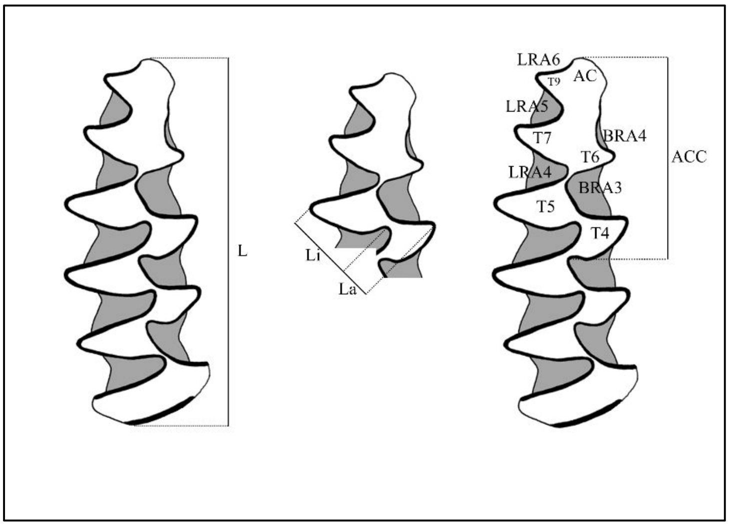


Figure 2. Nomenclature and measurement methods used for m1 in the description of arvicolines. L: total length; La: width of T4; Li: width of T5; ACC: anteroconid complex; AC: anterior cap; BRA: buccal re-entrant angle; LRA: lingual re-entrant angle; T4-T9: triangles 4–9.

There are characters in the first lower molars (m1s), i.e. in the anteroconid complex (ACC), that allow us to differentiate between the common vole and the field vole: symmetric T4-T5, opposite and widely confluent T6-T7, a rounded AC and parallel BRA4-LRA5 are typical of *Microtus arvalis*, while *M. agrestis* presents asymmetric T4-T5, alternating T6-T7 that sometimes results in the separation of these triangles, an angular AC and alternating BRA3-LRA4 and BRA4-LRA5 (Fig. 2).

The m1s of *M. arvalis* and *M. agrestis* were measured following the criteria defined by Van der Meulen (1973), Nadachowski (1984) and Cuenca-Bescós and Laplana (1995). Morphological characters have been described following Nadachowski (1982). L represents the total length of the tooth, La the width of T4, Li the width of T5; LRA and BRA are respectively the lingual and buccal re-entrant angles in the anterior part of the tooth (Fig.2). The La/Li index was calculated in order to quantify the degree of asymmetry between the buccal and the lingual side of the tooth.

When available, second upper molars (M2) were observed. In *M. agrestis* the M2s present a so-called "exsul-loop", an additional closed field at the posterior end of the tooth that is absent in *M. arvalis* (Zimmerman 1956).

The material from the sites in southern France, NE Iberia and NW Iberia was studied and photographed at the IPHES (Tarragona, Spain) using a Dino-Lite USB microscope. The material from Sierra de Atapuerca was studied and photographed at the Earth Science Department of the University of Zaragoza using an Olympus SZ-61 stereomicroscope.

Only complete teeth from adult specimens, both left and right, were measured. In sites with a high number of m1s, 30 specimens were selected randomly to provide a sample (showing no significant differences when the mean values of each random sample were compared to those of the corresponding whole sample: $p > 0.7$ for the F-test, and $p > 0.6$ for the t-test). All measurements were taken using ImageJ software and are given in millimetres.

The data were processed using PAST 3 software (Hammer & Harper 2006).

Site		coordinate	m. asl	date
Trinchera Dolina - layer 10.2	TD	42°33'06" N 3°53'55" W	1080	424-250 ka
Trinchera Galería-Zarpazos	TZG	42°33'06" N 3°53'55" W	1080	424-250 ka
Sima Elefante - layers 18-19	TE	42°33'06" N 3°53'55" W	1080	424-250 ka
Grotte de la Carrière	CAR	42° 33'94" N 2° 22'77" E	540	424-250 ka
Mollet Cave	Mollet	42°09'47" N 2°44'52" E	200	MIS 7
Valdavara-3	VAL-3	43°01'00" N 7°33'00" W	600	MIS 5
Teixoneres	TX	41°48'47" N 2°05'50" E	900	MIS 3
Xaragalls	XAR	41°23'02" N 1°02'56" E	590	MIS 3
Eirós	Eirós	42°46'3" N 7°12'13" W	780	MIS 3
Romanì - level O	AR	41°32’ N 1°41’30’’ E	265	MIS 3
Arbreda	ARB	42°09'38" N 2°44'49" E	211	MIS 3-2
Portalón	POR	42°33'06" N 3°53'55" W	1080	MIS 3-2
Valdavara-1	VAL-1	43°01'00" N 7°33'00" W	600	end MIS 2
Toll	Toll	41°48'25" N 2°09'02" E	760	end MIS 2
Colomera	COL	42°08'01" N 0°76'40" E	670	end MIS 2

Table 1. List of the sites with abbreviations and geographical and chronological indications.

2.1.3. Results and Discussion

The measurements taken on populations of *Microtus arvalis* and *M. agrestis* (Table 2) from different chronologies and different geographical locations, combined with our study of the morphology of the ACC of the m1s, allowed us to establish some remarkable differences within and between the two species.

Microtus agrestis

		L				La/Li x100			
Site	n.	min	max	mean	SD	min	max	mean	SD
TD	29	2.468	3.023	2.781	0.13	44.52	65.52	54.22	6.29
TZG	24	2.663	3.182	2.933	0.14	41.81	64.82	52.99	6.65
TE	5	2.82	3.049	2.903	0.08	51.48	61.9	56.57	4.41
CAR	11	2.664	2.939	2.796	0.09	51.4	63.6	56.0	3.7
Mollet	2	2.775	2.964	2.587	-	41.5	43.7	39.2	-
VAL-3	7	2.504	2.981	2.8	0.14	48.15	58.75	52.5	0.1
TX	30	2.369	3.053	2.713	0.14	37.56	69.81	61.13	4.66
XAR	6	2.688	3.18	2.91	0.16	60.33	67.8	63.59	2.67
Eirós	8	2.658	3.182	2.944	0.18	45.59	79.36	56	11.29
AR	4	2.587	3.01	2.895	0.2	62.6	67.58	65.46	2.47
ARB	30	2.586	3.222	2.905	0.19	51.01	67.92	62.35	4.05
POR	30	2.424	3.262	2.845	0.2	54.18	69.29	62.85	3.64
VAL-1	2	2.842	2.846	2.844	-	48.91	54.79	51.85	-
Toll	3	2.403	2.582	2.504	0.09	50.79	64.18	54.95	7.38
COL	10	2.603	3.234	2.974	0.2	59.46	72.48	64.16	3.69

Microtus arvalis

		L				La/Li x100			
Site	n.	min	max	mean	SD	min	max	mean	SD
TD	30	2.366	3.16	2.811	0.16	59.09	86.73	74.33	6.52
TZG	24	2.508	3.211	2.86	0.15	60.07	92.91	79.47	6.7
TE	6	2.611	2.823	2.743	0.07	65.29	78.34	72.4	4.9
CAR	1	-	-	2.832	-	-	-	70.04	-
VAL-3	2	2.579	3	2.785	-	71.11	73.39	72.25	-
TX	30	2.494	3.125	2.778	0.17	61.53	80.59	69.31	3.99
XAR	9	2.598	3.185	2.87	0.17	56.79	73.36	67.15	5.45
Eirós	10	2.766	3.499	3.09	0.23	67.17	83.51	76.3	4.81
AR	12	2.598	3.044	2.865	0.15	64.35	80.2	73.13	3.97
ARB	30	2.639	3.336	2.912	0.18	65.37	83.73	72.13	4.56
POR	30	2.618	3.259	2.954	0.19	67.72	91.62	75.21	5.48
VAL-1	12	2.748	3.28	3.001	0.16	61.8	78.16	68.74	5.53
Toll	10	2.664	3.009	2.795	0.1	64.74	77.36	70.18	4.14
COL	30	2.602	3.629	3.016	0.2	58.78	86.47	71.8	5.5

Table 2. Measurements for m1s of *Microtus agrestis* and *Microtus arvalis*. L: total length of m1; La/Li: index of asymmetry between the buccal and the lingual side of m1; n: number of individuals; min: minimum value obtained; max: maximum value obtained; mean: mean value; SD: standard deviation. TZG: Trinchera Galería-Zarpazos; TD: Trinchera Dolina; TE: Sima Elefante; CAR: Grotte de la Carrière; VAL-3: Valdavara-3; TX: Teixoneres; XAR: Xaragalls; AR: Romaní; ARB: Arbreda; POR: Portalón; VAL-1: Valdavara-1; COL: Colomera.

2.1.3.1. Morphometric separation between M. arvalis and M. agrestis

The degree of asymmetry between T4 and T5 has again proved to be a very good discriminant and a useful tool for identifying and separating the two species. In each pair of populations there are of course overlaps in the values due to intraspecific variations, i.e. when the minimum value of the La/Li index for *M. arvalis* is near to the maximum value for *M. agrestis*, but when these measurements are combined with the morphological characters it is always possible to assign the m1s to one of the two species. Even though a degree of uncertainty remains, as 5% to 10% of the whole samples cannot be clearly identified, this uncertainty is almost entirely restricted to juvenile specimens and broken or excessively digested m1s. During the Middle Pleistocene, the separation between *Microtus arvalis* and *M. agrestis* is clearly visible due to the marked asymmetry between the buccal and the lingual side of the tooth in the latter. On the other hand, during the Late Pleistocene, as the size of *M. arvalis* increases and its morphotypes become more complicated while the *M. agrestis* morphotypes simplify, the two sets come closer but maintain their separation (Fig. 3).

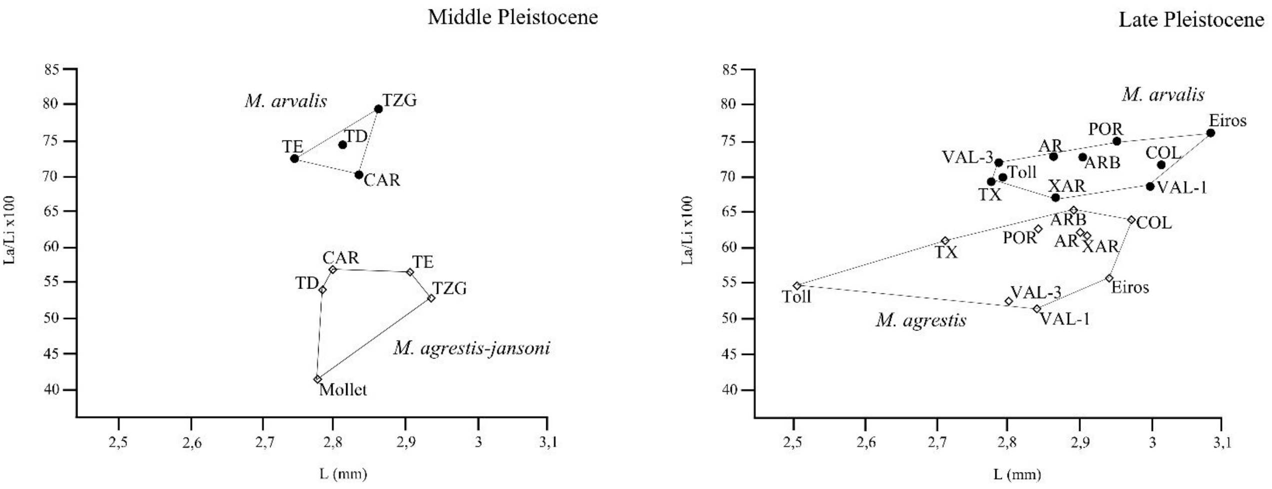


Figure 3. Morphometric differences between *Microtus agrestis* (black) and *Microtus arvalis* (white) of the Middle and Late Pleistocene. Correlation between L and La/Li index. L: total length of m1; La/Li: index of asymmetry between the buccal and the lingual side of m1. Site abbreviations: TZG: Trinchera Galería-Zarpazos; TD: Trinchera Dolina; TE: Sima Elefante; CAR: Grotte de la Carrière; VAL-3: Valdavara-3; TX: Teixoneres; XAR: Xaragalls; AR: Romaní; ARB: Arbreda; POR: Portalón; VAL-1: Valdavara-1; COL: Colomera.

Studies of fossil and recent populations of *M. arvalis* and *M. agrestis* from Poland (Nadachowski 1982; Nadachowski 1984), the Ukraine (Rekovets & Nadachowski 1995) and Croatia (Mauch Lenardić 2007) all agree in showing that during the Late Pleistocene the size of the m1s of common voles tends to remain stable, while those of field voles constantly increase in size.

Furthermore, *M. agrestis* always displays larger mean values of L than *M. arvalis*. By contrast, the samples from the Late Pleistocene of northern Iberia indicate that the interspecific relation between the two species is reversed, with the common vole m1s being slightly larger than those of the field vole (Fig. 3). For the common vole, six different mtDNA lineages have been identified: western-south, western-north, central, Italian, eastern and Balkan (Haynes et al. 2003; Tougard et al. 2008; Bužan et al. 2010; Stojak et al. 2015). It is possible that the western-south line (which includes Spain and western France), separated from the other lineages, developed a larger size during the Late Pleistocene, partly in response to environmental and climatic drives and partly as a consequence of this separation, testifying once again to the peculiarity of the Iberian Peninsula in comparison with the rest of continental Europe.

2.1.3.2. Microtus agrestis s.l.

Chaline (1972) first described a peculiar type of *M. agrestis* in the Middle Pleistocene of France based on material from Grotte de l'Escale (Saint-Estève-Janson, Bouches-du-Rhône, France). *Microtus agrestis jansoni* is a vole with *agrestis*-like morphology. The first lower molar is middle-large in size and presents five closed triangles with a clear labio-lingual asymmetry, alternatingly confluent T6 and T7, and an asymmetric anterior cap. Morphologically, the *jansoni*-type is characterized by a deep LRA4, the presence of T9 in the AC and a broad LRA5. In some cases, the populations from the late Middle Pleistocene develop a small BRA4 on T6, resulting in a T8 that recalls the mimomyan-fold. The material from the Middle Pleistocene of Sierra de Atapuerca (i.e. Sima del Elefante, Trinchera Dolina, and Trinchera Galería-Zarpazos), Mollet Cave, and Grotte de la Carrière displays all the diagnostic characters of *M. agrestis jansoni* (Fig. 4A.1-7). In the second upper molar, it is possible to observe the extra loop at the posterior end of the tooth that is typical of extant forms of *M. agrestis* (Fig. 4A.4).

During the Late Pleistocene, the values of L remain relatively stable while those of La/Li increase as the m1s become more symmetrical (Fig. 5A) and the morphology of the ACC tends to simplify (Fig. 4A.8-14). However, there are two remarkable exceptions.

The first concerns the sample from Toll Cave. *M. agrestis* specimens from this site are smaller and more asymmetrical than the others from the same region. This may be due to climatic and environmental factors. In fact, level 3 of Toll Cave can be related to the LGM (Fernández-García & López-García 2013), and small-sized individuals may have found it easier to thrive advantaged in the cold, dry climatic conditions typical of this phase (Dienske 1979; De Jonge 1983). As *M. arvalis* was more adapted to a mid-continental climate, it was probably less affected by this glacial stage than the field vole and its population does not differ much from the others in the same region (i.e. Xaragalls, Romaní, Arbreda, Teixoneres).

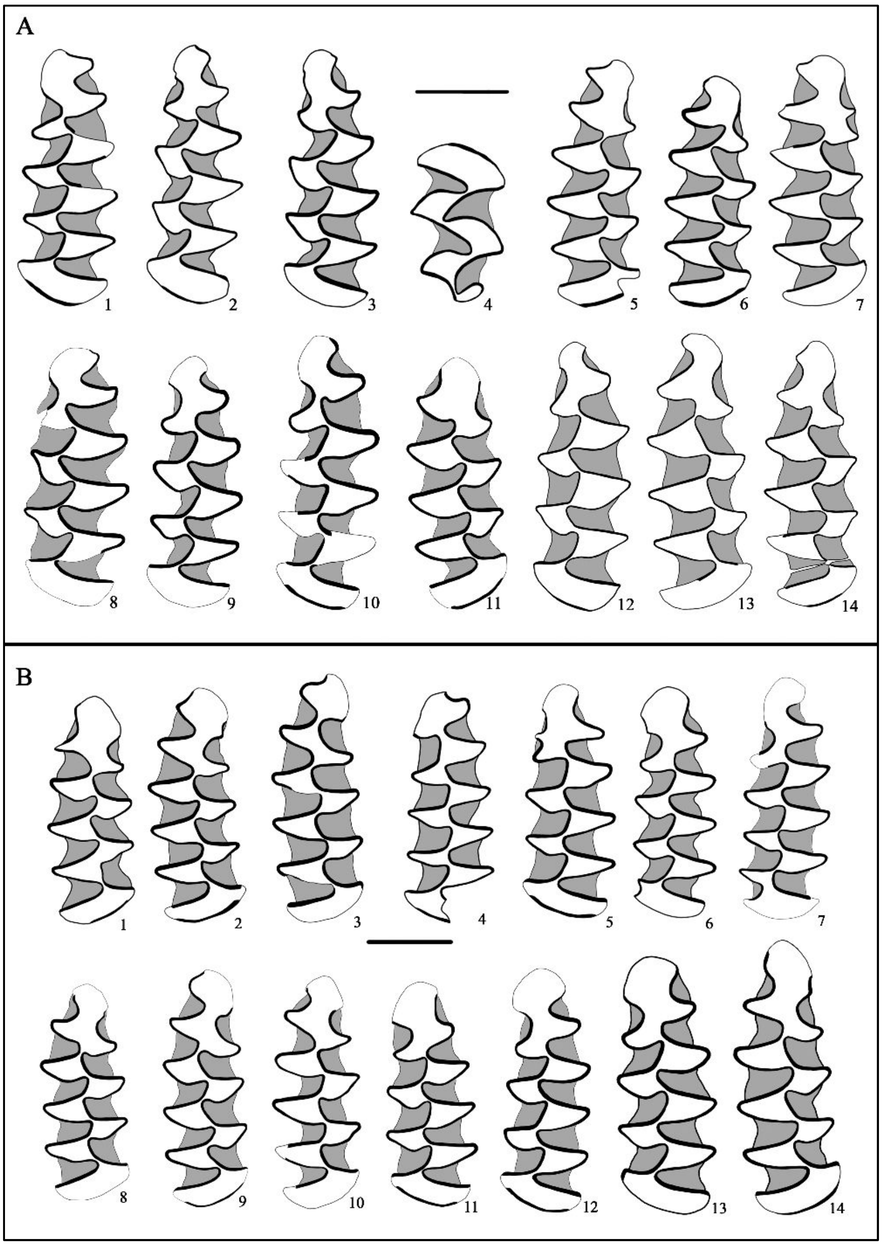


Figure 4. A: examples of *Microtus agrestis*. 1: TZGIIa_n3_280, left m1; 2: TZGIIa_p2_190_a, left m1; 3: TZGIIa_p2_190_b, left m1; 4: TD10-2_i20_300-310-8, right M2; 5: TD10-2_j16_250-270-37, right m1; 6: TD10-2_i13_210-220-3, right m1; 7: CAR_n4_d6-28b, right m1; 8: TX_n3b-5, left m1; 9: TX_n3a-3, left m1; 10: TX_n3a-4, left m1; 11: TX_n3b-2, right m1; 12: Eirós_CE3-3, left m1; 13: Eirós_CE3-5, right m1; 14: Eirós_CE3-8, right m1. Scale: 1 mm. B. examples of *Microtus arvalis*. 1: ARB_h_E2BE107-5, right m1; 2: ARB_e_E00E81-6, right m1; 3: ARB_d_E00E68-6, right m1; 4: ARB_f_E1AE87-14, left m1; 5: ARB_d_E00E68-11, left m1; 6: ARB_c_E00E65-13, left m1; 7: ARB_a_E00E52-17, left m1; 8: TX_n3a-5, right m1; 9: TX_n3a-4, right m1; 10: TX_n3b-6, right m1; 11: TX_n2b-2, left m1; 12: COL_ce14_x31_Fc-86, left m1; 13: COL_ce14_x31_Fc-75, left m1; 14: COL_ce15_x31-59, right m1. Scale: 1 mm. Site abbreviations: TZG: Trinchera Galería-Zarpazos; TD: Trinchera Dolina; CAR: Grotte de la Carrière; TX: Teixoneres; ARB: Arbreda; COL: Colomera.

The second exception is provided by the samples from the Late Pleistocene sites of Galicia, Eirós Cave and Valdavara-1. Their values are in fact close to those of Middle Pleistocene populations. However, even though they retain the same level of asymmetry and the same size as their older relatives, the morphology of the ACC in the m1s is clearly different, with a reduction in the AC, a less deep LRA4, a shallow LRA5 and an incipient T9, if present at all (Fig. 4A.12-14). Combining molecular and palaeontological data, it is possible to explain the morphological and morphometric peculiarity of the Late Peistocene field vole populations from Galicia. Two lineages of *M. agrestis* (northern and southern) were identified at an early stage on the basis of mtDNA studies (Jaarola & Searle 2002; Jaarola et al. 2004; Herman & Searle 2011; Beysard et al. 2012), and their splitting was related to the LGM. A third, highly divergent lineage (Portuguese) was subsequently identified (Giménez et al. 2012; Paupério et al. 2012), its distribution area located in the western Iberian Peninsula (including Galicia); the proposed time for its separation from the combined northern-southern group is 70 ka ± 30 (Paupério et al., 2012). Our data suggest that this Portuguese lineage might already be morphometrically and morphologically well characterized at least 40 ka BP (level 3 - Eirós Cave; Rey-Rodríguez et al., 2016), and the causes for this divergence might be ascribed to the relative geographical isolation provided by the Iberian Peninsula and to the climatic difference between Galicia and the rest of northern Spain. In the western Iberian Peninsula, the climate is influenced by the Atlantic Ocean. Temperate, with summers drier than winters (Köppen Climate Classification: Csb), it is considerably more humid than the climate of NE Iberia, influenced by the Mediterranean Sea, especially when autumn and winter mean precipitations are considered (AEMET 2011). During the Late Pleistocene, the same difference existed between those two regions (González-Sampériz et al. 2010). This climatic and environmental diversity led the eastern and the western sub-populations of northern Iberian Peninsula to diverge. Furthermore, the isolation provided by the Pyrenees and the steep Atlantic coastlines prevented any contact with populations from northern territories, enhancing the speciation process of the western populations.

2.1.3.3. Microtus arvalis

The La/Li index in the populations of *Microtus arvalis* remains relatively stable during the Middle and Late Pleistocene, although the overall size of the m1s increases slightly with time (Fig. 5B). This increase results in more complex Late Pleistocene morphotypes, with a slight alternation of T6 and T7, a greater degree of closure of AC, and the appearance of small T8 and T9 (Fig. 4B.1-11).

For this species too, the samples from Valdavara-1 and Eirós Cave represent an anomaly, together with that from Colomera Cave. These three populations display a larger size and a tendency towards a larger AC (Fig. 4B.12-14). The current distribution range of *M. arvalis* does not include Galicia and the area of Colomera Cave (Mitchell-Jones et al. 1999; Casals & Sanuy 2006).

Valdavara-1 is one of the last occurrences of this species in the region. The relative geographical isolation and the Oceanic climatic conditions have probably induced the populations of common vole in NW Spain to undergo a trend of increasing m1 and AC size during the Late Pleistocene in a natural process that resembles the one undergone by *M. arvalis* after its anthropic introduction into the Orkney Islands (northern UK, Cucchi et al., 2014).

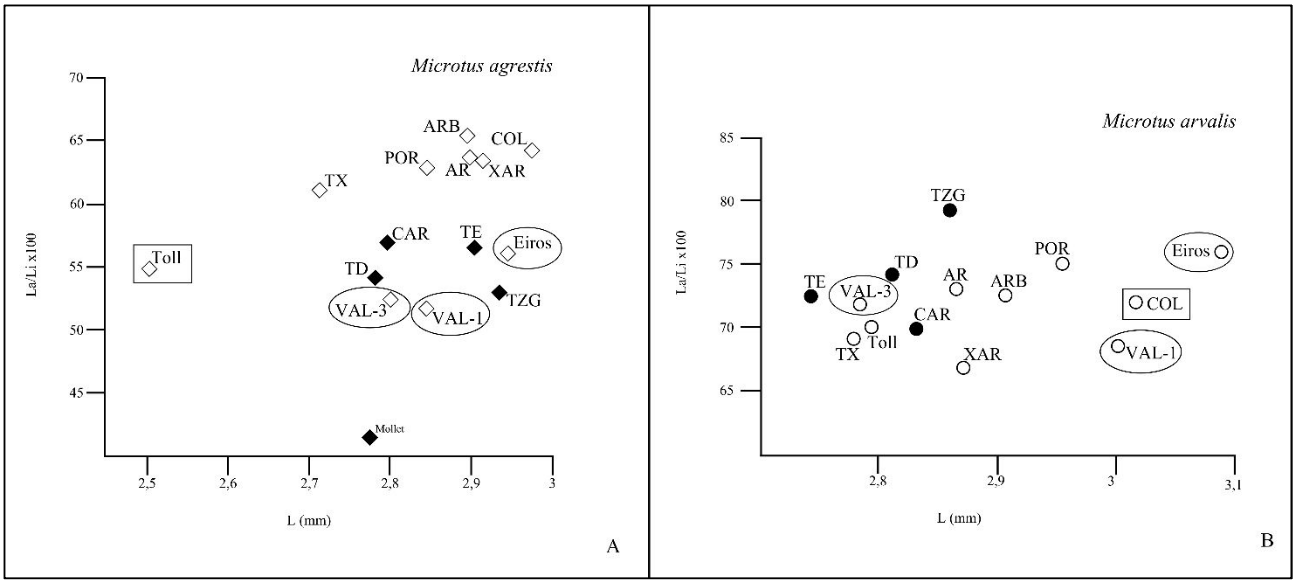


Figure 5. Correlation between L and La/Li index of *Microtus agrestis* (A) and *Microtus arvalis* (B) populations of the Middle Pleistocene (black) and the Late Pleistocene (white). L: total length of m1; La/Li: index of asymmetry between the buccal and the lingual side of m1. Site abbreviations: TZG: Trinchera Galería-Zarpazos; TD: Trinchera Dolina; TE: Sima Elefante; CAR: Grotte de la Carrière; VAL-3: Valdavara-3; TX: Teixoneres; XAR: Xaragalls; AR: Romaní; ARB: Arbreda; POR: Portalón; VAL-1: Valdavara-1; COL: Colomera.

A similar trend is observed in Colomera Cave, although for different reasons. The role of the Iberian Peninsula as glacial refugium during LGM for *M. arvalis* has long been known and it is reflected in the current distribution of living populations (Hewitt 1999; Stojak et al. 2015). At the end of the Late Pleistocene, Colomera Cave provided unique climatic and environmental conditions that allowed species adapted to cooler climate to survive at a low latitude, by the mean of altitude displacement, well into the Holocene and up to the Bronze Age (López-García et al. 2010). This "interglacial refugium" (Stewart et al. 2010) offered a favourable ecological setting for species with mid-European requirements such as *M. arvalis*. This population thus survived longer but was isolated from others living at lower altitudes and near the Mediterranean coast of NE Iberia.

The Orkney vole belonged the western lineage of *M. arvalis* (Haynes et al. 2003). More precisely, the western-north lineage and the coast of Belgium are most likely the point of origin of the colonization of the archipelago (Martinkova et al. 2013). The populations of common voles currently living in Spain belong to the western-south lineage (Stojak et al. 2016a). It is possible that the similar climatic conditions (of Late Pleistocene Galicia, of latest Pleistocene-Holocene Colomera Cave, and Holocene UK), and the isolation lead to parallel morphological and morphometric dental patterns. Common ancestry may have played a role too, since all the populations are part of the western lineage. This also support the hypothesis that a line of least resistance to evolution (Schluter 1996) exists in *M. arvalis*, despite the difference in phylogenetics (Cucchi et al. 2014).

2.1.3.4. The case of Valdavara-3

The populations of *M. arvalis* and *M. agrestis* from Valdavara-3 differ from the others of Late Pleistocene and, particularly for *M. arvalis*, from those of NW Iberia (Fig. 5A-B). In fact, both populations display morphologies and morphometric values close to those of Middle Pleistocene. The site has been dated by OSL to MIS 5 (unpubl. data, Vaquero et al.), at the beginning of Late Pleistocene, specifically in the earliest stage of MIS 5 (MIS 5d-a). The climatic conditions in this moments were milder and less arid than in MIS 3 and 2. Therefore, it is possible that the process of isolation leading *M. arvalis* toward an increased size of m1s and *M. agrestis* to differentiate from the *jansoni*-type was not yet started in Galicia. Another possible explanation may be that the separation between Middle and Late Pleistocene populations and between NW and NE Iberian Late Pleistocene populations already occurred in MIS 5e but cannot be seen in the fossil record of Valdavara-3. Given the chronological proximity to the splitting event, phenotypic changes may not have had time to arise.

2.1.4. Conclusions

The study of fossil populations of *M. arvalis* and *M. agrestis* as separated but related entities offers many points worthy of further examination, either for biochronological purposes or for a better understanding of the processes of isolation and divergence, or the influence of climatic and environmental fluctuations on dental characters at local or regional level.

- The La/Li index, combined with morphological characters, again showed its value as a useful tool for separating and identifying *M. arvalis* and *M. agrestis*.

- *Microtus agrestis jansoni* proved to be a good biochronological marker for the Middle Pleistocene of Spain and southern France, being morphometrically well separated from *M. arvalis* of the same period and morphologically well characterized within the group *M. agrestis*.

Further studies will be required to better understand the dynamics set in motion at the very beginning of the Late Pleistocene, as shown by the case of Valdavara-3, but during this age regionalism seems to play a key role in shaping the dental character of field and common voles:

- populations of the two species from the Late Pleistocene of Galicia (Cova Eirós and Valdavara-1) follow different evolutionary trends from the corresponding populations from Catalonia and Sierra de Atapuerca, partly because of the influence of the Atlantic climate and partly due to their relative geographical isolation;

- the peculiar climatic and environmental conditions brought on by the LGM are the most probable cause of the difference between the population of *M. agrestis* from Toll Cave and all the others from NE Iberia;

- the protection and isolation provided by the interglacial refugium of Colomera Cave acted on the *M. arvalis* population in such a way that it is more similar to those from Galicia than to those from Catalonia.

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2.2. 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)

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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.

2.2.1. 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). *M. 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 (Jaarola and Searle, 2004; Kapischke et al., 2009; Markova et al., 2010; Nadachowski, 1982).

Analysing 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 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. *M. 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).

2.2.1.1. 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 Moià (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 3 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 10 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 (López-García et al., 2012; Rosell et al., 2010; Rosell et al., 2016; Sánchez-Hernández et al., 2014; Talamo et al., 2016; Tissoux et al., 2006). Recent ^{14}C dating yields a chronological range of 33060 cal BP at 68.2% confidence at the top of unit II and >51000 to 40610 cal BP at 68.2% confidence for unit IIIb (Talamo et al. 2016).

2.2.2. Material and Methods

The material analysed 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 taxonomical 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 and separated (Nadachowski 1982; 1984). *M. 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 reduce the confluence between T6 and T7, giving a more angular shape to the ACC.

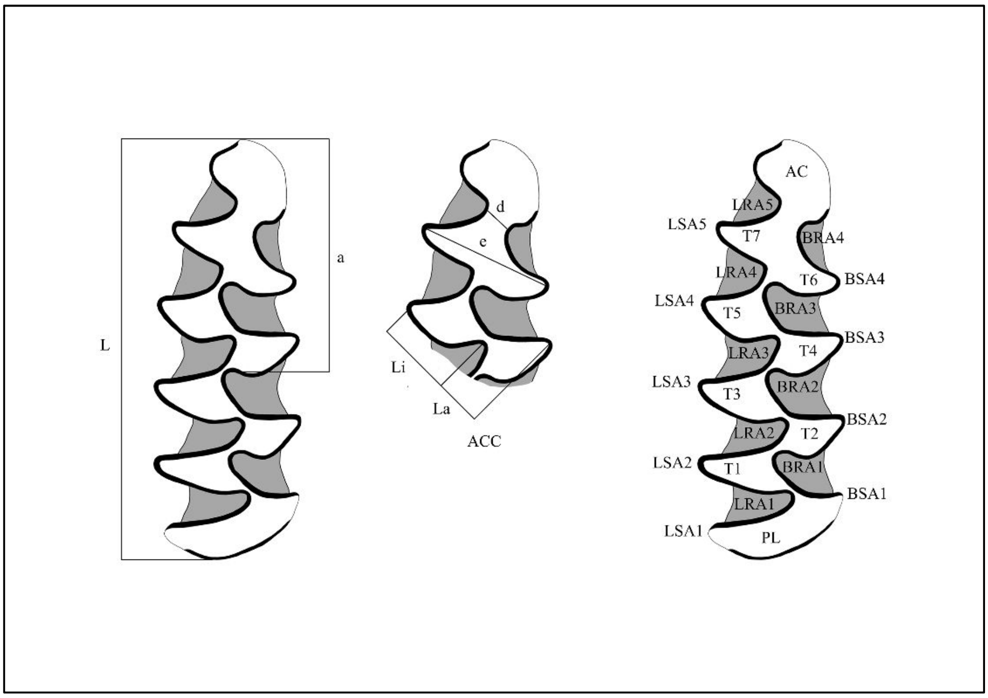

Figure 1. Nomenclature and measurement methods used for m1 in the description of arvicolines. **L**: total length; **a**: length of the anteroconid complex; **e**: width of the anteroconid complex; **d**: degree of closure of AC; **La**: width of T4; **Li**: width of T5; **PL**: posterior lobe; **ACC**: 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.

The nomenclature and measurement parameters used to analyse 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 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. Captures of the teeth have been taken using a Dino-lite USB microscope at 90x and measurements taken using ImageJ software. All measurements are given in millimetres.

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).

2.2.3. 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.

	Microtus arvalis of Teixoneres					*Microtus agrestis* 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

	Microtus arvalis - IIb					*Microtus agrestis* - 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

	Microtus arvalis - IIIa					*Microtus agrestis* - 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

	Microtus arvalis - IIIb					*Microtus agrestis* - 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

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.

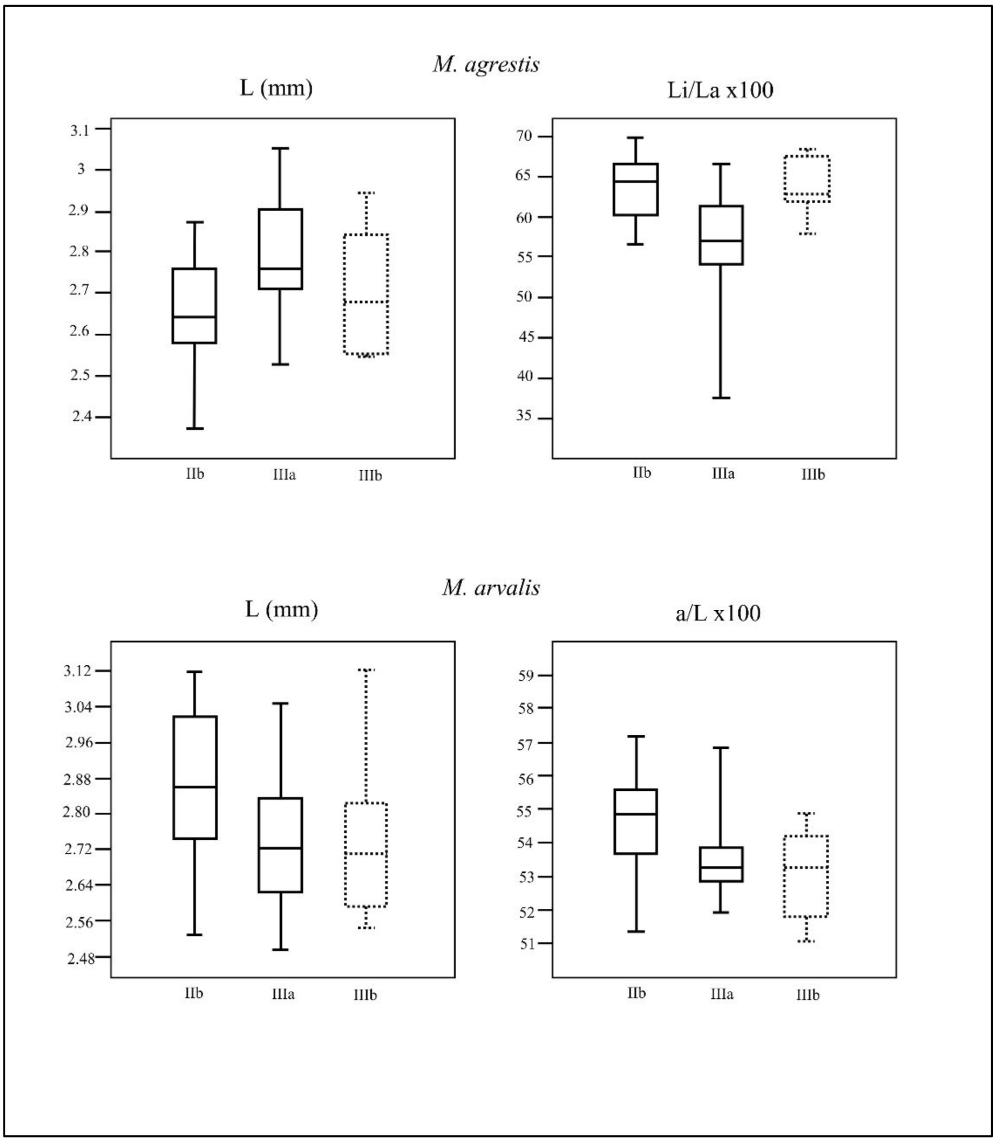

Figure 2. Box plot showing significant measurements of *M. agrestis* (L and Li/La) and *M. arvalis* (L and a/L). Black lines: levels IIb and IIIa. Dotted: level IIIb (not statistically significant).

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.

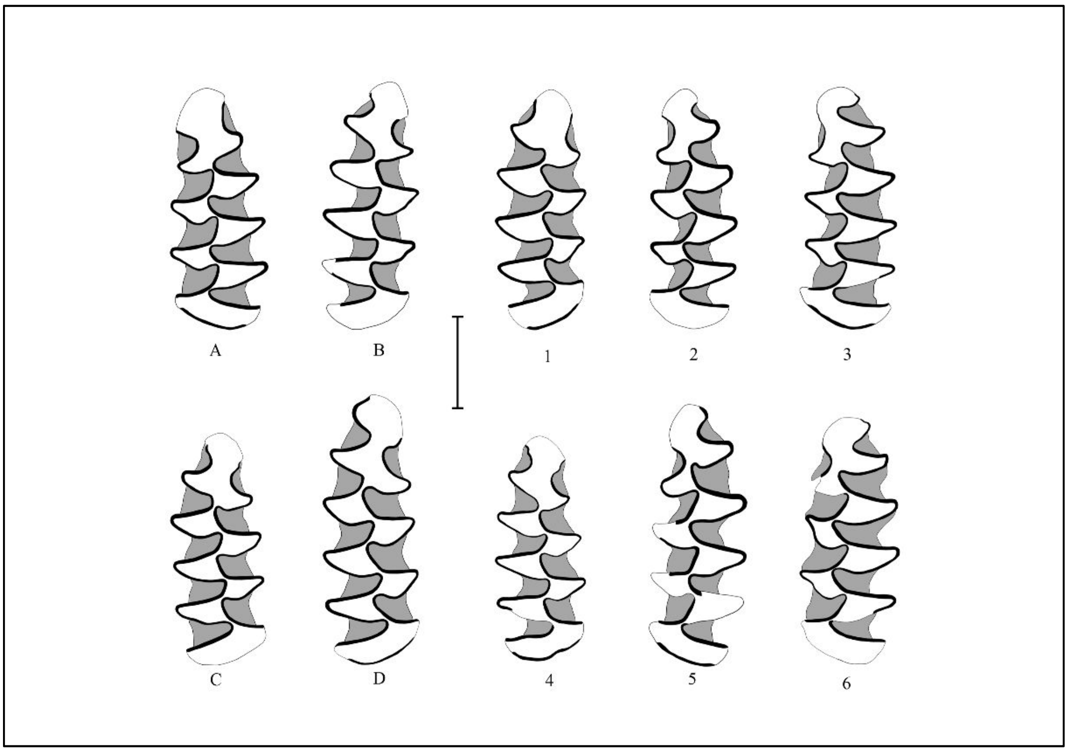

Figure 3. Morphotypes of *M. arvalis* (A: left m1; B-D: right m1, from level IIb) and *M. agrestis* (1 and 4: right m1, from level IIb; 2, 3, 5 and 6: left m1, from level IIIa). Occlusal view. Scale: 1 mm.

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

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

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

2.2.4. Discussion

Quantitative variations in small-mammal fossil assemblages linked to changes in climatic conditions have been studied extensively in the recent years (Berto et al. 2015; López-García et al. 2015; Rofes et al. 2015; Royer et al. 2016, among others). 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 cabrerae* and *Microtus* (*T.*) *duodecimcostatus*. The presence of *Capreolus capreolus* and *Equus hydruntinus* among the large-mammal record (Talamo et al. 2016) confirm 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 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 precipitations 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 favourable 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 m1 are large and asymmetrical, whereas in IIb they are smaller and more symmetrical (Fig. 4).

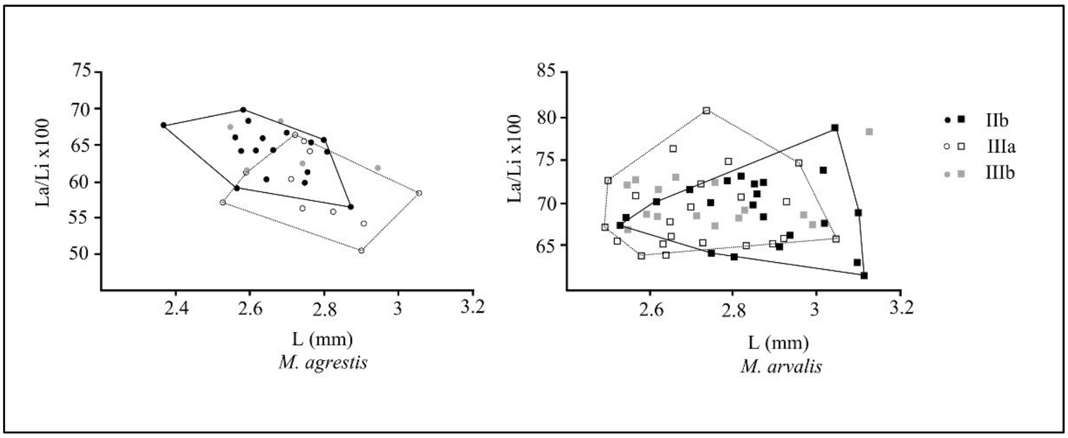

Figure 4. Graphic representation of the variations in the *M. agrestis* and *M. arvalis* populations.

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. Traditionally, these differences have been used in palaeontology 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* (Ledevin 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. 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 and privileged.

Dental patterns have proved to be strongly related to genetic factors in arvicolines (Stohl 1984; Polly et al. 2011; Markova et al. 2013a), and hereditability, 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 (Tougard et al. 2008; Ledevin et al. 2010a; Markova et al. 2010; Paupério 2012; Renvoisé et al. 2012; Tiunov et al. 2013; Markova et al. 2013b; Cucchi et al. 2014). While it is impossible to test directly the hypothesis of hereditability 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 favourable 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.

2.2.5. 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 favour of appropriately sized individuals. Bigger *M. arvalis* are favoured by drier conditions. In contrast, *M. agrestis* tends to get smaller when precipitations diminish.

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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2.3. Middle to Late Pleistocene *Microtus arvalis* and *Microtus agrestis* lineages from the Italian Peninsula: chronological insight and evolutionary

ELISA LUZI, CLAUDIO BERTO, and JUAN MANUEL LÓPEZ-GARCÍA

ABSTRACT: Rodents in general, and arvicolids in particular, have been usefully employed as biochronological markers for Pleistocene faunal sequences. In the present paper, populations belonging to *Microtus arvalis* and *M. agrestis* lineages from archaeological and palaeontological sites in the Italian Peninsula were analysed from a morphological and morphometric point of view in order to reveal possible patterns of evolution during the Middle and Late Pleistocene. Data obtained from the study of *M. nivaloides* populations were used to refine the chronological attribution of various sites from the Middle Pleistocene, calling into question the absolute dates assigned to them. It was also possible to establish the first clear occurrence of *M. arvalis* and *M. agrestis* in the Italian Peninsula during Marine Isotope Stage 12. Finally, comparison with sites from southwestern Europe enabled us to clarify the chronological position of Italian sites representing the transition between the late Middle Pleistocene and the Late Pleistocene, underlining shared evolutionary trends between southwestern Europe and the Italian Peninsula.

PALAIOS

Under Review

2.3.1. Introduction

In the last few decades, arvicolids have been widely employed as biochronological and biostratigraphic markers for Pleistocene sites and sequences (Abbassi et al. 1998; Markova 2005; Masini and Sala 2007; Ruddy 2011; Cuenca-Bescós et al. 2016, among others). The rapid rate of dental evolution, the extensive geographic distribution and the abundant presence of arvicolid taxa in the fossil record also make them useful tools in establishing interregional faunal correlations throughout Europe (Maul et al. 1998; Agadzhanyan 2012; López-García et al. 2015 among others). In the palaeontological record, the first lower molars are the anatomical element that provides diagnostic features for taxonomic identification, and many studies have thus focused on the analysis of their morphology (Kapischke et al. 2009; McGuire 2010; Polly et al. 2011; Markova et al. 2013; Tiunov et al. 2013; Borodin and Markova 2015, among others) and their morphometric characters (Ledevin et al. 2010; Maul et al. 2014; Klimowicz et al. 2015, among others), trying to establish patterns in their variations (Kolfschoten 1992; Kalthoff et al. 2007; Markova 2013, among others).

In this paper, populations of the common vole *Microtus arvalis* (Pallas, 1778) and field vole *Microtus agrestis* (Linnaeus 1761) belonging to evolutionary lineages from the Middle to Late Pleistocene of the Italian Peninsula were studied and the morphological and morphometric variations in their first lower molars were investigated in order to identify possible evolutionary patterns and help refine biochronological scales and attributions relating to the palaeontological and archaeological sites that contain these species.

2.3.2. Material and Methods

The samples analysed in this study come from 13 sites located in the Italian Peninsula, covering a chronological range spanning from the Middle to Late Pleistocene (Table 1). Spessa 10 (Bartolomei, 1964), Isernia la Pineta (Peretto et al., 2015), Bus de la Fadanana (Locatelli, 2005), Notarchirico (Sala, 1999; Pereira et al., 2015) and Visogliano (Bartolomei and Tozzi 1977; Falguères et al. 2008) belong to the Middle Pleistocene. Grotta Maggiore di San Bernardino (López-García et al., 2017) and Ciota Ciara (Berto et al., 2016) span from the Middle to Late Pleistocene. Caverna degli Orsi (Berto and Rubinato 2013), Grotta Fumane (López-García et al. 2015), Roccia San Sebastiano (Ruiu et al., 2012), Grotta della Ferrovia (Bartolomei, 1966; Sala, 2007), Grotta del Sambuco (Bietti, 1990) and Riparo Tagliente (Berto, 2013) date from the Late Pleistocene (Fig. 1).

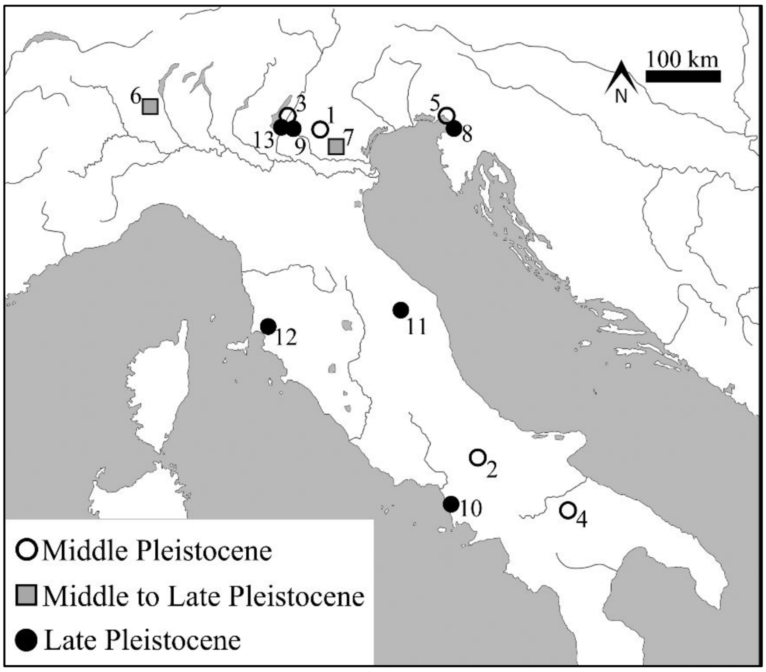

Figure 1. Geographical location of the sites. 1 = Spessa 10; 2 = Isernia; 3 = Bus de la Fadanana; 4 = Notarchirico; 5 = Visogliano; 6 = Ciota Ciara; 7 = Grotta Maggiore di San Bernardino; 8 = Caverna degli Orsi; 9 = Grotta Fumane; 10 = Roccia San Sebastiano; 11 = Grotta della Ferrovia; 12 = Grotta del Sambuco; 13 = Riparo Tagliente. White: Middle Pleistocene; grey: Middle to Late Pleistocene; black: Late Pleistocene.

Site		location (province-initials, region)	date
Spessa 10	1	Orgiano (VI, Veneto)	Middle Pleistocene
Isernia la Pineta	2	Isernia (IS, Molise)	MIS 15*
Bus de la Fada Nana	3	Bosco Chiesanuova (VR, Veneto)	Middle Pleistocene
Notarchirico	4	Venosa (PZ, Basilicata)	MIS 16*
Visogliano	5	Duino-Aurisina (TR, Friuli-Venezia Giulia)	MIS 12
Ciota Ciara	6	Borgosesia (VC, Piemonte)	Middle to Late Pleistocene
Grotta Maggiore San Bernardino	7	Mossano (VI, Veneto)	MIS 7-3
Caverna degli Orsi	8	San Dorligo della Valle (TR, Friuli-Venezia Giulia)	MIS 3
Grotta Fumane	9	Fumane (VR, Veneto)	MIS 3
Roccia San Sebastiano	10	Mondragone (CS, Campania)	MIS 3-2
Grotta della Ferrovia	11	Iesi (AN, Marche)	MIS 2
Grotta del Sambuco	12	Massa Marittima (GR, Toscana)	MIS 3-2
Riparo Tagliente	13	Grezzana (VR, Veneto)	MIS 2

Table 1. List of the sites, with their geographical location and chronology. MIS: Marine Isotope Stage. *: discussed in the paper.

The material was analysed with a Leica Ez4 D stereo microscope at x25 magnitude in the laboratory of the Dipartimento di Studi Umanistici, Sezione di Scienze Preistoriche e Antropologiche, Università degli Studi di Ferrara. The nomenclature for the description of the first lower molars (m1s) follows that proposed by Van der Meulen (1973): LRA and LSA represent respectively lingual reentrant and salient angles; BRA and BSA are buccal reentrant and salient angles; T refers to triangles. All triangles are numbered consecutively from the posterior lobe (LP) to the anterior cap (AC) (Fig. 2).

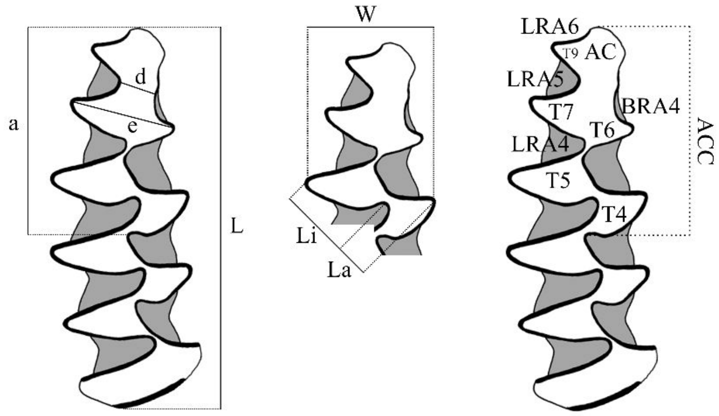

Figure 2. Nomenclature and measurements for the m1s. T = triangles; AC = anterior cap; BRA = buccal re-entrant angle; LRA = lingual re-entrant angle; ACC = anteroconid complex. L = total length of the tooth, a = length of the anteroconid; W = width of the anteroconid complex (ACC) measured at T4-T5; e = width of the anteroconid complex (ACC) measured at T6-T7; d = degree of closure of the anterior cap; La = width of T4; Li = width of T5 (after Van der Meulen 1974 and Cuenca-Bescós and Laplana 1995).

Measurements of the m1s were taken using ImageJ software and applying the criteria given by Van der Meulen (1973), Nadachowski (1984), and Cuenca-Bescós and Laplana (1995). "L" represents the total length of the tooth, "a" the length of the anteroconid, "W" the total width of the tooth measured at T4-T5, "e" the width of the anteroconid complex (ACC) measured at T6-T7, "d" the degree of closure of the anterior cap, "La" the width of T4, and "Li" the width of T5 (Fig. 2). The "La/Li" index is the ratio between the values La and Li and quantifies the degree of buccal-lingual asymmetry of the m1. The "a/L" index quantifies the development of the anterior part of the tooth compared to the total length of the m1. The "d/e" index reflects the degree of constriction of the AC. All indexes are expressed as percent. Only complete adult specimens, both right and left, were measured. All measurements are given in millimetres. The data were processed using PAST 3 software (Hammer and Harper, 2006). The mean values of the indexes a/L and La/Li for populations of different species and for populations of *M. agrestis* of different chronology were compared using the t-test and one-way ANOVA, with significance achieved at $p < 0.05$, while values of $p < 0.01$ were considered highly significant.

The diagnostic morphometric characters for the identification of *M. arvalis* and *M. agrestis* are those proposed by Nadachowski (1984).

The morphotypes of *Microtus nivaloides* were described following the criteria put forward by Nadachowski (1991), based on the different elements in the ACC:

- "nivalis-type": (1) BSA 4 and LRA5 well developed; (2) BRA 4 and LRA5 present; (3) short AC;
- "arvalis-type": (1); (4) BRA4 and LRA5 well developed; (5) high AC;
- "agrestis-type"; (2); (4); (5); LRA6 present;
- "coronensis-type": T6 and T7 strongly alternating;
- "extratriangulatus-type": T6 separated from T7;
- "tight-type": BRA4 and LRA5 very deep, T6-T7 widely confluent but separated from AC. This last morphotype was described in Rekovets and Nadachowski (1995) as the most complex of the arvaloid ones (see Results and Discussion, Fig. 4).

When possible, the upper second molars (M2s) were analysed in order to confirm the presence of *Microtus agrestis*. An additional closed field of dentine that occurs at the posterior end of these teeth in *M. agrestis* makes it possible to discriminate with certainty between this species and *M. arvalis* (Zimmerman, 1956; Chaline, 1972).

2.3.3. Results and Discussion

2.3.3.1. Populations of Microtus nivaloides from the early Middle Pleistocene (MIS 17-15): a tool for refining chronological attributions

Microtus nivaloides (Forsyth Major, 1902) was first described at West Runton as "recalling *M. nivalis*, but smaller and anterior loop more produced" (Forsyth Major 1902, p. 106, fig. 19). Subsequently, M.A.C. Hinton described *Microtus arvalinus* (Hinton, 1923) from the same site as with the "m1 in adults agreeing in form with that of *M. arvalis*; its size somewhat less and showing ephemeral and unusual complication of the anterior loop in early stage of wear", and *Microtus nivalinus* (Hinton 1923) as with the "m1 agreeing exactly in form and structure of anterior loop with recent *M. nivalis*. Size smaller" (Hinton 1923, p. 541). Reviewing the same material and following Van der Meulen (1973) and Stuart (1975), Nadachowski (1991) suggests ascribing *M. nivalinus* to the *M. oeconomus*-group, while *M. nivaloides* and *M. arvalinus* should be considered conspecific due to their striking morphological similarity, with priority of name given to *M. nivaloides*.

Microtus nivaloides presents high variability in the morphology of ACC, showing a range of continuous forms, from simple to more complex, both arvaloid and agrestoid. It has often been ascribed to the *M. arvalis*/*agrestis*-group, as an ancestor of both species but strong evidence points to a closer relationship with *M. agrestis* (Stuart, 1975; Rekovets and Nadachowski, 1995; Kowalski, 2001; Killick, 2012) (Fig. 3).

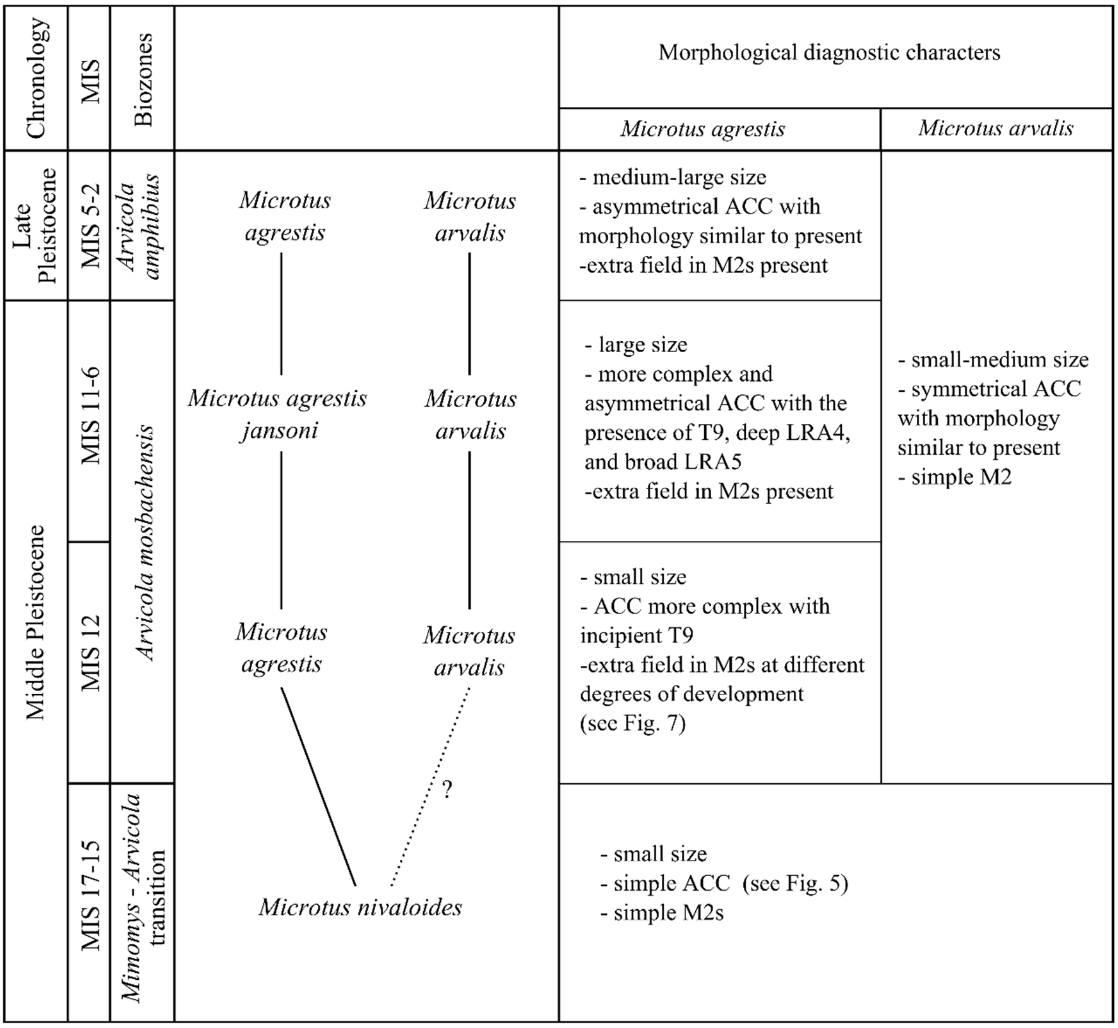

Figure 3. Chronological and phylogenetic succession of *Microtus nivaloides*, *M. agrestis* and *M. arvalis* with the morphological characters used for identification. MIS: Marine Isotope Stage. Biozones after Maul and Markova 2007.

In fossil populations from the Ukraine, the a/L index is never higher than 55 and d/e is never lower than 25 (Rekovets and Nadachowski 1995). The presence of *M. nivaloides* is recorded in central Europe, i.e. the Netherlands, Germany, Poland, Austria, Czechia, Slovakia, Hungary, Romania and parts of Italy and France, until Marine Isotope Stage (MIS) 15 or 13, when the first occurrence of *M. arvalis* is registered. In eastern Europe, i.e. Belarus, the Ukraine, Moldova and the European part of Russia, *M. arvalis* appears with certainty at MIS 12-11 (Maul and Markova 2007).

The populations from Spessa 10, Isernia la Pineta, Bus de la Fadanana and Notarchirico belong to *M. nivaloides*. The mean values of a/L x100 are always below 54, and d/e x100 is never lower than 30 (Fig. 4; Table 2).

Spessa 10

	n	min	mean	median	max	SD
L	5	2.333	2.673	2.686	2.888	0.21
a	5	1.212	1.332	1.332	1.467	0.09
e	3	0.758	0.81	0.831	0.842	0.04
d	3	0.198	0.387	0.469	0.496	0.16
a/L x100	5	47.65	49.91	50.36	51.95	2.08
d/e x100	3	26.12	47.84	55.7	59.68	18.33

Isernia

	n	min	mean	median	max	SD
L	17	2.34	2.677	2.719	2.898	0.17
a	23	1.097	1.356	1.409	1.583	0.4
e	28	0.64	0.774	0.76	0.88	0.05
d	25	0.86	0.323	0.324	0.454	0.06
La	28	0.186	0.36	0.355	0.417	0.02
Li	28	0.3	0.611	0.617	0.695	0.05
a/L x100	17	46.8	51.91	52.2	63.8	8.22
d/e x100	25	41.9	41.93	42	53.5	6.19

Bus de la Fadanana

	n	min	mean	median	max	SD
L	19	2.273	2.49	2.483	2.744	0.11
a	19	1.126	1.323	1.352	1.444	0.08
e	13	0.632	0.709	0.703	0.817	0.05
d	16	0.046	0.2	0.222	0.357	0.08
La	13	0.303	0.347	0.345	0.411	0.03
Li	13	0.449	0.521	0.506	0.674	0.06
a/L x100	19	49.53	53.09	53.1	55.73	1.79
d/e x100	13	6.71	30.57	34.73	43.69	1.18

Notarchirico

	n	min	mean	median	max	SD
L	6	2.359	2.692	2.731	2.993	0.1
a	7	1.213	1.463	1.535	1.624	0.05
e	7	0.647	0.744	0.768	0.84	0.02
d	8	0.132	0.265	0.248	0.373	0.02
La	4	0.346	0.388	0.4	0.407	0.01
Li	4	0.476	0.55	0.553	0.618	0.02
a/L x100	6	49.81	53.84	54.53	56.21	0.9
d/e x100	7	29.22	38	37.4	47.51	2.4

Table 2. Measurements of *Microtus nivaloides.*

However, there are differences among these populations. Even without absolute dating and on the basis of the evolutionary stage of the lineage *Mimomys-Arvicola* (Maul et al., 2000, 2014; Lozano-Fernández et al., 2013), the occurrence of an advanced *Mimomys savini* at Spessa 10 (B. Sala "pers. comm.", 2017) allows the site to be placed at the end of the Biharian (ca. 800-700 ka BP), hence prior to the others. Furthermore, the mean value of a/L for Spessa 10 is close to that for West Runton, tentatively assigned to MIS 17 (Maul and Parfitt 2010). The first occurrence of a primitive form of *Arvicola mosbachensis* at Isernia marks the beginning of the Toringian (ca. 600 ka BP), whereas the *Arvicola* of Notarchirico shows more advanced characters (Sala 1999; Sala and Masini 2007) and should thus be considered slightly younger than Isernia. Absolute dates suggest by contrast that Notarchirico, dated to MIS 16 (Pereira et al., 2015), should be older than Isernia, dated to the end of MIS 15 (Peretto et al., 2015). The position of Bus de la Fadanana is more complex: on the basis of the small-mammal assemblage (Locatelli, 2005), it can confidently be placed in the transition from the late Biharian to the early Toringian (ca. 700-600 ka BP), but it cannot be established whether it is younger or older than Isernia, although it is certainly older than Notarchirico. The study of the population of *M. nivaloides* may help to place these sites in their proper chronology.

Studies of several species of the genus *Microtus* suggest that the value of the a/L index increases over time (Maul et al. 1998; Maul et al. 2014; Klimowicz et al. 2015, among others). This relative elongation of the ACC allows for more complex morphologies to arise. In our samples, it can be observed that the value of a/L tends to increase over time (Fig. 4).

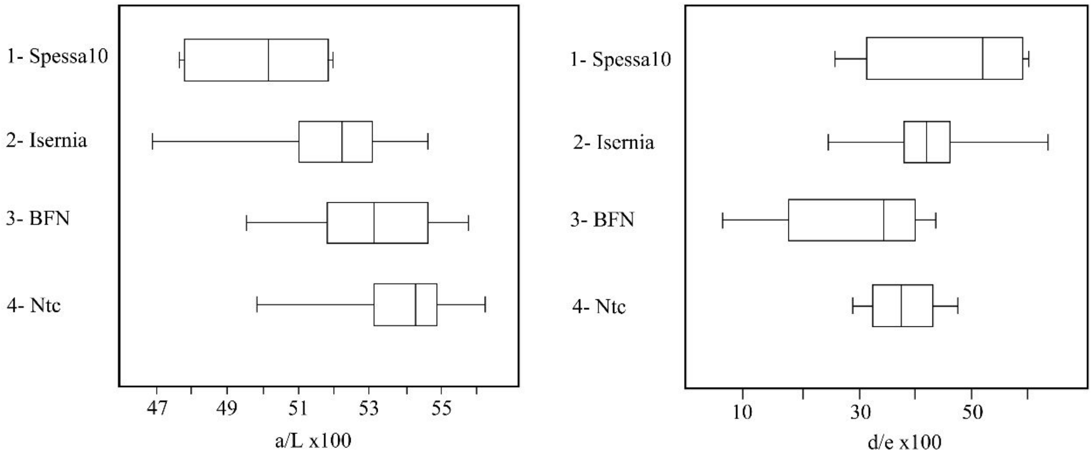

Figure 4. Box-plot with values of the a/L index and d/e index of *Microtus nivaloides* populations.

Furthermore, the distribution of the morphotypes changes: the simpler “nivalis-type” is not present at Notarchirico, the most recent site; the more complex types are absent from Spessa 10, the oldest site (Fig. 5). Therefore, the biochronological order of these sites suggested by *Microtus* is coherent with that of the *Mimomys*-*Arvicola* lineage rather than with the absolute chronological dating, placing Isernia before Notarchirico according to both the a/L and d/e indexes. In positioning Bus de la Fadanana, the value of a/L has been preferred because of its stronger evolutionary meaning. The low d/e values are in fact a reflection of the morphological peculiarity of this population, which presents a relatively high number of “tight-type” m1s.

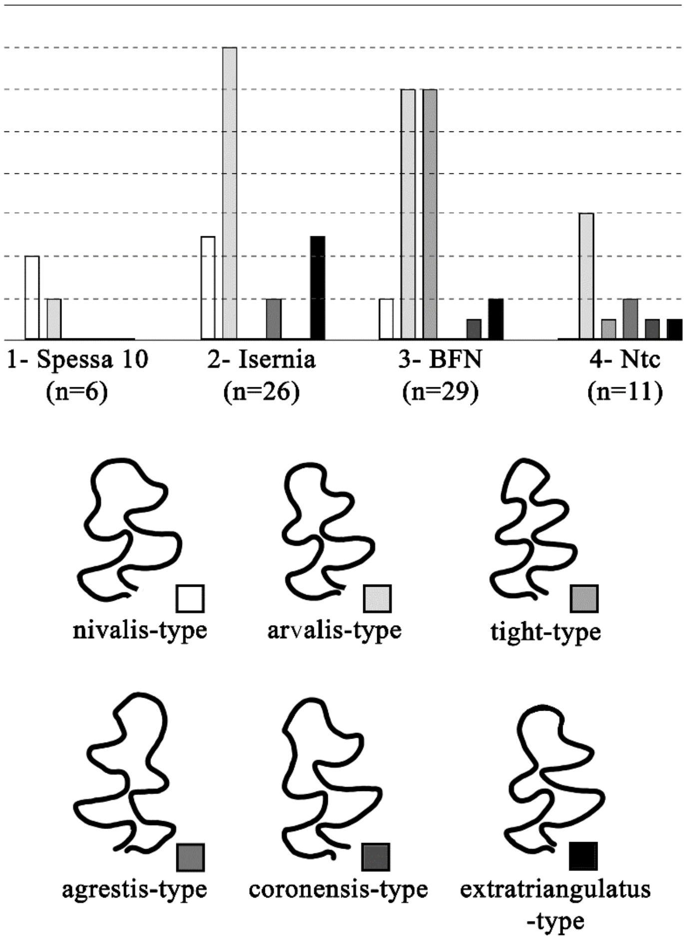

Figure 5. Outlines and distribution of morphotypes of *Microtus nivaloides* populations; in brackets: number of specimens. Morphotypes increase in complexity through time.

It is also notable that, in all the populations, the specimens with La/Li higher than 68 tend to present incomplete closure of T4-T5. This confluence is much narrower than the pitymyian rhombus typical of the subgenus *Terricola* but it is also visible in radical view, so it cannot be explained as a juvenile trait destined to disappear with growth. In Ukrainian populations this imperfect closure seems to be present (Rekovets and Nadachowski 1995, fig. 71), and the same character was observed by Nadachowski (1985) in two specimens from the Biharian fauna of Kozi Grzbiet, where it was associated with large size but with no mention regarding the symmetry of the m1s. Since this “defect” in the occlusal surface occurs, though only very rarely, in extant populations of *Microtus* s.l. (Nadachowski, 1985), this might be an archaic character with a tendency to resurface when the m1 is more symmetrical. Should this be the case, we would expect it to occur in the *M. arvalis* lineage, which displays a high degree of symmetry, rather than in *M. agrestis*, and to disappear through time.

2.3.3.2. The case of Visogliano rockshelter (MIS 12): the first occurrence of Microtus arvalis and Microtus agrestis in the Italian Peninsula

The site of Visogliano is composed of an external breccia (VisB) and a rock shelter (VisA). The 11-m-thick sequence of VisA was dated by ESR/U-series analysis to between 500 and 350 ka (Falguères et al., 2008). Analysis of the morphological and morphometric characters of *Arvicola mosbachensis* from level 34 allowed that level to be related to MIS 12 (Luzi et al., 2015). The sample of *Microtus* from Visogliano considered in this study comes from the same level. On the basis of morphological and morphometric data, it was possible to isolate two different populations. Even though they both present remarkable intraspecific morphological variations and are small in size, the morphotypes are already heading in the evolutionary direction of either the *agrestis*-group or the *arvalis*-group, the first characterized by an asymmetric ACC, alternating T6-T7 and the occurrence of LSA6; the latter by a symmetric ACC, opposing T6-T7 and a rounded AC. Furthermore, the a/L index and the La/Li index set the two groups apart (Fig. 6 and Table 3).

	M. nivaloides (1-4) mean ± SD	*M. agrestis* (5) mean ± SD	*p*
a/L x100	52.55 ± 2.17	53.38 ± 2.21	0.15
La/Li x100	64.80 ± 9.6	59.88 ± 4.31	0.21

	M. nivaloides (1-4) mean ± SD	*M. arvalis* (5) mean ± SD	*p*
a/L x100	52.55 ± 2.17	54.92 ±1.46	**0.01**
La/Li x100	64.80 ± 9.6	70.69 ± 5.11	**0.003**

	M. agrestis (5) mean ± SD	*M. arvalis* (5) mean ± SD	*p*
a/L x100	53.38 ± 2.21	54.92 ±1.46	**0.01**
La/Li x100	59.88 ± 4.31	70.69 ± 5.11	**< 0.001**

Table 3. Comparison of a/L index and La/Li index for *M. nivaloides*, *M. agrestis* and *M. arvalis* populations. T-test with significance achieved at *p*-value < 0.05; high significance at *p*-value < 0.01. Mean: mean value of the index; SD: standard deviation. Bold: significant values. In brackets: sites of origin of the samples, see Table 1.

Finally, in the M2s (n. 69), the additional dentine loop characteristic of *M. agrestis* is present (13%), although at different stages of development (Fig. 7). The same imperfect closure of T4-T5 spotted in the older populations of *M. nivaloides* is present (7 specimens out of the total 46), and here too it occurs only in the *M. arvalis*-group, supporting the hypothesis that it is a relict character from a primitive ancestor and linked to the symmetry of the molars.

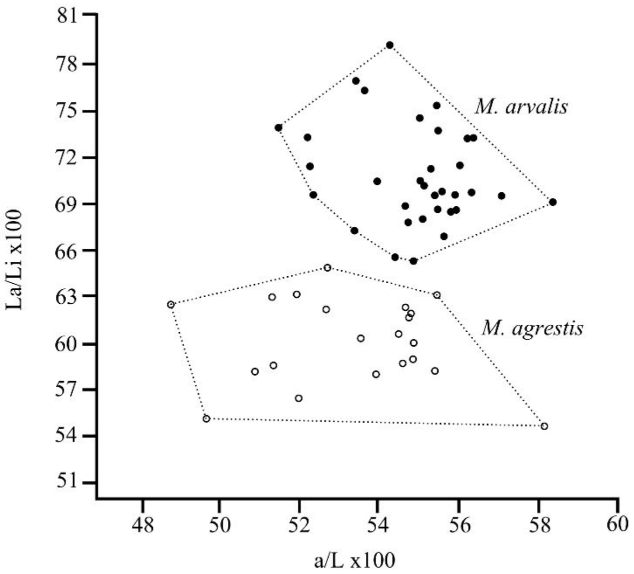

Figure 6. Relation between a/L index and La/Li index of Visogliano populations. Dotted lines: convex hulls. *Microtus arvalis* and *M. agrestis* are clearly separated.

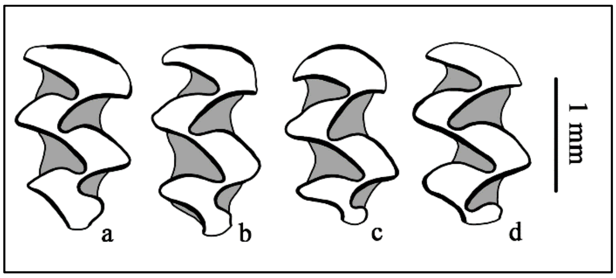

Figure 7. Different levels of development of M2s in the *M. agrestis* group: extra field in the posterior part of the tooth from incipient to closed (a to d). Scale: 1 mm.

Phylogenetic studies (Jaarola et al. 2004; Robovský et al. 2008; Fink et al. 2010; Martínková and Moravec 2012) have revealed that the split between the *M. arvalis* and *M. agrestis* lineages occurred early in the evolutionary history of the genus *Microtus* (2-1.2 Ma) and that the two species might have reached Europe from Asia in different colonization waves. Even though it may be possible to note the tendency of populations toward more "*arvalis*"-like or more "*agrestis*"-like morphologies and metrics, the continuous variations in the forms and measurements of the fossil specimens preclude definitive identification of the two groups in the early stages of their evolution. Kowalski (2001) suggests only ascribing to *M. arvalis* and *M. agrestis* fossil material that is younger than MIS 11. The study of the population from VisA shows that the two species at MIS 12 had reached a significant distance (Table 3) and that it is therefore possible to refer to them from this point on as *Microtus arvalis* and *Microtus agrestis*. Compared with *M. nivaloides*, *M. agrestis* from Visogliano shelter present a more complex ACC in m1 and the additional loop in M2. Despite the qualitative differences in morphological characters, there are no significant differences in the measurements of *M. nivaloides* and *M. agrestis* (Table 3), confirming the hypothesis of a more direct phylogenetic relations between these two species, whereas *M. arvalis* is morphologically and morphometrically well separated from both *M. nivaloides* and *M. agrestis*.

2.3.3.3. Evolutionary trends in Microtus arvalis (Pallas, 1778) through the late Middle Pleistocene and Late Pleistocene (MIS 11-2)

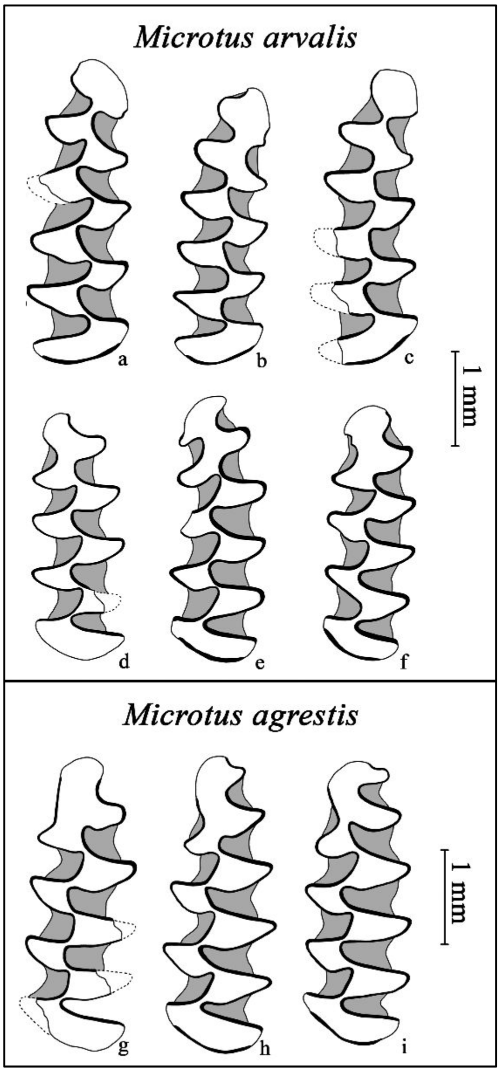

Figure 8. Morphological variation of first lower molars in *M. arvalis* (a-c: right m1s; d-f: left m1s) and *M. agrestis* (g-i: left m1s). Sample from the Late Pleistocene site of Grotta del Sambuco. Scale: 1 mm.

Microtus arvalis tends to follow a slow but steady pattern toward an increase in size and symmetry of the m1 but it shows remarkably stable values for a/L (Table 4). The intraspecific morphological variability is always very high (Fig. 8). The incomplete closure of T4-T5 is extremely rare. Compared to *M. agrestis*, it is always smaller in size (Fig. 9). This difference in size has already been noticed in population from Croatia (Mauch Lenardić, 2007), Poland (Nadachowski, 1982, 1984) and the Ukraine (Rekovets and Nadachowski 1995). Nevertheless, in our samples there are two exceptions. The first is the population from Riparo Tagliente, with the two species presenting almost equal mean values, and this is probably related to the peculiar chronology of this site, which is the only one in our sample dated to the very end of MIS 2. The climatic conditions following the end of the Last Glacial Maximum might be the cause of this altered trend: *M. arvalis* retains its size, while the unfavourable conditions lead *M. agrestis* to reduce its size. The same trend is visible at Toll Cave (north-eastern Iberia, Luzi and López-García 2017). The second exception is provided by the population from Roccia San Sebastiano. This is the only site in our sample from southern Italy and the relationship between *M. arvalis* and *M. agrestis* is comparable to that displayed by certain populations in the northern Iberian Peninsula, where m1s of *M. arvalis* are larger in size than those of *M. agrestis*, i.e. Teixoneres, Toll, Arbreda, Valdavara-1, Eirós, Portalon, Colomera (Luzi and López-García 2017). A latitudinal cline and/or similar climatic conditions might be supposed, but more data from other sites in the same region are needed to support any hypothesis.

Visogliano

	Microtus agrestis					*Microtus arvalis*				
	n	min	mean	max	SD	n	min	mean	max	SD
L	21	2.431	2.683	3.156	0.19	33	2.414	2.646	2.972	0.13
a	25	1.24	1.445	1.749	0.12	41	1.398	1.415	1.659	0.19
W	20	0.806	0.935	1.059	0.07	36	0.781	0.9	0.986	0.05
e	23	0.631	0.756	0.891	0.06	45	0.655	0.731	0.821	0.04
d	25	0.11	0.263	0.378	0.06	46	0.062	0.246	0.382	0.06
La	28	0.31	0.354	0.393	0.02	38	0.314	0.379	0.451	0.02
Li	26	0.521	0.59	0.701	0.04	37	0.488	0.536	0.581	0.02
a/L x100	21	48.81	53.38	58.15	2.21	33	51.53	54.92	58.32	1.46
La/Li x100	26	51.78	59.88	66.78	4.31	36	62.67	70.69	81.55	5.11

Ciota Ciara (unit 15)

	Microtus agrestis					*Microtus arvalis*				
	n	min	mean	max	SD	n	min	mean	max	SD
L	7	2.457	2.867	3.04	0.19	4	2.633	2.811	3.018	0.17
a	8	1.28	1.491	1.598	0.09	4	1.462	1.528	1.623	0.06
W	10	0.884	0.883	1.061	0.05	4	0.842	0.981	1.095	0.12
e	9	0.71	0.81	0.926	0.06	5	0.721	0.8	0.888	0.06
d	10	0.285	0.346	0.453	0.04	5	0.24	0.317	0.43	0.07
La	10	0.292	0.362	0.418	0.03	5	0.356	0.411	0.465	0.04
Li	12	0.548	0.622	0.692	0.04	5	0.494	0.581	0.67	0.06
a/L x100	5	48.85	51.35	52.56	1.52	4	52.16	54.42	56.23	1.82
La/Li x100	10	43.84	57.99	65.72	7.02	5	64.47	70.89	0.75	3.95

Ciota Ciara (unit 14)

	Microtus agrestis					*Microtus arvalis*				
	n	min	mean	max	SD	n	min	mean	max	SD
L	19	2.645	2.993	3.276	0.17	17	2.461	2.714	2.945	0.14
a	19	1.401	1.579	1.828	0.11	17	1.345	1.475	1.618	0.08
W	18	0.909	1.032	1.19	0.07	17	0.854	0.918	1.042	0.05
e	19	0.768	0.862	0.975	0.06	17	0.709	0.759	0.827	0.03
d	19	0.225	0.325	0.405	0.05	17	0.146	0.248	0.337	0.05
La	19	0.327	0.375	0.436	0.03	17	0.357	0.39	0.424	0.02
Li	19	0.57	0.669	0.796	0.04	17	0.501	0.541	0.615	0.03
a/L x100	19	48.9	52.72	55.79	1.72	17	50.45	54.34	56.3	1.48
La/Li x100	19	47.61	56.27	65.78	5.59	17	64.46	72.35	81.9	4.84

Grotta Maggiore di San Bernardino (units VIII-VII)

	Microtus agrestis					*Microtus arvalis*				
	n	min	mean	max	SD	n	min	mean	max	SD
L	25	2.647	2.892	3.073	0.12	5	2.57	2.637	2.67	0.03
a	25	1.406	1.554	1.687	0.08	5	1.444	1.468	1.471	0.01
W	25	0.9	0.997	1.102	0.04	5	0.829	0.895	0.987	0.06
e	25	0.8	0.789	0.906	0.05	5	0.733	0.77	0.824	0.03
d	25	0.05	0.269	0.381	0.06	5	0.156	0.18	0.214	0.02
La	25	0.296	0.348	0.415	0.02	5	0.344	0.371	0.442	0.04
Li	25	0.584	0.663	0.721	0.03	5	0.519	0.542	0.57	0.02
a/L x100	25	51.11	53.73	55.48	1.23	5	55.07	55.77	56.18	4.47
La/Li x100	25	43.4	52.69	60.76	4.78	5	65.07	68.41	77.54	5.17

Table 4. Measurements of *Microtus agrestis* and *M. arvalis*.

Grotta Maggiore di San Bernardino (units V-IV)

	Microtus agrestis					*Microtus arvalis*				
	n	min	mean	max	SD	n	min	mean	max	SD
L	21	2.625	2.935	3.314	0.18	24	2.471	2.675	3.004	0.14
a	21	1.378	1.574	1.766	0.09	24	1.264	1.463	1.73	0.1
W	21	0.895	1.02	1.123	0.06	24	0.82	0.921	1.016	0.04
e	20	0.709	0.833	0.931	0.05	24	0.669	0.763	0.852	0.05
d	20	0.086	0.259	0.408	0.08	24	0.117	0.214	0.303	0.04
La	21	0.311	0.373	0.433	0.02	24	0.349	0.389	0.442	0.02
Li	21	0.568	0.658	0.724	0.05	24	0.48	0.552	0.591	0.03
a/L x100	21	50.03	53.66	56.6	1.42	24	51.18	55.04	59.75	1.71
La/Li x100	21	46.07	56.89	64.96	4.89	24	66.47	70.71	79.51	3.95

Grotta Maggiore di San Bernardino (units III-II)

	Microtus agrestis					*Microtus arvalis*				
	n	min	mean	max	SD	n	min	mean	max	SD
L	14	2.616	2.797	3.002	0.12	6	2.318	2.577	2.896	0.19
a	14	1.347	1.505	1.636	0.08	6	1.226	1.409	1.6	0.13
W	14	0.857	0.969	1.087	0.06	6	0.793	0.9	0.969	0.06
e	14	0.664	0.775	0.897	0.07	6	0.671	0.741	0.826	0.06
d	14	0.198	0.294	0.411	0.06	6	0.24	0.254	0.267	0.01
La	14	0.316	0.353	0.39	0.02	6	0.336	0.386	0.44	0.03
Li	14	0.553	0.632	0.71	0.05	6	0.499	0.537	0.579	0.03
a/L x100	14	51.47	53.81	56.09	1.37	6	52.72	54.63	57.12	1.81
La/Li x100	14	47.39	56.17	66.07	6.17	6	64.76	72.19	86.95	7.77

Caverna degli Orsi

	Microtus agrestis					*Microtus arvalis*				
	n	min	mean	max	SD	n	min	mean	max	SD
L	15	2.342	2.652	2.97	0.16	19	2.319	2.518	2.746	0.11
a	15	1.218	1.436	1.62	0.1	19	1.23	1.383	1.479	0.08
W	15	0.853	0.904	1.039	0.05	19	0.807	0.877	0.994	0.04
e	13	0.662	0.738	0.808	0.04	19	0.674	0.742	0.828	0.04
d	14	0.164	0.268	0.378	0.05	19	0.056	0.212	0.275	0.04
La	15	0.307	0.335	0.403	0.02	19	0.321	0.36	0.43	0.02
Li	15	0.514	0.575	0.683	0.04	19	0.469	0.524	0.581	0.03
a/L x100	15	51.41	54.12	56.26	1.45	19	52.37	54.93	57.61	1.54
La/Li x100	15	45.82	58.53	66.03	5.66	19	59.85	68.84	91.68	6.79

Grotta Fumane

	Microtus agrestis					*Microtus arvalis*				
	n	min	mean	max	SD	n	min	mean	max	SD
L	30	2.478	2.861	3.238	0.2	30	2.04	2.604	2.882	0.16
a	30	1.326	1.549	1.764	0.11	30	1.269	1.434	1.549	0.08
W	30	0.829	0.991	1.159	0.11	30	0.794	0.879	1.051	0.05
e	29	0.667	0.819	1.003	0.08	30	0.662	0.733	0.888	0.04
d	30	0.135	0.265	0.535	0.08	30	0.131	0.221	0.323	0.05
La	30	0.313	0.363	0.42	0.03	30	0.294	0.363	0.425	0.02
Li	30	0.506	0.637	0.783	0.08	30	0.451	0.542	0.617	0.03
a/L x100	30	49.14	54.17	56.8	1.52	30	52.26	55.1	62.2	1.71
La/Li x100	30	39.97	57.75	69.9	6.27	30	61.68	69.34	81.39	4.98

Table 4. Measurements of *Microtus agrestis* and *M. arvalis*. Continued.

Roccia San Sebastiano										
			Microtus agrestis					*Microtus arvalis*		
	n	min	mean	max	SD	n	min	mean	max	SD
L	18	2.499	2.722	2.996	0.15	30	2.449	2.761	2.981	0.13
a	18	1.346	1.488	1.715	0.1	30	1.275	1.488	1.636	0.08
W	18	0.86	0.931	1.032	0.05	30	0.811	0.94	1.003	0.04
e	18	0.672	0.762	0.853	0.04	28	0.68	0.766	0.876	0.04
d	18	0.111	0.24	0.366	0.06	28	0.056	0.232	0.354	0.06
La	18	0.268	0.341	0.414	0.03	30	0.351	0.389	0.43	0.02
Li	18	0.525	0.6	0.708	0.05	30	0.479	0.555	0.597	0.02
a/L x100	18	51.35	54.63	58.01	1.93	30	51.32	53.89	57.5	1.43
La/Li x100	18	44.15	57.28	71.5	8.1	30	62.21	70.19	76.76	3.65
Grotta della Ferrovia										
			Microtus agrestis					*Microtus arvalis*		
	n	min	mean	max	SD	n	min	mean	max	SD
L	30	2.353	2.769	3.038	0.17	30	2.44	2.67	2.898	0.12
a	30	1.26	1.502	1.694	0.1	30	1.228	1.44	1.684	0.08
W	30	0.847	0.95	1.094	0.07	30	0.824	0.91	1.025	0.04
e	30	0.682	0.777	0.94	0.06	30	0.676	0.755	0.847	0.04
d	30	0.138	0.234	0.409	0.05	30	0.107	0.206	0.308	0.05
La	30	0.325	0.354	0.407	0.02	30	0.327	0.384	0.447	0.02
Li	30	0.511	0.605	0.745	0.06	30	0.49	0.542	0.584	0.02
a/L x100	30	52.82	54.22	56.36	0.94	30	50.82	53.92	58.1	1.61
La/Li x100	30	46.45	59.16	72.21	6.33	30	66.28	70.74	77.34	2.87
Grotta del Sambuco										
			Microtus agrestis					*Microtus arvalis*		
	n	min	mean	max	SD	n	min	mean	max	SD
L	23	2.476	2.852	3.034	0.14	30	2.474	2.782	2.816	0.08
a	23	1.364	1.558	1.686	0.08	30	1.32	1.489	1.541	0.05
W	21	0.78	0.951	1.044	0.07	30	0.806	0.944	1.007	0.05
e	21	0.683	0.803	0.847	0.04	29	0.642	0.791	0.836	0.04
d	23	0.12	0.23	0.399	0.08	30	0.123	0.258	0.412	0.06
La	23	0.316	0.362	0.374	0.01	30	0.325	0.397	0.427	0.02
Li	23	0.476	0.601	0.716	0.05	30	0.463	0.561	0.599	0.03
a/L x100	23	51.48	54.62	57.47	1.44	30	50.63	53.32	56.64	1.46
La/Li x100	23	45.82	60.94	67.77	5.76	30	60.9	75.8	79.96	4.64
Riparo Tagliente										
			Microtus agrestis					*Microtus arvalis*		
	n	min	mean	max	SD	n	min	mean	max	SD
L	30	2.525	2.724	2.942	0.12	30	2.484	2.721	3.027	0.14
a	30	1.368	1.479	1.675	0.07	30	1.318	1.469	1.684	0.09
W	26	0.825	0.926	1.012	0.04	29	0.822	0.93	1.014	0.04
e	24	0.666	0.784	0.863	0.04	27	0.676	0.787	0.877	0.04
d	24	0.067	0.248	0.35	0.05	29	0.071	0.262	0.423	0.06
La	26	0.303	0.36	0.399	0.02	29	0.34	0.392	0.436	0.02
Li	26	0.522	0.577	0.641	0.02	29	0.484	0.552	0.602	0.02
a/L x100	30	51.83	54.3	56.93	1.17	30	49.5	53.96	57.58	1.54
La/Li x100	26	57.95	62.37	66.84	2.59	29	65	71.11	80.14	3.7

Table 4. Measurements of *Microtus agrestis* and *M. arvalis*. Continued.

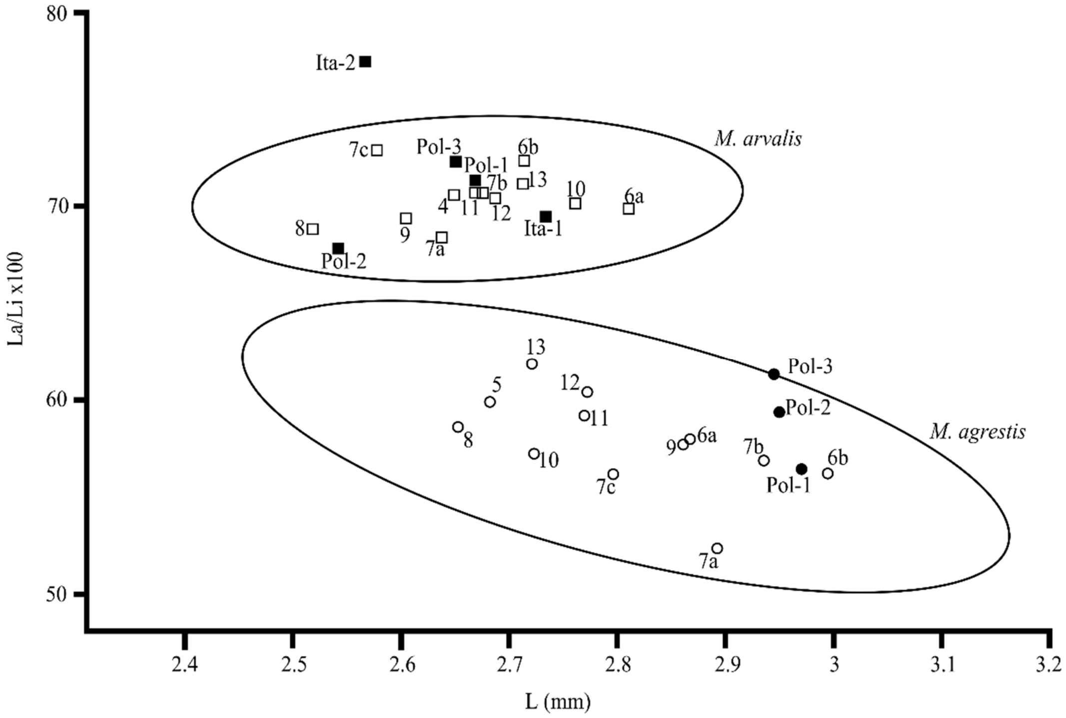

Figure 9. Relation between L and the La/Li index. Squares = *M. arvalis*; Circles = *M. agrestis*. White: fossil populations. 5 = Visogliano; 6a = Ciota Ciara (Middle Pleistocene); 6b = Ciota Ciara (MIS 5); 7a = Grotta Maggiore di San Bernardino (Middle Pleistocene); 7b = Grotta Maggiore di San Bernardino (MIS 5); 7c = Grotta Maggiore di San Bernardino (MIS 3) 8 = Caverna degli Orsi; 9 = Grotta Fumane; 10 = Roccia San Sebastiano; 11 = Grotta della Ferrovia; 12 = Grotta del Sambuco; 13 = Riparo Tagliente. Ellipses: 95% confidence for fossil population. Black: recent populations. Pol-1, Pol-2, Pol-3: Polish populations after Nadachowski 1984; Ita-1, Ita-2: Italian populations from the collection of Università of Ferrara. The two species are clearly separated.

2.3.3.4. Evolutionary trends in Microtus agrestis (Linnaeus, 1761) through the late Middle Pleistocene and Late Pleistocene (MIS 11-2)

In the Mediterranean region, Chaline (1972) recognized a specific type of *M. agrestis* from the late Middle Pleistocene, which he named *Microtus agrestis jansoni* after the type locality, Saint-Estève-Janson. He described it as clearly agrestoid, middle to large in size, with a highly variable ACC composed as a rule of alternating but confluent T6-T7, a deep LRA4, the presence of T9 in the AC and a broad LRA5. According to the same author, this species characterizes the Middle Pleistocene but survives until the first stage of the Late Pleistocene, when it occurs with a co-specific, *M. agrestis aubinensis*, which presents the same characters but is smaller in size.

In Italy, *M. a. jansoni* has been identified in the lower units (VIII-VII) of Grotta Maggiore di San Bernardino in association with *Arvicola mosbachensis* and an archaic form of *Dinaromys bogdanovi*, dated to the end of the Middle Pleistocene (MIS 7; López-García et al. 2017). It has also been identified in the lower level (unit 15) of Ciota Ciara, in association with *Allocricetus* sp., *Pliomys* sp. and *Arvicola* cf. *mosbachensis* (Angelucci et al., 2016), However, these two samples differ greatly as regards their a/L and La/Li values. Even though geographical differences exist between populations because of different climatic and environmental conditions or as a consequence of a different phylogenetic history, it may prove useful to compare these two populations with others of the same chronology from the Mediterranean region of southern Europe. The mean values of a/L within *M. agrestis* populations do not present a regular and constant increase, as already observed for *Microtus* populations across Europe (Maul et al. 2014).

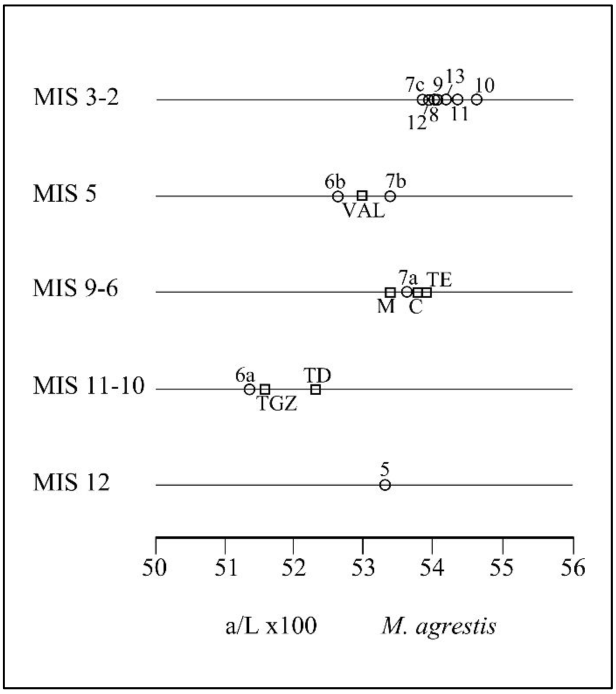

Figure 10. Variations in a/L index of *M. agrestis*. Circle = sample from the Italian Peninsula. MIS 12: 5 = Visogliano. MIS 11-10: 6a = Ciota Ciara; MIS 9-6: 7a = Grotta Maggiore di San Bernardino. MIS 5: 6b = Ciota Ciara, 7b = Grotta Maggiore di San Bernardino; MIS 3-2: 7c = Grotta Maggiore di San Bernardino (MIS 3) 8 = Caverna degli Orsi; 9 = Grotta Fumane; 10 = Roccia San Sebastiano; 11 = Grotta della Ferrovia; 12 = Grotta del Sambuco; 13 = Riparo Tagliente. Square = samples from southwestern Europe. TD = Trinchera Dolina; TGZ = Galeria-Zarpazos; TE = Sima del Elefante; C = Carrière; M = Mollet; VAL = Valdavara-3.

However, the fluctuations in the Mediterranean regions follow a pattern that allows a distinction to be drawn among late Middle Pleistocene and Late Pleistocene populations. Ciota Ciara (unit 15) sample is probably older than those from Grotta Maggiore di San Bernardino (units VIII-VII, MIS 7), Sima del Elefante (TE, layers 18-19, MIS 9-8, de Lombera Hermida et al. 2015), Mollet (M, MIS 7, Maroto et al., 2012) and Grotte de la Carrière (C, MIS 9-7, López-García et al. 2016) and comparable to those from the Middle Pleistocene of Trinchera Dolina (TD10.2; MIS 11-

10, Falguères et al. 2013) and Galeria-Zarpazos (TGZ II-III, MIS 11-10, Falguères et al. 2013) (Luzi and López-García, 2017) (Fig. 10; Table 5). It is noteworthy that the a/L values at sites from MIS 5, i.e. Ciota Ciara (unit 14), Grotta Maggiore di San Bernardino (units V-IV), and Valdavara-3 (VAL, MIS 5, Vaquero et al. 2017, submitted; Luzi and López-García 2017) are the lowest in the Late Pleistocene whereas the values at the sites dated to MIS 3 and MIS 2 are grouped together.

	M. agrestis (6a; TGZ; TD) MIS 11-10	*M. agrestis* (7a; M; C; TE) MIS 9-6	*M. agrestis* (6b; 7b; VAL) MIS 5	*M. agrestis* (7c-13) MIS 3-2
M. agrestis (6a; TGZ; TD) MIS 11-10		**< 0.001**	**< 0.001**	**< 0.001**
M. agrestis (7a; M; C; TE) MIS 9-6	**< 0.001**		0.058	0.77
M. agrestis (6b; 7b; VAL) MIS 5	**< 0.001**	0.58		**0.002**
M. agrestis (7c-13) MIS 3-2	**< 0.001**	0.77	**0.002**	

Table 5. Comparison of a/L index for *M. agrestis* populations. One-way ANOVA results, with significance achieved at p-value < 0.05; high significance at p-value < 0.01. Bold: significant values. MIS: Marine Isotope Stage. In brackets: sites of origin of the samples.

2.3.4. Conclusions

Our analysis of morphological and morphometric characters in populations belonging to the *Microtus arvalis* and *M. agrestis* lineages has proved to be a useful tool in refining the biochronological attributions of the Italian palaeontological and archaeological sites under consideration:

- our study of the frequency of morphotypes and comparison of values for the morphometric index a/L has allowed a chronological order to be proposed for the populations of *M. nivaloides*, highlighting Spessa as the oldest site, followed by Isernia, Bus de la Fadanana and Notarchirico. This is in contrast with absolute dating but in accordance with previous biochronological data;
- the first occurrence of early forms of *M. arvalis* and *M. agrestis* in the Italian Peninsula is attested at the Visogliano shelter, where the two species can be clearly differentiated in the fossil record;
- a/L values are useful tools for distinguishing between late Middle Pleistocene and Late Pleistocene populations of *M. agrestis*. This applies to Mediterranean populations from both southwestern Europe and the Italian Peninsula.

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2.4. The influence of climate on morphometric traits of fossil populations of *Microtus arvalis* and *M. agrestis* from the Carpathian Basin (northern Hungary)

Elisa Luzi, Piroska Pazonyi, Juan Manuel López-García

Abstract - In this study, we morphometrically analyse fossil populations of *Microtus arvalis* and *M. agrestis* from eight late Middle to Late Pleistocene archaeological and palaeontological sites in the Carpathian Basin. The intra- and inter-specific variations in both species can be related to climatic oscillations linked to the onset of the Eemian interglacial and the first phases of Marine Isotope Stage 5. The size of *M. agrestis* can be correlated with the presence/absence of relatively humid climatic and environmental conditions and of surface water resources (such as marshes and flooded areas). A possible immigration event of *M. arvalis* populations into the Carpathian Basin, also related to the Eemian interglacial, is also identified.

Keywords - Common Vole; Field Vole; Marine Isotope Stage 5; Middle to Late Pleistocene; Hungary; morphometrics.

Under Review

2.4.1. Introduction

The Carpathian Basin is situated between the latitudes of 45°45’N and 48°15’N, and between the longitudes of 16°5’E and 22°58’E. It is topographically sheltered by the Carpathian Mountains, the Alps and the Dinarides. In the Köppen classification of global climate it is assigned to the moist continental climate Cfb (Kottek *et al.* 2006) but at a local level there are substantial differences between regions (Vaszkó 2015; Hungarian Meteorological Service 2017). The westernmost region can be assigned to a mid-latitude west-coast climate; the southern region is subject to sub-Mediterranean climatic effects; a mild semi-arid climate characterizes the Hungarian Plain; the northern and eastern regions have a cold-humid climate; and finally, a highland climate is present in the mountains surrounding the Carpathian Basin (Rudner & Sümegi 2001; Zech *et al.* 2013). This climatic mosaic allows for a high diversity of landscapes and environments. Due to the influence of Mediterranean and Atlantic currents, the mean annual temperature is 2.5°C higher than the typical mean at the same latitude (Mezősi 2017). This favourable geographical and climatic setting made the area suitable as a refugium for temperate flora and fauna in the last part of the Pleistocene in an area further north than the lower-latitude Mediterranean refugia already identified in the Iberian, Italian and Balkan Peninsulas (Stewart & Lister 2001; Schmitt 2007; Provan & Bennett 2008; Fløjgaard *et al.* 2009; Herman *et al.* 2017). Evidence from recent molecular, phylogeographic and palaeontological studies proves that the Carpathian Basin was in fact a cryptic refugium for several vertebrate species during the Last Glacial Maximum (LGM), and that these refugial populations contributed to the post-glacial colonization of Europe (Hewitt 2000, 2004; Kotlík *et al.* 2006; Sommer & Nadachowski 2006; Schmitt & Varga 2012; Filipi *et al.* 2015).

The common vole *Microtus arvalis* and the field vole *Microtus agrestis* are present without interruption in the fossil record of the late Middle Pleistocene, the Late Pleistocene and the Holocene of the Carpathian Basin (Jánossy 1986). This area served as a refugium for these two species during the LGM (Jaarola & Searle, 2002). The eastern lineage of living *M. arvalis* expanded from this region to the Baltic and eastern Europe after the last glacial (Stojak *et al.* 2015).

In the present study, paired populations of *M. arvalis* and *M. agrestis* from the fossil record of the Carpathian Basin are analysed in order to shed light on the dynamics of the intra- and inter-specific relations of these two species in response to climatic changes in this particular region of Europe.

2.4.2. Material and Methods

The material analysed in this study belongs to the palaeontological collections of the Hungarian Natural History Museum (HNHM). It came from eight sites, located in four different areas of northern Hungary, in the north-eastern part of the Carpathian Basin (Fig. 1).

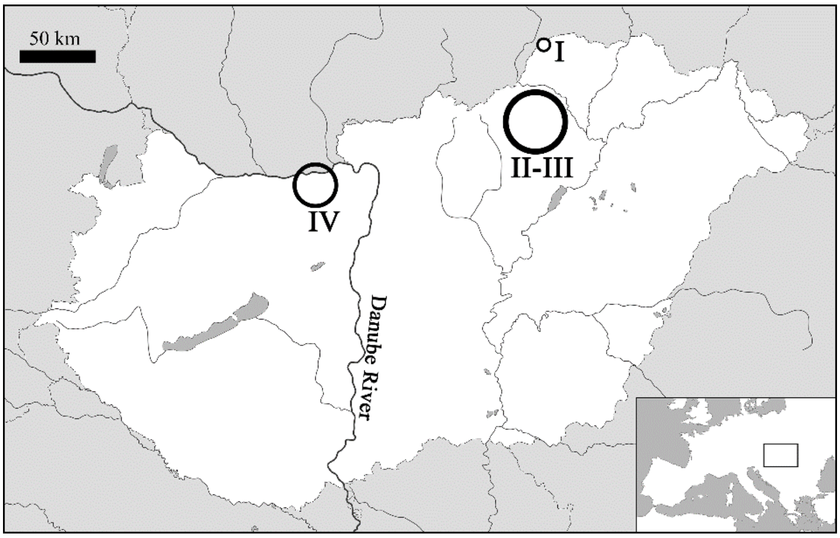

Figure 1. Geographic location of the studied sites. I- Aggtelek Mts. (Porlyuk Cave). II-III- Uppony Mts. and Bükk Mts. (Uppony I rock-shelter; Tarkő rock-shelter; Poroslyuk Cave; Lambrecht Cave; Istállóskő Cave). IV- Gerecse Mts. (Süttő 6, Tokod).

1. Aggtelek Mountains

   *Porlyuk Cave***.** The site is located approximately 4 km north of the municipality of Jósvafő in the Lófej Valley, at a height of 53 m above the bottom of the valley. The cave was formed in Middle Triassic Ladinian limestone. The palaeontological material was derived from the reddish brown infilling of the cave (Jánossy *et al.* 1972).

2. Uppony Mountains

   *Uppony I rock-shelter***.** The locality is situated approximately 400 m east of the municipality of Uppony, in a glen at an altitude of 287 m a.s.l. The rock-shelter, which was formed in Lower Carboniferous-Devonian limestone, is a remnant of a bigger cave. Eight layers were explored by Jánossy (1969*a*, *b*) in the infilling of the rock-shelter. Layers 7-8 are Holsteinian in age, whereas layers 1-6 are late Middle Pleistocene.

3. Bükk Mountains

   *Tarkő rock-shelter***.** The rock-shelter is located in the outskirts of the village of Felsőtárkány, on the peak of Tarkő Hill, at 850 m a.s.l. The cave was formed in Middle Triassic Anisian limestone. The rich assemblage of vertebrate fossils (85 species) was derived from the red clay infilling of 18 layers of the cave (Jánossy, 1986).

Poroslyuk Cave. The site is a narrow cave, situated 2 km south of the municipality of Répáshuta in the Balla Valley, at 420 m.a.s.l. The cave was formed in Upper Triassic limestone. The fossils were found in reddish brown clay (Jánossy, 1986). The fauna was correlated with MIS 5d by Pazonyi and Kordos (2004).

Lambrecht Cave. The locality is situated in the eastern Bükk Mts., approximately 5 km southwest of the municipality of Varbó on Nagygalya Hill, at 410 m.a.s.l. The cave was formed in Triassic limestone. The rich material, which was found in the dark grey clay layer of the infilling, is the stratotype of the Varbó Biochronological Phase (Jánossy, 1986), which was correlated to 80-90 ka B.P. by Kordos (1991).

*Istállóskő Cave***.** The site, where rich Aurignacian artefacts were found, is situated in the outskirts of the municipality of Szilvásvárad, at 535 m.a.s.l. The cave was formed in Triassic limestone, on the southwest side of Istállóskő Hill. Three layers of the infilling sediment contained significant palaeontological material: the uppermost layer comprised yellowish brown loess; below it was a dark brown infilling with limestone debris; and a light brown layer was at the bottom of the sequence (Vértes 1965). The age of the cultural layers is 27,933 – 33,101 B.P. (Ringer 2002).

4. Gerecse Mountains

Süttő 6. Süttő 6 is the most important site from a loess-palaeosol sequence. It is situated in the northwestern corner of the Diósvölgyi quarry, about 210 m above sea level, in sandy loess. The upper layers of this profile yielded fossils (vertebrates and molluscs, referred to site Süttő 5), but Jánossy started his excavation in 1973 from the paleosoil horizon situated in the lower tiers of the profile. He burrowed a 5-m-deep, 1-m-wide, 8-m-long trench to the surface of the travertine. Except for the paleosoil horizon, the loess seemed uniformly sandy, yet he collected material per 20–50 cm and separated 13 layers (Jánossy, 1986).

Süttő 6 is unique because, contrary to other loess sites, there is a co-occurrence of molluscs with a significant volume of vertebrate remains in each layer. This site is the type locality of the Süttő Biochronological Phase (Jánossy, 1986).

Tokod. The locality is situated west of Tokod, on the northern slope of the Hegyeskő Hill, in a deep ravine (175 m.a.s.l.). The vertebrate remains were found within a travertine body in a sandy loess layer containing travertine rubble (Jánossy 1971; Gasparik 1993). The lower part of the loess contains remains (e.g. *Lagurus lagurus* together with *Allactaga jaculus*, *Equus (Asinus) hydruntinus*, *Ursus* cf. *arctos*) characteristic of the mild and humid interglacial period of the local biochronological phase of Varbó (Kretzoi 1953; Pazonyi 2006), whereas the upper part contains slightly younger (probably MIS 3, ~40 ka) megafaunal elements typical of an open steppe environment (including *Mammuthus primigenius*, *Coelodonta antiquitatis* and *Megaloceros giganteus*).

For practical purposes, the ages of the localities and their biochronological position are given after Pazonyi (2011) and Kessler (2014). Uppony I rock-shelter (layers 1-4) and Tarkő rock-shelter (layers 1-7 and 8-12) (Jánossy 1986) belong to the late Middle Pleistocene and cover approximately Marine Isotope Stages (MIS) 10-6 (350-170 ka). Süttő 6 (layers 1-5) (Barta 2014; Pazonyi *et al.* 2014), Porlyuk Cave and Poroslyuk Cave (Jánossy 1986) are dated to the initial stages of MIS 5 (128-104 ka) at the beginning of the Late Pleistocene. Lambrecht Cave and the lower levels of Tokod (layers 4-6) (Gasparik 1993) pertain to the end of MIS 5 (82-80 ka), whereas the upper levels of Tokod (layers 1-3) (Jánossy 1986) and Istállóskő Cave (Jánossy 1986) belong to MIS 3 (40-30 ka) (Table 1).

site	zone	age	ref.
Tarkő rock-shelter - layer 8-12	III	MIS 10	1a
Tarkő rock-shelter - layer 1-7	III	MIS 9-8	1b
Uppony I. rock-shelter - layer 1-4	II	MIS 7-6	2
Süttő 6 - layers 1-5	IV	MIS 5	3
Porlyuk Cave	I	MIS 5	4
Poroslyuk Cave	III	MIS 5	5
Lambrecht Cave	III	MIS 5	6
Tokod - layers 4-6	IV	MIS 5	7a
Tokod - layers 1-3	IV	MIS 3	7b
Istállóskő Cave	III	MIS 3	8

Table 1 - List of the studied sites with geographical position (zone, according to Fig. 1), chronology (age) and reference number used in this paper for each site (ref.).

Microtus arvalis and *M. agrestis* can be recognized in the fossil record on the basis of the morphological and morphometric characters of the first lower molar (m1). The two species were identified following the morphological and morphometric criteria of Chaline (1974) and Nadachowski (1984); the morphologies of the m1s were analysed following Nadachowski (1982). The m1 of both species presents a posterior lobe (PL), seven triangles (T) and an anterior cap (AC) (Fig. 2). In the common vole, T6 and T7 are usually opposed and widely confluent, whereas in the field vole they tend to be alternate and the confluence between the two is reduced. Furthermore, whereas in the common vole the AC is rounded, in the field vole the AC presents an additional lingual salient angle (LSA), sometimes even a fully developed triangle. Finally, as a result of the difference of width between T4 and T5 and the sharp shape of the lingual and buccal salient (LSA and BSA) and reentrant (LRA and BRA) angles, *M. agrestis* presents a more asymmetric and angular shape than *M. arvalis*.

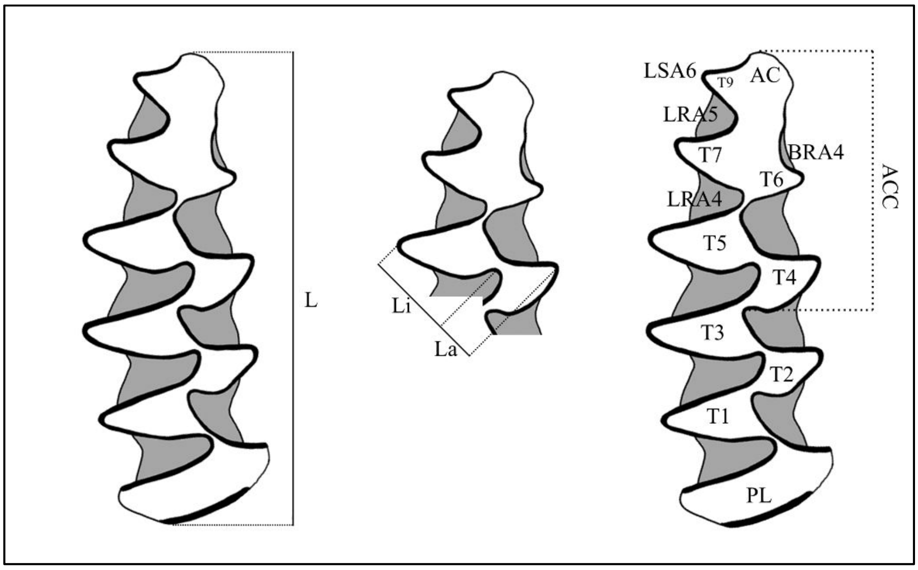

Figure 2. Nomenclature and measurements used for the description of the first lower molars of *Microtus*. L: total length; La: width of T4; Li: width of T5. ACC: anteroconid complex; AC: anterior cap; BRA: buccal reentrant angle; LRA: lingual reentrant angle; LSA: lingual salient angle; T: triangles; PL: posterior lobe.

The measurements were taken in accordance with Van der Meulen (1973) and Cuenca-Bescós and Laplana (1995): La is the width of T4; Li is the width of T5; L represents the total length of the tooth (Fig. 2). A total of 261 teeth belonging to both species were analysed. Only m1s of adult specimens, both right and left, were included in the study.

In order to quantify the fluctuations in size of the two species in relation to each other we use the following formula:

$$\frac{\mathrm{L\ agr}}{\mathrm{L\ arv}}\ \mathrm{x}100$$

where L_{agr} is the mean value of L for *M. agrestis* whereas L_{arv} is the mean value of L for *M. arvalis* in a specific site.

The material was analysed and photographed with a portable USB microscope with Celestron MicroCapture Pro at the HNHM. The measurements were taken using ImageJ software.

2.4.3. Results and Discussion

The measurements taken on the m1s are summarized in Table 2. In the lower levels of Tarkő rock-shelter only *Microtus agrestis* was present. The degree of asymmetry between T4 and T5 as expressed by the Li/La index (Nadachowski 1984) again proved to be a useful morphometric discriminant to separate *M. arvalis* from *M. agrestis* in both Middle and Late Pleistocene populations (Fig. 3). Both species present a wide range of intra-specific morphological variations (Fig. 4). The relative length of the m1s of *M. arvalis* and *M. agrestis* changes in time, as shown by the L_{agr}/L_{arv} index (Fig. 5A). During the Middle Pleistocene, *M. agrestis* m1s are larger than those of *M. arvalis*. This situation is reversed at the beginning of the Late Pleistocene but reverts to the initial state at the end of MIS 5.

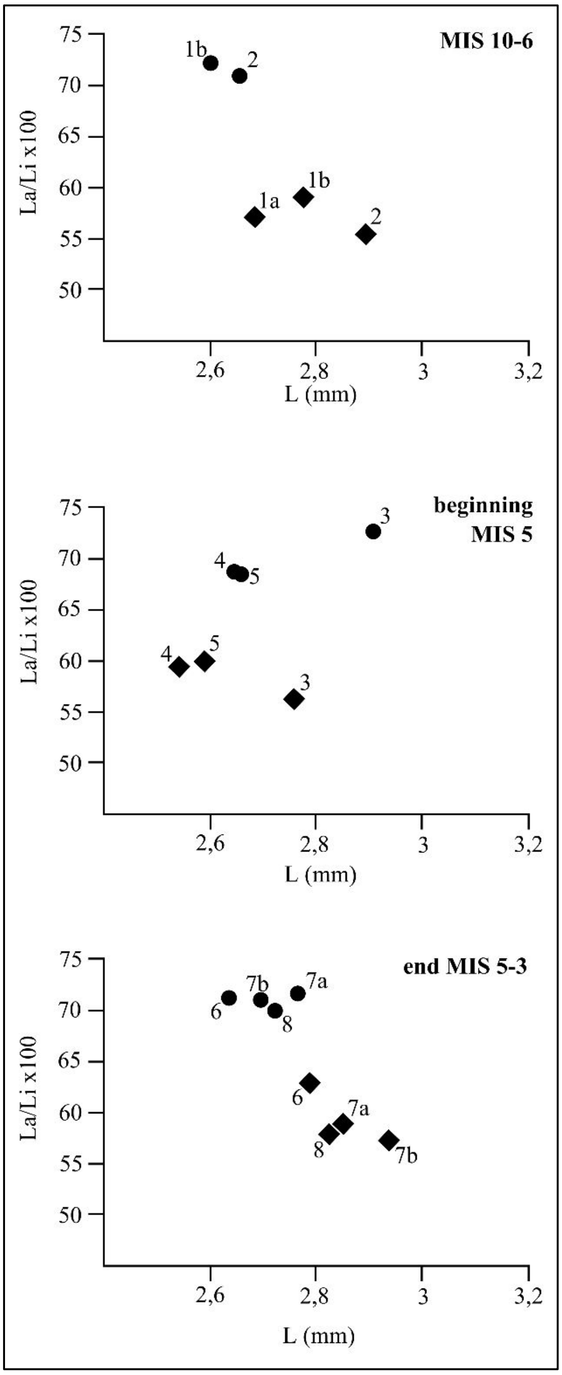

Figure 3. Relation between L and La/Li index of *Microtus arvalis* (circles) and *M. agrestis* (squares). 1a- Tarkő rock-shelter (layers 8-12); 1b- Tarkő rock-shelter (layers 1-7); 2- Uppony I rock-shelter (layers 1-4); 3- Süttő 6; 4- Porlyuk Cave; 5- Poroslyuk Cave; 6- Lambrecht Cave; 7a- Tokod (layers 4-6); 7b- Tokod (layers 1-3); 8- Istállóskő Cave.

2.4.3.1. First phases of the Late Pleistocene: the influence of the Eemian interglacial

The Late Pleistocene begins with the interglacial stage MIS 5. The early MIS 5 is characterized by a warm episode (MIS 5e) corresponding to the Eemian interglacial (Lisiecki & Raymo 2005; Dahl-Jensen *et al.* 2013; Rasmussen *et al.* 2013). The onset of this temperate period is registered in palynological records all across Europe, attested by the spread of arboreal taxa, the development of forest cover and an expansion in the range of temperate trees and thermophilus plants (Mamakowa, 1989; Zagwijn, 1996; Turner, 2000; Muller *et al.*, 2003, among others). Malacological records from Hungary for the first phases of MIS 5 register temperate conditions more arid than those in other parts of central Europe, with drier and more open woodlands intermixed with grassland (Krolopp 1983;

Krolopp & Sümegi 1995; Sümegi *et al.* 2011). After the climatic optimum of MIS 5e, a short period of dry, temperate conditions is detected in the speleothems of NE Hungary, followed by a progressive cooling and an increase in humidity (Demény *et al.* 2017). By the onset of MIS 5c, the climate was back to continental conditions, mostly similar to the present, with complex, mosaic-like environments (Zech *et al.* 2013; Demény *et al.* 2017; Salcher *et al.* 2017).

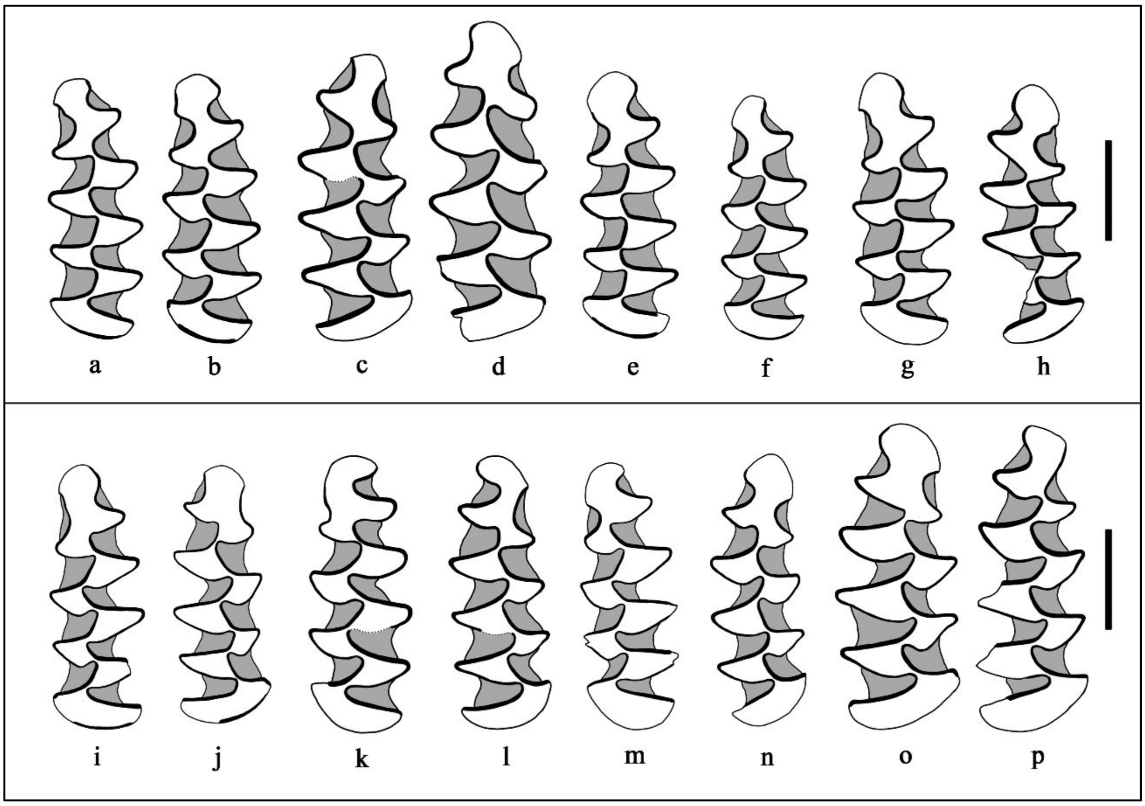

Figure 4. First lower molars of *Microtus arvalis* (a-h) and *Microtus agrestis* (i-p) from Tarkő rock-shelter (a: V.64.200_a, left m1; b: V.64.200_b, left m1; i: V.64.595_b, left m1; j: V.64.595_d, right m1), Süttő 6 (c: V.74.20_25, right m1; d: V.74.20_46, right m1; k: V.74.50, left m1; l: V.74.20_85, right m1), Porlyuk Cave (e: V.70.155_f, left m1; f: V.70.137_i, left m1; m: V.70.137_j, left m1; n: V.70.137_q, right m1), Istállóskő Cave (g: V.61.1943_85, left m1; h; V.61.1943_30, right m1; o: V.61.1943_33, right m1; p: V.61.1943_76 , right m1). Scale: 1 mm.

Values of the L_{agr}/L_{arv} index < 100 are typical of Late Pleistocene populations in Mediterranean regions (Fig. 5B): Spain (Luzi & López-García 2017), southern Italy (i.e. Roccia San Sebastiano; Luzi, unpub.) and coastal Croatia (i.e. Marlera I and Mujina Cave; Luzi, unpub.). Accordingly, the values of the L_{agr}/L_{arv} index for Süttő 6, Porlyuk Cave and Poroslyuk Cave (Fig. 5A) are possibly a consequence of the climatic shift towards more temperate and less humid conditions occurring at the onset of MIS 5. When the climate returned to more continental conditions, the L_{agr}/L_{arv} index was reversed, displaying values similar to those of recent and subfossil populations in central Europe and Late Pleistocene populations in northern and central

Italy (Fig. 5A-B), where the field vole always displays higher values than the common vole (Nadachowski, 1982; Niethammer and Krapp, 1982; Mauch Lenardić, 2007; Luzi et al., 2017, submitted).

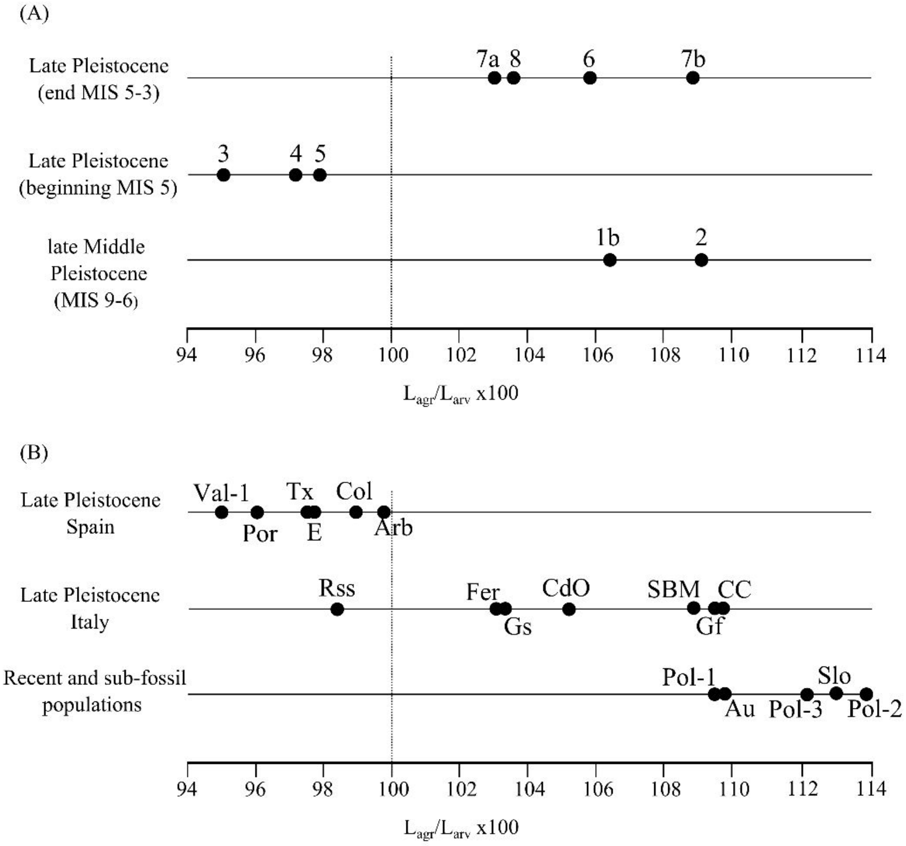

Figure 5. L_{agr}/L_{arv} index values. A: Values for Hungarian sites. 1b- Tarkő rock-shelter (layers 1-7); 2- Uppony I rock-shelter (layers 1-4); 3- Süttő 6; 4- Porlyuk Cave; 5- Poroslyuk Cave; 6- Lambrecht Cave; 7a- Tokod (layers 4-6); 7b-Tokod (layers 1-3); 8- Istállóskő Cave.

B: Values for other European sites. Late Pleistocene Spain - Tx: Teixoneres; Arb: Arbreda; Por: Portalón; Val-1: Valdavara-1; Col: Colomera; E: Eirós. Late Pleistocene Italy - CC: Ciota Ciara; SBM: San Bernardino Maggiore; CdO Caverna degli Orsi; Gf: Grotta Fumane; Rss: Roccia San Sebastiano; Fer: Grotta della Ferrovia; Gs: Grotta del Sambuco. Recent and sub-fossil populations - Pol-1, Pol-2, Pol-3: recent populations from Poland, data from Nadachowski (1984). Slo: recent populations from Slovenia; Au: sub-fossil populations from Austria, data from Mauch Lenardić (2007).

Tarkő rock-shelter - layer 8-12										
	Microtus agrestis					*Microtus arvalis*				
	n	min	mean	max	SD	n	min	mean	max	SD
L	9	2.278	2.686	2.903	0.18	-	-	-	-	-
La/Li x100	8	44.26	57.07	66.78	7.63	-	-	-	-	-

Tarkő rock-shelter - layer 1-7										
	Microtus agrestis					*Microtus arvalis*				
	n	min	mean	max	SD	n	min	mean	max	SD
L	16	2.473	2.776	2.95	0.11	3	2.394	2.602	2.87	0.24
La/Li x100	16	52.7	59.06	66.23	3.62	3	67.73	72.16	77.8	5.14

Uppony I. rock-shelter - layer 1-4										
	Microtus agrestis					*Microtus arvalis*				
	n	min	mean	max	SD	n	min	mean	max	SD
L	30	2.645	2.895	3.126	0.13	17	2.475	2.656	2.884	0.1
La/Li x100	30	43.58	55.24	66.66	5.7	18	63.71	70.89	86.21	5.06

Süttő 6 - layers 1-5										
	Microtus agrestis					*Microtus arvalis*				
	n	min	mean	max	SD	n	min	mean	max	SD
L	2	2.705	2.759	2.814	-	2	2.711	2.91	3.109	-
La/Li x100	2	55.02	56.29	57.56	-	2	68.28	72.49	72.49	-

Porlyuk Cave										
	Microtus agrestis					*Microtus arvalis*				
	n	min	mean	max	SD	n	min	mean	max	SD
L	7	2.345	2.543	2.806	0.14	7	2.304	2.615	2.851	0.19
La/Li x100	7	46.3	59.25	66.19	6.87	7	63.34	68.35	71.6	2.22

Poroslyuk Cave										
	Microtus agrestis					*Microtus arvalis*				
	n	min	mean	max	SD	n	min	mean	max	SD
L	23	2.299	2.585	3.075	0.17	14	2.386	2.645	2.876	0.15
La/Li x100	25	45.19	59.89	65.78	4.57	15	65.18	68.55	74.57	3.18

Lambrecht Cave										
	Microtus agrestis					*Microtus arvalis*				
	n	min	mean	max	SD	n	min	mean	max	SD
L	13	2.398	2.794	3.054	0.19	4	2.398	2.636	2.867	0.19
La/Li x100	13	50	62.82	77.49	7.67	4	66.09	71.21	77.49	5.25

Tokod - layers 4-6										
	Microtus agrestis					*Microtus arvalis*				
	n	min	mean	max	SD	n	min	mean	max	SD
L	19	2.492	2.852	3.238	0.2	17	2.539	2.767	2.983	0.13
La/Li x100	19	45.04	58.78	69.34	6.65	17	64.24	71.69	81.97	4.76

Tokod - layers 1-3										
	Microtus agrestis					*Microtus arvalis*				
	n	min	mean	max	SD	n	min	mean	max	SD
L	16	2.776	2.937	3.216	0.14	5	2.51	2.698	2.925	0.1
La/Li x100	16	49.44	57.17	65.69	5.78	5	68.78	71.02	75.67	2.71

Istállóskő Cave										
	Microtus agrestis					*Microtus arvalis*				
	n	min	mean	max	SD	n	min	mean	max	SD
L	30	2.521	2.827	3.153	0.18	19	2.502	2.724	2.981	0.12
La/Li x100	30	42.51	57.81	65.82	5.17	19	64.04	69.9	80.12	4.45

Table 2. Measurements of m1s of *Microtus agrestis* and *M. arvalis*. L: total length of m1, in mm; La/Li x100: relation between the length of T4 and T5. N: number of specimens; min: minimum value; mean: mean value; max: maximum value; SD: standard deviation.

2.4.3.2. Variations in first lower molar size in Microtus agrestis and M. arvalis: the role of interspecific competition and climatic changes

The climatic amelioration brought by the Eemian interglacial is also testified to in the small-mammal record of Süttő 6, Porlyuk Cave and Poroslyuk Cave by the disappearance of the root vole *Microtus oeconomus* and a strong reduction in the numbers of narrow-headed vole *M. gregalis* (Jánossy 1986). During the Late Pleistocene, the range of distribution of *M. gregalis* (or *Lasiopodomys* (*Stenocranius*) *gregalis*, following Petrova et al., 2015) covered all of Europe (Kowalski 2001), reaching as far west and south as central Spain (Laplana *et al.* 2016). The climatic changes occurring at the transition between Pleistocene and Holocene led to a major reduction in its area, and it currently inhabits tundra, forest-tundra and steppes in northern and central Asia (IUCN 2015). In terms of palaeoclimatic and palaeoenvironmental reconstruction, it indicates continental, relatively cold conditions (López-García *et al.* 2017). Its reduction in the fossil record of central Europe, together with the increased occurrence of the common vole, is characteristic of temperate phases (Nadachowski 1982; Horácev & Lozek 1988; Gasparik 1993).

M. oeconomus indicates relatively cold, humid conditions, in an open humid (i.e. tundra) or open woodland landscape (i.e. taiga or frost-resistant broad-leaved deciduous forests) (Hernández Fernández 2001; Hernández Fernández *et al.* 2007). The root vole currently inhabits densely-vegetated and dump areas at northern latitudes (IUCN 2015), although a relict population exists at the border between Slovakia and Hungary, separated from other populations in central Europe but with a common glacial origin (Brunhoff *et al.* 2003). The absence of *M. oeconomus* is indicative of the increase in temperature and the decrease in humidity, surface waters and precipitation at the beginning of MIS 5 in northern Hungary. The root vole, common vole and field vole compete with one another when their ranges overlap: *M. arvalis* is consistently dominant over *M. agrestis* and *M. oeconomus*, and forces them into areas with abundant surface water (such as marshes, bogs, fens, riverbanks and lake edges) that are not suitable for the common vole, which prefers dry fields with discontinuous cover (Grant 1972; De Jonge 1983; Ligtvoet & Wijngaarden 1994). Of the root vole and the field vole, the former is slightly dominant and can displace the latter locally into sub-optimal habitats (Henttonen *et al.* 1977; Hoset & Steen 2007).

Field vole m1s decrease in size in the first phases of MIS 5 but regain their Middle Pleistocene values at the end of MIS 5 and continue to grow during the Late Pleistocene (Fig. 6). Since large-sized *M. agrestis* needs more water (almost double the amount) with increased temperatures (Dienske 1979), small-sized field voles were probably favoured in the temperate settings at the beginning of MIS 5, leading to a decrease in mean values. However, under pressure from *M. arvalis* and without the competition of *M. oeconomus*, *M. agrestis* should have been able to gain access to and exploit dump areas and flooded areas, thus maintaining its size. The decrease in m1 size implies that such surface water resources were indeed very limited.

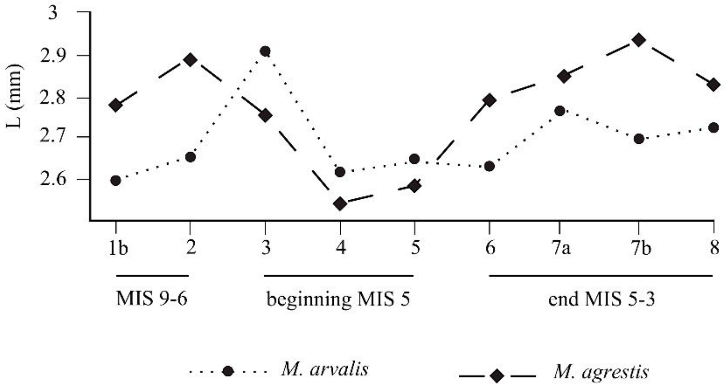

Figure 6. Variations in mean L values of *Microtus arvalis* (circles) and *M. agrestis* (squares). 1b- Tarkő rock-shelter (layers 1-7); 3- Uppony I rock-shelter (layers 1-4); 4- Süttő 6; 5- Porlyuk Cave; 6- Poroslyuk Cave; 7- Lambrecht Cave; 8a- Tokod (layers 4-6); 8b- Tokod (layers 1-3); 9- Istállóskő Cave.

On the other hand, *M. arvalis* m1s undergo a sudden increase in their mean L value at Süttő 6, clearly visible despite the low number of specimens; they go back to Middle Pleistocene values throughout MIS 5 and then start growing again (Fig. 6). Large-sized *M. arvalis* needs less water than small-sized individuals in warm climates (Dienske 1979), so a selection in favour of bigger specimens would be expected in the warm and dry environment of Süttő 6 (Pazonyi *et al.* 2014). Nevertheless, the sudden increase in m1 size at this site, followed by the sudden return to the earlier, Middle Pleistocene values, may be the sign of an immigration event. Populations of common voles from the Balkans, moving northwards from Mediterranean areas and searching for more suitable climatic conditions, might have entered the Carpathian Basin, thus influencing local populations at the beginning of MIS 5. If the incoming populations entered the Carpathian Basin from the southwest, the populations of Porlyuk Cave and Poroslyuk Cave (zone I and III, Fig. 1) were probably sheltered from the invasion by the River Danube and consequently do not show any signs of it.

2.4.3.3. The last phases of MIS 5 and MIS 3: the reversion to continental conditions

More continental and humid, but still temperate conditions are attested in the records for the last phases of MIS 5 (Mamakowa, 1989; Rudner & Sümegi, 2001; Helmens, 2013; Wohlfarth, 2013, among others). An increase in the general continentalization of the climate in the region, with colder temperatures and less precipitation but with pulses of humidity corresponding to interstadial moments, is registered during MIS 3 (Voelker 2002; Zech *et al.* 2013; Obreht *et al.* 2017). The

Carpathian Basin was then characterized by mosaic-like environments composed of closed and mixed taiga, pockets of deciduous trees, tundra elements, with treeless steppe components increasing with time (Krolopp & Sümegi 1995; Nádor *et al.* 2011). The occurrence of *M. oeconomus* at Lambrecht Cave, Tokod and Istállóskő Cave (Jánossy 1986) is consistent with the continental climatic settings of the late MIS 5 and MIS 3. The sizeable presence of *M. gregalis* at Tokod and Istállóskő Cave (Jánossy 1986; Gasparik 1993) and the L_{agr}/L_{arv} index > 100 (Fig. 6) are consistent with the restoration of mittel-European climatic and environmental settings.

At Tokod it is also noticeable that in the upper levels, which are relatively more humid and cooler than the lower ones, *M. agrestis* increases in size, whereas *M. arvalis* becomes smaller (Fig. 6). A similar change has been observed for the Late Pleistocene site of Teixoneres Cave (north-eastern Spain; (Luzi *et al.* 2017) where these oscillations in the m1 size of the field and common vole are linked to changes in humidity levels caused by variations in the amount of precipitation or in the seasonal distribution of rainfall.

2.4.4. Conclusions

This study of the variations in the m1 morphometric characters of *Microtus agrestis* and *M. arvalis* from northern Hungary enabled us to identify a change in the fossil populations related to the improved climatic conditions of MIS 5 and particularly of the Eemian interglacial.

- The L_{agr}/L_{arv} index shows an inversion at the sites of Süttő 6, Porlyuk Cave and Poroslyuk Cave that indicates the onset of more temperate and arid climatic conditions compared to the moist and cool continental setting present in the late Middle Pleistocene and from the end of MIS 5 onwards.
- The oscillations in the mean L values in the two species are also related to changes in climatic and environmental conditions and in particular to humidity and the presence/absence of surface water resources, dump areas and flooded areas, as suggested by the presence/absence of *M. oeconomus* in the fossil record.
- The sudden increase in the m1 size of *M. arvalis* at Süttő 6, followed by a similar sudden decrease, may be associated with an immigration event at the very beginning of MIS 5 that affected the local population, while populations east of the River Danube remained unaffected.

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3. OTHER STUDIED SITES: results and brief discussion

Other sites have been studied during the preparation of this PhD thesis, that have not been published for lack of time. The results of these studies are presented in this Chapter, together with brief discussion and conclusions. A more extensive discussion is going to be presented in Chapter 4.

Microtus arvalis and *M. agrestis* populations from three sites of Croatia (Vindija cave, Marlera I, and Mujina cave), one site of Italy (Paglicci cave), and two sites of Belgium (Scladina cave and Marie-Jeanne cave) are here described and analysed.

3.1. Adriatic area: Croatia and Italy

3.1.1. The sites

The samples from Croatia belong to the collection of the Institute for Quaternary Paleontology and Geology, in Zagreb. The samples from Grotta Paglicci belong to the collection of University of Siena. They represent populations from four different regions (Fig. 3.1.1).

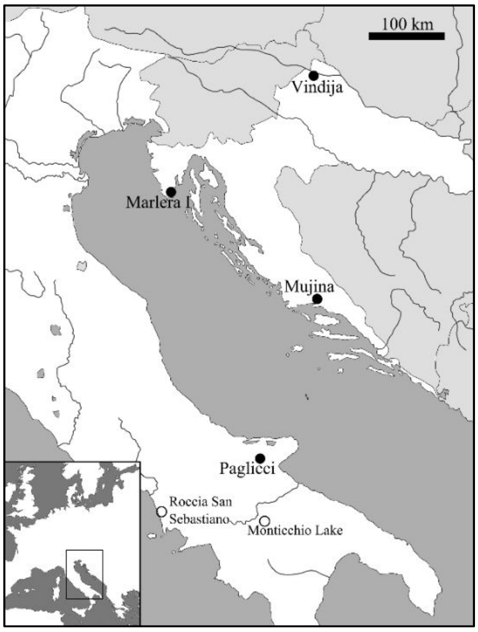
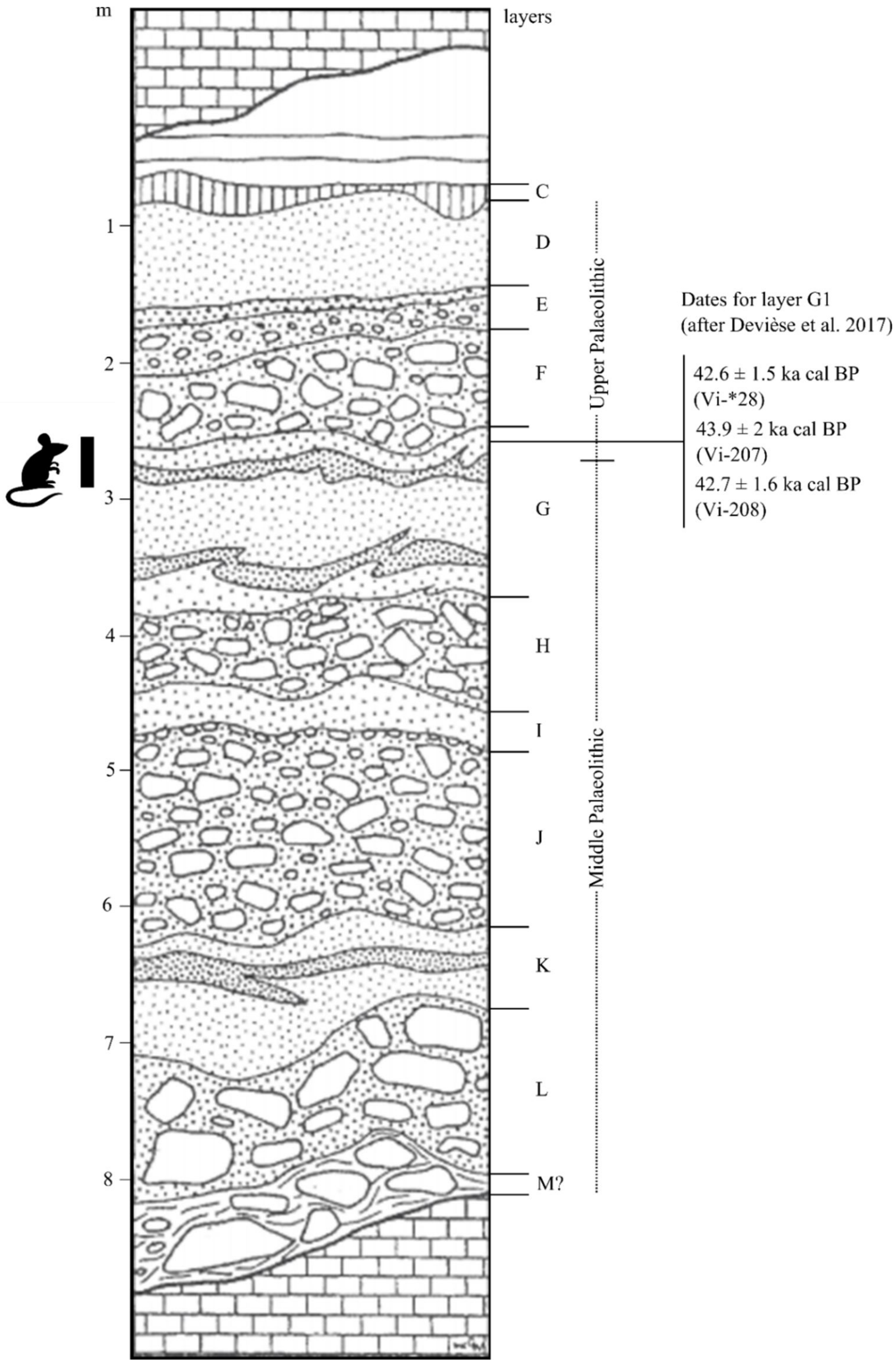


Figure 3.1.1. Geographic location of the studied sites in the Adriatic area (black dots) and of sites cited in the discussion (black circles).

Vindija cave is located in the NW of Croatia (46°18’12” N; 16°14’38” E), at 275 m a.s.l. The deposit is divided in 13 stratigraphic units (M to A, bottom to top). According to U/Th dates, two major complex can be identified: J-M that belong to the Middle Pleistocene with an age > 150 ka, and A-H, that span from the present to ca. 88 ka (Wild et al., 2001). In particular, levels D-H represent

Late Pleistocene. The site of Vindija yielded human remains of both *Homo sapiens* and *H. neanderthalensis*, and numerous artefacts, such as lithic tools and bone points, that are the focus of a long debate concerning the transition between Middle and Upper Palaeolithic (Karavanić 1995; Ahern et al. 2004; Higham et al. 2006; Zilhao 2009; Karavanić & Smith 2013, among others).



Dates for layer G1
(after Devièse et al. 2017)

42.6 ± 1.5 ka cal BP
(Vi-*28)
43.9 ± 2 ka cal BP
(Vi-207)
42.7 ± 1.6 ka cal BP
(Vi-208)

Figure 3.1.2. Stratigraphy of Vindija with indication of provenience of the samples (modified from Mauch Lenardić, 2011).

The remains of *Homo neanderthalensis* from the archaeological level G1 have been recently re-dated and this revision yielded results older than those previously obtained, suggesting a minimum age of at least ~44 ka BP (Deviѐse et al., 2017). The samples here analysed come from the so called "G complex" (i.e. from G1 and G2, Fig. 3.1.2). The large mammals assemblage indicates, for Marine Isotope Stage (MIS) 3 (levels F-H), a relatively stable climate without abrupt oscillations, and landscape characterized by patchy environment, with open grassland, evergreen taiga and spot of deciduous forest (Miracle et al., 2010). The analysis of pollen and spores, found only in layer F and G, highlighted the low frequency of arboreal pollen (AP), composed mainly by pine, the dominance of Cichoriaceae among non-arboreal pollen (NAP), and the occurrence of spikemoss. This point to a moist and cool climate, with open landscape and rare tree coverture (Paunović et al., 2001). The malacological assemblage, composed mainly by genus *Macrogastra* and *Clausilia,* and the avifaunal assemblage, composed by aquatic species such as Anatids, Rallids and Charadriidae, and by Galiform birds and birds of prey, reveal a mosaic landscape, with mixed open and forest environments, and dominant moist forest biotope (Paunović et al., 2001).

Figure 3.1.3. The site of Marlera I (photo from www.hazu.hr).

The site of Marlera I, located in the Istrian southern coast (44°48'60" N; 13°58'40" E, Fig. 3.1.3) was discovered in the year 2000, when quarry works revealed fissures filled with Quaternary sediments. Two sections (Sonda I e II), each about 3 m high, have been exposed, with Holocene and Pleistocene infill. The Pleistocene sediments do not present any stratification and have been dated to 45.199 ± 1.343 cal BP (Brajković et al., 2006). The site yielded numerous fossil remains of small and large vertebratez. Among ungulates, *Dama dama*, *Bos primigenius*, and *Cervus elaphus* are the most represented species; avifaunal assemblage includes Anseriformes, Falconiformes, Galliformes, Gruiformes, Charadriiformes, Passeriformes and Coraciiformes; the human presence at the site is testified by lithic tools (still under study) and cut marks on the bones (Mauch Lenardić, 2007, 2014; Brajković et al., 2010). Overall, the faunal assemblage testifies relatively temperate and humid conditions, with open grassland in the vicinity of the site (Brajković et al., 2010). Pollen analysis allowed to determine the presence of deciduous trees (maple and alder), conifers (pine and larch) and herbaceous, steppe taxa of *Artemisia* and *Compositae* (Oros Sršen, 2015).

Mujina cave is located in the area of Kaštela Bay (Dalmatia), at 260 m a.s.l., in the hills north of Trogir (43°33' N; 16°23' E). The site bears evidence of human occupations: Mousterian lithic industries, bone modification (burning, cut marks, impact points) and unpaved hearths (Rink et al., 2002; Karavanić et al., 2008; Nizek and Karavanić, 2012). Eight major archaeological stratigraphic levels (E3, E2, E1, D2, D1, C, B, A, from bottom to top) and 12 lithologic units have been identified in the profiles, with the sequence dated to MIS 3, between ~42 and ~49 ka BP (Rink et al., 2002; Karavanić et al., 2008; Boschian et al., 2017). All stratigraphic profiles suggest a short period of deposition without significant breaks (Rink et al., 2002) except for a major hiatus at the boundary between archaeological units E and D (Boschian et al., 2017). The samples here analysed belong to levels D and B (Fig. 3.1.4). Sedimentological and soil micromorphology analyses suggest that level E3 represent again a temperate period where, at level E2B, the arid and cold Heinrich Event 5 has been identified; levels E1 and E2A testify again temperate conditions while levels D1-2 represent a relatively cold one; levels B and C represent a relatively temperate oscillation (Boschian et al., 2017). Large mammals from levels D2 to B have been analysed from a zooarchaeological point of view: at levels D1-2, human frequentation is more intense compared to upper levels, and *Cervus elaphus*, *Rupicapra rupicapra*, and *Capra ibex* are dominant, while at levels C-B, the assemblage is dominated by caprids, large bovids and equids, with the presence of *Sus scrofa* (Miracle, 2005). This indicates a cooler but arid period in level D and more arid and relatively more temperate conditions in level B. Charcoals and pollen of pine, spruce and birch, and pollen of grassland vegetation and the heliophilic shrub joint-pine testify open environment with rare trees at level B; at level D2, charcoal of juniper and linden indicate a cool climatic oscillation (Karavanić et al., 2008; Boschian et al., 2017). All data suggest that the accumulation from level E2A to level B-3 took place under general cool and aridic conditions, with brief warm and cold spikes as it is typical of MIS 3 (Boschian et al., 2017).

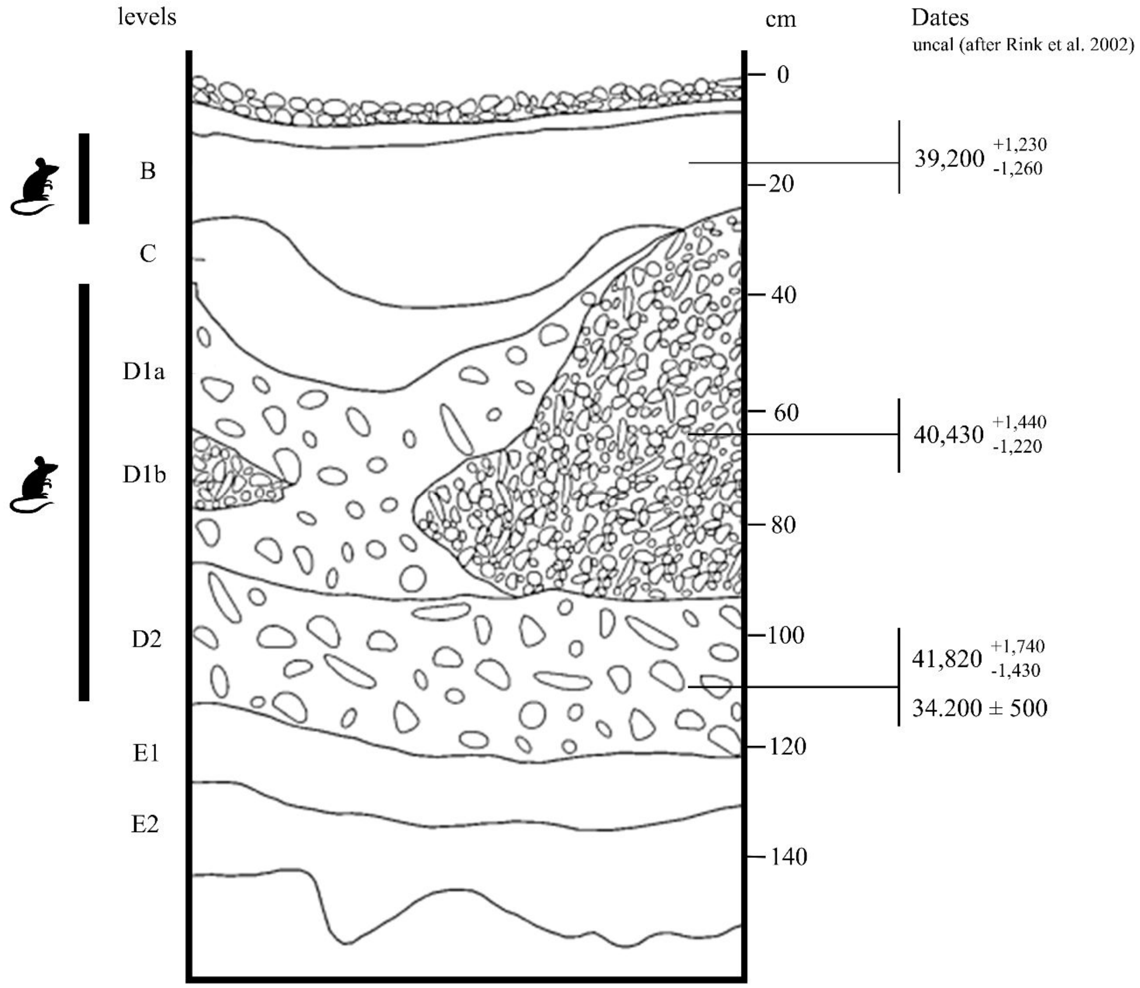


Figure 3.1.4. Stratigraphy of Profile A of Mujina with indication of provenience of the samples (modified from Karavanić et al., 2008).

Grotta Paglicci is located in the Gargano promontory (146 m a.s.l.), in the south-eastern side of the Italian Peninsula (41°41’ N; 15°35’ E). It yielded an interrupted cultural sequence of Upper Palaeolithic lithic, 12-m-thick, that has been divided in 24 archaeological layers. industries, ranging from the Aurignacian to the Late Epigravettian. According to the available radiocarbon dates, it accumulated almost continuously during the end of MIS 3, MIS 2 and the inset of MIS 1, between ~ 41 and ~12 ka BP (Palma di Cesnola, 2004). The samples here analysed come from level 22f to level 20c (Fig. 3.1.5), dated between ~33 and ~25 ka BP (Palma di Cesnola, 2006; Berto et al., 2017). This levels have been related with pollen zone 5a-b of Monticchio lake sequence (Allen et al. 2000; Watts et al. 2000; Berto et al. 2017): a relatively temperate period with increasingly arid conditions. The ungulate assemblage comprises *Bos primigenius*, *Equus ferus*, *Equus hydruntunus*, *Capra ibex*, *Rupicapra* sp., *Cervus elaphus*, *Sus scrofa* and *Capreolus capreolus*; from layer 24b to layer 6d the associations are generally dominated by open environment ungulates (Sala, 1983; Boscato, 2004;

Boschin, 2013). The analysis of the avifauna from the layers 24, 23 and 22 indicates the presence of steppe or grassland with bare rocks and rocky substrata, due to the high percentage of *Pyrrhocorax graculus* and *Columba livia* (Tagliacozzo and Gala, 2004).

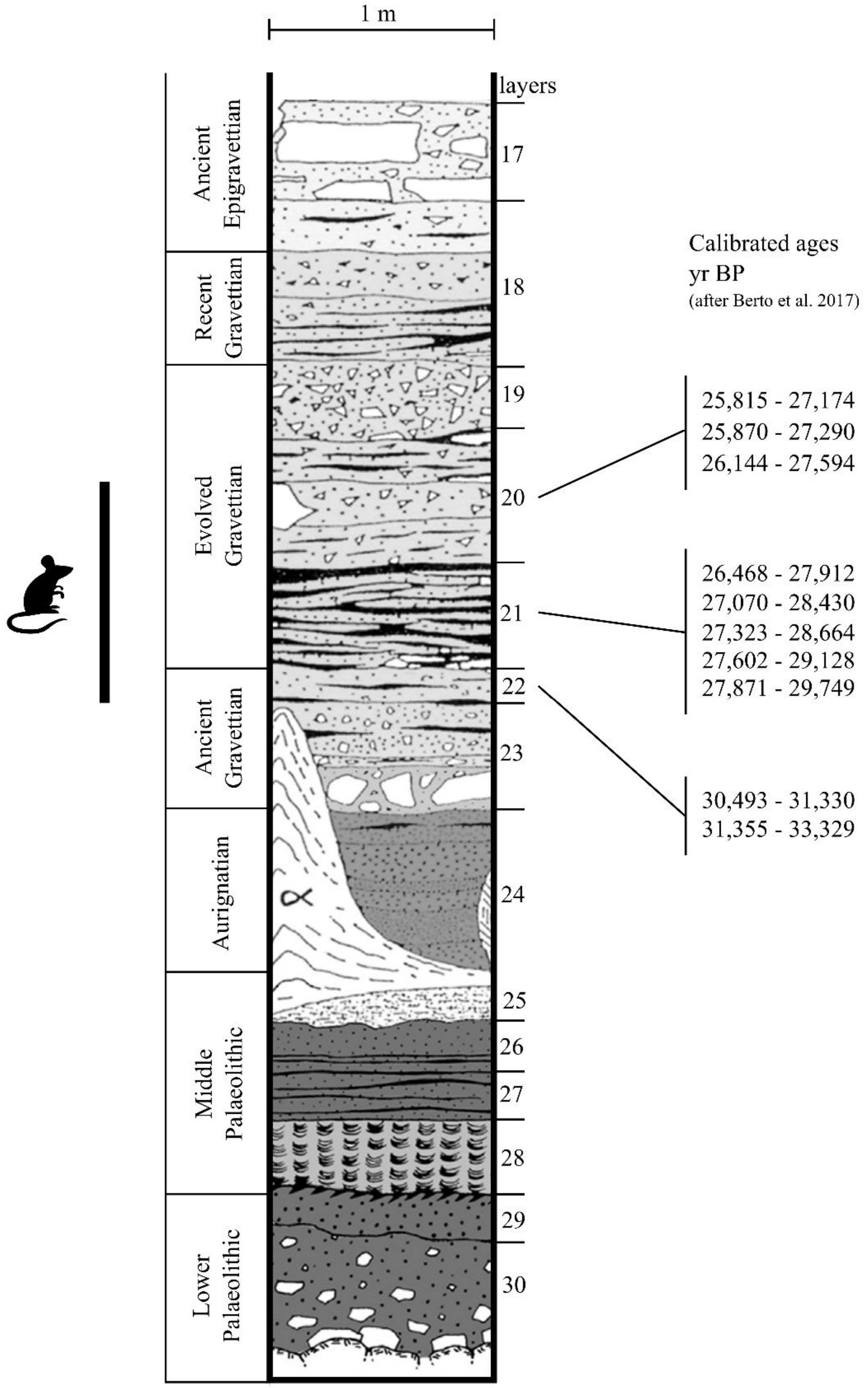


Figure 3.1.5. Partial stratigraphy of Paglicci with indication of provenience of the samples (modified from Berto et al., 2017).

3.1.2. Results and brief discussion

The populations of *Microtus arvalis* and *M. agrestis* from Vindija, Marlera I and Mujina were previously partially analysed and published by Mauch Lenardić (2007). In that study, the material belonging to each site (identified as *M.* ex gr. *arvalis*-*agrestis*) had been assigned entirely to either *M. arvalis* or *M. agrestis* on the base of morphometric characters: samples from Vindija were assigned to *M. arvalis*, while those from Marlera I and Mujina were assigned to *M. agrestis*. In our study, the material from each site has been divided between *M. arvalis* and *M. agrestis* following morphometric and morphological traits (Chaline, 1972; Nadachowski, 1984; Rekovets and Nadachowski, 1995).

There is a considerable difference in size between *M. arvalis* populations from different sites (Table 3.1.1). The common voles from Vindija are smaller than those from the Adriatic coast (Fig. 3.1.6). Furthermore, even though the all three Croatian sites dated to MIS 3, the index L_{agr}/L_{arv} displays different values for each site: 108.03 at Vindija; 100.81 at Marlera I; and 99.75 at Mujina.

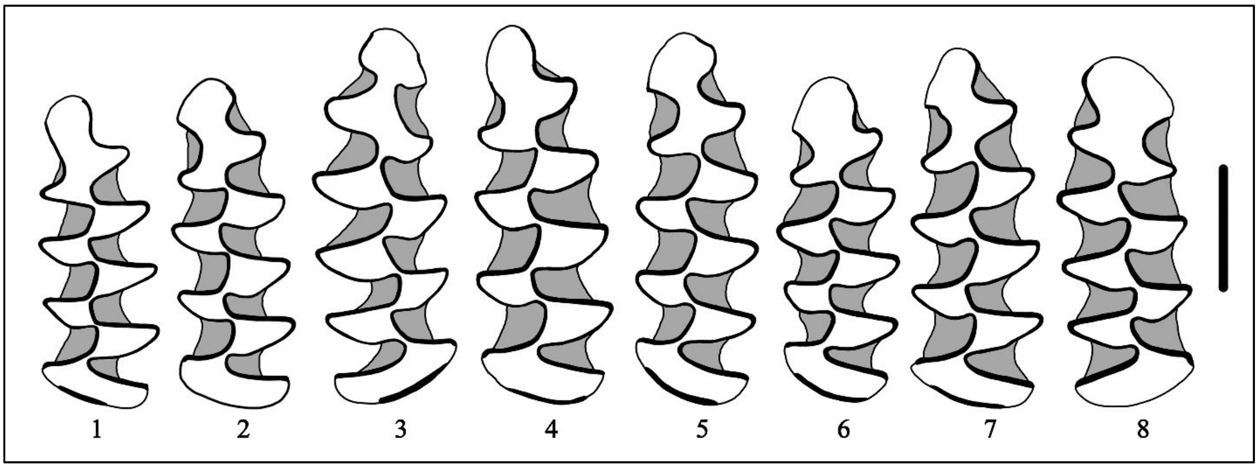


Figure 3.1.6. Sample of m1 of *Microtus arvalis* from Vindija (1-2), Marlera I (3-4), Mujina (5-6) and Paglicci (7-8). 1: Vin_G2_61, left m1; 2: Vin_G2_71, left m1; 3: MRL_10.5, right m1; 4: MRL_12.1, left m1; 5: MP2000_B-D2, left m1; 6: MP2000_D4, left m1; 7: P_019-1701, left m1; 8: P_024-1601, right m1. Scale: 1 mm.

There are differences in the climatic and environmental settings at the three sites during MIS 3. The root vole *M. oeconomus*, which indicates relatively cold and humid environment, is present in the fossil record of Vindija, but not in the other two sites (Mauch Lenardić, 2011). The bank vole *Clethrionomys glareolus*, a good indicator for woodlands, occurs at Vindija and Marlera I, while it is absent from Mujina (Mauch Lenardić, 2014). At this latter site, it is registered the presence of the Balkan snow vole *Dinaromys bogdanovi*, an endemic species of the Balkans, and the European snow vole *Chionomys nivalis*: both species require open landscape with exposed rocks. The values decrease following the decrease of general humidity: from the cool-humid conditions at Vindija, to the relatively temperate but still humid conditions of Marlera I, to finish with the cool-dry conditions at Mujina.

Vindjia (layers G2-G1)

	Microtus agrestis					*Microtus arvalis*				
	n	min	mean	max	SD	n	min	mean	max	SD
L	15	2.455	2.837	3.072	0.18	7	2.414	2.626	2.835	0.15
A	16	1.313	1.53	1.673	0.11	7	1.247	1.418	1.557	0.1
W	13	0.824	1.023	1.141	0.09	6	0.836	0.919	1.022	0.06
e	12	0.743	0.838	0.953	0.06	7	0.689	0.75	0.839	0.04
d	14	0.397	0.258	0.397	0.08	7	0.143	0.247	0.343	0.06
La	14	0.431	0.386	0.431	0.03	6	0.325	0.385	0.439	0.04
Li	13	0.504	0.641	0.729	0.07	6	0.46	0.537	0.616	0.05
a/L x100	15	51.05	53.62	55.84	1.47	7	51.65	53.95	54.92	1.23
La/Li x100	13	47.69	60.76	72.6	6.86	6	63.35	71.3	80.1	5.44

Marlera I

	Microtus agrestis					*Microtus arvalis*				
	n	min	mean	max	SD	n	min	mean	max	SD
L	17	2.653	2.965	3.23	0.16	9	2.639	2.941	3.187	0.18
a	16	1.345	1.57	1.745	0.12	7	1.381	1.99	1.695	0.11
W	11	0.933	1.018	1.11	0.05	7	0.933	1.012	1.121	0.07
e	15	0.767	0.85	0.962	0.05	7	0.747	0.856	1.011	0.09
d	14	0.188	0.252	0.402	0.06	8	0.175	0.256	0.358	0.06
La	10	0.337	0.404	0.437	0.02	6	0.386	0.425	0.464	0.03
Li	9	0.569	0.618	0.67	0.03	6	0.582	0.625	0.695	0.04
a/L x100	16	52.3	53.74	55.66	1.11	7	52.05	53.47	55.11	1.09
La/Li x100	9	59.22	64.82	66.45	2.17	6	63.74	68	74.47	3.66

Mujina

	Microtus agrestis					*Microtus arvalis*				
	n	min	mean	max	SD	n	min	mean	max	SD
L	15	2.592	2.828	3.114	0.12	7	2.62	2.835	3.078	0.17
a	15	1.388	1.53	1.734	0.09	7	1.424	1.539	1.659	0.09
W	17	0.863	0.94	1.075	0.06	7	0.856	0.941	0.997	0.05
e	15	0.67	0.79	0.907	0.05	7	0.757	0.777	0.824	0.02
d	16	0.119	0.23	0.335	0.05	5	0.202	0.258	0.372	0.06
La	17	0.333	0.363	0.423	0.02	7	0.375	0.402	0.428	0.02
Li	17	0.525	0.59	0.667	0.04	7	0.484	0.552	0.598	0.03
a/L x100	15	52.2	54.07	55.68	1.18	7	52.79	54.3	55.57	0.99
La/Li x100	17	53.65	61.62	66.55	3.85	7	64.04	73.18	81.4	6.52

Table 3.1.1. Measurements and indices of m1s of *Microtus agrestis* and *M. arvalis* from Croatia. n: number of specimens; min: minimum value; mean: mean value; max: maximum value; SD: standard deviation. Linear measures (L, a, W, d, e, La, Li) are given in mm.

The same climatic differences are present today. The current climate in Vindija, according to the Köppen classification (Kottek et al., 2006; Peel et al., 2007), is type Cfb. It indicates temperate climate (C), with warm summer (mean temperature of the warmest month < 22° C and at least 4 months with mean temperature > 10°C, b), without a clear dry season (f). At Marlera I, the climate is Cfa, which means that summers are hot (mean temperature of the warmest month > 22° C and at least 4 months with mean temperature > 10°C, a) but not dry. Mujina climate is Csa, characterized by hot and dry summer (less than 30 mm of precipitation in the driest month and less than 1/3 of the wettest month of winter, s). Therefore, the differences in L_{agr}/L_{arv} index might be related to the differences in geographic (and therefore climatic) settings, in particular to the difference in the distribution of annual precipitation, with values for more continental climate > 100, and values for more Mediterranean climate < 100.

The samples from Puglia belong to the end of MIS 3 and first phases of MIS 2, and are younger than those of Croatia. In the fossil record of Grotta Paglicci, *M. arvalis* dominates the assemblage, testifying the prevalence of open steppe landscape, and the presence of the northern water vole *Arvicola amphibius* is very scarce, which indicates that resources of superficial water were also scarce. This lack of superficial waters may explain the reduced size of *M. agrestis* from this site (Table 3.1.2).

	Paglicci (layers 22f-20c)									
	Microtus agrestis					*Microtus arvalis*				
	n	min	mean	max	SD	n	min	mean	max	SD
L	30	2.579	2.768	2.986	0.09	30	2.522	2.811	3.1	0.15
a	30	1.316	1.491	1.591	0.07	30	1.319	1.513	1.677	0.1
W	30	0.893	0.961	1.062	0.04	30	0.828	0.958	1.06	0.05
e	30	0.715	0.807	0.881	0.04	30	0.689	0.771	0.899	0.05
d	30	0.167	0.275	0.443	0.05	30	0.088	0.233	0.404	0.07
La	30	0.316	0.367	0.414	0.02	30	0.355	0.4	0.458	0.02
Li	30	0.557	0.603	0.66	0.02	30	0.498	0.566	0.623	0.03
a/L x100	30	51.02	53.83	56.43	1.55	30	51.12	53.82	56.78	1.3
La/Li x100	30	53.36	61.05	66.78	3.55	30	64.23	70.71	82.33	4.5

Table 3.1.2. Measurements and indices of m1s of *Microtus agrestis* and *M. arvalis* from Grotta Paglicci. n: number of specimens; min: minimum value; mean: mean value; max: maximum value; SD: standard deviation. Linear measures (L, a, W, d, e, La, Li) are given in mm.

Unlike at Mujina, the current climate in Paglicci is Cfa, but the mean precipitation per year at Paglicci is 545 mm, where in Mujina it reaches 813 mm (data from https://it.climate-data.org), thus indicating that conditions overall are drier in south-eastern Italy. At Paglicci, the value of the L_{agr}/L_{arv} index is, like at Mujina, below 100, i.e. 98.47. The samples from cut 10 of Roccia San Sebastiano (analysed in Chapter 2.3) belong to the same chronology of those of Paglicci and the current climate at the site is classified as Csa (with 893 mm of mean precipitation per year). In cut 10, the relative increase of the percentage of *Microtus* (*Terricola*) *savii*, Savi's pine vole, an endemic species that currently inhabits the Italian Peninsula and Sicily, indicates a temperate and dry climatic oscillation, and the value of the L_{agr}/L_{arv} index is 98.58. Thus, at the three sites (Mujina, Paglicci, and Roccia San Sebastiano) where relatively dry conditions have been detected and that currently present Csa/Cfa climate, the L_{agr}/L_{arv} values are < 100. These data confirm that populations belonging to relatively arid periods and Mediterranean geographic and climatic settings present values of the index L_{agr}/L_{arv} lower than 100.

The link between the L_{agr}/L_{arv} index and climatic conditions, with values < 100 in temperate-dry with Mediterranean settings and values > 100 related to more humid and continental frames is also confirmed by the variations of this index in the populations of Late Pleistocene of the Carpathian Basin (see Chapter 2.4). A small area characterized by a strong and stable Mediterranean influence is present nowadays in the south-western part of Hungary (Rudner and Sümegi, 2001; Hungarian Meteorological Service, 2017; Mezősi, 2017) and, during the climatic optimum of the Eemian Interglacial (MIS 5e), this influence area were extended further north and east, as testified by the presence of temperate trees and thermophilus plant in the palynological record of Central Europe (Mamakowa, 1989; Zagwijn, 1996; Muller et al., 2003, among others) and of warm-demanding snail species in the malacological record of the Carpathian Basin (Krolopp and Sümegi, 1995). Accordingly, in the sites belonging to the first phases of MIS 5, the values of the L_{agr}/L_{arv} index decrease below 100. Then the index increases again above 100 in the sites dated to the end of MIS 5 and MIS 3 with the return of more continental and humid conditions.

3.2. Belgium

3.2.1. The sites

The sites of Scladina cave (50°29'03" N, 05°01'30" E) and Marie-Jeanne cave (50°13' N, 4°47'06" E) are located in the province of Namur (south-eastern Belgium), in the Meuse River Basin (Fig. 3.2.1).

Scladina cave has been systematically excavated by the University of Liège and by the Scladina cave Archaeological Center since 1978. At least four Mousterian occupations had been identified along the sequence and 19 human fossil assigned to *Homo neanderthalensis* and thousands of lithics tools had been recovered in the last 40 years (Pirson et al., 2018). The samples of Scladina cave analysed here come from the square C4, at the entrance of the cave, from former levels VI to IV (Fig. 3.2.2), dated to MIS 5c-a (Pirson, 2014; López-García et al., 2017a).

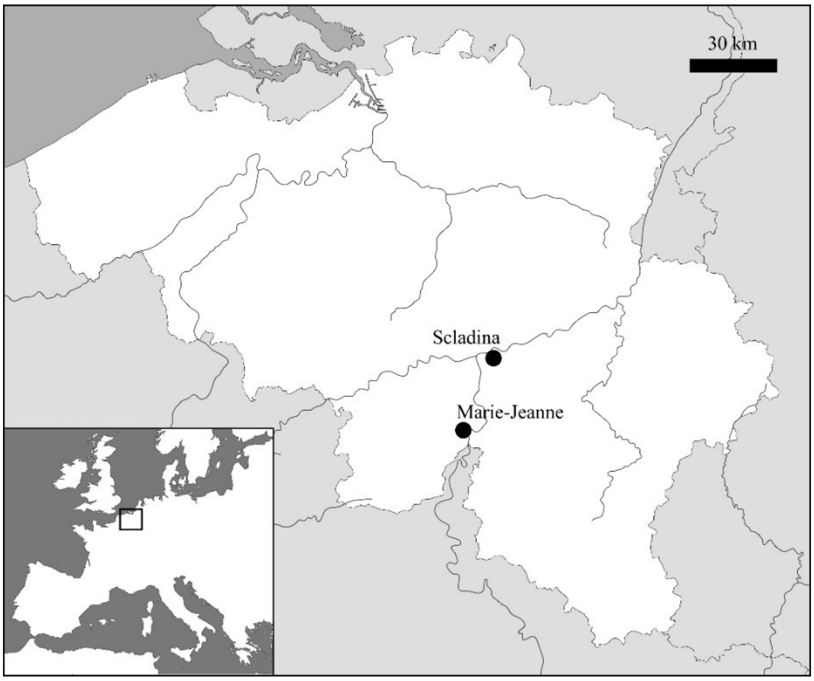


Figure 3.2.1. Geographic location of studied sites of Belgium.

Palynological and anthracological analysis point to temperate climatic conditions for levels VI and IV, with high percentage of AP, up to 80%, and the presence of temperate deciduous malacophyllous trees (Pirson et al., 2008). The large mammal assemblage, with the strong occurrence of *Dama dama*, *Capreolus capreolus* and *Cervus elaphus*, also indicates warm climatic conditions and extensive woodlands (Simonet, 1992).Recent herpetofaunal and small mammal studies agree in suggesting for levels VI and IV mild and humid climatic conditions, with good representation of forest formations (boreal and temperate), open humid meadows, and slow-water stream habitat (Blain et al., 2014; López-García et al., 2017a). Pollen assemblage, small mammal assemblage, and sedimentary structures for level V suggest instead a cooler and drier moment, with a reduction of tree coverture (Pirson et al., 2008; López-García et al., 2017a).

The material from Marie-Jeanne cave are deposited at the Royal Belgium Institute of Natural Science (RBINS). The deposits of Marie-Jeanne cave consist in 10 Pleistocene layers: layers 10-7 are sterile; layers 6-2 yielded abundant faunal remains and some Mousterian lithic tools; layer 1 presents a mix of fossil and modern faunas (Ballmann et al., 1980). Recent dating on lemmings revealed that layer 6-4 pertain to MIS 3, while layer 2 belong to MIS 2 but with divergent dates (14,850–13,925 and 25,456–24,497 yr cal BP).

The samples of Marie-Jeanne cave come from layers 6-5a (Fig. 3.2.3), dated between ca. 50 and ca. 40 ka BP (Brace et al., 2012). The large mammals, for this layers, suggest cool and dry conditions characterized by open cold steppe environments (i.e. *Coelodonta antiquitatis*, *Rangifer tarandus*, *Equus* cf. *remagensis*, *Bison priscus*), in accordance with the terrestrial molluscs recovered

(Ballmann et al., 1980).The small mammals assemblage indicates temperatures lower than at present and precipitation slightly higher than at present, together with an environment dominated by open woodlands and open dry grasslands (López-García et al., 2017b)

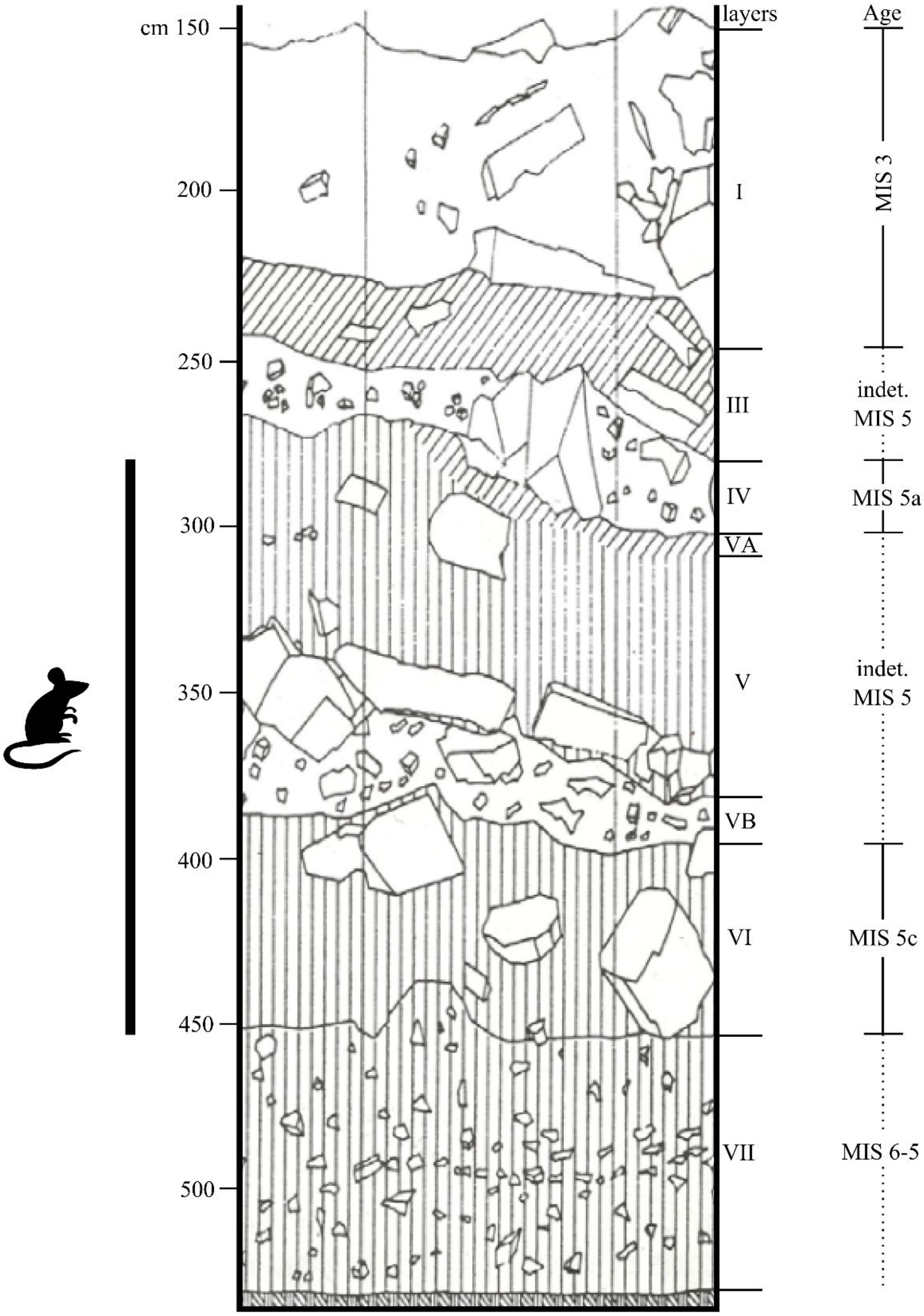


Figure 3.2.2. Scladina cave stratigraphy of square C4 with the indication of the provenience of the samples (modified from López-García et al., 2017a).

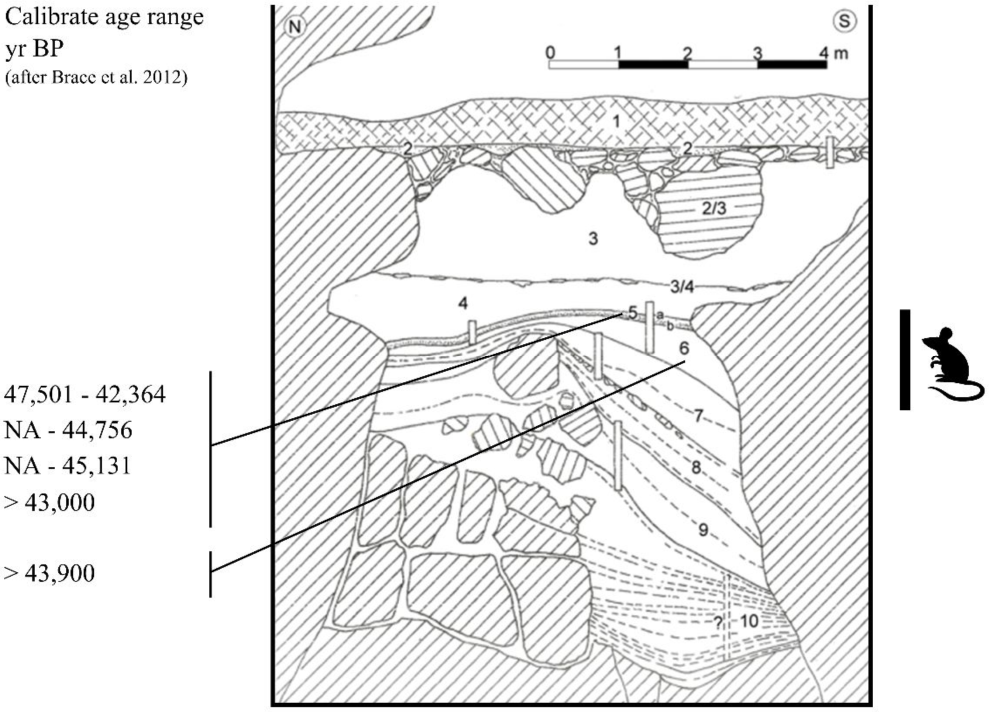


Figure 3.2.3. Stratigraphy of Marie-Jeanne cave, with indication of the provenience of the samples (modified from Ballmann et al., 1980).

3.2.2. Results and brief discussion

While *Microtus agrestis* remains stable in size, the mean values of L increase in *Microtus arvalis* from the MIS 5 of Scladina cave to the MIS 3 of Marie-Jeanne cave so that they almost reach the same length (Fig. 3.2.4). Both *M. arvalis* and *M. agrestis* from Scladina cave show lower values of the a/L index than those of Marie-Jeanne cave. (Table 3.2.1).

The difference in a/L values between populations of MIS 5 and populations of MIS 3 of *M. agrestis* has already been observed in Spain and Italy (see Chapter 2.3), and the mean value of *M. agrestis* from Scladina cave are comparable with those of other populations from MIS 5 (i.e. Ciota Ciara and San Bernardino Maggiore in Italy; Valdavara-3 in Spain; Süttő 6, Porlyuk cave, Poroslyuk cave, Tokod and Lambrecht cave in Hungary) while that of Marie-Jeanne cave is higher (Fig. 3.2.5).

During Late Pleistocene, for *M. arvalis* in south-western Europe, Italy, Croatia and Hungary, values of the a/L index are generally higher than 53 and there are no particular differences between populations of MIS 5 and MIS 3, except for the population of Scladina cave and Süttő 6 (Hungary). At Süttő 6, despite the low number of specimens, it is possible to note a punctual decrease of the index a/L that is not observed in the other Hungarian sites dated to MIS 5 (i.e. Porlyuk cave, Poroslyuk cave, Tokod and Lambrecht cave). This may be related to an event of displacement of demes from southern regions triggered by the major climatic shift of the Eemian interglacial (MIS 5e).

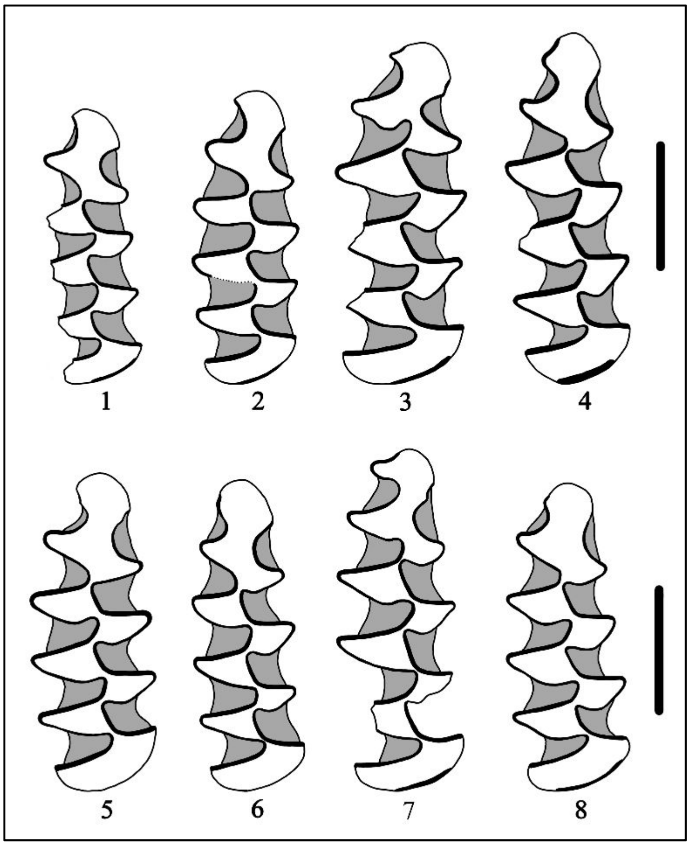


Figure 3.2.4. Sample of right m1s of Microtus arvalis (1-2-5-6) and Microtus agrestis (3-4-7-8) from Scladina cave (1-4) and Marie-Jeanne cave (5-8). 1: SCL-c4-IV-250-1; 2: SCL-c4-Vb-360-1; 3: SCL-c4-V-280-1; 4: SCL-c4-Vb-370-4 5: MJ-6-002; 6: MJ-6-023; 7: MJ-6-016; 8: MJ-6-029. Scale: 1 mm.

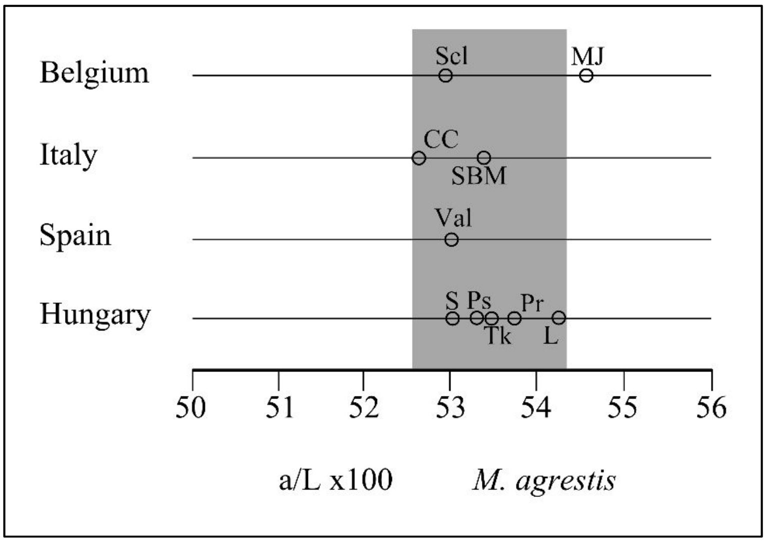


Figure 3.2.5. Mean values of a/L index for Microtus agrestis of Scladina cave and Marie-Jeanne cave compared to other European sites dated to MIS 5. Belgium - Scl: Scladina cave; MJ: Marie-Jeanne cave. Italy – CC: Ciota Cara; SBM: San Bernardino Maggiore. Spain – Val: Valdavara-3. Hungary – S: Süttő 6; Ps: Poroslyuk cave; Pr: Porlyuk cave; L: Lambrecht cave; Tk: Tokod. In grey: range of mean values of a/L index for MIS 5 sites.

At Scladina cave, it is not possible to know the values of the index for Middle Pleistocene populations, so that it is not possible to know if there is any variation with respect to older populations or to infer any correlation with the climatic conditions of MIS 5.

Scladina (C4. layers VI-IV)

	Microtus agrestis					*Microtus arvalis*				
	n	min	mean	max	SD	n	min	mean	max	SD
L	24	2.621	2.827	3.21	0.14	12	2.301	2.504	2.665	0.1
a	24	1.324	1.499	1.691	0.09	12	1.191	1.326	1.494	0.09
W	24	0.879	0.992	1.082	0.04	12	0.813	0.865	0.929	0.03
e	23	0.695	0.797	0.982	0.06	12	0.625	0.73	0.805	0.04
d	23	0.173	0.289	0.388	0.05	12	0.18	0.245	0.3	0.04
La	24	0.317	0.368	0.415	0.02	12	0.34	0.362	0.394	0.01
Li	24	0.561	0.634	0.718	0.04	12	0.478	0.519	0.56	0.02
a/L x100	24	49.07	52.99	55.29	1.56	12	47.83	52.94	57.39	2.51
La/Li x100	24	47.21	58.23	66	5.33	12	65.2	69.96	82.42	4.39

Marie-Jeanne (layers 6+5a)

	Microtus agrestis					*Microtus arvalis*				
	n	min	mean	max	SD	n	min	mean	max	SD
L	8	2.557	2.803	2.972	0.13	21	2.567	2.754	2.998	0.12
a	8	1.368	1.529	1.645	0.1	21	1.363	1.515	1.737	0.1
W	8	0.867	0.963	1.059	0.06	21	0.836	0.935	1.002	0.04
e	8	0.725	0.771	0.841	0.04	21	0.693	0.782	0.868	0.04
d	8	0.176	0.281	0.378	0.06	21	0.063	0.243	0.376	0.08
La	8	0.33	0.367	0.407	0.02	21	0.319	0.393	0.438	0.02
Li	8	0.547	0.617	0.666	0.04	21	0.498	0.553	0.613	0.03
a/L x100	8	52.5	54.52	57.46	1.75	21	51.7	55	59.2	1.81
La/Li x100	8	49.5	59.7	64.11	4.8	21	61.7	71.29	82.77	5.31

Table 3.2.1. Measurements and indices of m1s of *Microtus agrestis* and *M. arvalis* from Belgium. n: number of specimens; min: minimum value; mean: mean value; max: maximum value; SD: standard deviation. Linear measures (L, a, W, d, e, La, Li) are given in mm.

The index L_{agr}/L_{arv} show different values for the two sites. Both values are > 100, indicating a continental setting. Scladina cave (L_{agr}/L_{arv} = 112.89) presents a higher value compared with Marie-Jeanne cave (L_{agr}/L_{arv} = 101.77). This difference is due to the larger size of *Microtus arvalis* and slightly smaller size of *M. agrestis* from Marie-Jeanne. Since *M. agrestis* tends to reduce its size in drier environment where *M. arvalis* tends to become larger (Dienske, 1979; De Jonge, 1983), the data are coherent with the difference in mean annual precipitations inferred from the small mammals assemblages of the two sites: 1057,8 mm at Scladina cave and 1011,5 mm at Marie-Jeanne (López-García et al., 2017a, 2017b). Climatic and environmental conditions were different at the two sites, due to the different chronological settings: levels VI-IV of Scladina cave are related with the end of

MIS 5 (substages MIS 5c and 5a), with relatively warm and humid climate and a landscape characterized by woodland formation and water stream habitats (Simonet, 1992; Pirson et al., 2008; Blain et al., 2014), while layers 6-5a of Marie-Jeanne cave represent a relatively cold and dry moment of MIS 3, when open woodland and grasslands were dominant (Ballmann et al., 1980). Therefore, it is possible to observe that the values of the index L_{agr}/L_{arv} in the continental setting of Late Pleistocene in Belgium decrease as the climate become drier. The same phenomenon is visible at Tokod, where the value of the index L_{agr}/L_{arv} is lower in the drier lower levels (4-6) and increase in the more humid upper levels (1-3) (Chapter 2.4). These data are coherent with those from the Adriatic area and state again the link between L_{agr}/L_{arv} index and climatic context.

3.3 Conclusions

All data indicate that higher values of the L_{agr}/L_{arv} index are indicator of higher levels of precipitation and general humidity. Furthermore, in areas characterized by Mediterranean climate, the values of the index are generally < 100, where in areas characterized by continental climate the values are > 100.

The size of *Microtus arvalis* tends to increase in correspondence of dry periods and arid environmental conditions, while *M. agrestis* become larger during humid phases and in wet environments, as already observed at Teixoneres (Chapter 2.2).

4. GENERAL DISCUSSION

4.1. Evolutionary trends in *M. agrestis* during Middle and Late Pleistocene

We compare here the different populations of *Microtus agrestis* to each other, in chronological order. In order to do so, we used three fundamental measurements: the total length of the first lower molar (m1), L; the index La/Li that quantify the degree of asymmetry of the m1; the index a/L that quantify the degree of elongation of the anteroconid complex (ACC). We used alternatively the t-test, the Mann-Whitney test, the Kruskal-Wallis test, or the one-way ANOVA test to quantify the difference between the samples, with significance achieved for value of $p < 0.05$, and high significance for value of $p < 0.01$.

4.1.1. Morphology and morphometrics of *Microtus agrestis* sl. during late Middle Pleistocene

Reports of the occurrence of *Microtus* ex gr. *agrestis* dated the first appearance of this group to the glaciation B of the Cromerian complex (MIS 16, ca. 676-621 ka)) of Late Biharian of Poland (Nadachowski 1985; Markova & Puzachenko 2016), but it is after MIS 12 that *Microtus agrestis* s.str. becomes widespread across Europe (Kowalski 2001; Masini & Sala 2007; Maul & Markova 2007; Cuenca-Bescós *et al.* 2016).

A particular morphological type of *M. agrestis* for late Middle Pleistocene was identified by Chaline (1972) on the basis of material from Grotte de l'Escale (Saint-Estève-Janson, Bouches-du-Rhône, France): *M. agrestis jansoni*. The m1 presents a posterior loop, five closed triangles with a clear labio-lingual asymmetry, alternatingly confluent T6 and T7, and an asymmetric anterior cap. In particular, the *jansoni*-type is characterized by a middle-large size, a deep LRA4, the presence of T9 in the ACC and a broad LRA5. In some cases, the populations of the late Middle Pleistocene develop a small BRA4 on T6, resulting in a T8 that recalls the mimomyan-fold (Fig.4.1.1). This archaic character is rare in Late Pleistocene populations (1/1000).

The occurrence of *M. agrestis jansoni* have been signalled in late Middle Pleistocene sites of Western Europe: Caune de l'Arago (Brunet-Lecomte & Paunesco 2004), La Fage (Mourer-Chauvire *et al.* 2003), Grotte des Cèdres (Defleur *et al.* 1990), Combe Grenal (Chaline 1972), and Grotte de la Carrière (López-García *et al.* 2016) in France; Galeria, Zarpazos, Gran Dolina TD10, Sima del Elefante TE18-19 (Cuenca-Bescós *et al.* 1999; Galindo-Pellicena *et al.* 2011; López-García *et al.* 2011), and Mollet (López-García *et al.* 2014) in Spain; Ciota Ciara (unit 15) and Grotta Maggiore di San Bernardino (López-García *et al.* 2017c) in Italy.

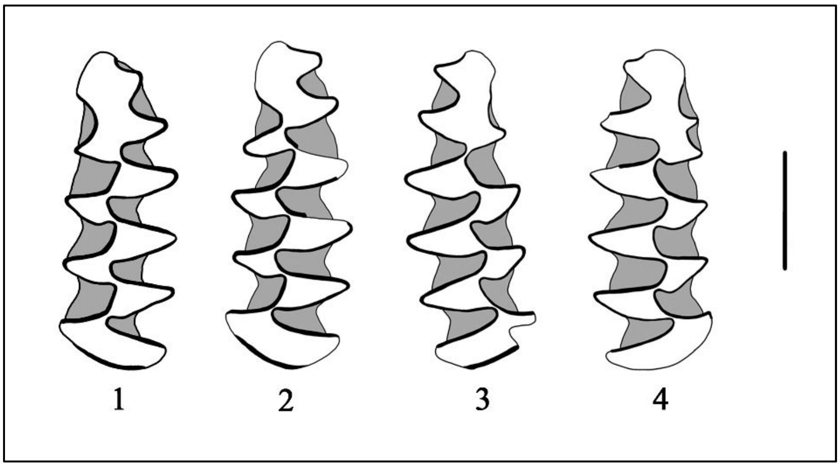


Figure 4.1.1. Samples of *Microtus agrestis jansoni*. 1: SBM_91_545_26_U8-1, left m1; 2: TGZIIa_n3_280, left m1; 3: TD10-2_j16_250-270-37, right m1; 4: 7: CAR_n4_d6-28b, right m1. SBM: Grotta Maggiore di San Bernardino; TGZ: Trinchera Galeria Zarpazos; TD10-2: Trinchera Dolina, level 10.2; CAR: Grotte de la Carrière. Occlusal view. Scale: 1mm.

Kormos (1933) described *Microtus coronensis* n. sp. from the Middle Pleistocene site of Brassó (now Brașov, in Transylvania, Romania). Its occurrence is reported in Middle Pleistocene sites of Central Europe, i.e. Czech Republic and Slovakia (Horácev & Lozek 1988; Ivanov & Vörös 2014). The holotype of this species belongs to the collection of the Hungarian Natural History Museum and in fact its morphology strongly resembles the *agrestis*-type. Its most prominent feature is the asymmetry of the ACC, with a deep LRA 4, a very developed LRA5 and a less deep BRA4. It presents five closed triangles, but in rare cases very deep BRA4 and LRA5 lead to the formation of a T6 almost separated from T7 and AC (Kormos 1933) (Fig.4.1.2).

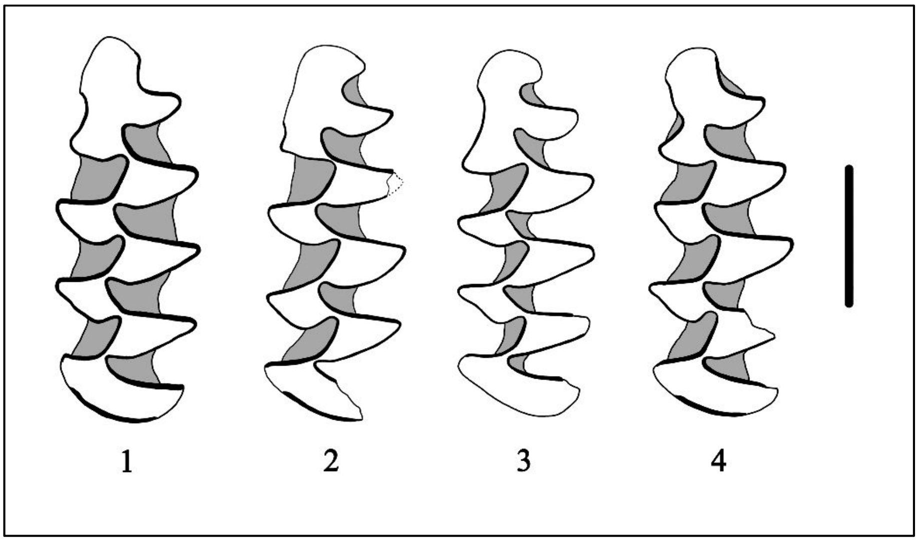


Figure 4.1.2. *Microtus coronensis*, Kormos 1933, from Brașov, Romania. Collection of the Hungarian Natural History Museum. 1-4: V61-1426, left m1s. 3: holotype. Occlusal view. Scale: 1 mm.

Similar morphological characters are displayed by the populations of *M. agrestis* of the Carpathian Basin, i.e. of Vértesszőlős, of Tarkő shelter and of Uppony I: they present an asymmetric ACC, a simple AC, without any additional triangle, and a pronounced LRA4 (Fig.4.1.3).

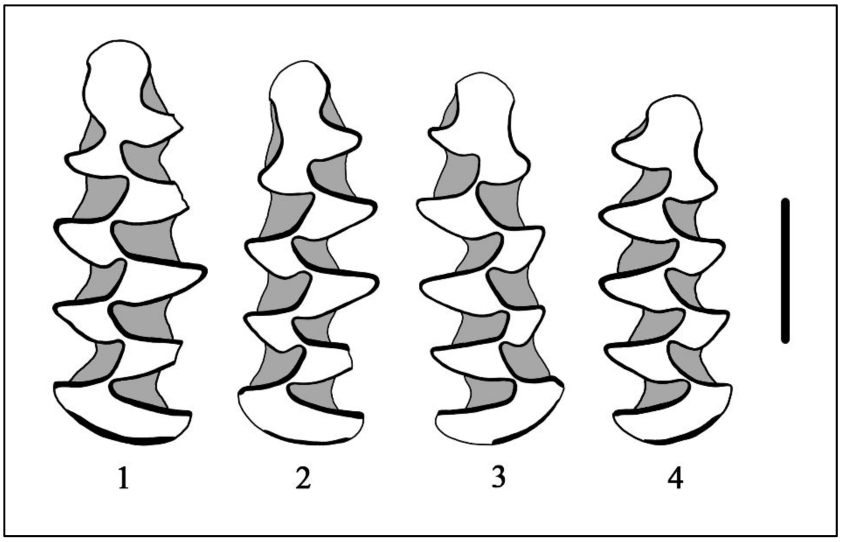


Figure 4.1.3. Samples of *Microtus agrestis* from the late Middle Pleistocene of Hungary of Tarkő (1-3) and Vértesszőlős (4). 1: V.64.595e, left m1; 2: V.64.595-b, left m1; 3: V.64.595-d, right m1; 4: V.64.666, right m1. Occlusal view. Scale: 1 mm.

Comparing the morphometric characters of the different populations, it is possible to observe that *M. coronensis* measurements correspond perfectly with those of others *M. agrestis* of the same chronology (MIS 11-10), i.e. Gran Dolina TD10, Galeria Zarpazos, Ciota Ciara – unit 15, Tarkő – level 8-12, and Vértesszőlős (Fig.4.1.4).

Given the morphometric similarities with *M. agrestis* from the same chronology and the morphological similarities with *M. agrestis* populations from the same geographic area, it is possible to consider *M. coronensis* as a subspecies of *M. agrestis*. The *coronensis*-type can be treated as a fixed morphotype of *M. agrestis*, more commonly found in Central Europe, in the same way that the *jansoni*-type is the more common fixed morphotype for the Mediterranean regions of Western Europe. The two morphotypes do not differ from a morphometric point of view but are easily identifiable.

Instead, morphometric differences exist between chronologies. The populations of late Middle Pleistocene of *Microtus agrestis* can be divided in two group regardless of their geographic provenience (Table 4.1.1): one composed by populations of MIS 11-10 and one composed by populations of MIS 9-6. Therefore, it is possible to say that the values of the index a/L increase significantly at the end of Middle Pleistocene.

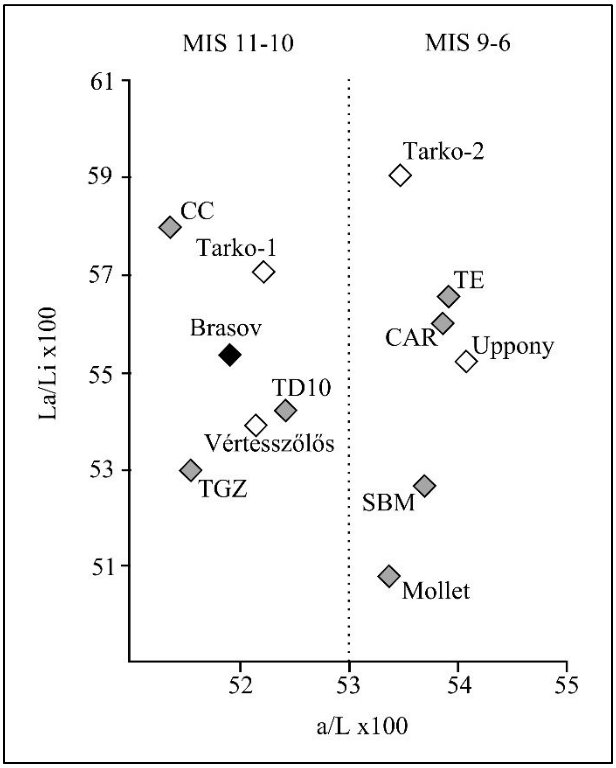


Figure 4.1.4. Relation between the a/L index and the La/Li index for populations of *M. agrestis* of late Middle Pleistocene. CC: Ciota Ciara, unit 15; Tarkő-1: Tarkő, level 8-12; Tarkő-2: Tarkő, level 7-1; TD10: Trinchera Dolina, level 10.2; TGZ: Trinchera Galeria-Zarpazos, level II-III; TE: Sima Elafante, layers 18-19; CAR: Grotte de la Carrière; SBM: Grotta Maggiore di San Bernardino, units VIII-VII.

	MIS 11-10 SW	MIS 11-10 I*	MIS 11-10 CB	MIS 9-6 SW	MIS 9-6 I*	MIS 9-6 CB
MIS 11-10 SW		0.8722	0.932	**1.14E-06**	**4.24E-05**	**1.68E-07**
MIS 11-10 I*	0.8722		0.8325	**0.001418**	**7.16E-03**	**4.20E-03**
MIS 11-10 CB	0.932	0.8325		**0.0007238**	**0.005679**	**0.0008868**
MIS 9-6 SW	**1.14E-06**	**0.001418**	**0.0007238**		0.3224	0.5945
MIS 9-6 I*	**4.24E-05**	**7.16E-03**	**0.005679**	0.3224		0.6315
MIS 9-6 CB	**1.68E-07**	**4.20E-03**	**0.0008868**	0.5945	0.6315	

Table 4.1.1. Results of the Kruskal-Wallis test (H = 48.57; p = 2.713E-09) showing highly significant differences (bold) between the a/L values of *M. agrestis* from MIS 11-10 and MIS 9-6 of Southwestern Europe (SW), Italian peninsula (I) and Carpathian Basin (CB). *: one single site.

4.1.2. The Middle-Late Pleistocene transition

The transition between Middle and Late Pleistocene affected the populations of *Microtus agrestis* living in the different areas under study in different ways. As already observed in Chapter 2.4, at the beginning of Late Pleistocene, because of the climatic changes brought by the Eemian Interglacial, *M. agrestis* from the Carpathian Basin suffer a reduction of size. On the other hand, the populations from the Mediterranean region retain the size of Middle Pleistocene ones.

	MIS 9-6 SW + I	MIS 9-6 CB	MIS 5 SW + I	MIS 5 CB
MIS 9-6 SW + I		0.996	**0.04528**	0.4725
MIS 9-6 CB	0.996		**0.03408**	0.4099
MIS 5 SW +I	**0.04528**	**0.03408**		0.65
MIS 5 CB	0.4725	0.4099	0.65	

Table 4.1.2. Results of the one-way ANOVA test (df = 210; F = 3.166; p = 0.02544) showing significant differences (bold) between the a/L values of *M. agrestis* from MIS 9-6 and MIS 5 of Mediterranean regions, Southwestern Europe (SW) and Italian peninsula (I), and Carpathian Basin (CB).

The values of the a/L index remain stable in the Carpathian Basin samples, while in Mediterranean region there are significant differences between MIS 9-6 and MIS 5 (Table 4.1.2): a decrease that is probably correlated with the climatic amelioration at the beginning of Late Pleistocene. During the first phases of MIS 5 (i.e. MIS 5e-d), the record of the Carpathian Basin registers temperate but relatively dry conditions, more arid than in other part of Central Europe, such as Poland, Germany, and France (Zagwijn 1996; Sümegi *et al.* 2011; Wohlfarth 2013; Zech *et al.* 2013; Demény *et al.* 2017). On the contrary, in SW Europe (i.e. northern Iberian Peninsula and southwestern France) and in Italy, the same period is characterized by warm and humid conditions (Sánchez-Goñi *et al.* 1999; Allen & Huntley 2009). The moister conditions in the Mediterranean region, that permit to *M. agrestis* to retain its size, can also be key to understand the shift toward lower values of a/L. Changes in a/L index are probably related to the functional advantage brought by the increased in the relative length and in the morphological complexity of the anteroconid complex: a longer ACC can reduce chewing pressure and therefore slow the wear of the tooth (Maul 2001). The decrease in the mean values of a/L may testify an ease from this functional pressure during a moment of climatic and environmental optimum: more quantity of available food, of improved quality, and with less silica. Instead, in the Carpathian Basin, where the conditions were not so favourable, the pressure to keep longer ACC remained and kept the a/L index stable.

Another possible explanation for this phenomenon may involve movement of populations. Immigration event at subspecific level are not easily spotted in the fossil record, unless morphological intraspecific differences existed between old inhabitants and new incomers. The most studied is the case of the water vole *Arvicola amphibius* (= *terrestris*): it was possible to identify a re-immigration event, dated to the beginning of Late Pleistocene (Kolfschoten van 1992). Living populations of this species show a variations in the relative thickness of the enamel of molars, quantified with the so-called SDQ index (Schmelzband-Differenzierungs-Quotient, enamel differentiation ratio, after

Heinrich 1978), and this variations are linked to a strong geographical cline: *A. amphibius* from Southern Europe present higher values of SDQ index, while in Central and North-western Europe values are lower (Röttger 1987). The same difference is visible between Southern Italy and Central Europe fossil populations of Late Pleistocene (Maul *et al.* 1998). The values of the SDQ index slowly decrease in time and marks the evolutionary stages of the lineage *Mimomys-Arvicola* (Heinrich 1990; Koenigswald von & Kolfschoten van 1996; Ruddy 2011; Agadzhanyan 2012; Lozano-Fernández *et al.* 2013, among others). Therefore, the important fluctuation toward higher values of the SDQ index interrupting the trend toward lower values has been interpreted as the results of an invasion of southern populations that recolonized northern territories as soon as the improved climatic conditions allow it (Kolfschoten van 1992; Kalthoff *et al.* 2007). Although the samples are very scarce, in the case of *M. agrestis* there seem to be no difference in the mean values of a/L index of subfossil and living populations coming from different geographic regions: 53.92 in Northern Spain (n = 6); 54.3 in Austria (n = 21, subfossil populations) (Mauch Lenardić 2007); in Poland (n = 30, living populations; n = 20, sub-fossil populations) the values vary between 53 and 54 (Nadachowski 1982). Furthermore, the fossil populations analysed in this work show no geographical cline and do not present differences when coeval samples are compared: during MIS 9-6, in SW Europe the mean values of a/L vary between 53.35 and 53.9 (Mollet: n = 2; Grotte del la Carrière: n = 13; Sima Elefante: n = 4); in Italy the mean is 53.73 (Grotta Maggiore di San Bernardino: n = 25); in Hungary 53.45 at Tarkő (levels 1-7: n = 16) and 54.1 at Uppony (n = 30). For these reasons, at the moment, the hypothesis that favourable environmental and climatic conditions allow a fluctuation toward lower values of a/L in Mediterranean populations has to be preferred.

4.1.3. Variations in Late Pleistocene populations

During Late Pleistocene, *Microtus agrestis* populations from the three studied geographic areas continue the process of differentiation started in MIS 5. The sample from Cova Eirós is highly divergent from any other of MIS 3-2 and is going to be analysed separately in the next sub-chapter 4.1.4.

The values of L in SW Europe remain rather stable while those of La/Li are relatively high, as the m1s become more symmetrical and the morphology of the ACC tends to simplify; the populations from Galicia differ from the others of northern Spain partly because of the influence of the Atlantic climate and partly due to their relative geographical isolation; *M. agrestis* of Toll cave present the smallest size among the samples, due to the peculiar climatic and environmental conditions brought on by the LGM (see Chapter 2.1). On the other hand, the populations of Late Pleistocene of the Italian Peninsula are very homogeneous, with values of L slightly reducing through time and the ACC present the complex morphotypes typical of *M. agrestis*, as described in Nadachowski (1982) and Kapischke *et al.* (2009) (see Chapter 2.3). The same can be said about the morphologies shown by populations from Carpathian Basin (see Chapter 2.4), but values of L show a decided increase from MIS 5 to MIS 3 (Fig.4.1.5).

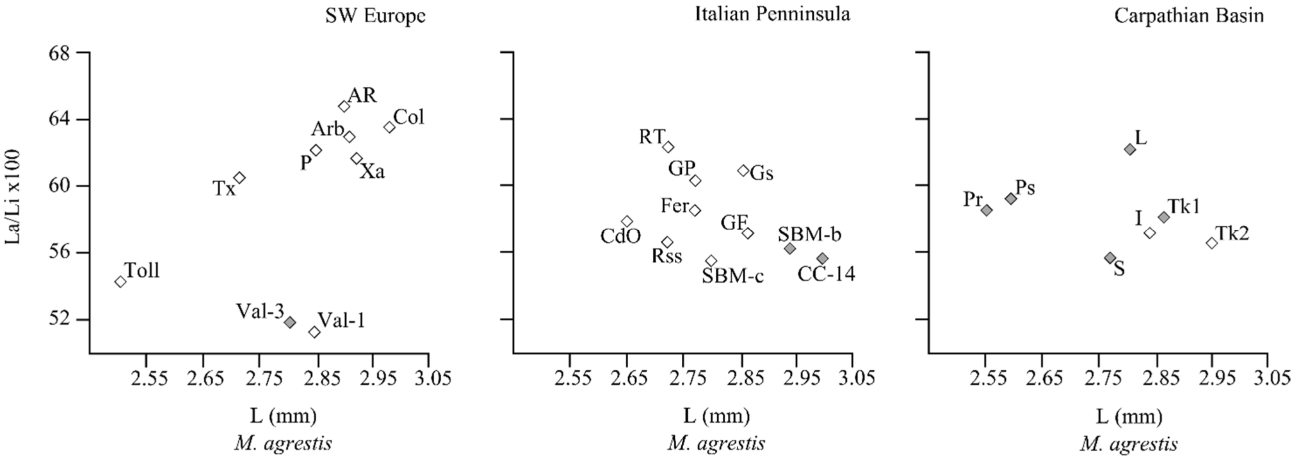


Figure 4.1.5. Relation between L and La/Li index of populations of *Microtus agrestis* from Late Pleistocene sites. Grey squares: MIS 5 samples. Southwestern Europe (SW): Val-3: Valdavara-3; Col: Colomera; Xa: Xaragalls; Tx: Teixoneres; P: Portalon; AR: Romaní, level O; Val-1: Valdavara-1; Arb: Arbreda. Italian Peninsula: CC-14: Ciota Ciara, unit 14; SBM-b: Grotta Maggiore di San Bernardino, units V-IV; SBM-c: Grotta Maggiore di San Bernardino, units III-II; CdO: Caverna degli Orsi; GF: Fumane; RSS: Roccia San Sebastiano; Fer: Ferrovia; GS: Grotta del Sambuco; RT: Riparo Tagliente; GP: Grotta Paglicci. Carpathian Basin: S: Süttő 6; Ps: Poroslyuk cave; Pr: Porlyuk cave; L: Lambrecht cave; Tk1: Tokod, levels 4-6; Tk2: Tokod, levels 1-3; I: Istállóskő.

	MIS 5 SW*	MIS 5 I	MIS 5 CB	MIS 3-2 SW	MIS 3-2 I	MIS 3-2 CB
MIS 5 SW*		0.5206	0.2819	**0.03746**	**0.01923**	0.07992
MIS 5 I	0.5206		0.3965	**0.00506**	**0.001623**	**0.03504**
MIS 5 CB	0.2819	0.3965		**0.02113**	**0.005011**	0.1928
MIS 3-2 SW	**0.03746**	**0.00506**	**0.02113**		0.6132	0.396
MIS 3-2 I	**0.01923**	**0.001623**	**0.005011**	0.6132		0.1614
MIS 3-2 CB	0.07992	**0.03504**	0.1928	0.396	0.1614	

Table 4.1.3. Results of the Kruskal-Wallis test ($H = 19.7$; $p = 0.001423$) showing significant differences (bold) between the a/L values of *M. agrestis* from MIS 5 and MIS 3-2 of Southwestern Europe (SW), Italian peninsula (I) and Carpathian Basin (CB). *: one single site.

It is also possible to identify two different patterns in the variations of the a/L index, one for the populations of *M. agrestis* from the Mediterranean region and one for Carpathian Basin. In the SW Europe and in the Italian Peninsula, the values of the index a/L of populations belonging to MIS

5 are significantly different from the values of those belonging to MIS 3-2, while the populations from MIS 5 and MIS 3-2 of the Carpathian Basin are similar to each other (Table 4.1.3). The samples from Belgium are small and belonging to just two sites, but the difference of a/L between MIS 5 and MIS 3 populations is significant ($p = 0.0348$ with Mann-Whitney test).

Increases size (in the case of Carpathian Basin), increased a/L values (in the case of the Mediterranean region) and increased morphological complexity of the ACC (in the case of Italy and Hungary) are effective strategies to contrast the wear of the tooth and therefore to acquire an evolutionary advantage in a more competitive environment. MIS 3 is characterized by repeated abrupt climatic changes (Heinrich 1988; Bond *et al.* 1993; Mogensen 2009), in a general context of continentalization of the climate, cool temperatures and few precipitation, but with pulse of humidity in correspondence of interstadial moments (Sánchez-Goñi *et al.* 1999; Muller *et al.* 2003; Pini *et al.* 2009; Zech *et al.* 2013; Obreht *et al.* 2017; Salcher *et al.* 2017). This climatic deterioration, with respect to the conditions of MIS 5, may have restored the trend toward higher values of the a/L index in the Mediterranean region, to obtain a functional advantage in a more competitive environment. In the context of the Carpathian Basin the same goal was reached by increasing size and complexity of the ACC, while in Italy both complexity and a/L value rise. These data are coherent with the hypothesis exposed in the previous sub-chapter 4.1.2: climatic changes have influence over the time and rhythm of the a/L evolutionary trend, by enhancing or loosing the need for increased functional optimum.

4.1.4. Cryptic speciation in the fossil record of Cova Eirós

Phylogenetic analysis of living populations of *M. agrestis* lead to the identification of three major lineages: an eastern lineage, distributed in Russia and eastern Scandinavia, a northern (or western) lineage, distributed in Northern and Central Europe, and a southern lineage, distributed in Spain, southwestern France, Italy and Dalmatia. Hungarian populations of south-western regions belong to the southern lineage, where those of the north and east belong to the northern one. The time of the separation among these three lines is set at the LGM (Jaarola & Searle 2002, 2004; Herman *et al.* 2014). The northern and southern lineages show today an elevated level of divergence and strong genetic structure that is retained also in parapatry, indicating that the speciation process is in a very advanced stage (Beysard *et al.* 2012). Recent studies identified a new lineage of *Microtus agrestis* within the range of the southern one. It has been located in central Portugal and north-western Spain and it is now considered as a separate cryptic species (Giménez *et al.* 2012; Paupério *et al.* 2012).

In Chapter 2.1, we observed that Late Pleistocene populations of *M. agrestis* from north-western Spain (Valdavara-3, Valdavara-1, and Eirós cave) differ from the others of northern Spain, in both morphology and morphometrics. In fact, the m1s present a more marked labio-lingual asymmetry (higher values of the La/Li index) and morphologies that resemble those of the populations of Middle Pleistocene. We suggested that these differences may be related to the early phases of the speciation process undergone by the populations of the Portuguese lineage. The analysis of the a/L index can provide additional data to investigate this question further.

The mean value of the a/L index in the sample from Valdavara-3 and Valdavara-1 are in line with those of the other populations in SW Europe of MIS 5 and MIS 3-2 respectively, while the one from Eirós cave is anomalous. When compared with the mean values of all the other populations of field vole belonging to Late Pleistocene (MIS 5 + MIS 3-2), the difference remains remarkable (Fig.4.1.6). Furthermore, this morphometric difference is highly significant with respect to all populations of *M. agrestis* of MIS 3-2 (Table 4.1.4). Hence, the fossil population of *M. agrestis* from Cova Eirós shows both morphological and morphometric characters that separate it from any other belonging to the same chronology.

Since the sample here analysed comes from level 3 of the site, dated at 41,299 to 38,390 yr. cal BP (95.4% probability) (Rey-Rodríguez *et al.* 2016) and since the proposed age of the separation between the Portuguese line and the combined northern-southern groups is 70 ± 30 ka (Paupério *et al.* 2012), our new data from Cova Eirós support the hypothesis that early signs of this speciation process can be spotted in the fossil record of Galicia at least 40 ka BP.

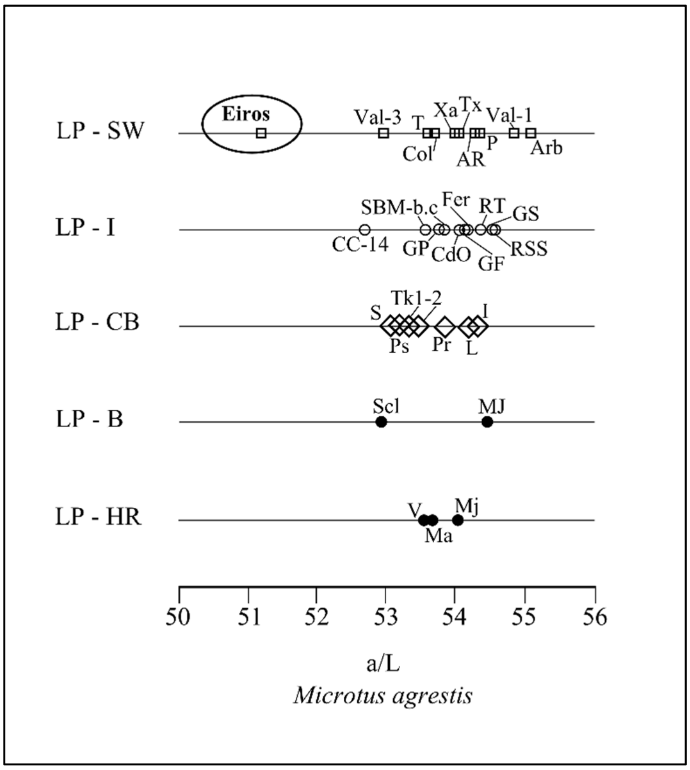


Figure 4.1.6. Mean values of the index a/L of *Microtus agrestis* in Late Pleistocene populations. The sample from Eirós cave is isolated from the others of its same chronology. Southwestern Europe (SW): Val-3: Valdavara-3; T: Toll; Col: Colomera; Xa: Xaragalls; Tx: Teixoneres; P: Portalon; AR: Romaní, level O; Val-1: Valdavara-1; Arb: Arbreda. Italian Peninsula (I): CC-14: Ciota Ciara, unit 14; SBM-b: Grotta Maggiore di San Bernardino, units V-IV; SBM-c: Grotta Maggiore di San Bernardino, units III-II; CdO: Caverna degli Orsi; GF: Fumane; RSS: Roccia San Sebastiano; Fer: Ferrovia; GS: Grotta del Sambuco; RT: Riparo Tagliente; GP: Grotta Paglicci. Carpathian Basin (CB): S: Süttő 6; Ps: Poroslyuk cave; Pr: Porlyuk cave; L: Lambrecht cave; Tk1: Tokod, levels 4-6; Tk2: Tokod, levels 1-3; I: Istállóskő. Belgium (B): Scl: Scladina; MJ: Marie-Jeanne. Croatia (HR): V: Vindija; Ma: Marlera I; Mj: Mujina.

	MIS 3-2 HR	MIS 3-2 B*	MIS 3-2 CB	MIS 3-2 I	MIS 3-2 SW	Eirós
MIS 3-2 HR		0.7861	0.8533	0.1801	0.4129	**0.005686**
MIS 3-2 B*	0.7861		0.4887	0.7847	0.7389	**0.01359**
MIS 3-2 CB	0.8533	0.4887		0.1614	0.396	**0.00112**
MIS 3-2 I	0.1801	0.7847	0.1614		0.6132	**0.0009907**
MIS 3-2 SW	0.4129	0.7389	0.369	0.6132		**0.001556**
Eirós	**0.005686**	**0.01359**	**0.00112**	**0.0009907**	**0.001556**	

Table 4.1.4. Results of the Kruskal-Wallis test ($H = 13.78$; $p = 0.01707$) showing significant differences (bold) between the a/L values of *M. agrestis* s.l. of Eirós cave and those of the other *M. agrestis* populations of the same chronology, MIS 3-2. HR: Croatia; B: Belgium; CB: Carpathian Basin; I: Italian Peninsula; SW: Southwestern Europe. *: one single site.

4.1.5. The index a/L as a chronological tool

The ratio a/L was first introduced by Van der Meulen (1973) in order to quantify the development of the anteroconid (a) of the first lower molar with respect to the total length (L) of the tooth. The fossil record provides evidence of an increase in the complexity of the anteroconid in arvicolids (Guthrie 1971; Gromov & Polyakov 1992; Markova 2013; Rekovets & Kovalchuk 2017, among others), hence an increase in time of the values of the a/L index. This increase is not so regular or homogeneous as previously thought, and its patterns of change can be gradual or varying in rate, and include stasis, fluctuations and, in some cases, non-directional variations, so that it can be used as biostratigraphic marker only in a general sense (Maul *et al.* 2014). Nevertheless, it proved to be a useful indicator of the level of complexity of the ACC and it is commonly used to compare different evolutionary stages within lineages in taxa with unrooted teeth, particularly for the species of the genus *Microtus* (Rekovets & Nadachowski 1995; Maul *et al.* 1998, 2007; López-García *et al.* 2015; Klimowicz *et al.* 2016, among others).

Comparing the mean values of the index a/L of the studied populations of *M. agrestis*, it is possible to point out similarities and differences across chronologies and geographic areas. The populations belonging to the Italian Peninsula and to SW Europe seem to undergo similar variations through time (Fig.4.1.7). If the entire Mediterranean region is considered, the difference between chronologies is significant (Table 4.1.5). In the case of the populations from SW Europe, each period differs significantly from the one preceding it and from the one following it: MIS 9-6 can be separated from both MIS 11-10 and MIS 5, as MIS 5 can be distinguished from both MIS 9-6 and MIS 3-2 (Table 4.1.6). In the case of the populations from the Italian Peninsula, although the index presents a slight shift toward lower values, there are no significant differences between *M. agrestis* from MIS

9-6 and those belonging to the Late Pleistocene (MIS 5 and MIS 3-2), but it is possible to separate populations dated to MIS 11-10 from populations of all the other chronologies, and populations dated to MIS 5 from population dated to MIS 3-2 (Table 4.1.7).

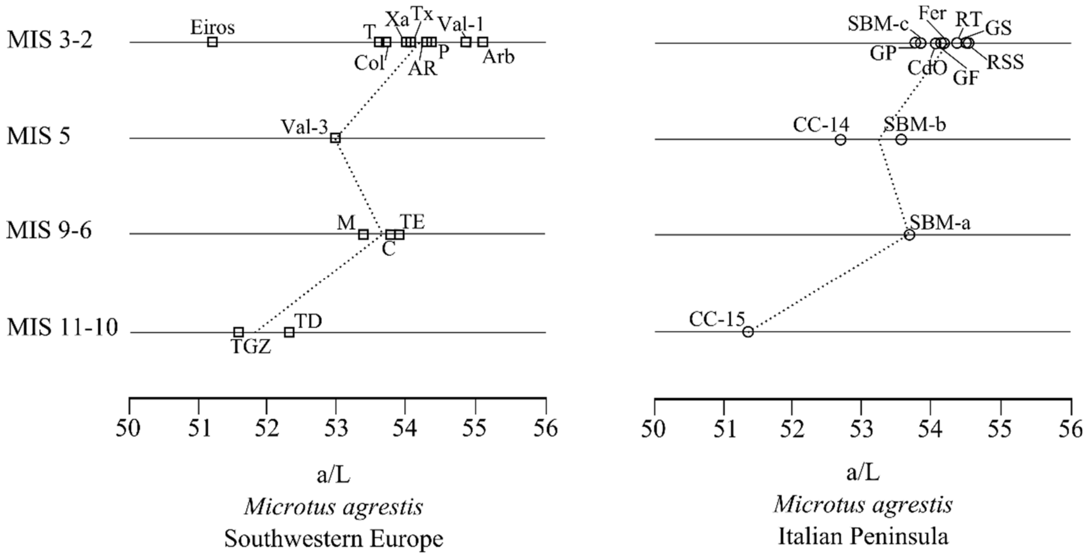


Figure 4.1.7. Mean values of the index a/L of *Microtus agrestis*. Dotted line: mean value of a/L for each chronological period. Southwestern Europe: TD: Trinchera Dolina, level 10.2; TGZ: Trinchera Galeria-Zarpazos, level II-III; TE: Sima Elafante, layers 18-19; C: Grotte de la Carrière; M: Mollet; Val-3: Valdavara-3; T: Toll; Col: Colomera; Xa: Xaragalls; Tx: Teixoneres; P: Portalon; AR: Romaní, level O; Val-1: Valdavara-1; Arb: Arbreda. Italian Peninsula: CC-15: Ciota Ciara, unit 15; CC-14: Ciota Ciara, unit 14; SBM-a: Grotta Maggiore di San Bernardino, units VIII-VII; SBM-b: Grotta Maggiore di San Bernardino, units V-IV; SBM-c: Grotta Maggiore di San Bernardino, units III-II; CdO: Caverna degli Orsi; GF: Fumane; RSS: Roccia San Sebastiano; Fer: Ferrovia; GS: Grotta del Sambuco; RT: Riparo Tagliente; GP: Grotta Paglicci.

	MIS 11-10 SW+I	MIS 9-6 SW+I	MIS 5 SW+I	MIS 3-2 SW+I
MIS 11-10 SW+I		**8.08E-09**	**0.0005442**	**9.24E-14**
MIS 9-6 SW+I	**8.08E-09**		**0.009068**	0.2868
MIS 5 SW+I	**0.0005442**	**0.009068**		**0.0002125**
MIS 3-2 SW+I	**9.24E-14**	0.2868	**0.0002125**	

Table 4.1.5. Results of the Kruskal-Wallis test (H = 65.68; p = 3.593E-14) showing significant differences (bold) between the a/L values of populations of *M. agrestis* from Mediterranean regions (SW Europe + Italian Peninsula).

	MIS 11-10 SW	MIS 9-6 SW	MIS 5 SW*	MIS 3-2 SW
MIS 11-10 SW		**1.14E-06**	0.1077	**2.33E-10**
MIS 9-6 SW	**1.14E-06**		**0.04024**	1
MIS 5 SW*	0.1077	**0.04024**		**0.03746**
MIS 3-2 SW	**2.33E-10**	1	**0.03746**	

Table 4.1.6. Results of the Kruskal-Wallis test (H = 46.3; p = 4.908E-10) showing significant differences (bold) between the a/L values of populations of *M. agrestis* from Southwestern Europe. Each period is significantly different from the one preceding and the one following it. *: one single site.

	MIS 11-10 I*	MIS 9-6 I*	MIS 5 I	MIS 3-2 I
MIS 11-10 I*		**0.007157**	**0.04691**	**0.001131**
MIS 9-6 I*	**0.007157**		0.1669	0.1205
MIS 5 I	**0.04691**	0.1669		**0.001623**
MIS 3-2 I	**0.001131**	0.1205	**0.001623**	

Table 4.1.7. Results of the Kruskal-Wallis test (H = 19.51; p = 0.0002) showing significant differences (bold) between the a/L values of populations of *M. agrestis* from Italian Peninsula. *: one single site.

In the case of *M. agrestis* from the Carpathian Basin, the species follow a different pattern: while the difference between populations dated to MIS 11-10 and the younger ones is evident, the index remains stable during MIS 9-2 showing no significant oscillations (Table 4.1.8): in particular, the mean values of the index do not decrease at the beginning of Late Pleistocene (Fig.4.1.8), contrarily to what observed in the populations from the Mediterranean area.

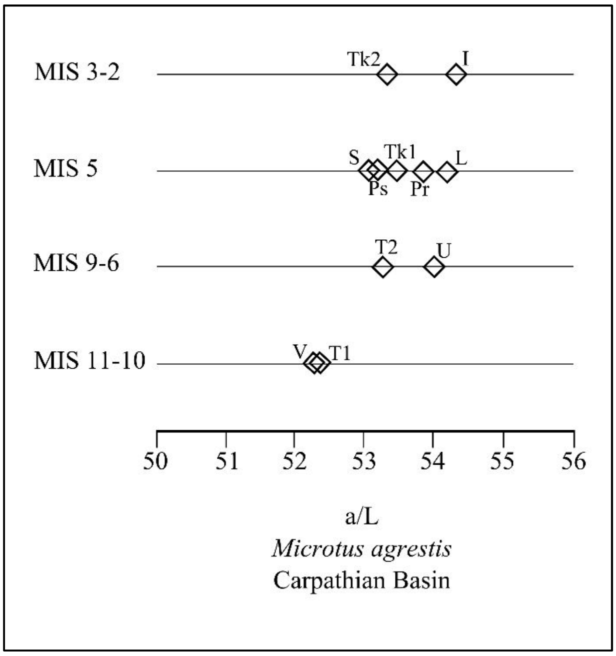


Figure 4.1.8. Mean values of the index a/L of *Microtus agrestis* in populations from the Carpathian Basin. V: Vértesszőlős II; T1: Tarkő, levels 8-12; T2; Tarkő, levels 7-1; U: Uppony I; S: Süttő 6; Ps: Poroslyuk cave; Pr: Porlyuk cave; L: Lambrecht cave; Tk1: Tokod, levels 4-6; Tk2: Tokod, levels 1-3; I: Istállóskő.

	MIS 11-10 CB	MIS 9-6 CB	MIS 5 CB	MIS 3-2 CB
MIS 11-10 CB		**0.008462**	**0.03665**	**0.007414**
MIS 9-6 CB	**0.008462**		0.1636	0.9484
MIS 5 CB	**0.03665**	0.1636		0.1928
MIS 3-2 CB	**0.007414**	0.9484	0.1928	

Table 4.1.8. Results of the Kruskal-Wallis test (H = 9.309; p = 0.02545) showing that significant differences (bold) in the a/L values of *M. agrestis* of Carpathian Basin (CB) are present only for MIS 11-10.

The data allow to find a pattern in the fluctuations of the a/L index, that seem to be strongly linked to their geographic and climatic context. It is possible to separate populations of belonging to MIS 11-10 from the younger populations of Middle Pleistocene in all geographic context analysed here. On the contrary, the distinction between MIS 9-6 and MIS 5 populations is clear only in the context of SW Europe but it is possible that the same pattern may occur in populations from the Italian Peninsula, given that the two datasets yielded a stronger signal when we jointed them. It is also possible to separate populations belonging to MIS 5 from younger populations of Late Pleistocene but only in Iberian and Italian Peninsulas. Even though more data are needed to confirm these patterns, the index a/L in populations of *M. agrestis* has a very high potential to be a useful tool to help refine the chronological attribution of archaeological and palaeontological sites in the Mediterranean area.

4.2. Evolutionary trends in *M. arvalis* during Middle and Late Pleistocene

We compare here the different populations of *Microtus arvalis* to each other. As in the study of *M. agrestis*, we used here three fundamental measurements: the total length L of the first lower molar (m1),; the index La/Li that quantify the degree of symmetry of the m1; the index a/L that quantify the degree of elongation of the anteroconid complex (ACC). We used alternatively the t-test or the Kruskal-Wallis test to quantify the difference between the samples, with significance achieved for value of $p < 0.05$, and high significance for value of $p < 0.01$.

4.2.1. Size differences in late Middle Pleistocene and Late Pleistocene *Microtus arvalis*

The first occurrence of *Microtus arvalis* is reported at Kärlich, Germany, during MIS 16, between ca. 621 – 676 ka (Kolfschoten & Turner 1996; Markova & Puzachenko 2016); in Italy, its first occurrence is testified at Visogliano shelter (MIS 12, ca. 424 – 478 ka; see Chapter 2.3) but it becomes widespread in Europe starting from MIS 11, ca. 324 - 374 ka (Chaline 1972; Kowalski 2001; Maul & Markova 2007; Pazonyi 2011; Cuenca-Bescós *et al.* 2016).

The samples from late Middle Pleistocene sites of SW Europe, Italy and Carpathian Basin show a difference in size: *M. arvalis* from SW Europe are larger than those of the Carpathian Basin; the sample from Ciota Ciara is similar in size to those from SW Europe, while the one from Grotta Maggiore of San Bernardino are closer to those of the Carpathian Basin (Fig.4.2.1).

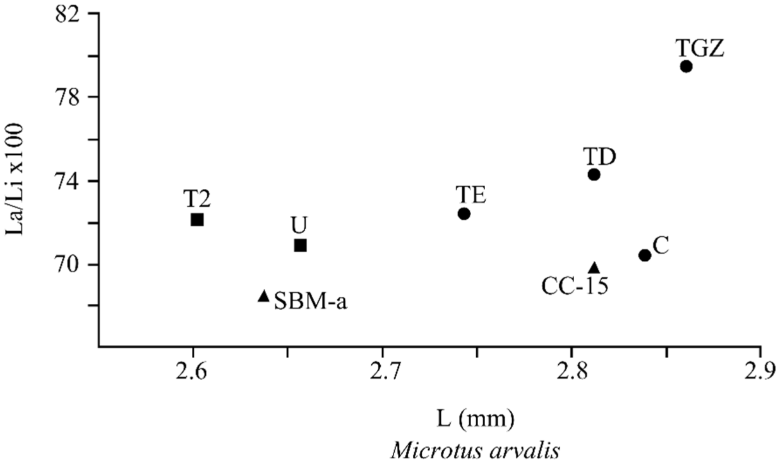


Figure 4.2.1. Relation between L and the La/Li index in *Microtus arvalis* of late Middle Pleistocene. Circles: SW Europe samples. TGZ: Trichera Galeria-Zarpazos; TD: Trinchera Dolina, level 10.2; TE: Sima Elefante, layers 18-19; C: Grotte de la Carrière. Squares: Carpathian Basin samples. U: Uppony; T2: Tarkő, level 1-7. Triangles: Italian samples. CC-15: Ciota Ciara; SBM-a: Grotta Maggiore di San Bernadino, units VIII-VII.

There is an obvious separation between populations from the Mediterranean region and populations from Hungary. According to Niethammer and Krapp (1982), in living populations of *M. arvalis* northern forms are generally larger than southern ones, mountain forms are slightly larger than plain forms, and insular forms are larger than continental ones. On the contrary, our data show that during late Middle Pleistocene, Mediterranean (southern) forms tend to be larger than continental (northern) ones. The two Italian populations seem to indicate that higher altitude correspond to larger size, since Ciota Ciara is at 670 m a.s.l. where San Bernardino in at 135 m a.s.l. but the two Hungarian populations seem instead to contradict that statement, since Uppony is at 278 m a.s.l. where Tarkő is at 850 m a.s.l. and both sample present similarly low values. Chronology might also play a role. The occurrences of *Allocricetus bursae* and *Pliomys* cf. *episcopalis* at Ciota Ciara – unit 15 (Angelucci *et al.* 2016) suggest an age older than San Bernardino units, and the value of the a/L index for *M. agrestis jansoni* indicates that unit 15 is possibly related to MIS 11-10 (see Chapter 4.1); both Trinchera

Dolina (level 10.2) and Galeria Zarpazos are related to the same chronology while Sima Elefante (level 18-19) is younger and dated to MIS 9-8 (Falguères *et al.* 2013; de Lombera Hermida *et al.* 2015); Grotte de la Carrière age ranges between 220 and 450 ka (López-García *et al.* 2016) The Middle Pleistocene units of Grotta Maggiore di San Bernardino are related to the end of MIS 7, as shown by the small mammals assemblage (López-García *et al.* 2017c) and confirmed by the absolute dating, with a minimum age range between 214 and 154 ka (Picin *et al.* 2013); Uppony also dates to the end of Middle Pleistocene, between 170 and 205 ka (Pazonyi 2011). Therefore, the end of MIS 7 seems to bring a reduction in size of *M. arvalis* m1s, but the sample of Tarkő, dated to MIS 9-8, presents the lowest mean value of L of all the Middle Pleistocene populations analysed. A factor to take into account is the peculiar geography of the Iberian Peninsula, that acted and acts as refugium and an area of endemism for both fauna and flora species (Gómez-Campo *et al.* 1984; Bilton *et al.* 1998; Gomez & Lunt 2006). From this point of view, the Iberian Peninsula can be considered as an "island" and SW Europe *M. arvalis* populations might have been relatively isolated from those of the continent during Middle and late Pleistocene and might have acquired and retain larger size as a consequence. Another possible agent to consider is climatic influence: since larger *M. arvalis* are better adapted to arid conditions than the smaller ones, due to a better management of body water dispersal, the difference in size might represent a difference in relative humidity of the environment.

Considering the size of m1s of Late Pleistocene *M. arvalis*, it is possible to notice that the samples from SW Europe continue to present larger mean size than those from Italy and the Carpathian Basin; the samples from Belgium are similar to those of the Carpathian Basin, and so it's Vindija, while the samples from Marlera I and Mujina are closer to those of SW Europe. Among the Italian samples, the largest m1s are those of Grotta Paglicci (Fig. 4.2.2).

Therefore, taking into account all the samples, there is no evidence of altitude affecting the size of m1s and since the differences between the Mediterranean and continental areas remain the same through time, also chronology proved to have little influence on *M. arvalis* size. Variations of size in *M. arvalis* of the Orkney archipelago were correlated with variations in latitude, mean and maximum annual precipitation and maximum annual temperature (Cucchi *et al.* 2014). Our data show that *M. arvalis* from southern latitude areas with Mediterranean characters (higher temperature and lower precipitation, sometimes concentrated in only one season) tend to be larger than those from continental climate and northern latitude, confirming that the climatic component has indeed an influence on the m1s size.

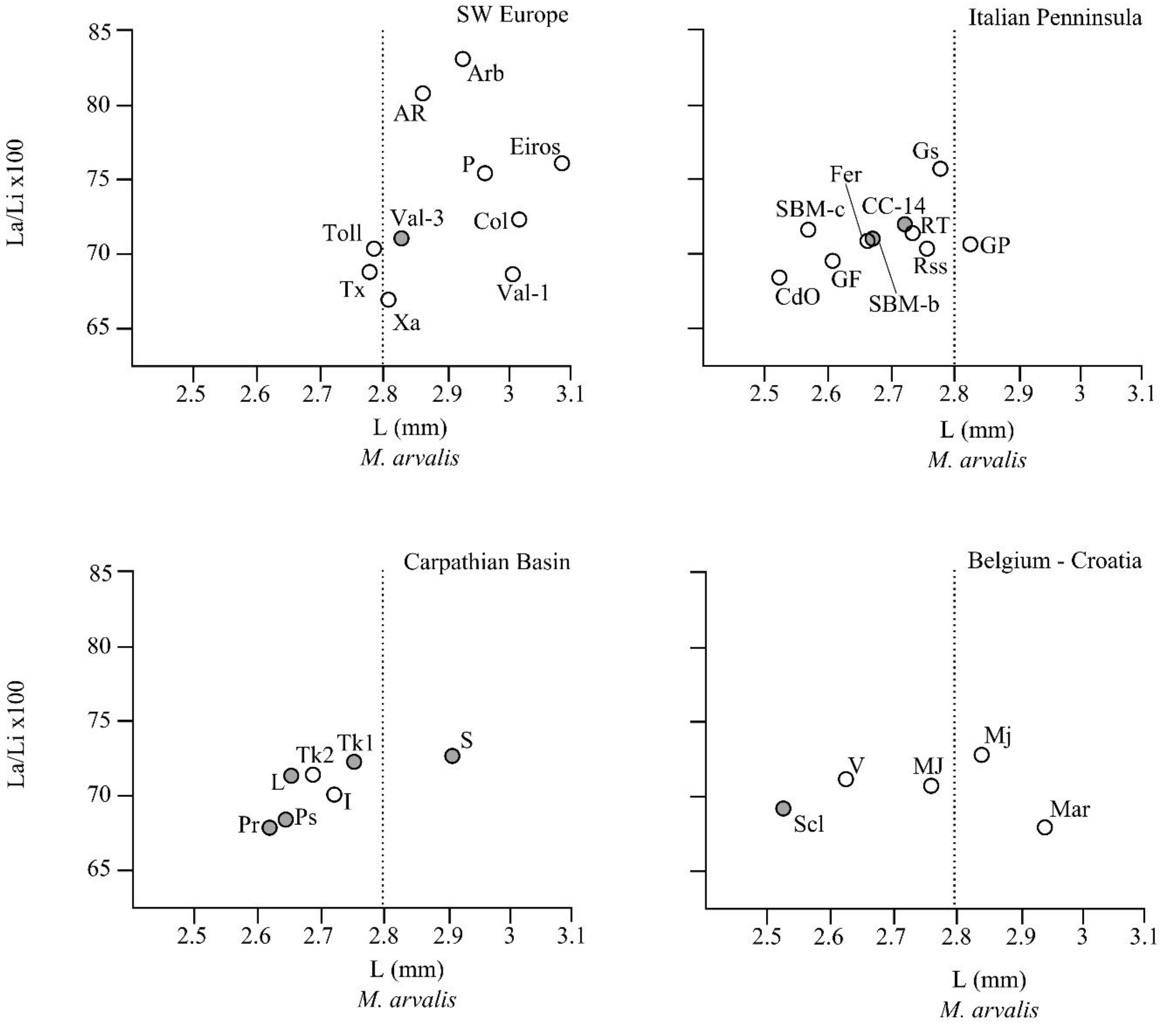


Figure 4.2.2. Relation between L and the La/Li index in *Microtus arvalis* of Late Pleistocene. In grey: MIS 5 samples. SW Europe: Val-3: Valdavara-3; Col: Colomera; Xa: Xaragalls; Tx: Teixoneres; P: Portalon; AR: Romaní (level O); Val-1: Valdavara-1; Arb: Arbreda. Italian Peninsula (I): CC-14: Ciota Ciara, unit 14; SBM-b: Grotta Maggiore di San Bernardino, units V-IV; SBM-c: Grotta Maggiore di San Bernardino, units III-II; CdO: Caverna degli Orsi; GF: Fumane; RSS: Roccia San Sebastiano; Fer: Ferrovia; GS: Grotta del Sambuco; RT: Riparo Tagliente; GP: Grotta Paglicci. Carpathian Basin (CB): S: Süttő 6; Ps: Poroslyuk cave; Pr: Porlyuk cave; L: Lambrecht cave; Tk1: Tokod, levels 4-6; Tk2: Tokod, levels 1-3; I: Istállóskő. Belgium (B): Scl: Scladina; MJ: Marie-Jeanne. Croatia (HR): V: Vindija; Ma: Marlera I; Mj: Mujina.

4.2.2 Stability of the a/L index in SW Europe and in the Carpathian Basin

In the samples from SW Europe, the low number of individuals for MIS 9-6, does not allow to have a clear picture of the end of Middle Pleistocene, but it is possible to notice that the mean values of the a/L index remain relatively stable: 54.22 for MIS 11-10; 54.07 for MIS 5; 54.37 for MIS 3-2, with no significant differences among them (Table 4.2.1).

	MIS 11-10 SW	MIS 5 SW*	MIS 3-2 SW
MIS 11-10 SW		0.5145	0.7393
MIS 5 SW*	0.5145		0.4851
MIS 3 SW	0.7393	0.4851	

Table 4.2.1. Results of the Kruskal-Wallis test (H = 0.6046; p = 0.7391) showing no significant differences between the a/L values of *M. arvalis* belonging to different chronologies from SW Europe (SW). *: one single site.

Despite the lack of *M. arvalis* for the MIS 11-10 chronology, in the samples from the Carpathian Basin it is possible to study the transition between Middle and Late Pleistocene, and the changes throughout MIS 5 to MIS 3. In chapter 2.4, the relative changes in size of *M. arvalis* and *M. agrestis* were analysed and related to the climatic and environmental oscillations of Late Pleistocene. Furthermore, it was possible to see how the size of *M. arvalis* remained rather stable through time, with the exception of a sudden increase during the first phases of MIS 5. The analysis of the a/L index shows no significant changes among the samples: 54.81 in MIS 9-6; 54.36 in MIS 5 e-c; 54.19 in MIS 5 b-a; 54.61 in MIS 3 (Table 4.2.2).

	MIS 9-6 CB	MIS 5 e-c CB	MIS 5 b-a CB	MIS 3
MIS 9-6 CB		0.3369	0.09851	0.4735
MIS 5 e-c CB	0.3369		0.76	0.5189
MIS 5 b-a CB	0.9851	0.76		0.3128
MIS 3	0.4735	0.5189	0.3128	

Table 4.2.2. Results of the Kruskal-Wallis test (H = 2.721; p = 0.4382) showing no significant differences between the a/L values of *M. arvalis* belonging to different chronologies from the Carpathian Basin (CB).

The Iberian Peninsula, together with the Italian and the Balkan Peninsulas, has been long known as a refugial area, due to the milder and relatively more stable climatic conditions provided by the lower latitude and by the influence of Mediterranean Sea and to the protection offered by the Pyreneans (Heckel *et al.* 2005; Schmitt 2007; Bailey *et al.* 2008; González-Sampériz *et al.* 2010). The peculiar geographic, topographic, climatic, and environmental setting of the Carpathian Basin allow several vertebrate species to survive in otherwise unfavourable conditions during glacial periods, acting as a cryptic refugium further north than the Mediterranean refugia (Hewitt 2000, 2004; Stewart & Lister 2001; Kotlík *et al.* 2006; Sommer & Nadachowski 2006; Fløjgaard *et al.* 2009; Schmitt & Varga 2012; Filipi *et al.* 2015). In particular, both areas functioned as refugium for *M. arvalis* during the LGM (Fink *et al.* 2004), and recent phylogenetic and phylogeographic studies proved that *M. arvalis* from the Carpathian Basin played a fundamental role in the post-glacial recolonization of Central and Eastern Europe (Stojak *et al.* 2015, 2016). In this context, the relative stability in the a/L index might be seen as an indicator of this privileged and protected contexts, that insured the surviving of the species during glacial periods. However, the samples belong to a limited latitudinal range: 48°30’39” N to 47°40’00” N in the Carpathian Basin, and 43°01’00” N to 41°23’ 02” N in Spain. Therefore, more sample will be necessary to establish if this stability is constant across the whole areas.

4.2.3. Latitudinal cline in a/L values in the Italian Peninsula during Late Pleistocene

During Late Pleistocene, it is possible to observe significant differences in the mean a/L values between northern and central-southern populations (Table 4.2.3): the mean value is sensibly higher in norther populations of MIS 5 and MIS 3-2. On the other hand, the values of northern fossil populations dated to post-LGM are closer to those of MIS 3-2 central-southern populations (Fig.4.2.3). This might be the indications of an immigration wave of *M. arvalis* from the south, similar to that observed for *A. amphibius* during the Eemian – MIS 5e (Kolfschoten van 1992; Paunescu *et al.* 2004; Kalthoff *et al.* 2007, among others). The amelioration of the climatic conditions brought by the end of the glaciation, the change in the environment and the pressing competition with Savii’s pine vole *Microtus* (*Terricola*) *savii*, better adapted to temperate Mediterranean conditions, might have lead *M. arvalis* to move north in search of more suitable territories.

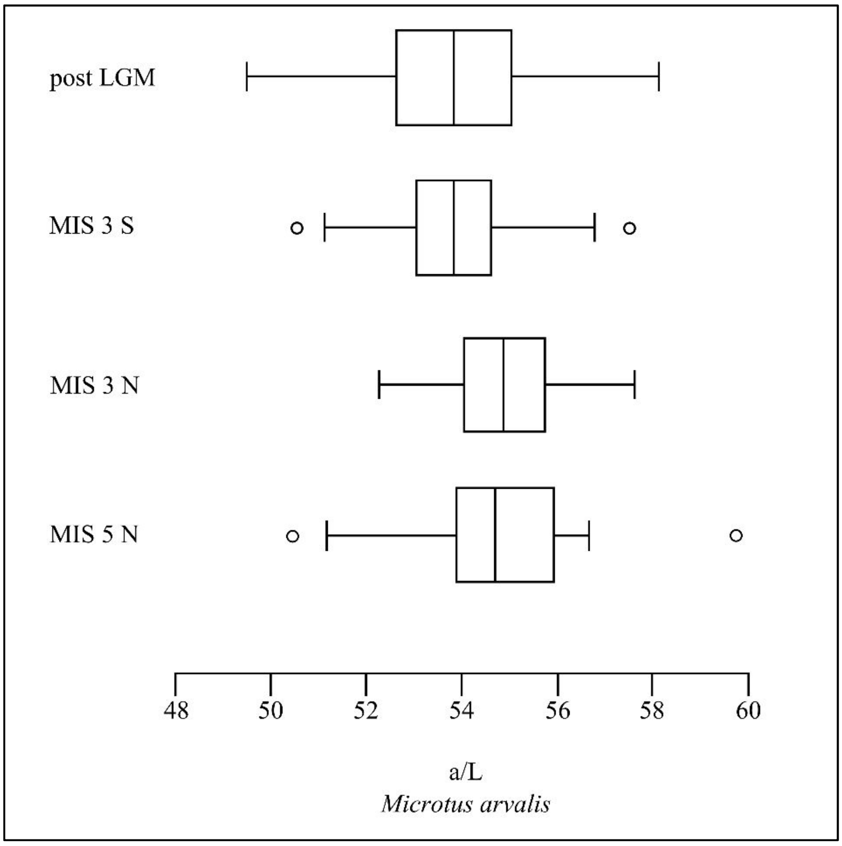


Figure 4.2.3. Box plot with outliers describing the oscillations of a/L index in *Microtus arvalis* samples from the Italian Peninsula. N: North; S: South; LGM: Last Glacial Maximum. MIS 5 N: Ciota Ciara-14; Grotta Maggiore di San Bernardino – units V-IV; MIS 3 N: Caverna degli Orsi, Grotta Fumane, Grotta Maggiore di San Bernardino – units III-II; MIS 3 S: Grotta del Sambuco – US6; Roccia San Sebastiano; Grotta Paglicci; post-LGM: Grotta del Sambuco – US5; Grotta della Ferrovia; Riparo Tagliente.

	MIS 5 N.I.	MIS 3 N.I.	MIS 3 S.I.	POST LGM I
MIS 5 N.I.		0.8006	**0.001214**	**0.002517**
MIS 3 N.I.	0.8006		**5.73E-05**	**0.0001602**
MIS 3 S.I.	**0.001214**	**5.73E-05**		0.8477
POST LGM I	**0.002517**	**0.0001602**	0.8477	

Table 4.2.3. Results of the Kruskal-Wallis test (H = 25.42; p = 1.261E-05) showing significant differences (bold) between the a/L values of *M. arvalis* coming from northern (N.I.) and southern (S.I.) Italian Peninsula but no significant differences between MIS 3 samples from southern Italy and post-LGM samples.

In Italy, the relative stability observed in the other two refugia analysed above is not present. This might be due to the larger latitudinal range analysed, 45° 42' 39" N to 41°06' N, and to the strong regionalism that characterized the Peninsula during the Late Pleistocene and in particular during and after the LGM: the Alps and the Apennine Mountains partially isolated Italy from the rest of the Europe; due to its peculiar geomorphology, there are clear differences between northern and southern faunal assemblages and between those from the eastern and the western side (Sala 1992, 2007; Kotsakis *et al.* 2003; Masini & Sala 2007; Sala & Masini 2007; Berto 2013). Because of the oscillations in the a/L index toward lower values, contrary to what is to be expected, it is possible to observe a slow, but steady decrease of the a/L values at the end of MIS 2. The trend is clearly visible at Grotta del Sambuco, where the mean a/L value for US 6, dated at 27,490-28,000 ka cal BP, is 53.78 while that of US 5, related to the Late Glacial, is 53.13. Living populations of *M. arvalis* from the Po Plain present even lower values, with a mean of 52.98 (n = 15), confirming the decreasing pattern. On the contrary, the a/L index remain relatively stable during Late Pleistocene in Hungary. A significant difference exists (F = 1.5455; t = 2.497; p = 0.0135 for student t-test) between the samples from the Iberian Peninsula dated to pre-LGM and those dated to post-LGM, when the mean a/L increase from 54.37 to 55.01. In Poland the a/L index increases its values between Late Glacial and Holocene, from 53 ± 1 to 55 ± 2, and then stabilize on mean values of 54 ± 2 in recent populations (Nadachowski 1982). Recent *M. arvalis* from Ukraine have an even higher mean a/L of 55.8 (Rekovets & Nadachowski 1995).

Being a peripherical population, living in less favourable conditions at the boundary of the species geographic range, it is possible that the relative isolation of Italian populations enhances this drift in the direction of a reduced ACC (García-Ramos & Kirkpatrick 1997). Another possible explanation might be the lack of direct competitors such as *M. agrestis*, *M. oeconomus* or *M. gregalis*, which do not currently inhabit the Po Plain, and the major anthropization of the region with the consequent abundance of food from cereal cultivations, two factors that can reduce the evolutive pressure for an elongated, more functional ACC.

4.2.4. Variations in a/L index during MIS 3-2 in Europe

During MIS 5 it is not possible to observe any clear pattern but during MIS 3-2, it is possible to divide the samples in two groups, according to the a/L values displayed by the different populations (Fig. 4.2.4). One group composed by central-southern Italian (i.e. Grotta Paglicci, Roccia San Sebastiano, Grotta del Sambuco) and Croatian populations, the other is composed by Iberian, northern Italian (i.e. Caverna degli Orsi, Grotta Fumane, Grotta Maggiore di San Bernardino – level III-II), Belgian and Hungarian populations (Table 4.2.4). Samples dated to the period following the Last Glacial Maximum (LGM) are analysed separately in section 4.2.5.

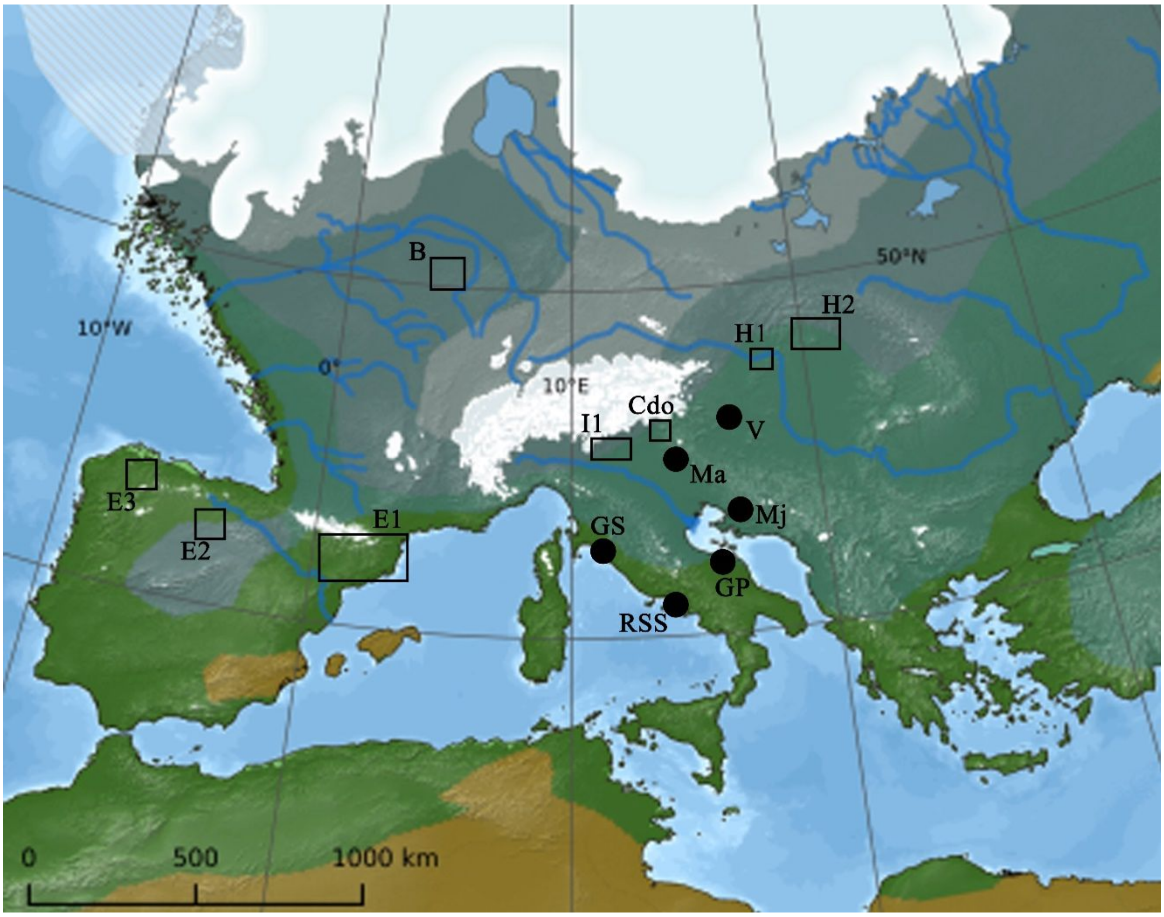


Figure 4.2.4. Geographic locations of MIS 3-2 sites, divided according to the a/L values. Circles: samples belonging to the southern group. Squares: samples belonging to the northern group. E1: Toll, Xaragalls, Teixoneres, Romaní, level O; E2: Portalon; E3: Cova Eirós. I1: Grotta Maggiore di San Bernardino, units III-II; Grotta Fumane; CdO: Caverna degli Orsi; RSS: Roccia San Sebastiano; GS: Grotta del Sambuco; GP: Grotta Paglicci. H1: Tokod; H2: Istállóskő. B: Scladina, Marie-Jeanne. V: Vindija; Ma: Marlera I; Mj: Mujina. Base map: Europe during the last Glaciation, modified from Becker *et al.* 2015.

	MIS 3-2 SW	MIS 3-2 N.I.	MIS 3-2 CB	MIS 3-2 B*	MIS 3-2 S.I.	MIS 3-2 HR
MIS 3-2- SW		0.07096	0.6696	0.1835	**0.0106**	**0.04646**
MIS 3-2 N.I.	0.07096		0.152	0.7893	**5.73E-05**	**0.001462**
MIS 3-2 CB	0.6696	0.152		0.3415	**0.009786**	**0.04893**
MIS 3-2 B*	0.1835	0.7893	0.3415		**0.008702**	**0.01272**
MIS 3-2 S.I.	**0.0106**	**5.73E-05**	**0.009786**	**0.008702**		0.9318
MIS 3-2 HR	**0.04646**	**0.001462**	**0.04893**	**0.01272**	0.9318	

Table 4.2.4. Results of the Kruskal-Wallis test ($H = 23.5$; $p = 0.0002714$) showing significant differences (bold) between the a/L values of *M. arvalis* southern Italian Peninsula (S.I.) and Croatia (HR) and those of the other *M. arvalis* populations of the same chronology, MIS 3-2. B: Belgium; CB: Carpathian Basin; N.I.: northern Italian Peninsula; SW: Southwestern Europe. *: one single site.

During MIS 3, the sea level in the Adriatic basin was between -30 and -70 m lower than it is today, and this marine regression reached its maximum during MIS 2, i.e. during the LGM, when the sea level dropped at -125 m. A large plain emerged, that at its maximum extended south down to the Pescara-Zadar line (Trincardi & Correggiari 2000; Surić & Juračić 2010; Anzidei *et al.* 2014, among others). These conditions might have favoured contacts between Italian and Croatian populations of *M. arvalis* and can explain the similarity between southern Italian and Croatian *M. arvalis*. On the other hand, although no clear geographic barriers are detectable, Croatian populations are significantly different from those of northern Italy and of the Carpathian Basin. Studies on present contact zones between different lineages of *M. arvalis* suggest that behavioural mechanisms such as female preferences in mate choice, can lead to partial reproductive isolation and enhance the process of divergence between groups (Beysard & Heckel 2014; Beysard *et al.* 2015). They also indicate that hybridization may be detrimental to one of the lineages, thus leading to further isolation. Landscape history might be another important factor: rocky environments, densely forested areas or extensive swamps are unsuitable habitats for *M. arvalis*, and these can be potential barriers not visible today that could have prevented contacts between neighbour populations.

4.2.5. Post Last Glacial Maximum divergence in Italian and SW Europe lineages

Studies on DNA and mitochondrial DNA of *Microtus arvalis* show the existence of six different lineages currently living in Europe: Western South, Western North, Central, Italian, Balkan, and Eastern (Fig. 4.2.5). The Eastern lineage probably originated from a cryptic refugium in the Carpathian Basin, while other three lineages originated in Mediterranean refugia: the Western South from Iberian Peninsula, the Italian from the Italian Peninsula and the Balkan from the Balkan Peninsula (Haynes *et al.* 2003; Fink *et al.* 2004; Heckel *et al.* 2005; Braaker & Heckel 2009; Bužan *et al.* 2010; Martinkova *et al.* 2013; Stojak *et al.* 2015, 2016). The separation between the lineages started during MIS 2, probably driven by the LGM, and by the inset of the Holocene all six group were already formed.

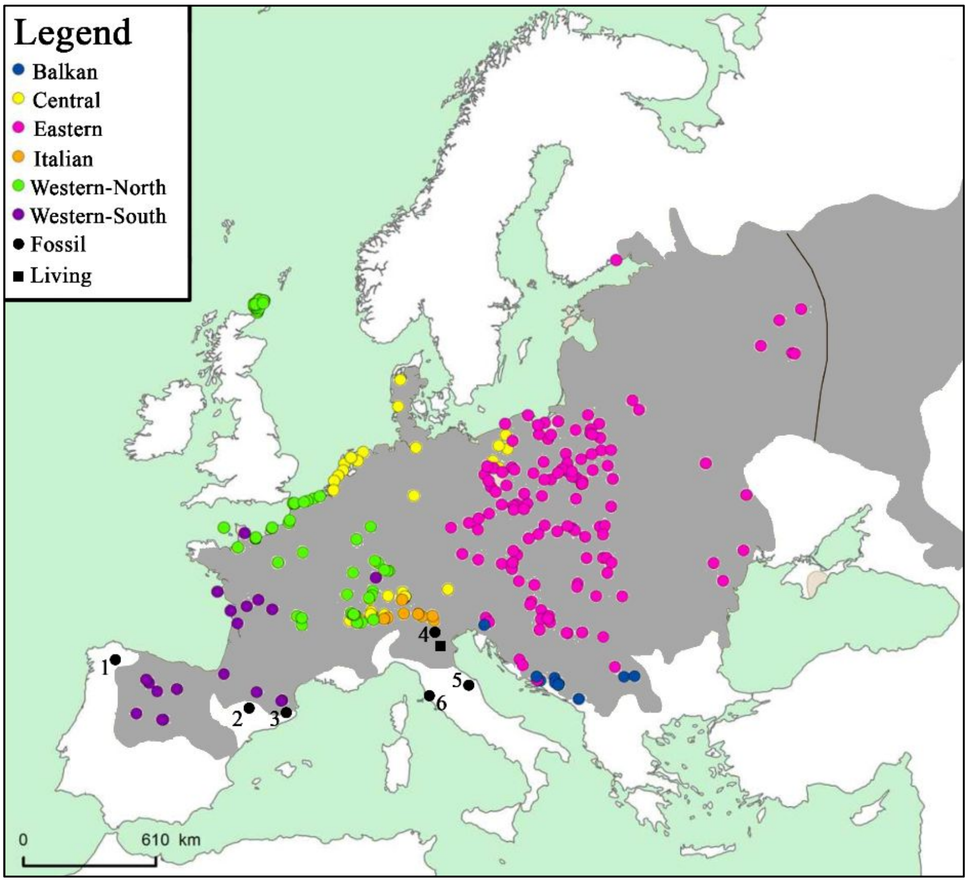


Figure 4.2.5. Distribution of the lineages of *M. arvalis*; in grey: current distribution of *M. arvalis*; black line: hybrid zone between *M. arvalis* and the eastern form *M. obscurus*. Modified from Stojak et al. 2016. Blue: Balkan; yellow: Central; pink: Eastern; orange: Italian; green: Western-North; purple: Western-South. Black: fossil populations dated to post-LGM analysed in this work. 1: Valdavara-1; 2: Colomera; 3: Arbreda; :4 Riparo Tagliente; 5: Grotta della Ferrovia; 6: Grotta del Sambuco. Black square: sample of living Italian population from the Po Plain.

We tried to discern in the fossil record traces of this pattern of divergence. Among the samples analysed for this thesis, five date to the post-LGM: Arbreda (level A), Valdavara-1 and Colomera, in Spain (López-García *et al.* 2010, 2011, 2014), and Riparo Tagliente, Grotta del Sambuco (US 5) and Grotta della Ferrovia in Italy (Bartolomei 1966; Calattini *et al.* 2016; Berto *et al.* 2017). Colomera, Valdavara-1, Grotta del Sambuco and Grotta della Ferrovia are located outside the current range of the geographic distribution of *M. arvalis* (IUCN 2017).

Grouping the samples by geographic area, and comparing the a/L values, it is possible to observe a significant difference between the Iberian and the Italian samples (table 4.2.5), as expected according to the phylogeographic studies.

	Post LGM-E	Post LGM-I	living I
Post LGM-E		**3.934E-06**	**8.314E-06**
Post LGM-I	**3.934E-06**		**0.02681**
living I	**8.314E-06**	**0.02681**	

Table 4.2.5. Results of the Kruskal-Wallis test (H = 32.72; p = 7.859E-8) showing significant differences (bold) between the a/L values of *M. arvalis* of Spain (E) and Italy (I) after the LGM, and between fossil and living Italian populations.

The suggested median age for the divergence of the Western South lineage is 23,442 years BP (37,340 – 12,114 years BP, 95% highest posterior density), while that of the Italian lineage is 12,484 years BP (19,869 – 6,123 years BP, 95% highest posterior density) (Stojak *et al.* 2015). Our data indicates that the two groups separation was completed and clearly visible in the a/L index at least at 15-14 ka. It is interesting to notice that the living population of *M. arvalis* from Italy differs completely from Iberian ones, but it also differs significantly from the Italian fossil populations, indicating that the evolutionary divergence is still on going.

4.3. The L_{agr}/L_{arv} as climatic indicator

In Chapter 2.4, the L_{agr}/L_{arv} index, that quantify the relative size variations of the two species, proved to be an excellent indicator in detecting shift in the climatic and environmental conditions of the Carpathian Basin during MIS 5. In Chapter 3, the index was applied in the context of the Adriatic area and of Belgium and the link between L_{agr}/L_{arv} values and level of general humidity was confirmed: higher values >100 indicates moist and wet environments; lower values <100 drier ones. Furthermore, values <100 seem to indicate a stronger Mediterranean influence in the Carpathian Basin (Chapter 2.4) and are typical of southern Italian Peninsula and of southern Adriatic regions, in both the eastern and western shores.

Therefore, we decided to apply the index to all the other samples analysed to try and confirm the connection between L_{agr}/L_{arv} values and environmental and climatic settings.

4.3.1. The Italian Peninsula

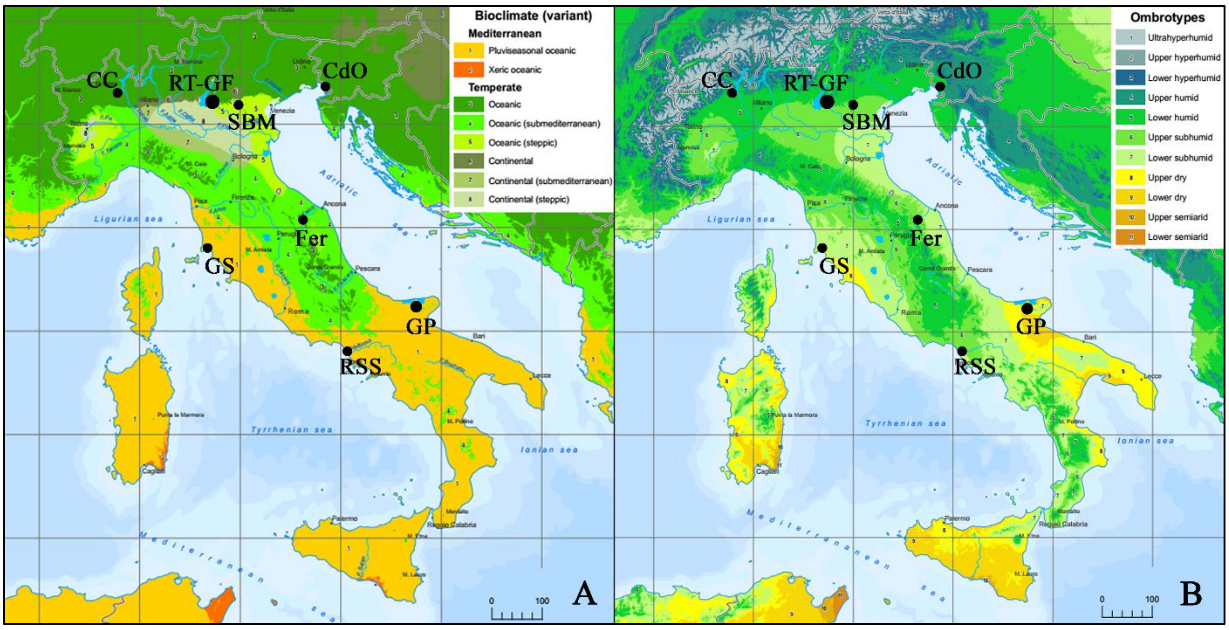


Figure 4.3.1. A. Bioclimatic map of the Italian Peninsula.; Mpo: Mediterranean pluviseasonal oceanic; Mexo: Mediterranean xeric oceanic; Toc: temperate oceanic; Tocsm: temperate oceanic submediterranean; Tocst: temperate oceanic steppic; Tco: temperate continental; Tcosm: temperate continental submediterranean; Tcost: temperate continental steppic. B. Ombrotypes of the Italian Peninsula. Modified from Pesaresi *et al.* (2014). CC: Ciota Ciara; SBM: Grotta Maggiore di San Bernardino; CdO: Caverna degli Orsi; GF: Grotta Fumane; RSS: Roccia San Sebastiano; Fer: Grotta della Ferrovia; GS: Grotta del Sambuco; RT: Riparo Tagliente; GP: Grotta Paglicci.

The Italian Peninsula presents a rich mosaic of climates in a relatively small territory: the south and western part of the Peninsula are strictly Mediterranean where the northern and eastern side are temperate and the Po Plain show continental traits (Fig.4.3.1A); the east-southern side tends to be more arid than the west-southern, the eastern-central to be more humid than the western-central, and the north-west to be slightly more humid than the north-east (Fig.4.3.1B) (Pesaresi *et al.* 2014).

As already noticed, sites from southern Italy, i.e. Roccia San Sebastiano e Grotta Paglicci, have values <100, while the other sites of northern Italy present values >100. The samples seem to follow the climatic pattern indicated by their geographic position and the current climatic conditions in the Italian Peninsula, with sites belonging to temperate-continental climate showing higher values, while those belonging to strictly Mediterranean climate present lower value, with the exception of the value from Riparo Tagliente, cuts 9-6 (Fig.4.3.2). The analysis of particular cases, such as that of Grotta Maggiore di San Bernardino, Grotta del Sambuco and Riparo Tagliente, that present variations of the index among different levels, might help to point out more subtle differences in the palaeoenvironmental conditions that characterized each site.

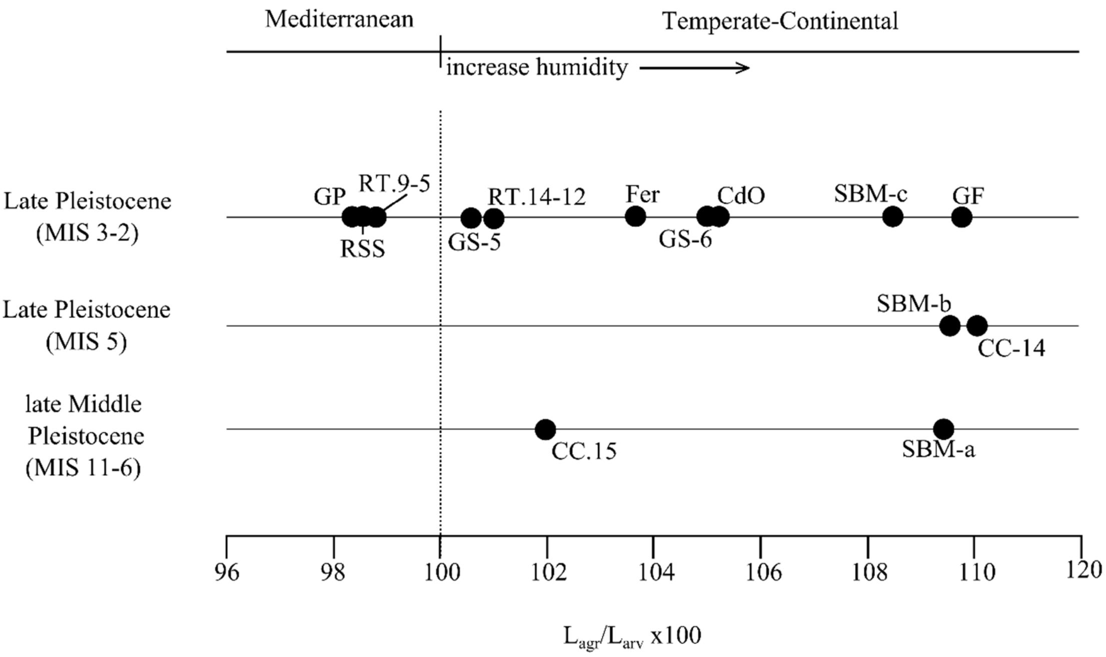


Figure 4.3.2. Values of the L_{agr}/L_{arv} index in the Italian Peninsula. CC-15: Ciota Ciara, unit 15; CC-14: Ciota Ciara, unit 14; SBM-a: Grotta Maggiore di San Bernardino, units VIII-VII; SBM-b: Grotta Maggiore di San Bernardino, units V-IV; SBM-c: Grotta Maggiore di San Bernardino, units III-II; CdO: Caverna degli Orsi; GF: Grotta Fumane; RSS: Roccia San Sebastiano; Fer: Grotta della Ferrovia; GS-6: Grotta del Sambuco, US 6; GS-5: Grotta del Sambuco, US 5 RT,9-6: Riparo Tagliente, cuts 9-6; RT,14-12: Riparo Tagliente, cuts 14-12; GP: Grotta Paglicci.

4.3.1.1. Grotta Maggiore di San Bernardino

The site of Grotta Maggiore di San Bernardino is located in north-eastern Italy (45°25' N, 11°33' E), at 135 m a.s.l., in the Berici Hills (Vicenza). It presents a discontinuous sequence dating from MIS 7 to MIS 3 (Picin *et al.* 2013; López-García *et al.* 2017c). In units VIII-VII, related to late Middle Pleistocene, the value of the L_{agr}/L_{arv} index is 109.67, while Mean Annual Precipitation (MAP) (calculated on the base of the small mammal assemblages, according to Hernández Fernández 2001; Hernández Fernández & Peláez-Campomanes 2005) reach 1,411 mm. While their L_{agr}/L_{arv} values are quite different, 109.71 for units V-IV and 108.53 for units III-II, MAP of the for MIS 5 and MIS 3 units of Grotta Maggiore di San Bernardino are very similar: 1,179 mm and 1,175 mm respectively. Therefore, it is possible to say that the index L_{agr}/L_{arv} is not linked directly to the amount of precipitation but is more likely to be connected to the general humidity of the environment, in particular to the distribution of precipitation through the year, the relative humidity of the air, the presence/absence of surface-water resources, such as stable rivers and streams, lake, pond, swampland, marsh or bog.

The difference in the L_{agr}/L_{arv} values between units V-IV (SBM-b, MIS 5) and units III-II (SBM-c, MIS 3) indicates that during MIS 5 the environment surrounding the site was more humid than during MIS 3 and it is possible to observe this difference in the small mammal assemblage. The *M. oeconomus* (Root Vole) occurs in units V-IV and its disappearance in units III-II coincides with the index decrease: coherently with the oscillations observed in the Carpathian Basin and in Croatian populations, the presence of the root vole is linked with wet environment and higher values of L_{agr}/L_{arv}. Also the presence of *Sicista betulina* (Northern Birch Mouse) at units V-IV and its absence in units III-II is consistent with a decrease in general humidity, since this species habitats include coniferous forests, mixed deciduous woodlands, bog forests, swampy meadows, moist clearings with bush coverture and fields bordering forests (Niethammer & Krapp 1982; Mitchell-Jones *et al.* 1999). The other site with the combined occurrence of *M. oeconomus* and *S. betulina* is Grotta Fumane (units D3+D6) which has the second highest value of L_{agr}/L_{arv} index in Late Pleistocene. Grotta Fumane is also located in north-eastern Italy, in the Veneto Pre-Alps (Monti Lessini, Verona), at 350 m a.s.l., 45° 35' N, 10° 54' E. Units D3+D6 of Grotta Fumane are dated at 38,895 – 37, 722 years cal BP (level D3ba) and represent a cold and humid oscillation of MIS 3 (López-García *et al.* 2015). MAP in this units reach 1,414 mm and are similar to those of SBM-a but higher than those of SBM-b. The L_{agr}/L_{arv} index for Fumane is 109.86, slightly higher than both SBM-a and SBM-b, confirming that the amount of precipitation is not the leading factor in determining the values of the index.

4.3.1.2. Grotta del Sambuco

Grotta del Sambuco (Massa Marittima, Grosseto) is located in central Italy, at a 20-km distance from the Tyrrhenian Sea, at 280 m ca. a.s.l., 43° 03' N 10° 53' E. Its current climatic attributions according to the Köppen–Geiger classification is Csa, temperate Mediterranean with hot and dry summer, while according to Pesaresi *et al.* (2014), it is a Mediterranean pluviseasonal-oceanic climate of subhumid type. Therefore, it should present L_{agr}/L_{arv} values typical of the Mediterranean regions with not uniformly distributed precipitation. Instead both Stratigraphic Units, US 6 and 5 present continental values (Table 4.3.1; Fig. 4.3.2). US 6 had been dated at 27,490 - 28,000 years cal BP, and its assemblage show a mosaic environment, dominated by open steppe but with diversified habitats, typical of the end of MIS 3 – beginning of MIS 2. The assemblage from US 5 is less diverse, indicating a monotonous environment dominated by open grassland and scarce forest coverture and it is probably related to the Late Glacial: in fact, the base of the superior US 4 had been dated at 16,704 – 16,161 years cal BP (Table 4.3.2). The value for US 6 is 105.05, for US 5 is 100.46, indicating more humid environmental conditions in US 6 than in US 5, but still in continental context.

Grotta del Sambuco					
Microtus arvalis - L					
	n	max	mean	min	SD
US 6	7	2.887	2.767	2.552	0.1
US 5	15	2.889	2.789	2.68	0.06
Microtus agrestis - L					
	n	max	mean	min	SD
US 6	10	3.108	2.907	2.715	0.12
US 5	11	2.715	2.802	2.596	0.12

Table 4.3.1. Total length (L) of the m1s of *Microtus arvalis* and *M. agrestis* from Grotta del Sambuco. n: number of specimens; max: maximum value; mean: mean value; min: minimum value; SD: standard deviation. Measurements are given in millimetres (mm).

Grotta del Sambuco		
	US5	US6
Erinaceus europaeus		x
Sorex minutus	x	x
Sorex ex gr *araneus*	x	x
Neomys anomalus		x
Arvicola amphibius	x	x
Chionomys nivalis		x
Clethrionomys glareolus	x	x
Microtus arvalis	xxx	xxx
Microtus agrestis	x	x
Microtus (*Terricola*) sp.	x	x
Microtus gregalis		x
Apodemus (*Sylvemus*) sp.	x	x
Sicista sp.		x
Eliomys quercinus		x

Table 4.3.2. Preliminary faunal list of the small mammals recovered at Grotta del Sambuco. x: present; xxx: dominant.

The presence in the small mammal assemblage of species like *Sicista* sp. and *Microtus gregalis* at US 6 indicate that the climatic and environmental changes that will lead to the Last Glacial Maximum (LGM) had shifted the climatic and environmental settings at Grotta del Sambuco toward less Mediterranean and more humid and continental conditions. Immediately after the LGM, conditions become more arid but still cool and continental. Palynological studies of sequence from Central Italy and from the nearby Accesa Lake suggest that full Late Glacial conditions, with reforestation and return of fully Mediterranean regimen does not occur before ca. 11 ka (Magri 1999; Magri *et al.* 1999; Magny *et al.* 2006; Drescher-Schneider *et al.* 2007), therefore confirming that continental conditions persist in the area during all MIS 2.

4.3.1.3. Riparo Tagliente

Riparo Tagliente is located in north-eastern Italy, on the left slope of Valpantena (Monti Lessini, Verona), at 226 m a.s.l. (45°32’ N, 10°59’ E). The site is composed by two deposits separated by river erosion: the lower one, with Mousterian and Aurignatian levels, has been related to MIS 4-3 (Arnaud *et al.* 2016), while the upper one, with Late Epigravettian level, has been dated to the end of MIS 2, at 17,219 to 13,472 years cal BP (Fontana *et al.* 2009).

Palaeontological, palynological and malacological analyses of the Late Epigravettian sequence indicate a series of climatic and environmental oscillations related to the latest part of the Older Dryas and the first half of the Bølling-Allerød Interstadial: cuts 18-13 correspond to an arid and cold phase; cuts 12-11 point to a transitional moments between stadial and interstadial while, starting from cut 10, temperate and more humid conditions are testified by the large mammal assemblage (Capuzzi & Sala 1980; Bartolomei *et al.* 1982). A recent study of the small mammal assemblage has reached the same chronological conclusions, but suggesting an increase in temperatures and a decrease in mean precipitation starting from cuts 11-10, and a relative stability of the open environments through the whole sequence (Berto *et al.* 2017).

After observing the oscillations of the L_{agr}/L_{arv} values provoked by the Eemian in Hungarian populations (Chapter 2.4), the sample from Riparo Tagliente was analysed again and divided into two samples: one related to the Late Glacial (cuts 14-13) and one related to the Bølling-Allerød Interstadial (cuts 9-5) (Table 4.3.3).

Riparo Tagliente					
Microtus arvalis - L					
	n	max	mean	min	SD
RT-14-13	17	3.027	2.724	2.484	0.16
RT-9-5	13	2.852	2.719	2.54	0.1
Microtus agrestis -L					
	n	max	mean	min	SD
RT-14-13	19	2.942	2.742	2.525	0.12
RT-9-5	11	2.94	2.694	2.529	0.11

Table 4.3.3. Total length (L) of the m1s of *Microtus arvalis* and *M. agrestis* from Riparo Tagliente. n: number of specimens; max: maximum value; mean: mean value; min: minimum value; SD: standard deviation. Measurements are given in millimetres (mm).

The objective was to find out if the same shift toward lower values of the L_{agr}/L_{arv} index would occur also in the context of northern Italy in correspondence to a major climatic improvement. The value of the L_{agr}/L_{arv} index for the lower cuts 14-12 is 100.84, while for the upper cuts 9-5 is 98.89. This shift in the values is similar to those occurring in the Carpathian Basin during the first phases of MIS 5. In both cases, a climatic oscillation toward more temperate and relatively drier conditions leads to lower values of the index. In the case of Riparo Tagliente, the inset of the Bølling-Allerød Interstadial causes the change in the balance between *Microtus arvalis* and *M. agrestis* that respond differently to the mutated climatic settings, the former becoming slightly larger to manage better the need for water in warmer and drier conditions, the latter reducing its size to adapt to the increasing aridity and diminished open humid environments.

The other two sites belonging to the Late Glacial in Italy are Grotta del Sambuco (US 5) and Grotta della Ferrovia (level E). Riparo Tagliente e Grotta del Sambuco present similar values (Chapter 4.3.1.2), while Grotta della Ferrovia has a higher value, 103.70. Grotta della Ferrovia is located in central Italy, on the Adriatic side of the Peninsula, 215 m a.s.l., 42° 26' N, 13° 00' E (Bartolomei 1966; Broglio *et al.* 2005). Level 3 of the sequence yielded a date of 11,700 ± 200 BP (14,003 – 13,140 years cal BP) (Sala 2007) The site is situated in the right slope of the "Gola della Rossa", a natural gorge excavated by the river Esino. The close proximity to the river and the consequent constant humidity and availability of water might explain the difference in the L_{agr}/L_{arv} values between this site and the other two. Furthermore, it is interesting to notice that *Sicista betulina* is present at Grotta della Ferrovia (Bartolomei 1966), but does not occur at cuts 14-12 of Riparo Tagliente or US 5 of Grotta del Sambuco.

4.3.2 The Southwestern Europe

The Iberian Peninsula is currently characterized by Mediterranean and temperate climate (Fig.4.3.3 A), with distribution of precipitation changing remarkably from North to South and from West to East (Fig.4.3.3 B). In particular Galicia, located in the north-western side of the Peninsula, tends to be hyperhumid or humid, due to the strong influence of the Atlantic Ocean; Catalonia, located in the north-eastern side, tends to be dry or subhumid, due to the stronger seasonality in the distribution of the precipitation and to the influence of the Mediterranean Sea (AEMET 2011; Rivas-Martínez *et al.* 2011). In this peculiar geographic and climatic context, we decided to analyse the different sites in relation with their geographic locations. The oscillations in the L_{agr}/L_{arv} index indicate the presence of more or less humid environmental conditions (Fig. 4.3.4), accordingly to what observed in the Carpathian Basin, Belgium, Croatia, and the Italian Peninsula (Chapters 2.4, 3 and 4.3.1).

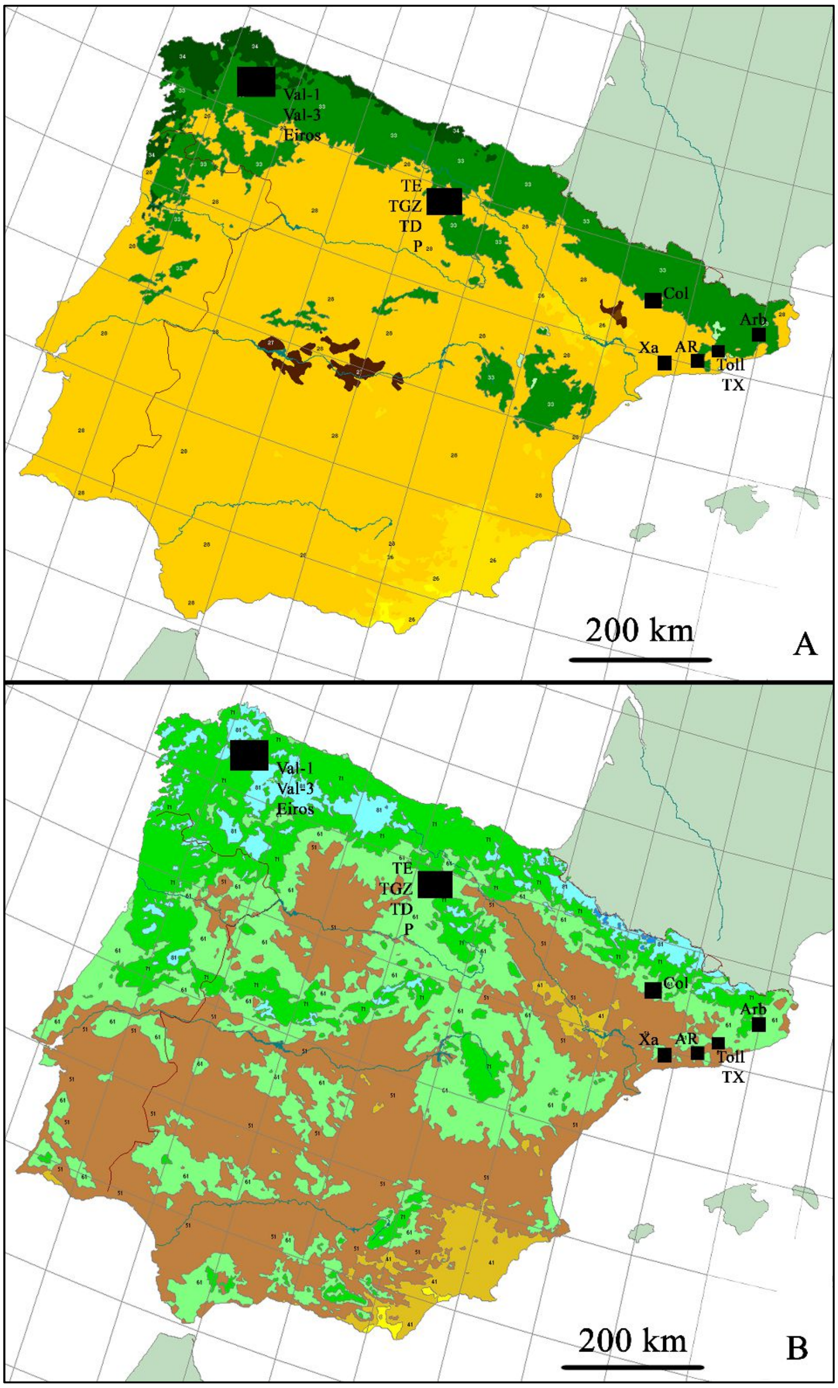


Figure 4.3.3. A. Bioclimatic map of the Iberian Peninsula. Light blue: temperate xeric; dark green: temperate hyperoceanic; green: temperate oceanic; dark yellow: Mediterranean pluviseasonal oceanic; light yellow: Mediterranean xeric oceanic; dark brown: Mediterranean pluviseasonal continental. B. Ombrotypes of the Iberian Peninsula. Light brown: semiarid; brown: dry; light green: subhumid; green: humid; blue: hyperhumid. Modified from Rivas-Martínez *et al.* (2011). TE: Trinchera Elefante; TGZ: Galeria-Zarpazos; TD: Trinchera Dolina. level 10.2; P: Portalón; Val-3: Valdavara-3; Val-1: Valdavara-1; XA: Xaragalls; TX: Teixoneres; AR: Romaní; Arb: Arbreda; Col: Colomera.

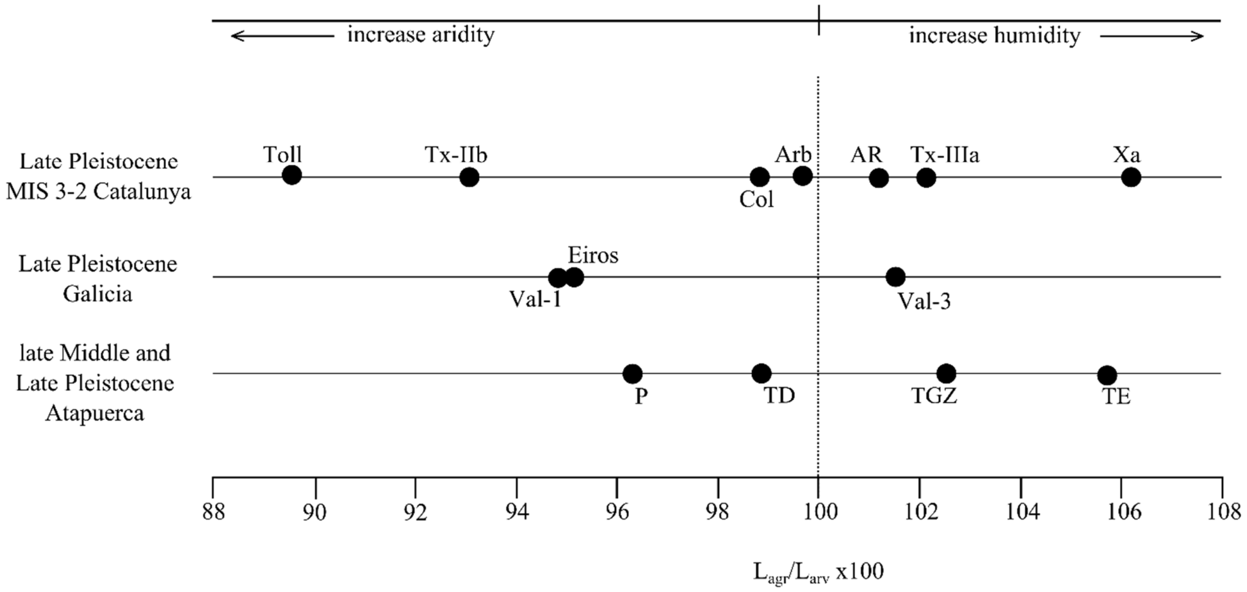


Figure 4.3.4. Values of the L_{agr}/L_{arv} index in SW Europe. TE: Trinchera Elefante; TGZ: Galeria-Zarpazos; TD: Trinchera Dolina. level 10.2; P: Portalón; Val-3: Valdavara-3; Val-1: Valdavara-1; XA: Xaragalls; TX-IIIa: Teixoneres. level IIIa; TX-IIb: Teixoneres. level IIb; AR: Romaní; Arb: Arbreda; Col: Colomera.

4.3.2.1. Mediterranean vs Atlantic climatic influence during late Middle and Late Pleistocene as reflected by the L_{agr}/L_{arv} index in the Sierra of Atapuerca

The majority of the samples from late Middle Pleistocene in south-western Europe come from the Sierra of Atapuerca (Buros, Spain). Sima del Elefante (TE), Trinchera Dolina (TD) and Galeria-Zarpazos (TGZ) are part of a karst complex located in the Bureba corridor, which connects the Ebro basin, subjected to the Mediterranean climatic influence, and the Duero basin, subject to the Atlantic climatic influence. Therefore, this area is particularly important to observe the interaction between the two different climatic realms, to understand the dynamics of the environmental changes in this transitional and migration zone (Montserrat 1991; Rosas González 1999; Cuenca-Bescós *et al.* 2005, among others). The L_{agr}/L_{arv} index indicates that at TE and TGZ environmental conditions were generally more humid than at TD. At TE and TGZ the dominant habitat is open humid, 40% and 50 % respectively, always in the presence of predominant Mediterranean conditions (Galindo-Pellicena *et al.* 2011; López-García *et al.* 2011b). On the other hand, at level 10 of TD open dry grasslands are the most represented habitat (Cuenca-Bescós *et al.* 2005). It is possible that the assemblages of TE and TGZ reflect two chronological moment in which the Atlantic climatic influence on Sierra of Atapuerca was stronger and provided the region with well distributed annual precipitation.

The other site from the Sierra of Atapuerca analysed here is Portalón: levels P9-P10 present the maximum peak of the sequence in the arboreal pollen and in micro-vertebrates associated with woodland and a high percentage of thermophilus and aquatic taxa, with MAP at 244 mm (López-García *et al.* 2010). The L_{agr}/L_{arv} index of P9-10 is 96.31. The occurrence of *Iberomys cabrerae* indicates that the Mediterranean influence was strong in the area and, contrary to what observed in Carpathian and Italian samples (Chapters 2.4; 4.3.1), the occurrence of *M. oeconomus* is not matched by value >100, even though the value of Portalón is the higher for the MIS 3-2 chronology, except for Colomera and Arbreda, two sites dated to the end of Late Pleistocene – beginning of Holocene and located in Catalonia (north-eastern Spain). In the small mammal record of Portalón, (López-García *et al.* 2010).

4.3.2.2. Late Pleistocene oscillations of the L_{agr}/L_{arv} index in Galicia

The values of Galicia sites reflect the general differences between MIS 5 and MIS 3-2, the former being warmer and more humid, the latter being colder and drier, with sudden and abrupt climatic changes, although in this region the Oceanic influence was always strong and the general level of humidity higher than in the rest of northern Iberian Peninsula (Gómez-Orellana *et al.* 2007, 2013). It is possible to observe that the sample from Valdavara-3, dated to MIS 5, does not present Mediterranean value, indicating that the Oceanic influence was indeed very strong and that humid environments were dominant, as also suggested by the studies of the small vertebrate assemblage (comm. pers. López-García). On the other hand, the values for Valdavara-1 and Cova Eirós (MIS 3-2) are very similar and < 100, indicating more arid conditions that at Valdavara-3, but still with dominant open humid habitats (López-García *et al.* 2011a; Rey-Rodríguez *et al.* 2016). The occurrence of *Iberomys cabrerae* at Valdavara-1 signalled a moment with a stronger Mediterranean influence, while the occurrence of *M. oeconomus* at Cova Eirós is not manifested in the L_{agr}/L_{arv} index, in agreement to what observed at Portalón.

4.3.2.3. Oscillation of the L_{agr}/L_{arv} values in Catalonia during MIS 3-2

The L_{agr}/L_{arv} index of Toll, Teixoneres-IIb, Colomera, and Arbreda present values below 100, indicating that temperate-Mediterranean climatic influence was dominant in this context even during MIS 3 and MIS 2. The sample from Toll cave, with a value lower than 90, represents an extreme and it is linked to the chronology of level 3 related to the LGM or to a phase immediately following it (see Chapter 2.2). The environmental conditions, according to the L_{agr}/L_{arv} index, were probably very arid and precipitation extremely reduced.

On the other hand, level IIIa of Teixoneres, level O of Romaní and layers C4-6 of Xaragalls present values above 100. All three sites are located in the Catalan Pre-Coastal Range: Teixoneres at 900 m a.s.l., Romaní at 265 m a.s.l. and Xaragalls at 590 m a.s.l. All three sites belong to the beginning of MIS 3: the top of unit III at Teixoneres has been dated at 46,660 – 44,810 years cal BP (Talamo *et al.* 2016); level O of Romaní was tentatively assigned to the Greenland Stadial 17 and it is dated ca. 56,291 years (Burjachs *et al.* 2012); layers C4 of Xaragalls yielded a date of 45,120 – 48,240 years cal BP (López-García *et al.* 2012). All three sites present Mean Annual Precipitation higher than today (+322 mm for Teixoneres, +350 mm for Romaní, and +200 mm for Xaragalls) and Mean Annual Temperature lower than current (-5.3°C per Teixoneres, -7.5°C per Romaní, and -5°C per Xaragalls).

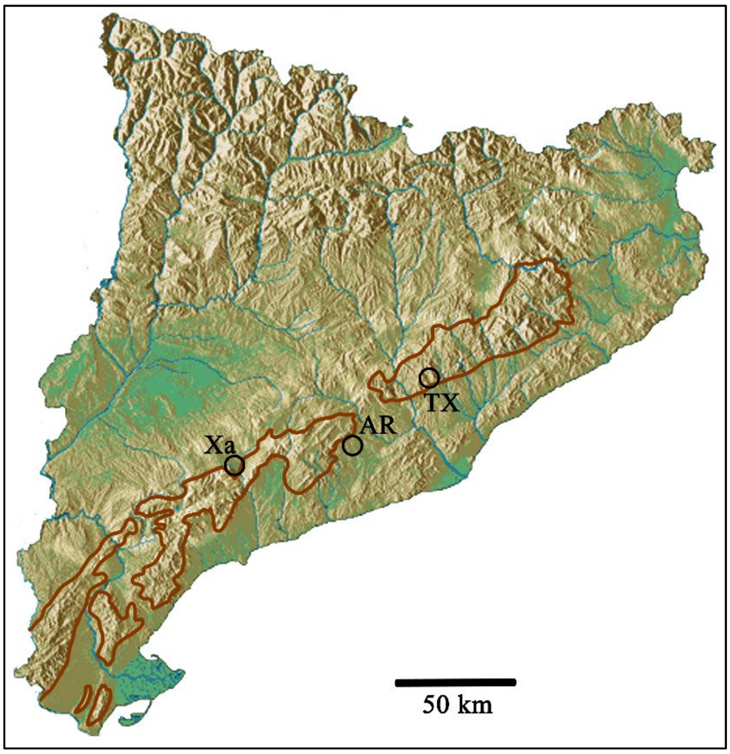


Figure 4.3.5. Physical map of Catalonia with the geographic location of the sites dated to the beginning of MIS 3 and presenting L_{agr}/L_{arv} index >100. TX: Teixoneres; AR: Romaní; XA: Xaragalls. In brown: Catalan Pre-Coastal Range.

In chapter 2.2, the morphological and morphometric variations in the m1s of *M. agrestis* from Teixoneres-IIIa, i.e. the appearance of more complex morphotypes and the increase in size, were related to small-scale regional movements of populations triggered by an increase of available and suitable habitat due to the higher humidity detected in that layer with respect to layer IIb: local displacements along rivers and streams, more connections between the coastal and the central part of the region and between populations living at different altitude. This might be a possible explanation for the higher values of Xaragalls and Romaní, since these two sites are also located in key-points of passage and intersection among different geographic areas (Fig. 4.3.5). Another viable hypothesis might be that, in Catalonia, the environmental conditions tends to become drier in time during MIS 3 and MIS 2, with an increase in general humidity after the LGM. Xaragalls dates are similar to that of Teixoneres-IIIa, therefore the values of L_{agr}/L_{arv} index >100 might indeed indicate that at the beginning of MIS 3 the general humidity of the area was higher than in the following part of MIS 3. The date for level O of Romaní seems to confirm it, since it is older than the other two. Teixoneres-IIb and Toll presents lower values, while at Colomera and Arbreda, the values are close to 100, indicating a return to more humid conditions. More samples will be needed in order to test this last hypothesis.

5. GENERAL CONCLUSIONS

The study of the morphological and morphometric variations of *Microtus arvalis* and *M. agrestis* during late Middle and Late Pleistocene allow us to draw the following conclusions:

1 - the index La/Li that quantify the degree of asymmetry between the labial and the lingual side of the first lower molar (m1), combined with the total length (L) of the tooth proved to have a **high taxonomic value** also in the context of Mediterranean regions and allows to identify and separate specimens of *M. arvalis* and *M. agrestis*;

2 - a/L index, that quantifies the relative elongations of the anteroconid complex (ACC) to the total length of the m1 proved to be a useful tool:

> - to **refine the chronological attributions** of palaeontological and archaeological sites of the Mediterranean region (i.e. Spain and Italy) based on the mean values obtain for *M. agrestis* populations;
>
> - to **identify divergent lineages**, as in the case of *M. arvalis* of MIS 3-2 from southern/northern Europe, of MIS 3-2 from southern/northern Italy and of western-south/Italian living lineages;
>
> - to **detect immigration events** and **displacement of populations**, i.e. at Riparo Tagliente (Italy), at Teixoneres (Spain) and possibly at Süttő 6 (Hungary)

3 - during late Middle Pleistocene, two morphotypes of *M. agrestis* existed, one typical of Mediterranean areas (i.e. Spain, southern France and Italy) **the *jansoni*-type**, and one typical of Central Europe (i.e. Hungary, Slovakia and Romania**) the *coronensis*-type**. However, the two morphotypes does not differ morphometrically from each other (to separate the samples of *M. agrestis* belonging to Marine Isotope Stage (MIS) 11-10 from the samples of MIS 9-6, regardless their geographic provenance) it was possible or from *M. agrestis* from other chronologies and present the exsul-loop in the second upper molar (M2) typical of the field vole, therefore they **cannot be treated as separate species from *M. agrestis***;

4 - comparing our data with the data available from phylogenetic studies, it is possible to recognize in the fossil record of Cova Eirós (Galicia, Spain) **early signs of speciation**: the population of *M. agrestis* shows a/L values that are significantly different from those of all the other populations of MIS 3-2 and very typical morphological traits (high asymmetry and relatively simple ACC);

5 - The relative stability of the a/L index in both *M. arvalis* and *M. agrestis* from the Carpathian Basin during the Late Pleistocene might represent another proof of the protection offered by this **refugial area** to both species.

6 - Furthermore, we propose the use of a new index, $\mathbf{L_{agr}/L_{arv}}$, to quantify the variations in size of *M. agrestis* and *M. arvalis* in relation to each other. This index proved to be an excellent **indicator of the general humidity** level that characterized environmental conditions in the surrounding of a given site. In particular, it was possible to:

- detect differences between strictly Mediterranean (index values < 100) and temperate/continental areas (index values > 100) of Italy and Croatia;

- detect oscillations in humidity through the sequence of the sites of Grotta Maggiore di San Bernardino (Italy), Grotta del Sambuco (Italy), Teixoneres (Spain), Tokod (Hungary), in accordance with the changes in percentage and composition of the small mammal assemblage and with previous palaeoenvironmental reconstructions;

- detect fluctuations in the Atlantic vs Mediterranean climatic influence in the areas of Sierra of Atapuerca, in accordance with previous palaeoenvironmental reconstructions;

- detect shift in general environmental humidity reflecting the general differences between MIS 5 (more humid), MIS 3-2 (increasing in aridity until the end of LGM) and the very end of MIS 2 (return of humidity) in the Iberian Peninsula and Belgium;

- detect the shift in environmental conditions (toward Mediterranean values) brought by major climatic ameliorations after the Eemian (beginning of MIS 5) in the Carpathian Basin and during the Interstadial Bølling/Allerød (end MIS 2) at Riparo Tagliente.

6. FUTURE PERSPECTIVES

This PhD thesis offers a staring point for the study of intra- and inter-specific variations in morphology and morphometrics of fossil populations of *Microtus arvalis* and *Microtus agrestis*.
To further investigate the subject, we propose some short- and long-term objectives.

Short-term:

- study of the long sequences already available, i.e. Arbreda, Portalón, Paglicci and Fumane;
- application of geometric morphometric methods of analysis to the samples already available.

Long-term:

- expand the samples of fossil populations of *M. arvalis* and *M. agrestis* from southern Europe;
- expand the samples collecting material from different geographic areas;
- extend the study to other *Microtus* species to try and find broader interspecific correlations;
- obtain further phylogenetics data to compare with those obtain with palaeontological studies.

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APPENDIX 1

It presents a list of all the sites of Middle and Late Pleistocene where *Microtus arvalis* and *Microtus agrestis* occur and the complete tables with the measurements and indices of the two species.

Site	coordinates	m a.s.l.	age	climate	P (mm)	T (°C)
Trinchera Dolina - layer 10.2	42°33'06" N 3°53'55" W	1080	MIS 11-10	Cfb	575	10.5
Trinchera Galería-Zarpazos	42°33'06" N 3°53'55" W	1080	MIS 11-10	Cfb	575	10.5
Sima Elefante - layers 18-19	42°33'06" N 3°53'55" W	1080	MIS 9-6	Cfb	575	10.5
Grotte de la Carrière	42° 33'94" N 2° 22'77" E	540	MIS 9-6	Cfb	810	12.5
Mollet Cave	42°09'47" N 2°44'52" E	200	MIS 7	Cfa	733	14.8
Valdavara-3	43°01'00" N 7°33'00" W	600	MIS 5	Csb	941	11.6
Teixoneres	41°48'47" N 2°05'50" E	900	MIS 3	Cfb	749	12.3
Xaragalls	41°23'02" N 1°02'56" E	590	MIS 3	Cfa	596	13.6
Eirós	42°46'3" N 7°12'13" W	780	MIS 3	Csb	978	11.3
Romanì - level O	41°32’ N 1°41’30’’ E	265	MIS 3	Cfa	619	14.8
Portalón	42°33'06" N 3°53'55" W	1080	MIS 3-2	Cfb	575	10.5
Arbreda (levels tr-a)	42°09'38" N 2°44'49" E	211	end MIS2	Cfa	733	14.8
Valdavara-1	43°01'00" N 7°33'00" W	600	end MIS2	Csb	941	11.6
Toll	41°48'25" N 2°09'02" E	760	end MIS2	Cfb	749	12.3
Colomera	42°08'01" N 0°76'40" E	670	end MIS2	Cfb	801	10.4

List of *M. arvalis* and *M. agrestis* sites from southwestern Europe, with coordinates, altitude (m a.s.l.), age, Köppen climatic classification, current Mean Annual Temperature (MAT) and current mean annual precipitation (MAP).

Trinchera Dolina - TD10.2

	Microtus agrestis					*Microtus arvalis*				
	n	min	mean	max	SD	n	min	mean	max	SD
L	29	2.468	2.782	3.063	0.13	30	2.366	2.811	3.16	0.16
a	29	1.299	1.457	1.649	0.08	30	1.266	1.531	1.735	0.11
W	29	0.935	0.999	1.088	0.04	30	0.83	0.962	1.091	0.06
e	29	0.725	0.797	0.884	0.04	30	0.692	0.812	0.932	0.06
d	29	0.048	0.245	0.317	0.05	30	0.046	0.196	0.329	0.05
La	29	0.286	0.355	0.419	0.03	30	0.314	0.414	0.497	0.04
Li	29	0.603	0.657	0.735	0.03	30	0.481	0.558	0.619	0.03
a/L x100	29	50.03	52.4	54.89	1.39	30	47.15	54.43	57.58	1.78
La/Li x100	29	44.52	54.2	65.52	6.29	30	59.09	74.33	86.67	6.52

Trinchera Galeria-Zarpazos

	Microtus agrestis					*Microtus arvalis*				
	n	min	mean	max	SD	n	min	mean	max	SD
L	24	2.663	2.933	3.182	0.14	24	2.508	2.86	3.211	0.15
a	24	1.331	1.512	1.72	0.1	24	1.316	1.546	1.725	0.09
W	24	0.864	1.023	1.162	0.06	24	0.888	0.973	1.149	0.05
e	24	0.683	0.816	0.93	0.06	24	0.684	0.81	0.967	0.05
d	24	0.209	0.278	0.36	0.04	24	0.026	0.202	0.317	0.06
La	24	0.283	0.359	0.442	0.04	24	0.343	0.436	0.517	0.03
Li	24	0.58	0.68	0.756	0.04	24	0.504	0.549	0.622	0.03
a/L x100	24	48.46	51.53	55.37	1.67	24	52.45	54.07	55.64	0.98
La/Li x100	24	41.81	52.99	64.82	6.65	24	60.07	79.47	92.29	6.7

Sima Elefante - TE18-19

	Microtus agrestis					*Microtus arvalis*				
	n	min	mean	max	SD	n	min	mean	max	SD
L	4	2.82	2.903	3.049	0.1	5	2.11	2.743	2.823	0.08
a	4	1.484	1.565	1.691	0.08	4	1.484	1.545	1.6	0.06
W	5	0.974	1.031	1.079	0.03	6	0.87	0.953	0.998	0.04
e	4	0.789	0.83	0.863	0.03	6	0.706	0.787	0.846	0.05
d	4	0.206	0.247	0.289	0.04	6	0.19	0.239	0.278	0.03
La	5	0.354	0.374	0.403	0.01	7	0.348	0.404	0.431	0.02
Li	5	0.608	0.664	0.707	0.03	7	0.531	0.558	0.607	0.02
a/L x100	4	51.85	53.9	55.46	1.79	4	54	56.7	58.6	1.96
La/Li x100	5	51.48	56.57	61.9	4.93	7	65	72.24	78.34	5.29

Grotte de la Carrière

	Microtus agrestis					*Microtus arvalis*				
	n	min	mean	max	SD	n	min	mean	max	SD
L	13	2.652	2.788	2.939	0.09	1	-	2.832	-	-
a	13	1.412	1.502	1.598	0.05	1	-	1.522	-	-
W	13	0.892	0.977	1.067	0.05	1	-	1.022	-	-
e	11	0.725	0.782	0.856	0.04	1	-	0.85	-	-
d	10	0.219	0.301	0.419	0.05	1	-	0.307	-	-
La	13	0.311	0.353	0.416	0.02	1	-	0.428	-	-
Li	13	0.592	0.631	0.666	0.02	1	-	0.611	-	-
a/L x100	13	51.82	53.87	55.02	0.92	1	-	54.8	-	-
La/Li x100	13	51.06	56.04	63.6	3.83	1	-	70.04	-	-

Mollet Cave

	Microtus agrestis				
	n	min	mean	max	SD
L	2	2.595	2.764	2.934	-
a	4	1.373	1.475	1.608	0.09
W	4	0.974	1.031	1.051	0.03
e	4	0.809	0.847	0.882	0.02
d	4	0.215	0.207	0.298	0.03
La	4	0.289	0.333	0.368	0.03
Li	4	0.66	0.696	0.745	0.03
a/L x100	2	52.9	53.35	54.8	-
La/Li x100	4	43.35	50.85	52.74	5.08

Valdavara-3

	Microtus agrestis					*Microtus arvalis*				
	n	min	mean	max	SD	n	min	mean	max	SD
L	7	2.814	2.85	2.981	0.07	5	2.579	2.81	3.144	0.22
a	7	1.456	1.51	1.643	0.07	5	1.405	1.516	1.71	0.12
W	11	0.929	1.017	1.112	0.05	6	0.855	0.909	0.966	0.04
e	12	0.748	0.808	0.877	0.04	5	0.696	0.785	0.838	0.05
d	12	0.145	0.236	0.323	0.04	6	0.176	0.272	0.401	0.08
La	11	0.269	0.346	0.398	0.03	5	0.362	0.389	0.411	0.18
Li	11	0.607	0.667	0.778	0.05	5	0.509	0.555	0.598	0.04
a/L x100	7	52.03	53	55.11	1.1	5	53.11	53.9	54.47	0.66
La/Li x100	11	34.57	52.44	64.71	7.52	5	63.87	70.53	78.82	6.07

Teixoneres

			Microtus agrestis					*Microtus arvalis*		
	n	min	mean	max	SD	n	min	mean	max	SD
L	30	2.369	2.713	3.053	0.14	30	2.494	2.778	3.125	0.17
a	30	1.225	1.456	1.635	0.08	30	1.3	1.496	1.725	0.11
W	30	0.851	0.945	1.117	0.05	30	0.876	0.963	1.07	0.04
e	30	0.656	0.784	0.916	0.06	30	0.64	0.772	0.925	0.05
d	30	0.137	0.227	0.404	0.05	30	0.145	0.232	0.368	0.05
La	30	0.278	0.359	0.408	0.02	30	0.349	0.395	0.474	0.02
Li	30	0.516	0.592	0.74	0.04	30	0.474	0.57	0.626	0.02
a/L x100	30	50.61	54.16	56.94	1.53	30	51.03	53.2	57.17	2.07
La/Li x100	30	37.56	61.13	69.81	6.83	30	61.53	69.31	80.59	3.99

Xaragalls

			Microtus agrestis					*Microtus arvalis*		
	n	min	mean	max	SD	n	min	mean	max	SD
L	8	2.688	2.979	3.185	0.18	9	2.598	2.803	2.926	0.1
a	10	1.471	1.609	1.787	0.1	12	1.395	1.531	1.73	0.08
W	8	0.878	1.007	1.089	0.07	7	0.862	0.937	0.985	0.04
e	11	0.739	0.853	0.961	0.07	12	0.733	0.787	0.868	0.04
d	10	0.212	0.262	0.3	0.03	12	0.049	0.193	0.349	0.08
La	9	0.343	0.4	0.457	0.03	7	0.343	0.388	0.414	0.02
Li	9	0.544	0.627	0.684	0.04	9	0.532	0.574	0.605	0.02
a/L x100	8	50.36	54	56.19	1.85	9	51.67	53.53	54.86	0.97
La/Li x100	8	60.33	63.59	67.8	2.66	7	56.78	67.15	73.35	5.44

Romanì – level O

			Microtus agrestis					*Microtus arvalis*		
	n	min	mean	max	SD	n	min	mean	max	SD
L	4	2.587	2.895	3.01	0.2	12	2.598	2.865	3.044	0.15
a	4	1.342	1.575	1.737	0.16	12	1.409	1.597	1.749	0.11
W	4	0.914	1.019	1.09	0.08	12	0.893	1.02	1.099	0.06
e	4	0.738	0.844	0.901	0.07	12	0.764	0.857	0.94	0.04
d	4	0.03	0.138	0.289	0.11	12	0.041	0.175	0.3	0.09
La	4	0.362	0.41	0.442	0.03	12	0.364	0.434	0.474	0.03
Li	4	0.564	0.626	0.682	0.05	12	0.519	0.595	0.657	0.03
a/L x100	4	51.87	54.32	57.7	2.44	12	53.12	55.69	57.81	1.53
La/Li x100	4	62.6	65.46	67.58	0.247	12	64.35	73.13	80.2	3.97

Portalón

	Microtus agrestis					*Microtus arvalis*				
	n	min	mean	max	SD	n	min	mean	max	SD
L	30	2.424	2.845	3.262	0.2	30	2.618	2.954	3.259	0.19
a	30	1.287	1.549	1.815	0.13	30	1.085	1.59	1.815	0.15
W	30	0.902	0.996	1.108	0.05	30	0.935	1.04	1.187	0.06
e	30	0.758	0.847	0.953	0.05	30	0.76	0.883	1.02	0.05
d	30	0.192	0.268	0.389	0.05	30	0.129	0.253	0.411	0.06
La	30	0.337	0.387	0.44	0.03	30	0.389	0.452	0.553	0.03
Li	30	0.555	0.617	0.687	0.03	30	0.539	0.6	0.677	0.03
a/L x100	30	51.08	54.44	62.01	1.96	30	33.39	53.85	57.04	4.02
La/Li x100	30	54.18	62.85	69.29	3.64	30	67.72	75.21	91.62	5.48

Eirós

	Microtus agrestis					*Microtus arvalis*				
	n	min	mean	max	SD	n	min	mean	max	SD
L	8	2.658	2.944	3.182	0.18	10	2.766	3.09	3.499	0.23
a	8	1.343	1.511	1.699	0.14	10	1.509	1.673	1.891	0.13
W	8	0.972	1.062	1.131	0.05	10	0.978	1.082	1.194	0.06
e	8	0.697	0.844	0.931	0.07	10	0.761	0.897	0.979	0.06
d	8	0.21	0.262	0.286	0.02	10	0.145	0.255	0.349	0.06
La	8	0.321	0.38	0.5	0.04	10	0.434	0.624	0.537	0.03
Li	8	0.63	0.684	0.746	0.04	10	0.567	0.475	0.706	0.04
a/L x100	8	44.9	51.26	53.39	2.91	10	51.99	54.12	56.38	1.4
La/Li x100	8	45.59	56.06	71.93	9.21	10	67.17	76.3	83.35	4.81

Valdavara-1

	Microtus agrestis					*Microtus arvalis*				
	n	min	mean	max	SD	n	min	mean	max	SD
L	2	2.842	2.844	2.846	-	13	2.748	3.001	3.28	0.16
a	2	1.55	1.559	1.563	-	14	1.407	1.637	1.866	0.11
W	2	0.997	1.006	1.015	-	12	0.965	1.05	1.089	0.04
e	2	0.868	0.881	0.895	-	14	0.784	0.837	0.908	0.04
d	2	0.233	0.242	0.251	-	14	0.167	0.216	0.251	0.03
La	2	0.388	0.346	0.354	-	12	0.377	0.419	0.468	0.02
Li	2	0.646	0.668	0.691	-	13	0.545	0.611	0.686	0.03
a/L x100	2	54.71	54.81	54.91	-	13	51.2	54.74	56.9	1.68
La/Li x100	2	48.91	51.85	54.79	-	12	59.91	68.74	78.16	5.78

Arbreda

	Microtus agrestis					*Microtus arvalis*				
	n	min	mean	max	SD	n	min	mean	max	SD
L	30	2.586	2.905	3.22	0.19	30	2.639	2.912	3.336	0.18
a	30	1.357	1.604	1.868	0.13	30	1.423	1.61	1.925	0.13
W	30	0.934	1.009	1.172	0.06	30	0.9	1.014	1.169	0.05
e	30	0.759	0.861	0.972	0.05	30	0.763	0.848	0.961	0.04
d	30	0.125	0.224	0.341	0.05	30	0.12	0.239	0.361	0.05
La	30	0.339	0.391	0.466	0.03	30	0.387	0.432	0.502	0.03
Li	30	0.566	0.629	0.706	0.04	30	0.525	0.6	0.698	0.02
a/L x100	30	50.21	55.17	58.37	2.05	30	52.65	55.24	57.74	1.42
La/Li x100	30	51.01	62.35	67.92	4.05	30	65.37	72.13	83.73	4.56

Toll

	Microtus agrestis					*Microtus arvalis*				
	n	min	mean	max	SD	n	min	mean	max	SD
L	3	2.403	2.504	2.582	0.09	13	2.664	2.795	3.009	0.13
a	5	1.254	1.336	1.38	0.05	14	1.325	1.512	1.748	0.12
W	7	0.854	0.92	0.992	0.08	10	0.91	0.948	0.997	0.03
e	7	0.68	0.792	0.876	0.06	12	0.764	0.799	0.845	0.02
d	7	0.093	0.18	0.268	0.05	13	0.15	0.247	0.463	0.08
La	7	0.272	0.33	0.385	0.04	10	0.356	0.39	0.427	0.02
Li	7	0.541	0.6	0.656	0.04	10	0.539	0.563	0.6	0.01
a/L x100	3	52.45	53.61	53.44	1.13	13	45.43	53.48	57.23	3.51
La/Li x100	7	50.27	54.95	64.18	5.12	10	64.74	70.18	77.36	4.14

Colomera

	Microtus agrestis					*Microtus arvalis*				
	n	min	mean	max	SD	n	min	mean	max	SD
L	10	2.603	2.974	3.234	0.21	30	2.602	3.016	3.629	0.2
a	10	1.377	1.598	1.722	0.11	30	1.422	1.647	2.005	0.11
W	10	0.965	1.031	1.087	0.03	30	0.904	1.048	1.164	0.05
e	10	0.811	0.881	0.928	0.03	30	0.76	0.883	1.02	0.05
d	10	0.16	0.279	0.494	0.09	30	0.093	0.269	0.37	0.06
La	10	0.377	0.407	0.461	0.02	30	0.383	0.443	0.518	0.03
Li	10	0.599	0.635	0.649	0.01	30	0.542	0.618	0.706	0.04
a/L x100	10	52.57	53.75	56.57	1.31	30	46.78	54.62	56.36	1.74
La/Li x100	10	59.46	64.16	72.48	3.91	30	58.78	71.8	86.47	5.6

Site	coordinates	m a.s.l.	age	climate	P (mm)	T (°C)
Visogliano	45°47' N 13°35' E	-	MIS 12	Cfa	1121	13.6
Ciota Ciara (unit 15)	45°42'39'' N 8°18'39'' E	670	MIS 11-10	Cfb	1099	10.7
Grotta Maggiore di San Bernardino (units VIII-VII)	45°25' N 11°33' E	135	MIS 7	Cfa	895	13.5
Ciota Ciara (unit 14)	45°42'39'' N 8°16'	670	MIS 5	Cfb	1099	10.7
Grotta Maggiore di San Bernardino (units V-IV)	45°25' N 11°33' E	135	MIS 5	Cfa	895	13.5
Grotta Maggiore di San Bernardino (units III-II)	45°25 N 11°33' E	135	MIS 3	Cfa	895	13.5
Caverna degli Orsi	45°36'15'' N 15°53'02'' E	360	MIS 3	Cfa	1095	14.2
Grotta Fumane (layers D3+D6)	45°35'30'' N 10°54'18'' E	350	MIS 3	Cfa	827	12.4
Roccia San Sebastiano (level 10)	41°06' N 13°53' E	-	MIS 3-2	Csa	893	15.5
Grotta del Sambuco	43°03' N 10°53' E	-	MIS 3-2	Csa	699	14
Paglicci	41°41' N 15°35' E	135	MIS 3-2	Cfa	545	12.8
Grotta della Ferrovia (level E)	43°26' N 13° E	215	end MIS 2	Cfa	775	13.9
Riparo Tagliente	45°32' N 10°59' E	226	end MIS 2	Cfa	831	12.3

List of *M. arvalis* and *M. agrestis* sites from the Italian Peninsula, with coordinates, altitude (m a.s.l., when available), age, Koppen climatic classification, current Mean Annual Temperature (MAT) and current Mean Annual Precipitation (MAP).

Visogliano

	Microtus agrestis					*Microtus arvalis*				
	n	min	mean	max	SD	n	min	mean	max	SD
L	21	2.431	2.683	3.156	0.19	33	2.414	2.646	2.972	0.13
a	25	1.24	1.445	1.749	0.12	41	1.398	1.415	1.659	0.19
W	20	0.806	0.935	1.059	0.07	36	0.781	0.9	0.986	0.05
e	23	0.631	0.756	0.891	0.06	45	0.655	0.731	0.821	0.04
d	25	0.11	0.263	0.378	0.06	46	0.062	0.246	0.382	0.06
La	28	0.31	0.354	0.393	0.02	38	0.314	0.379	0.451	0.02
Li	26	0.521	0.59	0.701	0.04	37	0.488	0.536	0.581	0.02
a/L x100	21	48.81	53.38	58.15	2.21	33	51.53	54.92	58.32	1.46
La/Li x100	26	51.78	59.88	66.78	4.31	36	62.67	70.69	81.55	5.11

Ciota Ciara (unit 15)

	Microtus agrestis					*Microtus arvalis*				
	n	min	mean	max	SD	n	min	mean	max	SD
L	7	2.457	2.867	3.04	0.19	4	2.633	2.811	3.018	0.17
a	8	1.28	1.491	1.598	0.09	4	1.462	1.528	1.623	0.06
W	10	0.884	9.883	1.061	0.05	4	0.842	0.981	1.095	0.12
e	9	0.71	0.81	0.926	0.06	5	0.721	0.8	0.888	0.06
d	10	0.285	0.346	0.453	0.04	5	0.24	0.317	0.43	0.07
La	10	0.292	0.362	0.418	0.03	5	0.356	0.411	0.465	0.04
Li	12	0.548	0.622	0.692	0.04	5	0.494	0.581	0.67	0.06
a/L x100	5	48.85	51.35	52.56	1.52	4	52.16	54.42	56.23	1.82
La/Li x100	10	43.84	57.99	65.72	7.02	5	64.47	70.89	0.75	3.95

Ciota Ciara (layer 14)

	Microtus agrestis					*Microtus arvalis*				
	n	min	mean	max	SD	n	min	mean	max	SD
L	19	2.645	2.993	3.276	0.17	17	2.461	2.714	2.945	0.14
a	19	1.401	1.579	1.828	0.11	17	1.345	1.475	1.618	0.08
W	18	0.909	1.032	1.19	0.07	17	0.854	0.918	1.042	0.05
e	19	0.768	0.862	0.975	0.06	17	0.709	0.759	0.827	0.03
d	19	0.225	0.325	0.405	0.05	17	0.146	0.248	0.337	0.05
La	19	0.327	0.375	0.436	0.03	17	0.357	0.39	0.424	0.02
Li	19	0.57	0.669	0.796	0.04	17	0.501	0.541	0.615	0.03
a/L x100	19	48.9	52.72	55.79	1.72	17	50.45	54.34	56.3	1.48
La/Li x100	19	47.61	56.27	65.78	5.59	17	64.46	72.35	81.9	4.84

Grotta Maggiore di San Bernardino (units VIII-VII)

	Microtus agrestis					*Microtus arvalis*				
	n	min	mean	max	SD	n	min	mean	max	SD
L	25	2.647	2.892	3.073	0.12	5	2.57	2.637	2.67	0.03
a	25	1.406	1.554	1.687	0.08	5	1.444	1.468	1.471	0.01
W	25	0.9	0.997	1.102	0.04	5	0.829	0.895	0.987	0.06
e	25	0.8	0.789	0.906	0.05	5	0.733	0.77	0.824	0.03
d	25	0.05	0.269	0.381	0.06	5	0.156	0.18	0.214	0.02
La	25	0.296	0.348	0.415	0.02	5	0.344	0.371	0.442	0.04
Li	25	0.584	0.663	0.721	0.03	5	0.519	0.542	0.57	0.02
a/L x100	25	51.11	53.73	55.48	1.23	5	55.07	55.77	56.18	4.47
La/Li x100	25	43.4	52.69	60.76	4.78	5	65.07	68.41	77.54	5.17

Grotta Maggiore di San Bernardino (units V-IV)

	Microtus agrestis					*Microtus arvalis*				
	n	min	mean	max	SD	n	min	mean	max	SD
L	21	2.625	2.935	3.314	0.18	24	2.471	2.675	3.004	0.14
a	21	1.378	1.574	1.766	0.09	24	1.264	1.463	1.73	0.1
W	21	0.895	1.02	1.123	0.06	24	0.82	0.921	1.016	0.04
e	20	0.709	0.833	0.931	0.05	24	0.669	0.763	0.852	0.05
d	20	0.086	0.259	0.408	0.08	24	0.117	0.214	0.303	0.04
La	21	0.311	0.373	0.433	0.02	24	0.349	0.389	0.442	0.02
Li	21	0.568	0.658	0.724	0.05	24	0.48	0.552	0.591	0.03
a/L x100	21	50.03	53.66	56.6	1.42	24	51.18	55.04	59.75	1.71
La/Li x100	21	46.07	56.89	64.96	4.89	24	66.47	70.71	79.51	3.95

Grotta Maggiore di San Bernardino (units III-II)

	Microtus agrestis					*Microtus arvalis*				
	n	min	mean	max	SD	n	min	mean	max	SD
L	14	2.616	2.797	3.002	0.12	6	2.318	2.577	2.896	0.19
a	14	1.347	1.505	1.636	0.08	6	1.226	1.409	1.6	0.13
W	14	0.857	0.969	1.087	0.06	6	0.793	0.9	0.969	0.06
e	14	0.664	0.775	0.897	0.07	6	0.671	0.741	0.826	0.06
d	14	0.198	0.294	0.411	0.06	6	0.24	0.254	0.267	0.01
La	14	0.316	0.353	0.39	0.02	6	0.336	0.386	0.44	0.03
Li	14	0.553	0.632	0.71	0.05	6	0.499	0.537	0.579	0.03
a/L x100	14	51.47	53.81	56.09	1.37	6	52.72	54.63	57.12	1.81
La/Li x100	14	47.39	56.17	66.07	6.17	6	64.76	72.19	86.95	7.77

Caverna degli Orsi

	Microtus agrestis					*Microtus arvalis*				
	n	min	mean	max	SD	n	min	mean	max	SD
L	15	2.342	2.652	2.97	0.16	19	2.319	2.518	2.746	0.11
a	15	1.218	1.436	1.62	0.1	19	1.23	1.383	1.479	0.08
W	15	0.853	0.904	1.039	0.05	19	0.807	0.877	0.994	0.04
e	13	0.662	0.738	0.808	0.04	19	0.674	0.742	0.828	0.04
d	14	0.164	0.268	0.378	0.05	19	0.056	0.212	0.275	0.04
La	15	0.307	0.335	0.403	0.02	19	0.321	0.36	0.43	0.02
Li	15	0.514	0.575	0.683	0.04	19	0.469	0.524	0.581	0.03
a/L x100	15	51.41	54.12	56.26	1.45	19	52.37	54.93	57.61	1.54
La/Li x100	15	45.82	58.53	66.03	5.66	19	59.85	68.84	91.68	6.79

Grotta Fumane

	Microtus agrestis					*Microtus arvalis*				
	n	min	mean	max	SD	n	min	mean	max	SD
L	30	2.478	2.861	3.238	0.2	30	2.04	2.604	2.882	0.16
a	30	1.326	1.549	1.764	0.11	30	1.269	1.434	1.549	0.08
W	30	0.829	0.991	1.159	0.11	30	0.794	0.879	1.051	0.05
e	29	0.667	0.819	1.003	0.08	30	0.662	0.733	0.888	0.04
d	30	0.135	0.265	0.535	0.08	30	0.131	0.221	0.323	0.05
La	30	0.313	0.363	0.42	0.03	30	0.294	0.363	0.425	0.02
Li	30	0.506	0.637	0.783	0.08	30	0.451	0.542	0.617	0.03
a/L x100	30	49.14	54.17	56.8	1.52	30	52.26	55.1	62.2	1.71
La/Li x100	30	39.97	57.75	69.9	6.27	30	61.68	69.34	81.39	4.98

Roccia San Sebastiano

	Microtus agrestis					*Microtus arvalis*				
	n	min	mean	max	SD	n	min	mean	max	SD
L	18	2.499	2.722	2.996	0.15	30	2.449	2.761	2.981	0.13
a	18	1.346	1.488	1.715	0.1	30	1.275	1.488	1.636	0.08
W	18	0.86	0.931	1.032	0.05	30	0.811	0.94	1.003	0.04
e	18	0.672	0.762	0.853	0.04	28	0.68	0.766	0.876	0.04
d	18	0.111	0.24	0.366	0.06	28	0.056	0.232	0.354	0.06
La	18	0.268	0.341	0.414	0.03	30	0.351	0.389	0.43	0.02
Li	18	0.525	0.6	0.708	0.05	30	0.479	0.555	0.597	0.02
a/L x100	18	51.35	54.63	58.01	1.93	30	51.32	53.89	57.5	1.43
La/Li x100	18	44.15	57.28	71.5	8.1	30	62.21	70.19	76.76	3.65

	Paglicci (layers 20c-22f)									
	Microtus agrestis					*Microtus arvalis*				
	n	min	mean	max	SD	n	min	mean	max	SD
L	30	2.579	2.768	2.986	0.09	30	2.522	2.811	3.1	0.15
a	30	1.316	1.491	1.591	0.07	30	1.319	1.513	1.677	0.1
W	30	0.893	0.961	1.062	0.04	30	0.828	0.958	1.06	0.05
e	30	0.715	0.807	0.881	0.04	30	0.689	0.771	0.899	0.05
d	30	0.167	0.275	0.443	0.05	30	0.088	0.233	0.404	0.07
La	30	0.316	0.367	0.414	0.02	30	0.355	0.4	0.458	0.02
Li	30	0.557	0.603	0.66	0.02	30	0.498	0.566	0.623	0.03
a/L x100	30	51.02	53.83	56.43	1.55	30	51.12	53.82	56.78	1.3
La/Li x100	30	53.36	61.05	66.78	3.55	30	64.23	70.71	82.33	4.5

	Grotta della Ferrovia									
	Microtus agrestis					*Microtus arvalis*				
	n	min	mean	max	SD	n	min	mean	max	SD
L	30	2.353	2.769	3.038	0.17	30	2.44	2.67	2.898	0.12
a	30	1.26	1.502	1.694	0.1	30	1.228	1.44	1.684	0.08
W	30	0.847	0.95	1.094	0.07	30	0.824	0.91	1.025	0.04
e	30	0.682	0.777	0.94	0.06	30	0.676	0.755	0.847	0.04
d	30	0.138	0.234	0.409	0.05	30	0.107	0.206	0.308	0.05
La	30	0.325	0.354	0.407	0.02	30	0.327	0.384	0.447	0.02
Li	30	0.511	0.605	0.745	0.06	30	0.49	0.542	0.584	0.02
a/L x100	30	52.82	54.22	56.36	0.94	30	50.82	53.92	58.1	1.61
La/Li x100	30	46.45	59.16	72.21	6.33	30	66.28	70.74	77.34	2.87

	Grotta del Sambuco									
	Microtus agrestis					*Microtus arvalis*				
	n	min	mean	max	SD	n	min	mean	max	SD
L	23	2.476	2.852	3.034	0.14	30	2.474	2.782	2.816	0.08
a	23	1.364	1.558	1.686	0.08	30	1.32	1.489	1.541	0.05
W	21	0.78	0.951	1.044	0.07	30	0.806	0.944	1.007	0.05
e	21	0.683	0.803	0.847	0.04	29	0.642	0.791	0.836	0.04
d	23	0.12	0.23	0.399	0.08	30	0.123	0.258	0.412	0.06
La	23	0.316	0.362	0.374	0.01	30	0.325	0.397	0.427	0.02
Li	23	0.476	0.601	0.716	0.05	30	0.463	0.561	0.599	0.03
a/L x100	23	51.48	54.62	57.47	1.44	30	50.63	53.32	56.64	1.46
La/Li x100	23	45.82	60.94	67.77	5.76	30	60.9	75.8	79.96	4.64

	Riparo Tagliente									
	Microtus agrestis					*Microtus arvalis*				
	n	min	mean	max	SD	n	min	mean	max	SD
L	30	2.525	2.724	2.942	0.12	30	2.484	2.721	3.027	0.14
a	30	1.368	1.479	1.675	0.07	30	1.318	1.469	1.684	0.09
W	26	0.825	0.926	1.012	0.04	29	0.822	0.93	1.014	0.04
e	24	0.666	0.784	0.863	0.04	27	0.676	0.787	0.877	0.04
d	24	0.067	0.248	0.35	0.05	29	0.071	0.262	0.423	0.06
La	26	0.303	0.36	0.399	0.02	29	0.34	0.392	0.436	0.02
Li	26	0.522	0.577	0.641	0.02	29	0.484	0.552	0.602	0.02
a/L x100	30	51.83	54.3	56.93	1.17	30	49.5	53.96	57.58	1.54
La/Li x100	26	57.95	62.37	66.84	2.59	29	65	71.11	80.14	3.7

Site	coordinates	m a.s.l.	age	climate	P (mm)	T (°C)
Tarkő rock-shelter	48°08'30" N 20°50' E	850	MIS 11-10 MIS 9-6	Cfb	551	10
Vértesszőlős	47°40' N 18°20' E	270	MIS 11-10	Cfb	547	10.4
Uppony I rock-shelter	48°21'51" N 20°43'44" E	278	MIS 7-6	Dfb	555	9.5
Süttő 6 - layers 1-5	47°75' N 18°43'80" E	240	MIS 5	Cfb	545	10.5
Porosluyk Cave	48°33'30" N 20°53'30" E	420	MIS 5	Cfb	543	9.9
Porlyuk Cave	48°30'39" N 20°32'49" E	410	MIS 5	Dfb	562	9.2
Lambrecht Cave	48°16'70" N 20°58'30" E	410	MIS 5	Cfb	551	10
Tokod	47°71'91" N 18°65' E	170	MIS 5 MIS 3	Cfb	557	10.7
Istállóskő Cave	48°06'67" N 20°40' E	535	MIS 3	Cfb	543	9.9

List of *M. arvalis* and *M. agrestis* sites from the Carpathian Basin, with coordinates, altitude (m a.s.l.), age, Köppen climatic classification, current Mean Annual Temperature (MAT) and current Mean Annual Precipitation (MAP).

Tar-kői rock-shelter - layer 8-12

	Microtus agrestis				
	n	min	mean	max	SD
L	9	2.278	2.686	2.903	0.18
a	9	1.164	1.405	1.578	0.13
W	8	0.771	0.94	1.033	0.08
e	6	0.627	0.759	0.817	0.06
d	8	0.273	0.354	0.465	0.06
La	8	0.278	0.339	0.389	0.04
Li	8	0.469	0.597	0.649	0.05
a/L x100	9	50.19	52.23	55.6	1.86
La/Li x100	8	44.26	57.07	66.78	7.63

Tar-kői rock-shelter - layer 1-7

	Microtus agrestis					*Microtus arvalis*				
	n	min	mean	max	SD	n	min	mean	max	SD
L	16	2.473	2.776	2.95	0.11	3	2.394	2.602	2.87	0.24
a	16	1.283	1.484	1.653	0.08	3	1.27	1.407	1.534	0.13
W	16	0.803	0.916	1.01	0.05	3	0.753	0.857	0.949	0.09
e	16	0.608	0.741	0.836	0.05	2	0.668	0.692	0.717	-
d	16	0.228	0.315	0.431	0.05	2	0.127	0.176	0.225	-
La	16	0.308	0.343	0.406	0.02	3	0.33	0.362	0.382	0.02
Li	16	0.499	0.581	0.643	0.03	3	0.465	0.503	0.564	0.05
a/L x100	16	51.64	53.45	56.03	1.46	3	53.04	54.08	55.74	1.45
La/Li x100	16	52.7	59.06	66.23	3.62	3	67.73	72.16	77.8	5.14

Vértesszőlős II

	Microtus agrestis				
	n	min	mean	max	SD
L	2	3	3.095	3.186	-
a	3	1.48	1.571	1.738	0.14
W	4	0.955	1.023	1.088	0.06
e	3	0.809	0.832	0.854	0.02
d	3	0.183	0.303	0.382	0.1
La	4	0.335	0.364	0.391	0.03
Li	4	0.624	0.675	0.719	0.04
a/L x100	2	49.86	52.2	54.55	-
La/Li x100	4	50.75	53.92	54.38	2.33

Uppony I rock-shelter - layer 1-4

	Microtus agrestis					*Microtus arvalis*				
	n	min	mean	max	SD	n	min	mean	max	SD
L	30	2.645	2.895	3.126	0.13	17	2.475	2.656	2.884	0.1
a	30	1.348	1.568	1.742	0.08	18	1.31	1.469	1.61	0.07
W	30	0.875	1.023	1.135	0.08	18	0.851	0.914	0.999	0.04
e	30	0.656	0.821	0.922	0.06	17	0.682	0.757	0.833	0.04
d	30	0.126	0.257	0.369	0.06	18	0.088	0.228	0.351	0.05
La	30	0.275	0.368	0.434	0.03	18	0.345	0.382	0.419	0.02
Li	30	0.558	0.668	0.753	0.05	18	0.486	0.539	0.597	0.03
a/L x100	30	50.54	54.1	57	1.41	17	52.9	54.99	56.65	1.07
La/Li x100	30	43.58	55.24	66.66	5.7	18	63.71	70.89	86.21	5.06

Süttő 6 - layers 1-6

	Microtus agrestis					*Microtus arvalis*				
	n	min	mean	max	SD	n	min	mean	max	SD
L	2	2.705	2.759	2.814	-	2	2.711	2.91	3.109	-
a	3	1.44	1.542	1.646	0.1	2	1.422	1.514	1.607	-
W	3	0.896	0.927	0.954	0.02	2	1.041	1.1	1.16	-
e	3	0.762	0.767	0.777	0.008	2	0.773	0.852	0.931	-
d	3	0.186	0.233	0.284	0.04	2	0.229	0.311	0.393	-
La	2	0.334	0.36	0.411	-	2	0.409	0.458	0.507	-
Li	2	0.57	0.586	0.607	-	2	0.599	0.63	0.661	-
a/L x100	2	52.84	53.03	53.23	-	2	51.68	52.07	52.45	-
La/Li x100	2	55.02	56.29	57.56	-	2	68.28	72.49	72.49	-

Porlyuk Cave

	Microtus agrestis					*Microtus arvalis*				
	n	min	mean	max	SD	n	min	mean	max	SD
L	7	2.345	2.543	2.806	0.14	7	2.304	2.615	2.851	0.19
a	7	1.191	1.371	1.537	0.1	7	1.211	1.42	1.521	0.11
W	7	0.816	0.86	0.94	0.04	7	0.818	0.886	0.966	0.05
e	7	0.68	0.716	0.756	0.02	7	0.678	0.728	0.788	0.04
d	7	0.136	0.258	0.343	0.06	7	0.203	0.266	0.462	0.09
La	7	0.295	0.32	0.348	0.01	7	0.345	0.363	0.387	0.01
Li	7	0.494	0.554	0.663	0.05	7	0.493	0.532	0.582	0.03
a/L x100	7	50.78	53.87	55.38	1.57	7	52.56	54.29	56.18	1.34
La/Li x100	7	46.3	59.25	66.19	6.87	7	63.34	68.35	71.6	2.22

Poroslyuk Cave

	Microtus agrestis					*Microtus arvalis*				
	n	min	mean	max	SD	n	min	mean	max	SD
L	23	2.299	2.585	3.075	0.17	14	2.386	2.645	2.876	0.15
a	25	1.15	1.38	1.608	0.11	15	1.281	1.451	1.64	0.09
W	25	0.825	0.904	1.018	0.04	15	0.837	0.926	1.091	0.06
e	24	0.474	0.741	0.865	0.07	15	0.67	0.762	0.838	0.04
d	25	0.109	0.253	0.382	0.06	15	0.179	0.257	0.381	0.05
La	25	0.296	0.342	0.379	0.02	15	0.337	0.38	0.44	0.02
Li	25	0.517	0.573	0.669	0.03	15	0.494	0.555	0.596	0.02
a/L x100	23	50.02	53.25	56.45	1.73	14	53.32	54.73	57.02	1.18
La/Li x100	25	45.19	59.89	65.78	4.57	15	65.18	68.55	74.57	3.18

Lambrecht Cave

	Microtus agrestis					*Microtus arvalis*				
	n	min	mean	max	SD	n	min	mean	max	SD
L	13	2.398	2.794	3.054	0.19	4	2.398	2.636	2.867	0.19
a	13	1.251	1.519	1.638	0.1	4	1.251	1.4	1.566	0.13
W	13	0.863	0.98	1.137	0.08	4	0.863	0.898	0.947	0.03
e	12	0.685	0.793	0.893	0.06	4	0.685	0.71	0.742	0.02
d	13	0.079	0.221	0.333	0.07	4	0.079	0.203	0.292	0.09
La	13	0.343	0.38	0.427	0.02	4	0.347	0.38	0.427	0.03
Li	13	0.506	0.612	0.17	0.07	4	0.506	0.533	0.552	0.02
a/L x100	13	51.5	54.38	57.18	1.53	4	52.16	54.95	57.18	2.13
La/Li x100	13	50	62.82	77.49	7.67	4	66.09	71.21	77.49	5.25

Tokod - layers 4-6

	Microtus agrestis					*Microtus arvalis*				
	n	min	mean	max	SD	n	min	mean	max	SD
L	19	2.492	2.852	3.238	0.2	17	2.539	2.767	2.983	0.13
a	19	1.285	1.527	1.755	0.12	17	1.355	1.494	1.629	0.07
W	19	0.811	0.9891	1.172	0.1	17	0.865	0.935	1.073	0.05
e	17	0.693	0.814	1.046	0.09	17	0.669	0.751	0.839	0.03
d	19	0.157	0.258	0.398	0.06	17	0.047	0.244	0.362	0.06
La	19	0.259	0.368	0.457	0.04	17	0.345	0.394	0.483	0.03
Li	19	0.519	0.629	0.762	0.07	17	0.51	0.55	0.607	0.02
a/L x100	19	51.37	53.51	56.78	1.4	17	52.25	54.01	55	0.79
La/Li x100	19	45.04	58.78	69.34	6.65	17	64.24	71.69	81.97	4.76

Tokod - layers 1-3

	Microtus agrestis					*Microtus arvalis*				
	n	min	mean	max	SD	n	min	mean	max	SD
L	16	2.776	2.937	3.216	0.14	5	2.51	2.698	2.925	0.1
a	16	1.43	1.566	1.758	0.08	5	1.335	1.449	1.564	0.09
W	16	0.871	1.022	1.12	0.06	5	0.894	0.958	1.086	0.07
e	16	0.696	0.821	0.77	0.05	5	0.746	0.798	0.913	0.06
d	16	0.141	0.272	0.443	0.07	5	0.202	0.296	0.363	0.06
La	16	0.34	0.379	0.46	0.02	5	0.368	0.399	0.45	0.03
Li	16	0.546	0.666	0.737	0.05	5	0.518	0.563	0.644	0.04
a/L x100	16	51.28	53.32	54.66	1.15	5	52.68	53.69	55.29	0.98
La/Li x100	16	49.44	57.17	65.69	5.78	5	68.78	71.02	75.67	2.71

Istállóskő Cave

	Microtus agrestis					*Microtus arvalis*				
	n	min	mean	max	SD	n	min	mean	max	SD
L	30	2.521	2.827	3.153	0.18	19	2.502	2.724	2.981	0.12
a	30	1.349	1.532	1.726	0.1	19	1.336	1.502	1.657	0.08
W	30	0.849	0.97	1.157	0.09	19	0.826	0.92	1.018	0.05
e	30	0.704	0.794	0.919	0.06	18	0.665	0.763	0.854	0.05
d	30	0.093	0.245	0.382	0.06	19	0.121	0.221	0.341	0.06
La	30	0.281	0.358	0.427	0.03	19	0.339	0.384	0.436	0.02
Li	30	0.523	0.623	0.739	0.06	19	0.488	0.549	0.595	0.02
a/L x100	30	51.56	54.21	56.25	1.17	19	53.39	55.16	58.73	1.36
La/Li x100	30	42.51	57.81	65.82	5.17	19	64.04	69.9	80.12	4.45

Site	coordinates	m a.s.l.	age	climate	P (mm)	T (°C)
Vindija (G1-G2)	46°18'12" N 16°14'38" E	275	MIS 3	Cfb	917	10.5
Marlera I	44°48' 60" N 13°58'40" E	30	MIS 3	Cfa	947	14.4
Mujina	43°33' N 16°23' E	260	MIS 3	Csa	813	15.8

List of *M. arvalis* and *M. agrestis* sites from Croatia, with coordinates, altitude (m a.s.l.), age, Köppen climatic classification, current Mean Annual Temperature (MAT) and current Mean Annual Precipitation (MAP).

	Vindjia (layer G1-G2)									
			Microtus agrestis					*Microtus arvalis*		
	n	min	mean	max	SD	n	min	mean	max	SD
L	15	2.455	2.837	3.072	0.18	7	2.414	2.626	2.835	0.15
a	16	1.313	1.53	1.673	0.11	7	1.247	1.418	1.557	0.1
W	13	0.824	1.023	1.141	0.09	6	0.836	0.919	1.022	0.06
e	12	0.743	0.838	0.953	0.06	7	0.689	0.75	0.839	0.04
d	14	0.397	0.258	0.397	0.08	7	0.143	0.247	0.343	0.06
La	14	0.431	0.386	0.431	0.03	6	0.325	0.385	0.439	0.04
Li	13	0.504	0.641	0.729	0.07	6	0.46	0.537	0.616	0.05
a/L x100	15	51.05	53.62	55.84	1.47	7	51.65	53.95	54.92	1.23
La/Li x100	13	47.69	60.76	72.6	6.86	6	63.35	71.3	80.1	5.44

	Marlera I									
			Microtus agrestis					*Microtus arvalis*		
	n	min	mean	max	SD	n	min	mean	max	SD
L	17	2.653	2.965	3.23	0.16	9	2.639	2.941	3.187	0.18
a	16	1.345	1.57	1.745	0.12	7	1.381	1.99	1.695	0.11
W	11	0.933	1.018	1.11	0.05	7	0.933	1.012	1.121	0.07
e	15	0.767	0.85	0.962	0.05	7	0.747	0.856	1.011	0.09
d	14	0.188	0.252	0.402	0.06	8	0.175	0.256	0.358	0.06
La	10	0.337	0.404	0.437	0.02	6	0.386	0.425	0.464	0.03
Li	9	0.569	0.618	0.67	0.03	6	0.582	0.625	0.695	0.04
a/L x100	16	52.3	53.74	55.66	1.11	7	52.05	53.47	55.11	1.09
La/Li x100	9	59.22	64.82	66.45	2.17	6	63.74	68	74.47	3.66

	Mujina Pecina									
	Microtus agrestis					*Microtus arvalis*				
	n	min	mean	max	SD	n	min	mean	max	SD
L	15	2.592	2.828	3.114	0.12	7	2.62	2.835	3.078	0.17
a	15	1.388	1.53	1.734	0.09	7	1.424	1.539	1.659	0.09
W	17	0.863	0.94	1.075	0.06	7	0.856	0.941	0.997	0.05
e	15	0.67	0.79	0.907	0.05	7	0.757	0.777	0.824	0.02
d	16	0.119	0.23	0.335	0.05	5	0.202	0.258	0.372	0.06
La	17	0.333	0.363	0.423	0.02	7	0.375	0.402	0.428	0.02
Li	17	0.525	0.59	0.667	0.04	7	0.484	0.552	0.598	0.03
a/L x100	15	52.2	54.07	55.68	1.18	7	52.79	54.3	55.57	0.99
La/Li x100	17	53.65	61.62	66.55	3.85	7	64.04	73.18	81.4	6.52

Site	coordinates	m a.s.l.	age	climate	P (mm)	T (°C)
Scladina Cave	50°29'03" N 05°01'30" E	137	MIS 5	Cfb	830	9.7
Marie-Jeanne Cave	50°13' N 4°47'06" E	ca. 120	MIS 3	Cfb	840	9.9

List of *M. arvalis* and *M. agrestis* sites from Belgium, with coordinates, altitude (m a.s.l.), age, Köppen climatic classification, current Mean Annual Temperature (MAT) and current Mean Annual Precipitation (MAP).

Scladina (C4. layers IV-VI)										
	Microtus agrestis					*Microtus arvalis*				
	n	min	mean	max	SD	n	min	mean	max	SD
L	24	2.621	2.827	3.21	0.14	12	2.301	2.504	2.665	0.1
a	24	1.324	1.499	1.691	0.09	12	1.191	1.326	1.494	0.09
W	24	0.879	0.992	1.082	0.04	12	0.813	0.865	0.929	0.03
e	23	0.695	0.797	0.982	0.06	12	0.625	0.73	0.805	0.04
d	23	0.173	0.289	0.388	0.05	12	0.18	0.245	0.3	0.04
La	24	0.317	0.368	0.415	0.02	12	0.34	0.362	0.394	0.01
Li	24	0.561	0.634	0.718	0.04	12	0.478	0.519	0.56	0.02
a/L x100	24	49.07	52.99	55.29	1.56	12	47.83	52.94	57.39	2.51
La/Li x100	24	47.21	58.23	66	5.33	12	65.2	69.96	82.42	4.39

Marie-Jeanne (layers 5a+6)										
	Microtus agrestis					*Microtus arvalis*				
	n	min	mean	max	SD	n	min	mean	max	SD
L	8	2.557	2.803	2.972	0.13	21	2.567	2.754	2.998	0.12
a	8	1.368	1.529	1.645	0.1	21	1.363	1.515	1.737	0.1
W	8	0.867	0.963	1.059	0.06	21	0.836	0.935	1.002	0.04
e	8	0.725	0.771	0.841	0.04	21	0.693	0.782	0.868	0.04
d	8	0.176	0.281	0.378	0.06	21	0.063	0.243	0.376	0.08
La	8	0.33	0.367	0.407	0.02	21	0.319	0.393	0.438	0.02
Li	8	0.547	0.617	0.666	0.04	21	0.498	0.553	0.613	0.03
a/L x100	8	52.5	54.52	57.46	1.75	21	51.7	55	59.2	1.81
La/Li x100	8	49.5	59.7	64.11	4.8	21	61.7	71.29	82.77	5.31

APPENDIX 2

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Patterns of variation in *Microtus arvalis* and *Microtus agrestis* populations from Middle to Late Pleistocene in southwestern Europe

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ABSTRACT
Fifteen paired fossil populations of *Microtus arvalis* and *Microtus agrestis* from southwestern Europe have been analysed from a morphological and morphometric point of view. The sites under consideration are located in the northern Iberian Peninsula and southern France, from the Middle Pleistocene to the end of the Late Pleistocene. The aim of this study is to stress once again the importance of keeping these two species separated in the fossil record in order to recognize specific trends of evolution and divergence and to obtain more precise information on palaeoclimatic and palaeoenvironmental conditions. It was possible to observe remarkable intraspecific differences between Middle and Late Pleistocene populations of both species. Furthermore, in synchronic co-specific populations from the Late Pleistocene, climatic and geographic conditions seem to exert a major influence in shaping intraspecific changes in dental pattern.

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Morphology; morphometric; dental variation; *Microtus*

Introduction

The common vole *Microtus arvalis* (Pallas, 1778) and the field vole *Microtus agrestis* (Linnaeus, 1761) are commonly found in Middle and Late Pleistocene palaeontological and archaeological sites of France (Chaline 1972), Italy (Sala and Masini 2007) and Spain (Cuenca-Bescós et al. 2016).

Their first occurrence in Spain is dated to the Holstein Interglacial, corresponding to Marine Isotopic Stage (MIS) 11 at roughly 424–374 thousand years (ka) ago (Lisiecki and Raymo 2005), in the sites of Sierra de Atapuerca (Kowalski 2001), and they are constantly present in the northern Iberian Peninsula throughout the Saalian glaciation (MIS 10 to 6) (López-García, Blain, Julià, Alcover, et al. 2014; Cuenca-Bescós et al. 2016) and the Late Pleistocene (MIS 5 to 2) (López-García, Blain, Bennàsar, et al. 2014; Rofes et al. 2015; Bañuls-Cardona et al. 2017, among many others).

The taxonomic identification of fossils belonging to the genus *Microtus* is based on the recognition of dental patterns, particularly the features of the first lower molars (m1s), the most abundant and best diagnostic element. *M. arvalis* and *M. agrestis* have similar m1 morphology, and the distinction between the two species can present some difficulties due to the considerable intraspecific variations and the partial superposition of the shapes and measurements of their m1s. Nevertheless, morphological and morphometric characters inferred from living populations (Chaline 1974; Nadachowski 1984; Niethammer and Krapp 1982; Gromov and Polyakov 1992) provide useful references in order to achieve reliable identification. In numerous studies of small-mammal assemblages (Popov and Marinska 2007; Lebreton et al. 2016; Bogićević et al. 2017 among others), they appear under the denomination '*Microtus arvalis-agrestis*', which is enough to account for the presence/absence of the taxa but leaves important issues unaddressed.

Even though they are both grassland species, the field vole and the common vole differ slightly in their ecological preferences, the latter inhabiting open dry terrain with discontinuous herbaceous cover such as crop fields and steppe, while the former favours dump areas such as marshes, peat-bogs and river-banks (IUCN, 2015). Hence, it is important to keep them separated in the fossil record, particularly in order to obtain more precise palaeoclimatic and palaeoenvironmental reconstructions.

Furthermore, recent molecular studies of their mitochondrial DNA (mtDNA) have revealed that after the Last Glacial Maximum (27–19 ka BP) (Clark et al. 2009) *M. arvalis* and *M. agrestis* underwent two very different evolutionary histories (Jaarola et al. 2004; Heckel et al. 2005; Braaker and Heckel 2009; Bužan et al. 2010; Herman et al. 2014) leading to the current intraspecific genetic diversity and the geographical distribution of the extant lineages (Jaarola and Searle 2002; Haynes et al. 2003; Paupério et al. 2012; Beysard and Heckel 2014; Stojak, McDevitt, Herman, et al. 2016a, Stojak, Wójcik, Ruczyńska, et al. 2016). It may thus be useful to analyse also the fossil record to try and recognize early patterns of isolation and divergence.

In this paper, *M. arvalis* and *M. agrestis* populations will be studied in order to underline the different patterns of change undergone by these two species during the Middle and Late Pleistocene in northern Spain and southwestern France.

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Material and methods

The samples analysed in this study come from 14 archaeological and palaeontological sites located in the northern Iberian Peninsula. Valdavara-1, Valdavara-3 (Vaquero Rodríguez et al. 2009; López-García, Blain, Cuenca-Bescós, et al. 2011) and Eirós Cave (Rey-Rodríguez et al. 2016) are located in Galicia, in the NW Atlantic region of the Iberian Peninsula. Mollet Cave (Maroto et al. 2012; López-García, Blain, Julià, Alcover, et al. 2014), Teixoneres (Rosell et al. 2008; López-García, Blain, Burjachs, et al. 2012; Luzi et al. 2016; Talamo et al. 2016), Xaragalls (López-García, Blain, Bennàsar, et al. 2012), Abric Romaní (López-García 2008), Arbreda (Soler Masferrer and Maroto 1987; López-García, Blain, Bennàsar, Fernández-García 2014), Toll (Fernández-García and López-García 2013) and Colomera Cave (López-García, Blain, Allué, et al. 2010) are located in the NE of Iberia, facing the Mediterranean Sea. Sima del Elefante (López-García, Blain, De Marfá, et al. 2011), Trinchera Dolina (Cuenca-Bescós et al. 2010; Falguères et al. 2013), Trinchera Galería-Zarpazos (Galindo-Pellicena et al. 2011; Demuro et al. 2014) and Portalón (López-García, Blain, Cuenca-Bescós, et al. 2010; Bañuls-Cardona et al. 2014) belong to the Sierra de Atapuerca complex, in the Bureba Corridor, connecting these two geographical regions. One last site, Grotte de la Carrière (Lopez-Garcia et al. 2016), is located in the French Eastern Pyrenees region, approximately 20 km from the Spanish border (Figure 1). These sites cover a chronological range spanning from the Middle Pleistocene to the end of the Late Pleistocene (Table 1).

There are characters in the first lower molars (m1s), i.e. in the anteroconid complex (ACC), that allow us to differentiate between the common vole and the field vole: symmetric T4-T5, opposite and widely confluent T6-T7, a rounded AC and parallel BRA4-LRA5 are typical of *Microtus arvalis*, while *M. agrestis* presents asymmetric T4-T5, alternating T6-T7 that sometimes results in the separation of these triangles, an angular AC and alternating BRA3-LRA4 and BRA4-LRA5 (Figure 2).

The m1s of *M. arvalis* and *M. agrestis* were measured following the criteria defined by Van der Meulen (1973), Nadachowski (1984) and Cuenca-Bescós and Laplana (1995). Morphological characters have been described following Nadachowski (1982). L represents the total length of the tooth, La the width of T4, Li the width of T5; LRA and BRA are respectively the lingual and buccal re-entrant angles in the anterior part of the tooth (Figure 2). The La/Li index was calculated in order to quantify the degree of asymmetry between the buccal and the lingual side of the tooth.

When available, second upper molars (M2) were observed. In *M. agrestis* the M2s present a so-called 'exsul-loop', an additional closed field at the posterior end of the tooth that is absent in *M. arvalis* (Zimmerman 1956).

The material from the sites in southern France, NE Iberia and NW Iberia was studied and photographed at the IPHES (Tarragona, Spain) using a Dino-Lite USB microscope. The material from Sierra de Atapuerca was studied and photographed at the Earth Science Department of the University of Zaragoza using an Olympus SZ-61 stereomicroscope.

Only complete teeth from adult specimens, both left and right, were measured. In sites with a high number of m1s, 30 specimens were selected randomly to provide a sample (showing no significant differences when the mean values of each random sample were compared to those of the corresponding whole sample: $p > 0.7$ for the F-test, and $p > 0.6$ for the t-test). All measurements were taken using ImageJ software and are given in millimetres.

The data were processed using PAST 3 software (Hammer and Harper 2006).

Results and discussion

The measurements taken on populations of *Microtus arvalis* and *M. agrestis* (Table 2) from different chronologies and different geographical locations, combined with our study of the morphology of the ACC of the m1s, allowed us to establish some remarkable differences within and between the two species.

Morphometric separation between M. arvalis and M. agrestis

The degree of asymmetry between T4 and T5 has again proved to be a very good discriminant and a useful tool for identifying and separating the two species. In each pair of populations there are of course overlaps in the values due to intraspecific variations, i.e. when the minimum value of the La/Li index for *M. arvalis* is near to the maximum value for *M. agrestis*, but when these measurements are combined with the morphological characters it is always possible to assign the m1s to one of the two species. Even though a degree of uncertainty remains, as 5–10% of the whole samples cannot be clearly identified, this uncertainty is almost entirely restricted to juvenile specimens and broken or excessively digested m1s. During the Middle Pleistocene, the separation between *Microtus arvalis* and *M. agrestis* is clearly

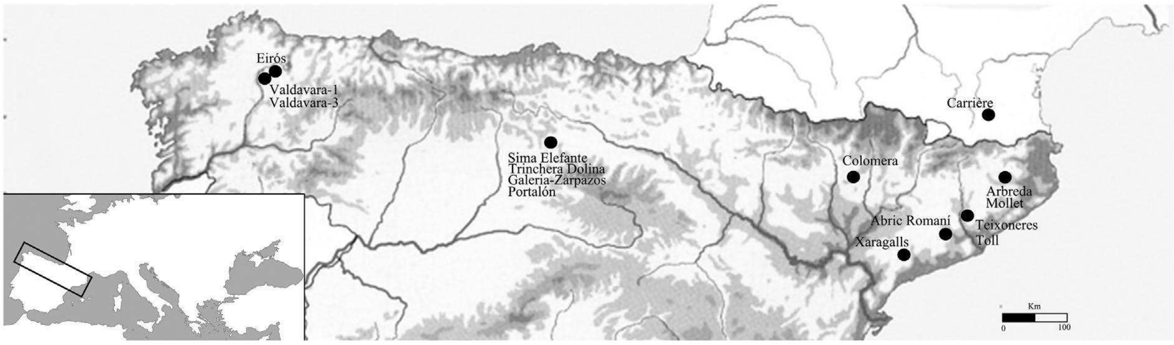

Figure 1. Geographical location of the sites.

visible due to the marked asymmetry between the buccal and the lingual side of the tooth in the latter. On the other hand, during the Late Pleistocene, as the size of *M. arvalis* increases and its morphotypes become more complicated while the *M. agrestis* morphotypes simplify, the two sets come closer but maintain their separation (Figure 3).

Studies of fossil and recent populations of *M. arvalis* and *M. agrestis* from Poland (Nadachowski 1982, 1984), the Ukraine (Rekovets and Nadachowski 1995) and Croatia (Mauch Lenardić 2007) all agree in showing that during the Late Pleistocene the size of the m1s of common voles tends to remain stable, while those of field voles constantly increase in size. Furthermore, *M. agrestis* always displays larger mean values of L than *M. arvalis*. By contrast, the samples from the Late Pleistocene of northern Iberia indicate that the interspecific relation between the two species is reversed, with the common vole m1s being slightly larger than those of the field vole (Figure 3). For the common vole, six different mtDNA lineages have been identified: western-south, western-north, central, Italian, eastern and Balkan (Haynes et al. 2003; Tougard et al. 2008; Bužan et al. 2010; Stojak et al. 2015). It is possible that the western-south line (which includes Spain and western France), separated from the other lineages, developed a larger size during the Late Pleistocene, partly in response to environmental and climatic drives and partly as a consequence of this separation, testifying once again to the peculiarity of the Iberian Peninsula in comparison with the rest of continental Europe.

Table 1. List of the sites with abbreviations and geographical and chronological indications.

Site		Coordinate	m. asl	Date
Trinchera Dolina – layer 10.2	TD	42°33′06″ N 3°53′55″ W	1080	424–250 ka
Trinchera Galería-Zarpazos	TZG	42°33′06″ N 3°53′55″ W	1080	424–250 ka
Sima Elefante – layers 18–19	TE	42°33′06″ N 3°53′55″ W	1080	424–250 ka
Grotte de la Carrière	CAR	42° 33′94″ N 2° 22′77″ E	540	424–250 ka
Mollet Cave	Mollet	42°09′47″ N 2°44′52″ E	200	MIS 7
Valdavara-3	VAL-3	43°01′00″ N 7°33′00″ W	600	MIS 5
Teixoneres	TX	41°48′47″ N 2°05′50″ E	900	MIS 3
Xaragalls	XAR	41°23′02″ N 1°02′56″ E	590	MIS 3
Eirós	Eirós	42°46′3″ N 7°12′13″ W	780	MIS 3
Romanì – level O	AR	41°32′ N 1°41′30″ E	265	MIS 3
Arbreda	ARB	42°09′38″ N 2°44′49″ E	211	MIS 3-2
Portalón	POR	42°33′06″ N 3°53′55″ W	1080	MIS 3-2
Valdavara-1	VAL-1	43°01′00″ N 7°33′00″ W	600	End MIS 2
Toll	Toll	41°48′25″ N 2°09′02″ E	760	End MIS 2
Colomera	COL	42°08′01″ N 0°76′40″ E	670	End MIS 2

Microtus agrestis s. l.

Chaline (1972) first described a peculiar type of *M. agrestis* in the Middle Pleistocene of France based on material from Grotte de l'Escale (Saint-Estève-Janson, Bouches-du-Rhône, France). *Microtus agrestis jansoni* is a vole with *agrestis*-like morphology. The first lower molar is middle-large in size and presents five closed triangles with a clear labio-lingual asymmetry, alternatingly confluent T6 and T7, and an asymmetric anterior cap. Morphologically, the *jansoni*-type is characterized by a deep LRA4, the presence of T9 in the AC and a broad LRA5. In some cases, the populations from the late Middle Pleistocene develop a small BRA4 on T6, resulting in a T8 that recalls the mimomyan-fold. The material from the Middle Pleistocene of Sierra de Atapuerca (i.e. Sima del Elefante, Trinchera Dolina, and Trinchera Galería-Zarpazos), Mollet Cave, and Grotte de la Carrière displays all the diagnostic characters of *M. agrestis jansoni* (Figure 4(A).(1)–(7)). In the second upper molar, it is possible to observe the extra loop at the posterior end of the tooth that is typical of extant forms of *M. agrestis* (Figure 4(A).(4)).

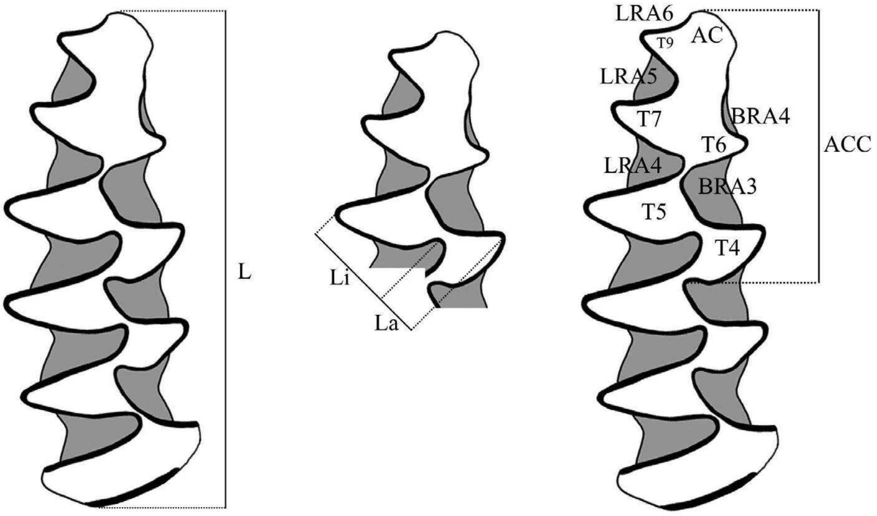

Figure 2. Nomenclature and measurement methods used for m1 in the description of arvicolines.

Notes: L: total length; La: width of T4; Li: width of T5; ACC: anteroconid complex; AC: anterior cap; BRA: buccal reentrant angle; LRA: lingual re-entrant angle; T4-T9: triangles 4–9.

Table 2. Measurements for m1s of *Microtus agrestis* and *Microtus arvalis*.

		L				La/Li ×100			
Site	*n*	Min.	Max.	Mean	SD	Min.	Max.	Mean	SD
Microtus agrestis									
TD	29	2.468	3.023	2.781	0.13	44.52	65.52	54.22	6.29
TZG	24	2.663	3.182	2.933	0.14	41.81	64.82	52.99	6.65
TE	5	2.82	3.049	2.903	0.08	51.48	61.9	56.57	4.41
CAR	11	2.664	2.939	2.796	0.09	51.4	63.6	56.0	3.7
Mollet	2	2.587	2.964	2.775	–	39.2	43.7	41.5	–
VAL-3	7	2.504	2.981	2.8	0.14	48.15	58.75	52.5	0.1
TX	30	2.369	3.053	2.713	0.14	37.56	69.81	61.13	4.66
XAR	6	2.688	3.18	2.91	0.16	60.33	67.8	63.59	2.67
Eirós	8	2.658	3.182	2.944	0.18	45.59	79.36	56	11.29
AR	4	2.587	3.01	2.895	0.2	62.6	67.58	65.46	2.47
ARB	30	2.586	3.222	2.905	0.19	51.01	67.92	62.35	4.05
POR	30	2.424	3.262	2.845	0.2	54.18	69.29	62.85	3.64
VAL-1	2	2.842	2.846	2.844	–	48.91	54.79	51.85	–
Toll	3	2.403	2.582	2.504	0.09	50.79	64.18	54.95	7.38
COL	10	2.603	3.234	2.974	0.2	59.46	72.48	64.16	3.69
Microtus arvalis									
TD	30	2.366	3.16	2.811	0.16	59.09	86.73	74.33	6.52
TZG	24	2.508	3.211	2.86	0.15	60.07	92.91	79.47	6.7
TE	6	2.611	2.823	2.743	0.07	65.29	78.34	72.4	4.9
CAR	1	–	–	2.832	–	–	–	70.04	–
VAL-3	2	2.579	**3**	**2.785**	–	71.11	73.39	72.25	–
TX	30	2.494	3.125	2.778	0.17	61.53	80.59	69.31	3.99
XAR	9	2.598	3.185	2.87	0.17	56.79	73.36	67.15	5.45
Eirós	10	2.766	3.499	3.09	0.23	67.17	83.51	76.3	4.81
AR	12	2.598	3.044	2.865	0.15	64.35	80.2	73.13	3.97
ARB	30	2.639	3.336	2.912	0.18	65.37	83.73	72.13	4.56
POR	30	2.618	3.259	2.954	0.19	67.72	91.62	75.21	5.48
VAL-1	12	2.748	3.28	3.001	0.16	61.8	78.16	68.74	5.53
Toll	10	2.664	3.009	2.795	0.1	64.74	77.36	70.18	4.14
COL	30	2.602	3.629	3.016	0.2	58.78	86.47	71.8	5.5

Notes: L: total length of m1; La/Li: index of asymmetry between the buccal and the lingual side of m1; *n*: number of individuals; min: minimum value obtained; max: maximum value obtained; mean: mean value; SD: standard deviation. TZG: Trinchera Galería-Zarpazos; TD: Trinchera Dolina; TE: Sima Elefante; CAR: Grotte de la Carrière; VAL-3: Valdavara-3; TX: Teixoneres; XAR: Xaragalls; AR: Romaní; ARB: Arbreda; POR: Portalón; VAL-1: Valdavara-1; COL: Colomera.

During the Late Pleistocene, the values of L remain relatively stable while those of La/Li increase as the m1s become more symmetrical (Figure 5(A)) and the morphology of the ACC tends to simplify (Figure 4(A).(8)–(14)). However, there are two remarkable exceptions.

The first concerns the sample from Toll Cave. *M. agrestis* specimens from this site are smaller and more asymmetrical than the others from the same region. This may be due to climatic and environmental factors. In fact, level 3 of Toll Cave can be related to the LGM (Fernández-García and López-García 2013), and small-sized individuals may have found it easier to thrive advantaged in the cold, dry climatic conditions typical of this phase (Dienske 1979; De Jonge 1983). As *M. arvalis* was more adapted to a mid-continental climate, it was probably less affected by this glacial stage than the field vole and its population does not differ much from the others in the same region (i.e. Xaragalls, Romaní, Arbreda, Teixoneres).

The second exception is provided by the samples from the Late Pleistocene sites of Galicia, Eirós Cave and Valdavara-1. Their values are in fact close to those of Middle Pleistocene populations. However, even though they retain the same level of asymmetry and the same size as their older relatives, the morphology of the ACC in the m1s is clearly different, with a reduction in the AC, a less deep LRA4, a shallow LRA5 and an incipient T9, if present at all (Figure 4(A).12–14). Combining molecular and palaeontological data, it is possible to explain the morphological and morphometric peculiarity of the Late Peistocene field vole populations from Galicia. Two lineages of *M. agrestis* (northern and southern) were identified at an early stage on the basis of mtDNA studies (Jaarola and Searle 2002; Jaarola et al. 2004; Herman and Searle 2011; Beysard et al. 2012), and their splitting was related to the LGM. A third, highly divergent lineage (Portuguese) was subsequently identified (Giménez et al. 2012; Paupério et al. 2012), its distribution area located in the western Iberian Peninsula (including Galicia); the proposed time for its separation from the combined northern-southern group is 70 ka ± 30 (Paupério et al. 2012). Our data suggest that this Portuguese lineage might already be morphometrically and morphologically well characterized at least 40 ka BP (level 3 – Eirós Cave; Rey-Rodríguez et al. 2016), and the causes for this divergence might be ascribed to the relative geographical isolation provided by the Iberian Peninsula and to the climatic difference between Galicia and the rest of northern Spain. In the western Iberian Peninsula, the climate is influenced by the Atlantic Ocean. Temperate, with summers drier than winters (Köppen Climate Classification: Csb), it is considerably more humid than the climate of NE Iberia, influenced by the Mediterranean Sea, especially when autumn and winter mean precipitations are considered (AEMET 2011). During the Late Pleistocene, the same difference existed between those two regions (González-Sampériz et al. 2010). This climatic and environmental diversity led the eastern and the western sub-populations of northern Iberian Peninsula to diverge. Furthermore, the isolation provided by the Pyrenees and the steep Atlantic coastlines prevented any contact with populations from northern

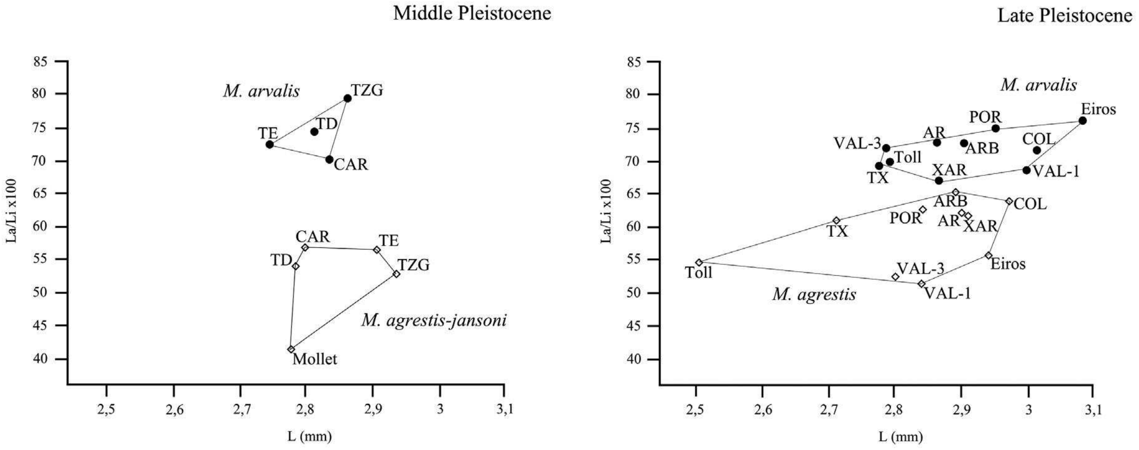

Figure 3. Morphometric differences between *Microtus agrestis* (black) and *Microtus arvalis* (white) of the Middle and Late Pleistocene. Correlation between L and La/Li index.

Notes: L: total length of m1; La/Li: index of asymmetry between the buccal and the lingual side of m1. Site abbreviations: TZG: Trinchera Galería-Zarpazos; TD: Trinchera Dolina; TE: Sima Elefante; CAR: Grotte de la Carrière; VAL-3: Valdavara-3; TX: Teixoneres; XAR: Xaragalls; AR: Romaní; ARB: Arbreda; POR: Portalón; VAL-1: Valdavara-1; COL: Colomera.

territories, enhancing the speciation process of the western populations.

Microtus arvalis

The La/Li index in the populations of *Microtus arvalis* remains relatively stable during the Middle and Late Pleistocene, although the overall size of the m1s increases slightly with time (Figure 5(B)). This increase results in more complex Late Pleistocene morphotypes, with a slight alternation of T6 and T7, a greater degree of closure of AC, and the appearance of small T8 and T9 (Figure 4(B).1–11).

For this species too, the samples from Valdavara-1 and Eirós Cave represent an anomaly, together with that from Colomera Cave. These three populations display a larger size and a tendency towards a larger AC (Figure 4(B).12–14). The current distribution range of *M. arvalis* does not include Galicia and the area of Colomera Cave (Mitchell-Jones et al. 1999; Casals and Sanuy 2006).

Valdavara-1 is one of the last occurrences of this species in the region. The relative geographical isolation and the Oceanic climatic conditions have probably induced the populations of common vole in NW Spain to undergo a trend of increasing m1 and AC size during the Late Pleistocene in a natural process that resembles the one undergone by *M. arvalis* after its anthropic introduction into the Orkney Islands (northern UK, Cucchi et al. 2014).

A similar trend is observed in Colomera Cave, although for different reasons. The role of the Iberian Peninsula as glacial refugium during LGM for *M. arvalis* has long been known and it is reflected in the current distribution of living populations (Hewitt 1999; Stojak et al. 2015). At the end of the Late Pleistocene, Colomera Cave provided unique climatic and environmental conditions that allowed species adapted to cooler climate to survive at a low latitude, by the mean of altitude displacement, well into the Holocene and up to the Bronze Age (López-García et al. 2010). This 'interglacial refugium' (Stewart et al. 2010) offered a favourable ecological setting for species with mid-European requirements such as *M. arvalis*. This population thus survived longer but was isolated from others living at lower altitudes and near the Mediterranean coast of NE Iberia.

The Orkney vole belonged the western lineage of *M. arvalis* (Haynes et al. 2003). More precisely, the western-north lineage and the coast of Belgium are most likely the point of origin of the colonization of the archipelago (Martínková et al. 2013). The populations of common voles currently living in Spain belong to the western-south lineage (Stojak, McDevitt, Herman, et al. 2016a). It is possible that the similar climatic conditions (of Late Pleistocene Galicia, of latest Pleistocene-Holocene Colomera Cave, and Holocene UK), and the isolation lead to parallel morphological and morphometric dental patterns. Common ancestry may have played a role too, since all the populations are part of the western lineage. This also support the hypothesis that a line of least resistance to evolution (Schluter 1996) exists in *M. arvalis*, despite the difference in phylogenetics (Cucchi et al. 2014).

The case of Valdavara-3

The populations of *M. arvalis* and *M. agrestis* from Valdavara-3 differ from the others of Late Pleistocene and, particularly for *M. arvalis*, from those of NW Iberia (Figure 5(A) and (B)). In fact, both populations display morphologies and morphometric values close to those of Middle Pleistocene. The site has been dated by OSL to MIS 5 (unpubl. data, Vaquero et al.), at the beginning of Late Pleistocene, specifically in the earliest stage of MIS 5 (MIS 5d-a). The climatic conditions in this moments were milder and less arid than in MIS 3 and 2. Therefore, it is possible that the process of isolation leading *M. arvalis* toward an increased size of m1s and *M. agrestis* to differentiate from the *jansoni*-type was not yet started in Galicia. Another possible explanation may be that the separation between Middle and Late Pleistocene populations and between NW and NE Iberian Late Pleistocene populations already occurred in MIS 5e but cannot be seen in the fossil record of Valdavara-3. Given the chronological proximity to the splitting event, phenotypic changes may not have had time to arise.

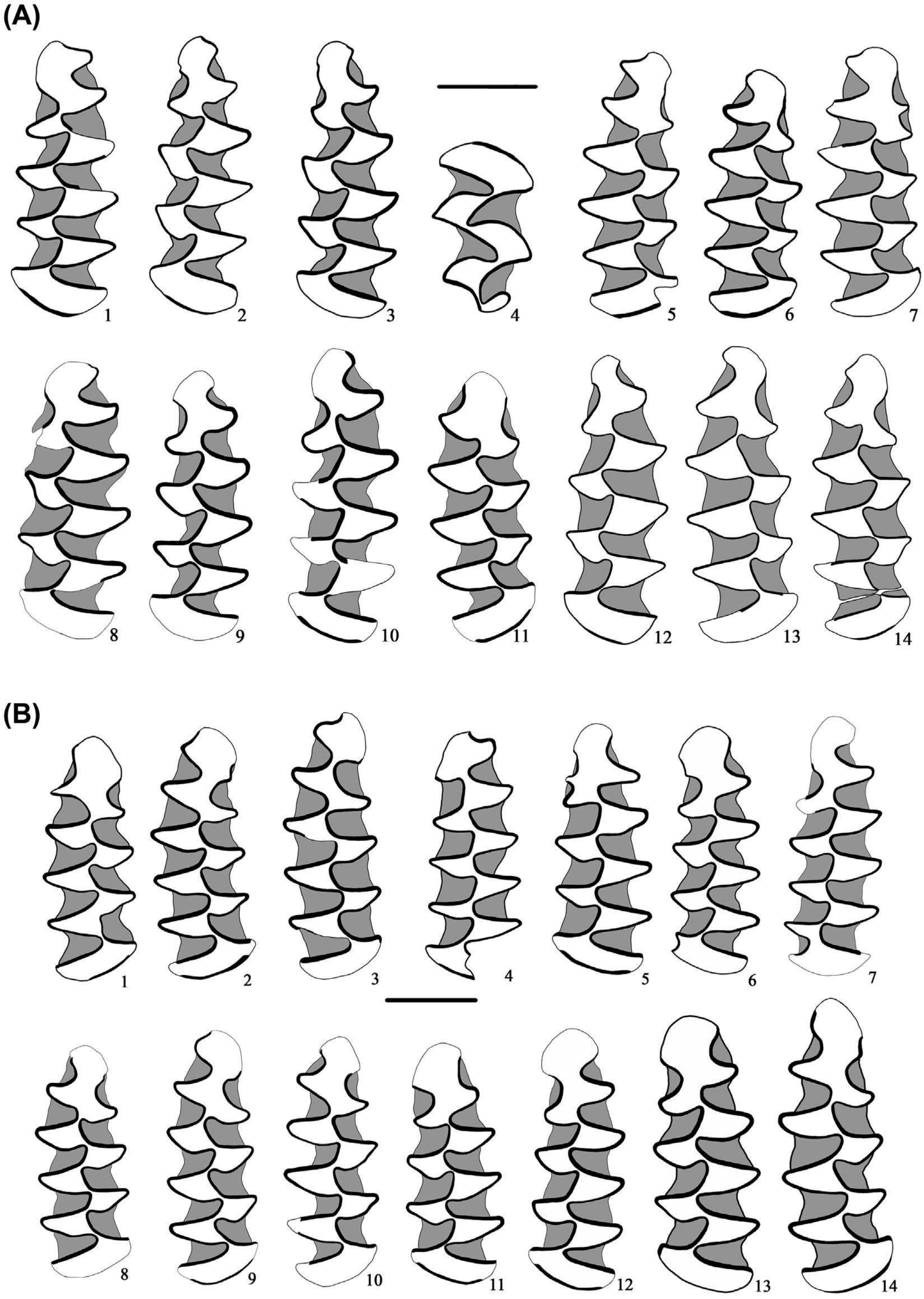

Figure 4. (A): examples of *Microtus agrestis*. (1): TZGIIa_n3_280, left m1; (2): TZGIIa_p2_190_a, left m1; (3): TZGIIa_p2_190_b, left m1; (4): TD10-2_i20_300-310-8, right M2; (5): TD10-2_j16_250-270-37, right m1; (6): TD10-2_i13_210-220-3, right m1; (7): CAR_n4_d6-28b, right m1; (8): TX_n3b-5, left m1; (9): TX_n3a-3, left m1; (10): TX_n3a-4, left m1; (11): TX_n3b-2, right m1; (12): Eirós_CE3-3, left m1; (13): Eirós_CE3-5, right m1; (14): Eirós_CE3-8, right m1. Scale: 1 mm. (B) examples of Microtus arvalis. (1): ARB_h_E2BE107-5, right m1; (2): ARB_e_E00E81-6, right m1; (3): ARB_d_E00E68-6, right m1; (4): ARB_f_E1AE87-14, left m1; (5): ARB_d_E00E68-11, left m1; (6): ARB_c_E00E65-13, left m1; (7): ARB_a_E00E52-17, left m1; (8): TX_n3a-5, right m1; (9): TX_n3a-4, right m1; (10): TX_n3b-6, right m1; 11: TX_n2b-2, left m1; (12): COL_ce14_x31_Fc-86, left m1; (13): COL_ce14_x31_Fc-75, left m1; (14): COL_ce15_x31-59, right m1.

Notes: Scale: 1 mm. Site abbreviations: TZG: Trinchera Galería-Zarpazos; TD: Trinchera Dolina; CAR: Grotte de la Carrière; TX: Teixoneres; ARB: Arbreda; COL: Colomera.

Conclusions

The study of fossil populations of *M. arvalis* and *M. agrestis* as separated but related entities offers many points worthy of further examination, either for biochronological purposes or for a better understanding of the processes of isolation and divergence, or the influence of climatic and environmental fluctuations on dental characters at local or regional level.

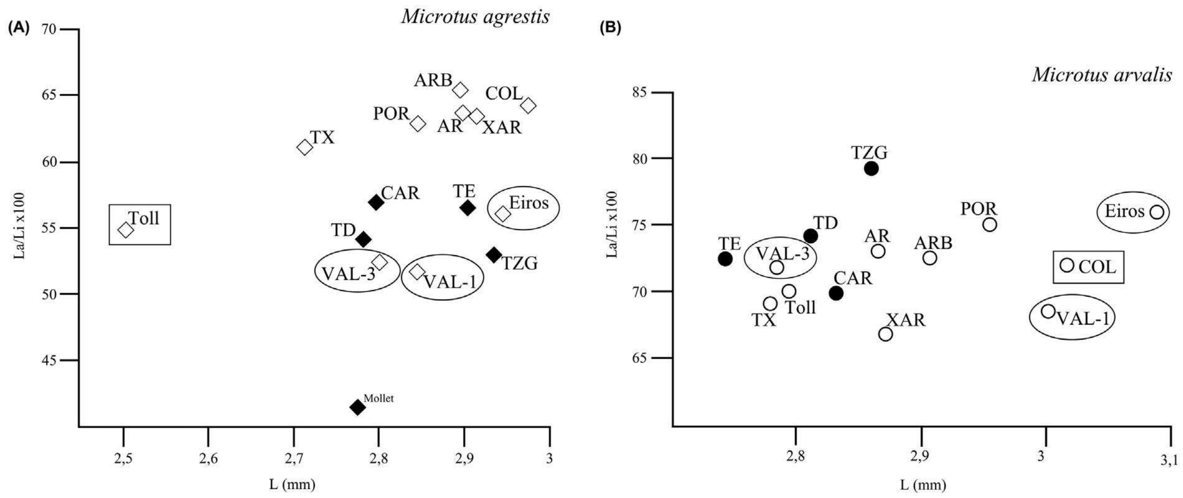

Figure 5. Correlation between L and La/Li index of *Microtus agrestis* (A) and *Microtus arvalis* (B) populations of the Middle Pleistocene (black) and the Late Pleistocene (white). L: total length of m1; La/Li: index of asymmetry between the buccal and the lingual side of m1.

Notes: Site abbreviations: TZG: Trinchera Galería-Zarpazos; TD: Trinchera Dolina; TE: Sima Elefante; CAR: Grotte de la Carrière; VAL-3: Valdavara-3; TX: Teixoneres; XAR: Xaragalls; AR: Romaní; ARB: Arbreda; POR: Portalón; VAL-1: Valdavara-1; COL: Colomera.

- The La/Li index, combined with morphological characters, again showed its value as a useful tool for separating and identifying *M. arvalis* and *M. agrestis*.
- *Microtus agrestis jansoni* proved to be a good biochronological marker for the Middle Pleistocene of Spain and southern France, being morphometrically well separated from *M. arvalis* of the same period and morphologically well characterized within the group *M. agrestis*.

Further studies will be required to better understand the dynamics set in motion at the very beginning of the Late Pleistocene, as shown by the case of Valdavara-3, but during this age regionalism seems to play a key role in shaping the dental character of field and common voles:

- populations of the two species from the Late Pleistocene of Galicia (Cova Eirós and Valdavara-1) follow different evolutionary trends from the corresponding populations from Catalonia and Sierra de Atapuerca, partly because of the influence of the Atlantic climate and partly due to their relative geographical isolation;
- the peculiar climatic and environmental conditions brought on by the LGM are the most probable cause of the difference between the population of *M. agrestis* from Toll Cave and all the others from NE Iberia;
- the protection and isolation provided by the interglacial refugium of Colomera Cave acted on the *M. arvalis* population in such a way that it is more similar to those from Galicia than to those from Catalonia.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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ORIGINAL PAPER

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-García**[1] · **Ruth Blasco**[3] · **Florent Rivals**[1,2,4] · **Jordi Rosell**[1,2]

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

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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 Moià (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 ^{14}C 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

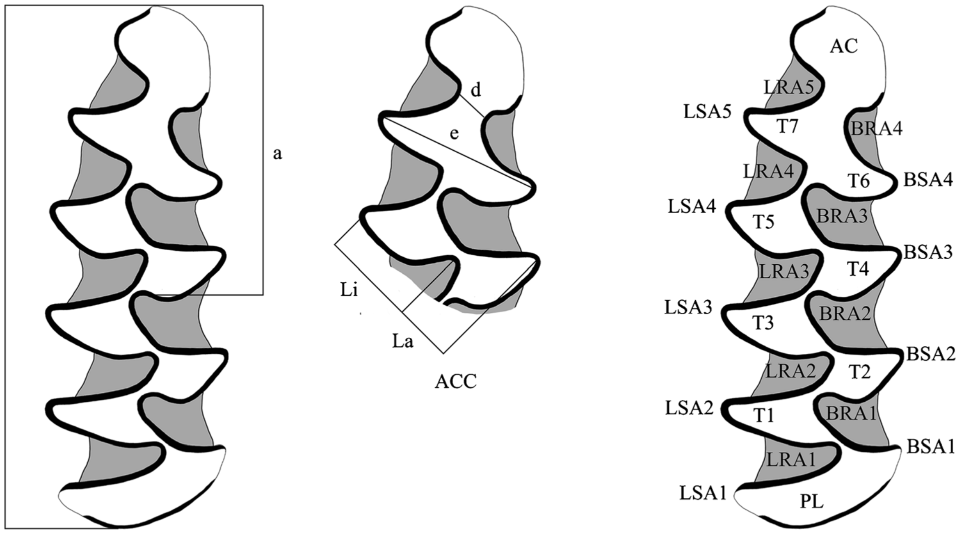

Fig. 1 Nomenclature and measurement methods used for m1 in the description of arvicolines. **L**: total length; **a**: length of the anteroconid complex; **e**: width of the anteroconid complex; **d**: degree of closure of AC; **La**: width of T4; **Li**: width of T5; **PL**: posterior lobe; **ACC**: 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

	Microtus arvalis of Teixoneres					*Microtus agrestis* 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
	Microtus arvalis - IIb					*Microtus agrestis* - 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
	Microtus arvalis - IIIa					*Microtus agrestis* - 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
	Microtus arvalis - IIIb					*Microtus agrestis* - 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 ×100	15	70.26	78.34	67.03	3.03	5	63.71	68.43	57.85	4.35

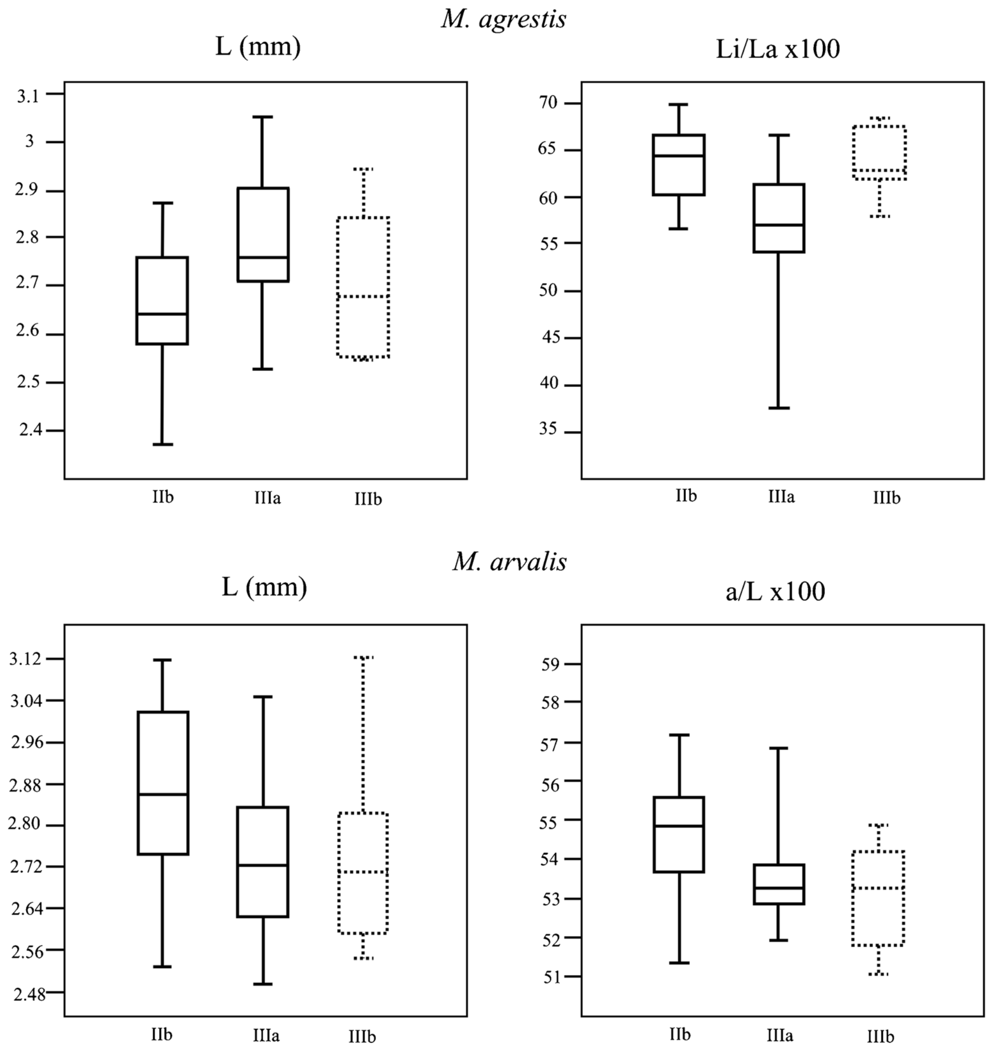

Fig. 2 Box plot showing significant measurements of *M. agrestis* (L and Li/La) and *M. arvalis* (L and a/L). *Black lines*: levels IIb and IIIa. Dotted: level IIIb (not statistically significant)

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 cabrerae* 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

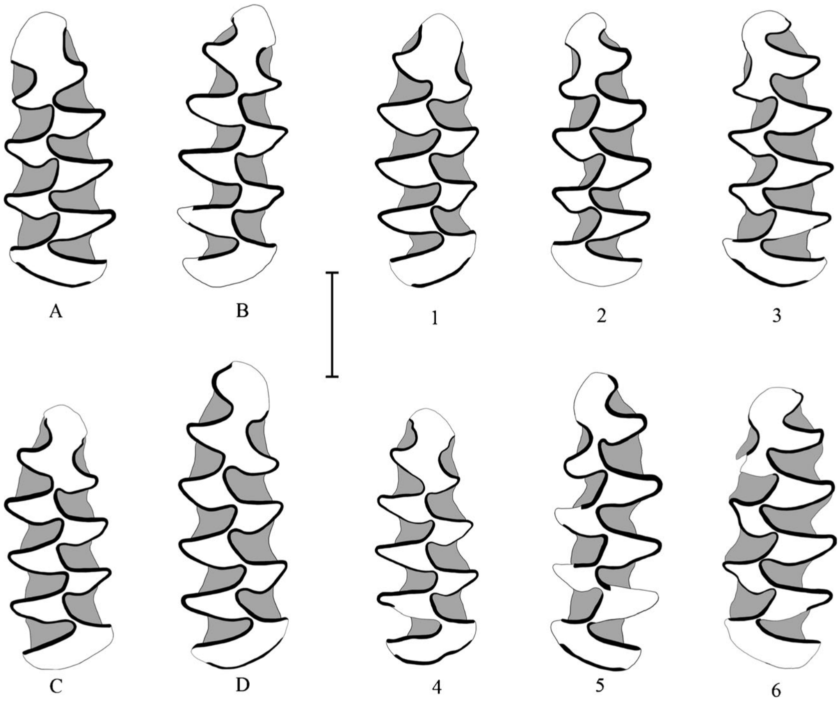

Fig. 3 Morphotypes of *M. arvalis* (**a**: *left* m1; **b-d**: *right* m1, from level IIb) and *M. agrestis* (1 and 4: *right* m1, from level IIb; 2, 3, 5 and 6: *left* m1, from level IIIa). Occlusal view. Scale: 1 mm

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* (Ledevin 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.

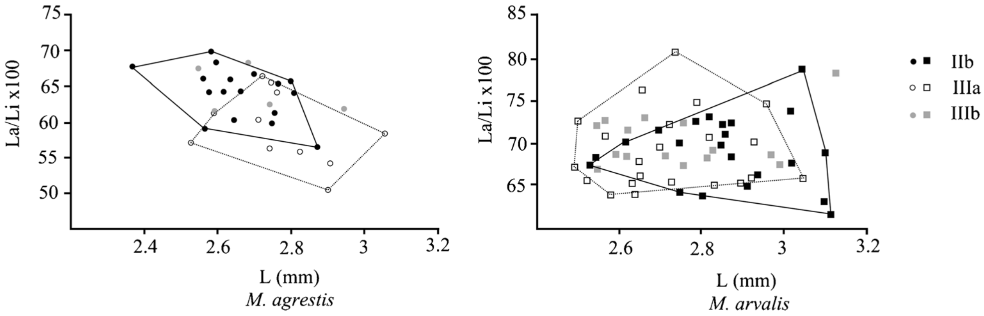

Fig. 4 Graphic representation of the variations in the *M. agrestis* and *M. arvalis* populations

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 hereditability, 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 (Tougard 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 hereditability 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 subpopulations 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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APPENDIX 3

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Paleoenvironmental and paleoclimatic context during the Upper Palaeolithic (late Upper Pleistocene) in the Italian Peninsula. The small mammal record from Grotta Paglicci (Rignano Garganico, Foggia, Southern Italy)

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ABSTRACT

Changes in large mammal population and biotic regionalism of the Italian Peninsula during Upper Pleistocene have been well documented over the last twenty years. On the other hand, only few studies have focused on the changes in small mammal fossil assemblages.

Grotta Paglicci is a key archaeological site for Italian prehistory. It is well dated and it shows an uninterrupted chronological sequence of Upper Palaeolithic lithic industries, ranging from the Aurignacian to the Late Epigravettian.

Small mammal remains from the Upper Palaeolithic layers of this cave have been identified and the assemblage has been analysed through the application of Simpson diversity index, Habitat Weighting and Bioclimatic model methods. The results show remarkable differences through the record: major climatic changes (GS2 is particularly well defined) are visible and a clear turning point is observable at the Bølling-Allerød interstadial transition. This is in line with environmental and climatic oscillations already detected in the Italian Peninsula. These data also suggest that a strong regionalism characterized the south-eastern Italian Peninsula during the Late Pleistocene.

1. Introduction

In the Italian Peninsula faunal assemblages dating to the Upper Pleistocene and especially to its last phases (end of MIS 3 and MIS 2) are characterized by a strong regionalism (Gliozzi et al., 1997; Masini and Sala, 2011, 2007; Sala, 2007; Sala et al., 1992; Sala and Masini, 2007). This is mostly due to the geomorphology and to the position of the Peninsula. Differences are clearly visible between assemblages from northern and southern areas (Sala, 2007) especially during the Late Glacial (Sala, 2007, 1990). Nonetheless, differences due to site position (i.e. mountain, valley, coastal area) must also be taken into account.

Among ungulates, *Capra ibex* and *Rupicapra rupicapra* were dominant in the Pre-Alps during glacial phases and were replaced by *Cervus elaphus* during warming up phases. On the other hand, in the Po plain, the dominant species was *Bison priscus* accompanied by the noteworthy presence of *Alces alces* (Sala, 2007). In Southern Italy, ungulate assemblages reflect differences between Adriatic and Tyrrhenian sides. During cold phases on the eastern side *Capra ibex*, *Bos primigenius* and *Equus ferus* were dominant, replaced by *Equus hydruntinus* and *Cervus elaphus* probably during the Bølling-Allerød Interstadial. During the Greenland Interstadial 1 on the western side, *Sus scrofa* and *Capreolus capreolus* tend to replace

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Cervus elaphus dominated assemblages (Boscato, 2007; Sala, 2007, 1983). Such East-West difference continues during the first phases of the Holocene (Bon and Boscato, 1996).

Recent studies on small mammal assemblages (Berto, 2013; López-García et al., 2015, 2014) show a division of the Italian Peninsula in at least four biogeographic regions: two in Northern-central Italy and two in Southern Italy. The Apennine chain acts as a divide between the eastern and western sides especially in Southern Italy. The presence of *Microtus* (*Terricola*) *savii* among arvicolids is a common element between the two regions. Although the origins and evolution of this species are still unclear, the molecular data shows that it originated in Italy probably during the Middle Pleistocene, even if no fossil evidences related to this Age have been found (Tougard et al., 2008). Morphological differences between MIS 5 and MIS 3 *Microtus* (*Terricola*) *savii* populations, especially at Cavallo Cave (Salento, Southern Apulia), have been interpreted as the result of geographic isolation during the warm phases. Nevertheless, during the Upper Pleistocene this species seems to be endemic to the southern Italian Peninsula (Berto, 2013; Petruso et al., 2011).

In the eastern side of the southern Italian peninsula, small mammal assemblages attest to arid conditions. The biodiversity is always low, one species (*Microtus arvalis* or *Microtus* (*Terricola*) *savii*) usually dominates the assemblages and forest adapted species are rare or absent.

The climate of the western side was influenced by Atlantic disturbances. Therefore, small mammal assemblages are characterized in this area by high percentages of forest adapted species (*Apodemus* gr. *sylvaticus-flavicollis* and *Glis glis*), sometimes dominant during warming up phases (Berto, 2013; Bon and Boscato, 1996; López-García et al., 2014).

In this context, Grotta Paglicci is a key sequence for the knowledge of climatic changes and environmental conditions in Southern Italy during the Upper Palaeolithic. This site also contributes to understand the evolution of regional differences among small mammal communities in the Italian Peninsula.

2. Grotta Paglicci

Grotta Paglicci is one of the most important Upper Palaeolithic sites in the Mediterranean Basin. It is located on the western slope of the Gargano promontory (Foggia, Apulia, Southern Italy), 143 m above sea level (Fig. 1A and B). The Cave's position was of strategic importance for Paleolithic populations, as it lies not far both from the Foggia plain and from the highest rocky peaks of the promontory. The site comprises the present-day cave and a rock shelter that was once part of the same cave system (Palma di Cesnola, 2004a, 1993).

Research at Grotta Paglicci has a long history. The site was discovered at the end of the 1950s and first excavated by the Natural History Museum of Verona between 1961 and 1963. From 1971 up to now research has been carried out by the University of Siena in collaboration with the local Soprintendenza Archeologica (Palma di Cesnola, 2004a; Zorzi, 1964).

Two main areas have been excavated, one in the present external rock-shelter and one in the underground cave. The external area yielded archaeological artefacts ranging from the late Acheulean to the ancient Mousterian (Crezzini et al., 2016; Palma di Cesnola, 2004a). In the excavation of the inner cave, a 12-m-thick sequence with 26 archaeological layers (Fig. 1C) was investigated. This covers a time span from the Lower-Middle Palaeolithic (layers 30-25) through the whole Upper Palaeolithic which is present in a continuous sequence comprising Aurignacian with marginally backed bladelets (layer 24), Gravettian (Ancient: layers 23 and 22; Evolved: layers 21 to 19b; Late: layers 19a to 18b) and Epigravettian (Ancient: layers 18a to 12; Evolved: layers 11 to 8; Late: layers 7 to 3a) (Cremaschi and Ferraro, 2007; Palma di Cesnola, 2004a, 2004b, 2004c; Ricci et al., 2016; Wierer, 2013).

The discovery of two Gravettian burials (Pa12 and Pa25) and 146 human remains attributed to *Homo sapiens* (69 in the Gravettian layers and 47 in the Epigravettian layers) and the presence of the only example of Palaeolithic rock painting in Italy make of Grotta Paglicci one of the most important sequences of the European Upper Palaeolithic (Arrighi et al., 2008, 2012a, 2012b; Bietti, 1990; Borgia et al., 2016; Fu et al., 2016; Palma di Cesnola, 1993; Posth et al., 2016; Ricci et al., 2016; Ronchitelli et al., 2015). Recently, also important evidences of Gravettian plant food processing and consumption were discovered (Mariotti Lippi et al., 2015; Revedin et al., 2015).

Most of the radiocarbon dates have been obtained during the 1970's and, therefore, without decontamination of sample by pretreatment chemistry (i.e. ABOX-SC treatment) (Higham et al., 2009; Higham, 2011). However, the 52 available radiocarbon dates (Fig. 2) indicate that the sequence accumulated quite continuously during the last phases of MIS 3, MIS 2, and the first phases of MIS 1 (from 40,939–36,570 years cal BP to 13,712–12,970 years cal BP) (Palma di Cesnola, 2004a). Considering available radiocarbon dates, a possible chronological gap is present between ca 20,000 and 24,000 years cal. BP.

A first paleoenvironmental study based on macro-mammal remains was carried out by Sala (1983) on a limited sample of materials recovered before 1983 (Layers 3a-22a). Boscato (2004) analysed large mammal remains from layers 22a-24b.

The ungulate assemblage comprises *Bos primigenius*, *Equus ferus*, *Equus hydruntunus*, *Capra ibex*, *Rupicapra* sp., *Cervus elaphus*, *Sus scrofa* and *Capreolus capreolus* (Arobba et al., 2004; Boscato, 2007, 2004; Boschin, 2013; Sala, 1983). From layer 24b to layer 6d associations are generally dominated by more or less open-environment ungulates (*Bos primigenius*, *Equus ferus*, and *Capra ibex*). A change is visible at the end of the sequence: from layer 6c to layer 3a *Cervus elaphus*, *Sus scrofa*, *Bos primigenius* and *Equus hydruntinus* become dominant suggesting a more forested environment and the presence of more abundant water sources. With regard to carnivores, the Aurignacian-Early Gravettian sequence and the Epigravettian one are dominated by *Canis lupus* and *Vulpes vulpes* (Boscato, 2004; Boschin, 2013). *Crocuta crocuta spelaea* has been individuated in layers 24 and 23 (Boscato and Crezzini, 2005; Crezzini et al., 2016). No data are available for the evolved/final Gravettian sequence.

A complete revision of the large mammal record is underway, and its description and interpretation will be the aim of further works.

Bartolomei (2004, 1980, 1975) published preliminary studies on small mammals from the lower sequence (layers 24, 23, 22, and 21). According to this author, *Microtus arvalis* dominates the sequence suggesting an environment characterized by wooden or continental steppe with a cooling phase recorded from layer 22D to layer 21A.

Further paleoenvironmental studies on avifauna from the Aurignacian and Ancient Gravettian layers (layers 24, 23 and 22) have highlighted the presence of steppe or grassland with bare rocks and rocky substrata, as testified by the high percentage of *Pyrrhocorax graculus* and *Columba livia*. In layer 23B, the occurrence of boreal and alpine species suggests a cold climatic oscillation (Tagliacozzo and Gala, 2004).

Finally, the study of stable isotopes on *Cervus elaphus*, *Bos primigenius* and *Equus ferus* bones from the Gravettian and Epigravettian layers shows the occurrence of a climatic improvement between 19,500 ka and 16,000 ka related to a shift from arid to humid conditions with the development of forest habitats (Delgado

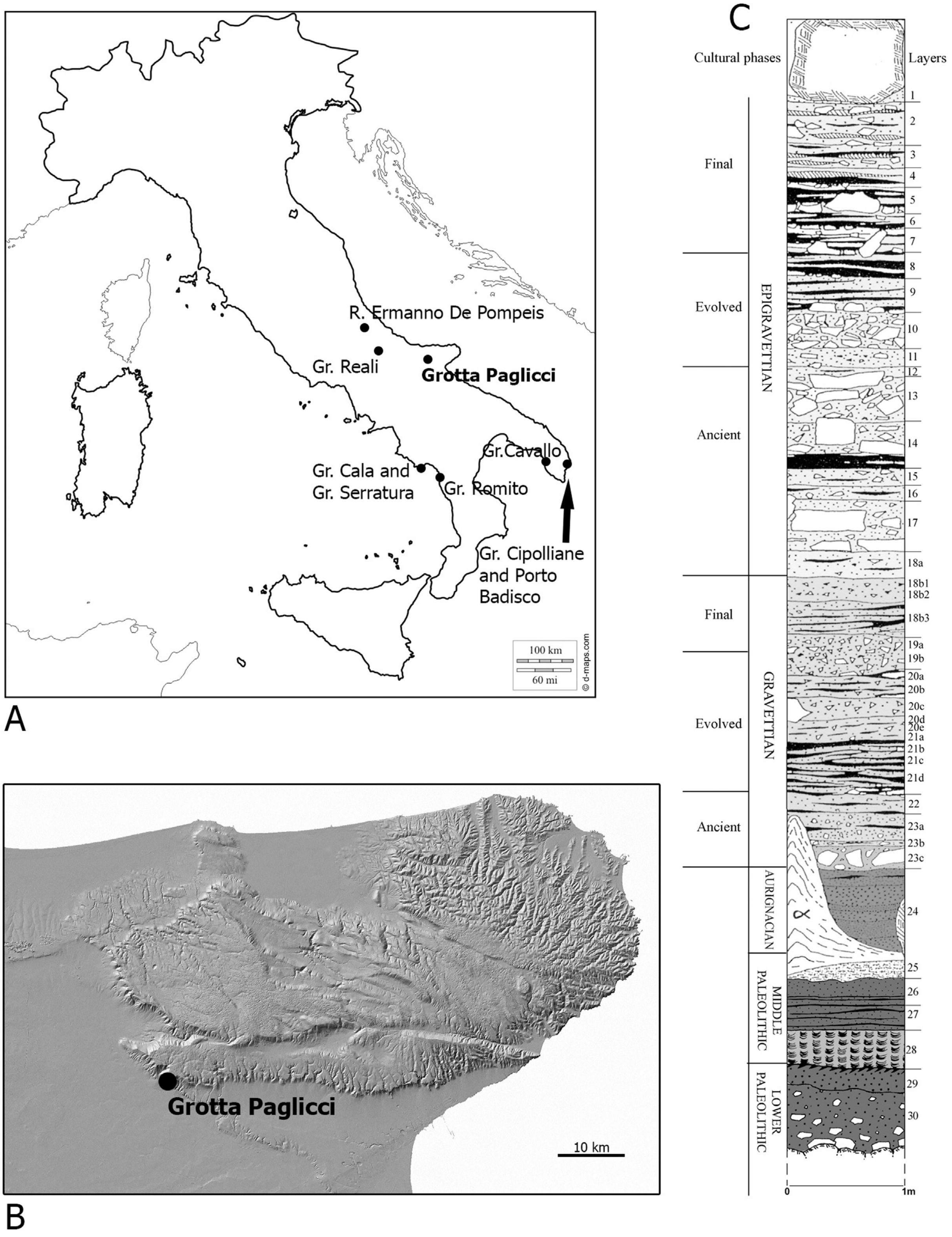

Fig. 1. Location of the most important Upper Pleistocene (MIS 3, 2 and 1) sites in Southern Italy (A); Location of Grotta Paglicci (B); Stratigraphy of the cave (C).

Huertas et al., 1997; Iacumin et al., 1997).

3. Materials and methods

The small mammal remains mainly comprise disarticulated bone fragments collected during the last forty years of excavation campaigns. This material was retrieved by water-screening using 1 mm mesh sieves.

The small mammal assemblage includes a total of 9779 remains, corresponding to a minimum number of 5047 individuals (Table 1,

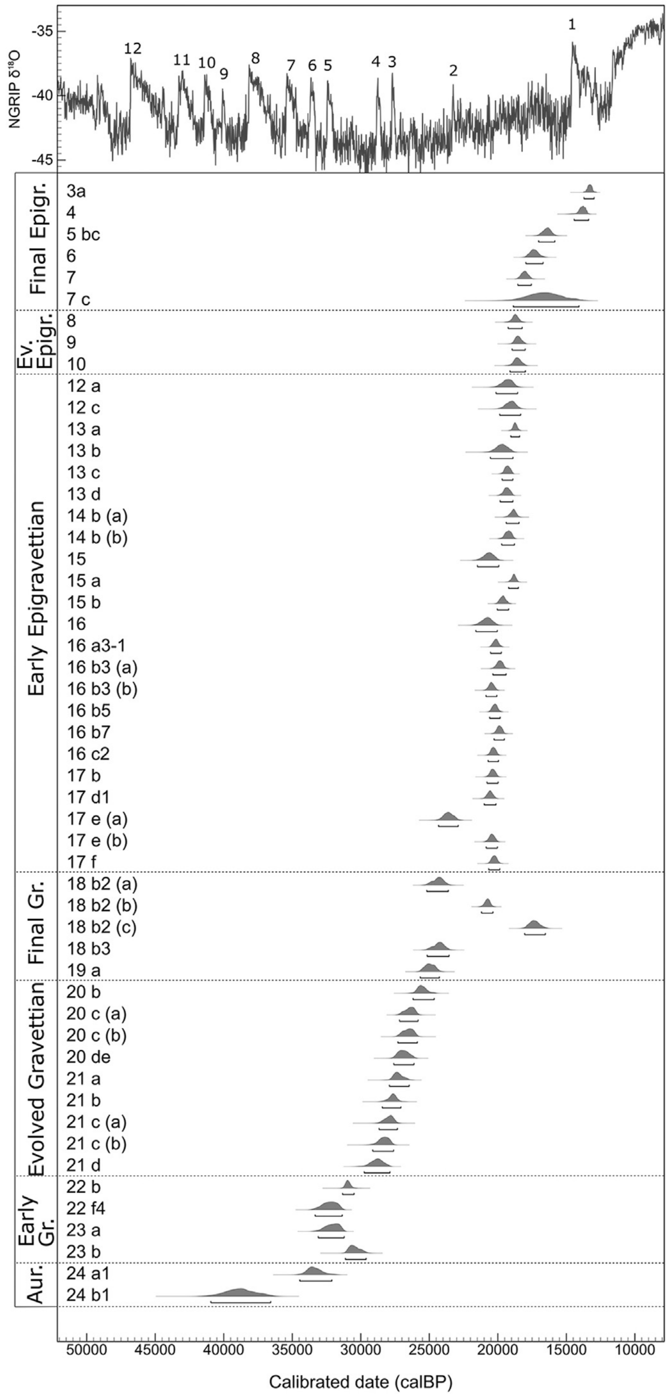

Fig. 2. Radiocarbon dates for the layers of Grotta Paglicci. Ages are calibrated with the OxCal 4.2 software (Bronk Ramsey, 2009) using the IntCal13 curve (Reimer et al., 2013).

Table 2 and Fig. 3). The specific attribution of this material was mainly based on the best diagnostic elements: mandible, maxilla and isolated teeth for rodents, mandible and maxilla for shrews, mandible, maxilla, isolated teeth and postcranial bones for talpidae.

The taxonomic classification follows Wilson and Reeder (2005), except for *Clethrionomys glareolus* (for the priority over *Myodes*, see Tesakov et al. (2010)). Data on the distribution and habitat of the species were taken from Amori et al. (2008), Boitani et al. (2003), and Mitchell-Jones et al. (1999).

We calculated the paleodiversity using the Simpson index of Evenness $= 1-\sum(\mathrm{pi}^2)$, where pi is the proportion of individuals in the ith species (Harper, 2005; Magurran, 2004). The evenness index is constrained between 0 and 1. The index has been calculated using PAST 3.04 avoiding redundant determinations (i.e., for *Arvicola amphibius*, the individuals determined as *Arvicola* cf. *amphibius* and *Arvicola* sp. have not been included in the Simpson index calculation) (Hammer et al., 2001).

3.1. *Environmental reconstruction*

In order to reconstruct the paleoenvironment at Grotta Paglicci we used the habitat weighting method (Andrews, 2006; Evans et al., 1981), assigning each small mammal taxon to habitat(s) where it can be found today in Europe. To this purpose, habitats have been divided up into six types (Cuenca-Bescós et al., 2009; López-García et al., 2010, 2015): open land with either dry or wet meadows (OD and OH, respectively); woodland environments, divided into open woodland, woodland margins and forest patches (OW) and woodland and mature forest habitat (W); water, areas along streams, lakes and ponds (Wa); and habitats with a suitable rocky or stony substratum (R). For better understanding changes in habitat along the sequence, Open Dry habitats have been subdivided into two sub categories: OD Continental, characterized by *Microtus arvalis*, and OD mediterranean, characterized by *Microtus* (*Terricola*) *savii* (Table 3).

3.2. *Climatic reconstruction*

Paleoclimatic data from Grotta Paglicci have been calculated using the Bioclimatic Model described by Hernández-Fernández (2001, 2005). First, the mammal assemblage has been assigned to climatic types described in Hernández-Fernández (2001) and Walter (1970) following the values established in Hernández-Fernández and Peláez-Campomanes (2005): IV Subtropical with winter rains and summer droughts; VI Typical temperate; VII Arid-temperate; VIII Cold-temperate (boreal) and IX Polar. The assemblage of each unit has been analysed using the Climatic Restriction Index ($\mathrm{CRI}_i = 1/n$, where “n” is the number of climatic zones inhabited by the species and “i” is the climatic zone where the species appears). A value of 1 has been assigned in climate type IV (winter rain and summer drought) for *Microtus* (*Terricola*) *savii* because this species is considered as a Mediterranean one (Amori et al., 2008). The presence of values in climate types I, II, II/III and III are due to the occurrence of *Rattus rattus* in layer 1. This layer, together with layer 2, has been considered as reworked and has not been taken into consideration for paleoclimatic and paleoenvironmental interpretations.

Afterwards, the Bioclimatic Component (BC) has been calculated using the following formula: $\mathrm{BCi} = (\Sigma\ \mathrm{CRI}_i) \times 100/S$, where S is the number of species by unit at Grotta Paglicci. From the BC, climatic parameters have been estimated with multiple linear regression method using the values given by Hernández-Fernández and Peláez-Campomanes (2005). Mean Annual Temperatures (MAT), Mean Temperatures of the Coldest and Warmest months (MTC and MTW respectively) and Mean Annual Precipitation (MAP) has been obtained. The data has been compared to the present conditions registered at Amendola meteorological station (Foggia, Apulia, 41°32′N, 15°42′E), approximately 10 km SE from the site. The current data are: MAT = 15.4 °C, MTW = 24.8 °C, MTC = 7.3 °C and MAP = 494.7 mm.

4. Results and discussion

4.1. *The small mammal assemblage from Grotta Paglicci*

The main accumulation cause for small mammal assemblages is

Table 1

Small mammals MNI percentages from layer 1 to 16 of Grotta Paglicci.

	1	2	3	4a	4b	4c	5a	5b	5c	6	7	8a	8b	8c	8d	9	10	11	14	15	16
Arvicola amphibius	17.65	27.03	35.18	38.00	37.84	24.00	26.83	26.09	11.76	10.53	14.29	22.22	15.38	6.67	33.33	28.57	6.17		33.33	16.67	18.18
Chionomys nivalis											33.33			6.67			6.17				9.09
Microtus (*Terricola*) sp.			7.69		2.70					5.26											
cf. *Microtus* (*Terricola*) *savii*						32.00				15.79											
Microtus (*Terricola*) *savii*	55.88	59.46	45.05	42.00	35.14	22.00	46.34	56.52	79.41	57.89	14.29	22.22	46.15	40.00	66.67	14.29	7.41		33.33	16.67	9.09
cf. *Microtus arvalis*																					
Microtus arvalis			1.10	2.00	2.70		4.88				23.81	44.44	7.69	6.67		57.14	55.56	50.00	33.33	41.67	45.45
cf. *Microtus agrestis*																				16.67	
Microtus agrestis							2.44						7.69	6.67			2.47				
Clethrionomys glareolus											4.76			6.67			2.47	50.00			9.09
Apodemus gr. *sylvaticus-flavicollis*	20.59	8.11	3.30	10.00	16.22	12.00	12.20	8.70	5.88		9.52	11.11	7.69	20.00			6.17			8.33	9.09
Rattus rattus	2.94																				
cf. *Eliomys quercinus*																					
Eliomys quercinus	2.94	5.41	3.30	2.00	2.70	6.00	7.32	4.35	2.94	5.26			7.69				2.47				
cf. *Talpa europaea*				2.00																	
Talpa europaea																					
cf. *Talpa romana*			1.10														7.41				
Talpa romana			1.10	4.00	2.70	4.00		4.35		5.26							2.47				
Sorex minutus																	1.23				
Crocidura suaveolens			1.09											6.67							
Erinaceus europaeus			1.09										7.69								
TOTAL NMI	**34**	**37**	**91**	**50**	**37**	**50**	**41**	**23**	**34**	**19**	**21**	**9**	**13**	**15**	**9**	**7**	**81**	**2**	**3**	**12**	**11**

Table 2

Small mammals MNI percentages from layer 17 to 24 of Grotta Paglicci.

	17	18	19a	19b	20a	20b	20c	20d	20e	21a	21b	21c	21d	22a	22b	22c	22d	22e	22f	23a	23b	23c	24
Arvicola amphibius	2.44	7.69	2.78	3.57	2.38	1.04	0.98	2.50	0.97	1.03	1.51	3.13	0.85	0.69	2.33	1.16	1.15	0.85	8.33	2.24	2.30	3.41	5.56
Chionomys nivalis		3.85		2.38	2.38	2.60	1.31	0.63	1.94	1.24	1.01	2.08	0.17								0.57	2.27	
Microtus (*Terricola*) sp.			1.39	0.40						0.41				0.93			1.15	2.56		0.75			
cf. *Microtus* (*Terricola*) *savii*								0.63															
Microtus (*Terricola*) *savii*	11.38	3.85	4.17	2.78	6.55	6.25	5.25	7.50	6.07	5.57	5.03	6.25	4.94	5.09	2.33	3.49	4.60	13.68	8.33	11.94	6.32	4.55	16.67
cf. *Microtus arvalis*							0.98			0.41													
Microtus arvalis	73.17	66.67	68.06	76.98	79.76	81.77	77.70	81.25	85.92	81.65	84.92	80.21	89.95	87.04	79.07	91.86	81.61	75.21	75.00	74.63	81.03	68.18	61.11
cf. *Microtus agrestis*	0.81	1.28	4.17	1.59	1.19	1.04	2.95	0.63		1.44	1.51		0.17	2.08		1.16	6.90			0.75	1.72	1.14	
Microtus agrestis	3.25	2.56	1.39	0.79	1.19	0.52	3.28	1.88	2.43	2.68	2.51	1.04	0.51	0.23	6.98		2.30			2.24			
Clethrionomys glareolus	3.25	2.56	2.08	3.57	1.19	1.04	2.30	2.50	1.21	1.86	1.01	1.04	0.85	0.69				0.85		2.24	1.72	2.27	5.56
Apodemus gr. *sylvaticus-flavicollis*	2.44	7.69	7.64	4.37	4.17	4.69	2.62	1.88	1.21	2.68	1.51	5.21	1.70	2.08	6.98	2.33	1.15	4.27	8.33	2.99	3.45	10.23	2.78
cf. *Eliomys quercinus*										0.21													
Eliomys quercinus	1.63	2.56	2.78	0.79			0.33		0.24		0.50		0.34	0.23	2.33			0.85		1.49	2.30	7.95	5.56
Talpa sp.			1.39	0.40										0.46									
cf. *Talpa europaea*																				0.75			
Talpa europaea														0.23									
cf. *Talpa romana*																		0.85					
Talpa romana		1.28	2.08	1.19			0.33			0.41	0.50		0.17										
Sorex ex gr. *araneus*	1.63		0.69	0.79	1.19	1.04	1.64	0.63		0.21		1.04	0.17	0.23			1.15	0.85					2.78
Sorex minutus			0.69	0.40			0.33			0.21			0.17								0.57		
TOTAL NMI	**123**	**78**	**144**	**252**	**168**	**192**	**305**	**160**	**412**	**485**	**199**	**96**	**587**	**432**	**43**	**86**	**87**	**117**	**24**	**134**	**174**	**88**	**36**

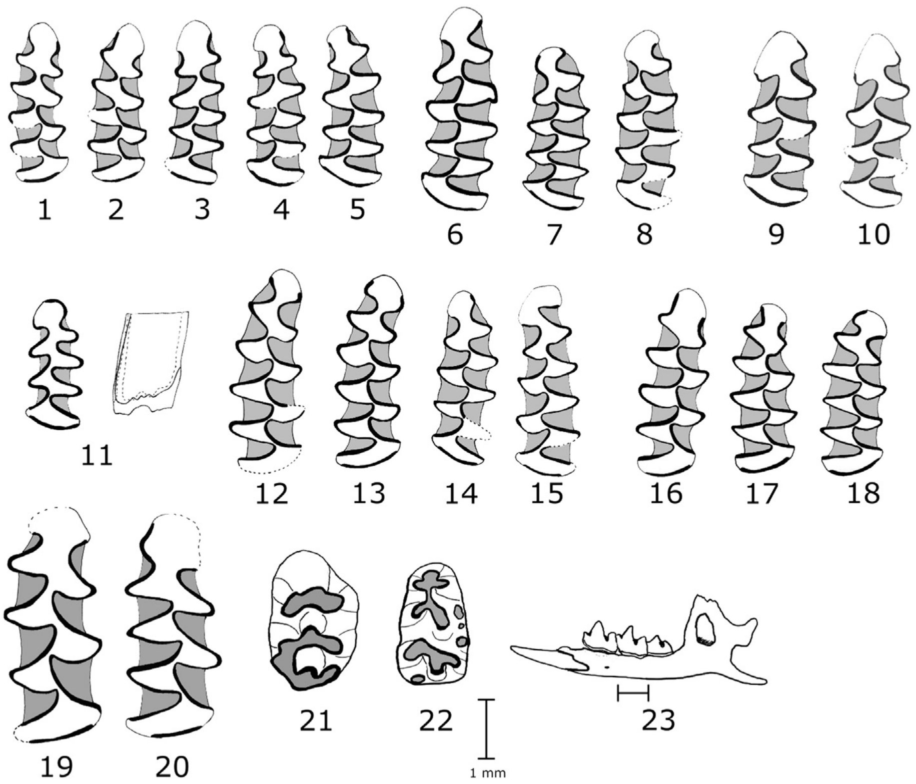

Fig. 3. Some identified small mammals from Grotta Paglicci, all scales are 1 mm long. 1 and 2: *Microtus* (*Terricola*) *savii*, right m1, layer 20 a; 3–5: *Microtus* (*Terricola*) *savii*, left m1, layer 20 a; 6–7: *Microtus agrestis*, left m1, layer 23 a; 8: *Microtus agrestis*, left m1, layer 23 c2; 9–10: *Chionomys nivalis*, left m1, layer 10 c; 11: *Clethrionomys glareolus*, left m1 (occlusal view and labial view), layer 10 e; 12–13: *Microtus arvalis*, right m1, layer 23 a; 14: *Microtus arvalis*, left m1, layer 23 a; 15: *Microtus arvalis*, left m1, layer 23 c2; 16–18: *Microtus arvalis*, right m1, layer 23 a; 19: *Arvicola amphibius*, right m1, layer 10 e; 20: *Arvicola amphibius*, right m1, layer 7 a; 21: *Apodemus* gr. *sylvaticus-flavicollis*, right M1, layer 8 c; 22: *Apodemus* gr. *sylvaticus-flavicollis*, right m1, layer 8 b; 23: *Crocidura suaveolens*, left mandible with i1, m1, m2 and m3, layer 8 c.

Table 3
Species distribution by habitat (OD: Open Dry; OH: Open Humid; OW: Open Woodland; R: Rocky; Wa: Water) and by climatic preferences (Hernández-Fernández, 2001): I: equatorial; II: tropical with summer rains; II/III: transition tropical semi-arid; III: sub-tropical arid; IV: winter rain and summer drought; V: warm-temperate; VI: typical temperate; VII: arid-temperate; VIII: cold-temperate (boreal); IX: Arctic.

	Habitat							Climatic Zone									
	OD continental	OD mediterranean	OH	OW	W	R	Wa	I	II	II/III	III	IV	V	VI	VII	VIII	IX
Arvicola amphibius							1	0	0	0	0	0.25	0	0.25	0.25	0.25	0
Chionomys nivalis						1		0	0	0	0	0.25	0	0.25	0	0.25	0.25
Microtus (*Terricola*) *savii*		1						0	0	0	0	1	0	0	0	0	0
Microtus arvalis	0.75			0.25				0	0	0	0	0	0	1	0	0	0
Microtus agrestis			1					0	0	0	0	0	0	0.5	0	0.5	0
Clethrionomys glareolus				0.25	0.75			0	0	0	0	0	0	0.5	0	0.5	0
Apodemus flavicollis					1			0	0	0	0	0	0	1	0	0	0
Apodemus sylvaticus					1			0	0	0	0	0.5	0	0.5	0	0	0
Rattus rattus								0.143	0.143	0.143	0.143	0.143	0.143	0.143	0	0	0
Eliomys quercinus					0.75	0.25		0	0	0	0	0.5	0	0.5	0	0	0
Talpa europaea			0.5	0.5													
Talpa romana			0.5	0.5													
Sorex ex gr. *araneus*			0.75	0.25													
Sorex minutus				0.25	0.5		0.25										
Crocidura suaveolens			0.5	0.5													
Erinaceus europaeus				0.25	0.75												

predation (Andrews, 1990; Fernández-Jalvo et al., 2016); usually, three main categories of predators can be distinguished: nocturnal raptors, diurnal bird of prey and small carnivores; each category leaves different digestion marks on the sample (Fernández-Jalvo et al., 2016). Although a complete taphonomic analysis of the fossil small mammals has not been completed yet, light and moderate digestion evidence have been observed, especially on arvicolid molars, suggesting that the Grotta Paglicci small mammals have been accumulated mainly by nocturnal birds of prey.

The sequence is subdivided into two main parts (Fig. 4). In the first part (layers 24 to 19b) (Table 4) the assemblage is characterized by a low diversity (Simpson 1-D from 0.1 in layer 22c and 21d to 0.5 in layer 24) and by a preponderance of *Microtus arvalis*. The frequency of this arvicolid is always over 60% and it reaches its maximum in layer 22c, where the species percentage is 91.86%. Although it is difficult to appreciate the faunal variations along this

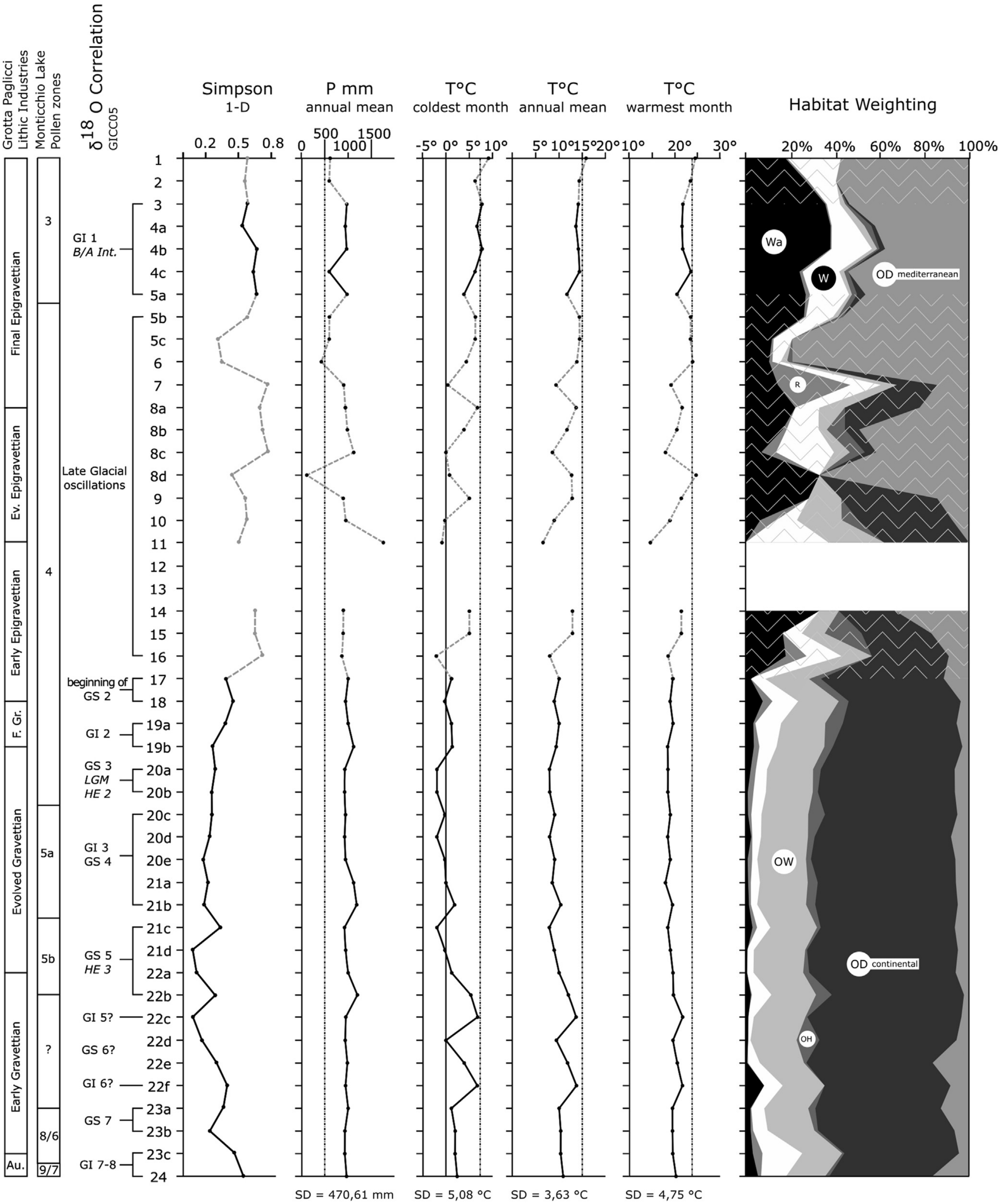

Fig. 4. Representation of the small mammal Simpson diversity index (1-D), the mean annual precipitation (MAP), the mean annual temperature of the coldest month (MTC), the mean annual temperature (MAT) the mean annual temperature of the warmest month (MTW) and the landscape percentages (OD mediterranean: open meadows related to Mediterranean conditions; OD continental: open meadows related to continental conditions; OH: open humid meadows; W: woodlands; R: rocky areas; Wa: areas along streams, lakes and ponds); Habitat Weighting white lines (from layer 16 to 5b, layers 3 and 2): low MNI.

Table 4
Biodiversity, Climate and Landscape values. Number of taxa in each layer; values obtained for evenness: Simpson diversity index $= 1\text{-}\Sigma(p_i^2)$; Relation of temperature and precipitation for Grotta Paglicci sequence: MAT: Mean Annual Temperature, MTW: Mean Temperature of the Warmest month, MTC: Mean Temperature of the Coldest month; Percentage representation of small mammal taxa associated with open dry meadows (OD, mediterranean and continental), open humid meadows (OH), open woodland environments (OW), woodland environments (W), rocky environments (R) and landscapes constituted by river, lakes and ponds (Wa).

Layer	Biodiversity		Climate				Landscape						
	Taxa	Simpson 1-D	MAT	MTW	MTC	MAP	OD cont.	OD Med.	OH	OW	W	R	Wa
1	5	0.5795	15.8	24.5	9.0	619	0.0	57.6	0.0	0.0	23.5	0.8	18.2
2	4	0.555	14.4	23.4	6.2	599	0.0	59.5	0.0	0.0	12.2	1.4	27.0
3	8	0.5793	14.2	21.7	7.7	973	0.8	53.5	1.1	2.2	5.8	0.8	35.7
4a	5	0.533	13.7	21.6	6.7	943	1.5	42.0	3.0	3.5	11.5	0.5	38.0
4b	6	0.6617	14.2	21.7	7.7	973	2.0	37.8	1.4	2.0	18.2	0.7	37.8
4c	5	0.6312	14.4	23.4	6.2	599	0.0	54.0	2.0	2.0	16.5	1.5	24.0
5a	6	0.6706	11.8	20.5	3.9	989	3.7	46.3	2.4	1.2	17.7	1.8	26.8
5b	5	0.5847	14.4	23.4	6.2	599	0.0	56.5	2.2	2.2	12.0	1.1	26.1
5c	4	0.3105	14.4	23.4	6.2	599	0.0	79.4	0.0	0.0	8.1	0.7	11.8
6	4	0.3508	13.8	23.9	4.4	434	0.0	78.9	2.6	2.6	3.9	1.3	10.5
7	6	0.7662	9.3	19.2	0.3	900	17.9	14.3	0.0	7.1	13.1	33.3	14.3
8a	4	0.6852	13.7	21.6	6.7	943	33.3	22.2	0.0	11.1	11.1	0.0	22.2
8b	7	0.7111	11.8	20.5	3.9	989	6.1	49.0	8.2	4.1	14.3	2.0	16.3
8c	9	0.7685	8.6	18.1	0.0	1117	5.2	41.4	6.9	6.9	25.9	6.9	6.9
8d	2	0.4331	12.6	24.8	0.7	105	0.0	66.7	0.0	0.0	0.0	0.0	33.3
9	3	0.5628	12.8	21.5	5.0	894	42.9	14.3	0.0	14.3	0.0	0.0	28.6
10	10	0.5759	9.0	19.0	−0.2	945	41.9	7.5	7.5	19.9	9.9	6.8	6.5
11	2	0.5	6.5	14.7	−0.8	1770	37.5	0.0	0.0	25.0	37.5	0.0	0.0
14	3	0.66	12.8	21.5	5.0	894	25.0	33.3	0.0	8.3	0.0	0.0	33.3
15	4	0.66	12.8	21.5	5.0	894	31.3	16.7	16.7	10.4	8.3	0.0	16.7
16	6	0.7218	8.0	18.6	−2.0	862	34.1	9.1	0.0	13.6	15.9	9.1	18.2
17	8	0.391	10.1	19.7	1.2	1000	54.9	11.4	5.3	19.5	6.1	0.4	2.4
18	9	0.4642	9.0	19.0	−0.2	945	50.0	3.8	4.5	17.9	11.5	4.5	7.7
19a	12	0.399	10.1	19.7	1.2	1000	51.0	5.6	7.8	19.6	11.6	1.0	3.3
19b	13	0.2798	9.5	18.5	1.3	1115	57.9	3.2	3.8	21.3	7.7	2.6	3.7
20a	8	0.2992	8.0	18.5	−1.9	924	59.8	6.5	3.3	20.5	5.1	2.4	2.4
20b	8	0.2666	8.0	18.5	−1.9	924	61.3	6.3	2.3	21.0	5.5	2.6	1.0
20c	11	0.2683	9.0	19.0	−0.2	945	59.1	5.3	7.6	20.9	4.6	1.4	1.1
20d	8	0.2496	8.0	18.5	−1.9	924	60.9	8.1	3.0	21.1	3.8	0.6	2.5
20e	8	0.1935	9.0	19.0	−0.2	945	64.4	6.1	2.4	21.8	2.3	2.0	1.0
21a	10	0.2272	8.6	18.1	0.0	1117	61.6	6.0	4.5	21.3	4.2	1.3	1.1
21b	9	0.2057	10.3	19.5	1.8	1181	63.7	5.0	4.3	21.7	2.6	1.1	1.5
21c	8	0.335	8.0	18.5	−1.9	924	60.2	6.3	1.8	20.6	6.0	2.1	3.1
21d	11	0.09724	9.0	19.0	−0.2	945	67.5	4.9	0.9	22.9	2.6	0.3	0.9
22a	10	0.1225	10.1	19.7	1.2	1000	65.3	6.0	2.8	22.3	2.8	0.1	0.7
22b	6	0.2939	12.0	19.7	5.3	1201	59.3	2.3	7.0	19.8	8.7	0.6	2.3
22c	4	0.09858	13.7	21.6	6.7	943	68.9	3.5	1.2	23.0	2.3	0.0	1.2
22d	6	0.1761	9.5	19.7	0.0	938	61.2	5.7	10.1	20.7	1.1	0.0	1.1
22e	7	0.3032	11.8	20.5	3.9	989	56.4	16.2	1.1	19.7	5.6	0.2	0.9
22f	4	0.4048	13.7	21.6	6.7	943	56.3	8.3	0.0	18.8	8.3	0.0	8.3
23a	7	0.3748	10.1	19.7	1.2	1000	56.0	12.7	3.4	19.6	5.8	0.4	2.2
23b	8	0.2548	10.3	19.6	1.9	927	61.0	6.3	1.7	20.9	6.5	1.2	2.4
23c	7	0.4715	10.3	19.6	1.9	927	51.1	4.5	1.1	17.6	17.9	4.3	3.4
24	7	0.5529	10.9	20.2	2.3	968	45.8	16.7	2.1	17.4	11.1	1.4	5.6

part of the sequence, it is possible to detect some differences between different layers: in layers 24 and 23c the diversity is relatively high (1-D = 0.55 and 0.47 respectively). *Microtus arvalis* is always dominant but other species have relatively high percentages, such as *Microtus* (*Terricola*) *savii* in layer 24 (16.67%), *Apodemus* gr. *sylvaticus-flavicollis* and *Eliomys quercinus* in layer 23c (10.23% and 7.95% respectively). Thus, the associations of these two layers record a sensible percentage of woodland component (11.11% in layer 24 and 17.91% in layer 23c) if compared to the other layers of this part of the sequence. The environment surrounding the cave was mainly open with the presence of woodland, woodland margin and forest patches.

The MAT, MTC and MTW calculated for these layers are around 5 °C lower than the current means suggesting colder climatic conditions with respect to present day. The MAP variations along the first part of the sequence are not significant except in layers 22b, 21b and 21a where a slight increase in precipitation is registered together with a rise in temperature.

The woodland component decreases quickly in unit 23b (6.48%) and it continues to be lower than 10% up to layer 19a. From layer 23b to layer 19b the biodiversity index ranges from 0.4 (layer 22f) to 0.1 (layers 22c and 21d). This means that, during the deposition of these layers, the diversity was poor with an assemblage characterized by few species and dominated by *Microtus arvalis*. A recrudescence in climate is registered too. The MAT, MTC and MTW values decrease reaching 7–9 °C lower than the current means. In these layers, at least three warming-up events are present. One in layer 22f (also showing a low value in MNI), one in layer 22c and a weak one in layer 19b. These warming peaks do not always reflect a change in habitat distribution. Open environments characterized by dry meadows continue to be the most represented and only slight increases can be identified in the forest component in layers 22f, 22b, 21c and 19b.

The second part of the sequence (Table 4) begins at the transition between the Final Gravettian and the Early Epigravettian layers (from 19a to 17) and continues up to the top of the sequence (Final Epigravettian, layer 3a), reflecting a radical change in both climate and environment. Climate shifts from cold continental to mediterranean. It can be argued that this change was gradual, even though several layers of this section have a low MNI and no small mammals were identified in layers 12 and 13. The change seems to start in layer 19a-17 with a slight decrease in *Microtus arvalis* frequency which also corresponds to an increase in diversity. The increase of *Microtus* (*Terricola*) *savii*, a species that will dominate the assemblage in the upper part of the sequence, begins in layer 17 (11.38%). A woodland and water increase is recorded among habitat components and there is a rise in mean temperatures even though they still remain below present day means. After several layers with low MNI or with no individuals at all, layer 10 shows similar conditions to the ones recorded in layers 19a-17, both in terms of habitats and climate. *Microtus arvalis* still dominates the assemblage but diversity is still relatively high ($1\text{-}D = 0.58$) and there is a relevant percentage of *Chionomys nivalis*, suggesting that climate was still cold and arid if compared to present day conditions.

The major changes occur from layer 9 to 4, where an assemblage dominated by *Microtus arvalis* is replaced by one dominated by *Microtus* (*Terricola*) *savii* and *Arvicola amphibius*. There is a well distributed diversity, even if the number of species remains low throughout. The open environments with dry meadows continue to be dominant but are set within a more Mediterranean context with a patchy presence of mature woodlands. Water streams, ponds or rivers close to the site which were not recorded in the lower layers, were the right habitat for *Arvicola amphibius*. The environmental change is related to a general warming that took place during the deposition of layers 9-4. MAT, MTW and MTC are close to present-day conditions (from 0.3 to 4.3 °C lower than the present means). Since the MNI in most of these layers is low, it is not possible to identify the exact moment when this change occurred in the small mammal assemblage.

The sequence ends with layer 3, where the climatic conditions do not change significantly and only a reduction of the forest component due to a decrease in the percentage of *Apodemus* gr. *sylvaticus-flavicollis* is recorded.

4.2. Correlation between $\delta^{18}O$, pollen records and ungulates record

The long stratigraphy of Grotta Paglicci, the many radiometric dates available for it and the studies of other bioclimatic indicators allow us to correlate the sequence of Grotta Paglicci to the $\delta^{18}O$ curve (GICC05, Andersen et al., 2006; Svensson et al., 2006) and to the pollen sequence of Lago Grande di Monticchio (Allen et al., 2000; Allen and Huntley, 2009).

The first part of the sequence (layers 24 and 23c) can be correlated to Greenland Interstadials 7 or 8 (Fig. 4). This imprecision is caused by two factors: the high σ of the radiometric date and the low MNI in the small mammal assemblages. This relatively temperate phase can be related to PAZ 9 or 7 of Lago Grande di Monticchio where woody taxa are relatively abundant. The climatic recrudescence recorded in layers 23b and 23a can be related to GS 7 according to radiometric dates and to PAZ 8 or 6. This temperate phase followed by a cold one is visible in the large mammals record where *Equus hydruntinus* decreases and *Bos primigenius* and *Capra ibex* increase. The presence of *Sus scrofa* from layers 23c to 22e confirms that the forest component was present up to GS 5.

The two warming up peaks recorded in layers 22f and 22c can be tentatively linked to GI 6 and GI 5. These two chronologically close interstadials are difficult to detect in continental deposits (Berto, 2013). Furthermore, the correlation between 22f and GI 6 is uncertain because of the low MNI (MNI = 24). In the large mammals record this part of the sequence is initially characterized by an assemblage dominated by *Bos primigenius* (from layer 22f to layer 22d) followed by one dominated by *Capra ibex* and *Rupicapra* sp. (22c), with a strong decrease in wild boar and hydruntinus. Taking these data into account, it is more prudent to attribute layers 22f, 22e, 22d and 22c to a warm-cold oscillation which took place around GI 6, GS 6 and GI 5.

The cold and arid oscillation recorded between 22b and 21c probably falls in Heinrich Event 3 (GS 5); this phase can be related to Lago Grande di Monticchio PAZ 5b/beginnings of 5a. The best represented Ungulates are caprines and horse. Layers 21b to 20c probably formed during GI 4, 3 and GS 4 corresponding to PAZ 5a. Also these latter oscillations are difficult to distinguish because the time interval between them is short and the small mammal assemblage does not vary significantly. Furthermore, it is also possible that the onset of the Last Glacial Maximum has to be placed in layer 20e, where small mammals indicate low temperatures and arid environments characterized mainly by open meadows. Among ungulates, the highest percentage of *Capra ibex* of the whole sequence is recorded from layer 21b to layer 20e. Layers 20b and 20a represent the LGM peak: at this moment MAT, MTW and MTC record the lowest values of the whole sequence.

The end of LGM (GI 2) corresponds to the increase in temperatures and in woody habitats identified in layers 19b and 19a. Lago Grande di Monticchio sequence does not record this moment. Herbaceous pollen (PAZ 4) dominates until the Bølling-Allerød Interstadial (PAZ 3). The climatic recrudescence recorded in layer 18 represents the beginning of the Late Glacial (GS 2).

From this point onwards, the correlation between the Grotta Paglicci small mammal record and $\delta^{18}O$ become difficult to draw due to a lack of material or to a low MNI. Considering the radiometric dates, the first part of the Late Glacial (Ravazzi et al., 2007) is represented from layer 17 to layer 5. It is probably during this phase that climate conditions starts to vary from continental to mediterranean. Small mammal remains fail to identify the exact layer where this change happened but the large mammal assemblage helps to better understand this moment. Starting from the upper portion of layer 6 (layer 6a: 18,223–16,360 cal BP) forest related ungulates (mainly *Sus scrofa* and *Cervus elaphus*) percentages rise, while *Capra ibex* and *Equus ferus* almost disappear in favour of *Equus hydruntinus*.

This moment precedes onset of the Bølling-Allerød Interstadial (GI 1) which is represented by layer 4 and 3. In these latter layers, the presence of *Capreolus capreolus* among ungulates is significant and temperatures values are close to present-day means.

4.3. Grotta Paglicci in the bioclimatic context of the Southern Italian Peninsula during the Upper Palaeolithic

The small mammal assemblage from Grotta Paglicci confirms the peculiarity of the South-Eastern region of the Italian Peninsula. During the Late Pleistocene cold oscillations this area may have acted as a glacial refuge, especially for *Microtus* (*Terricola*) *savii* (Curcio et al., 2005; Kotsakis et al., 2003; Sommer and Nadachowski, 2006 among others).

In the small mammal assemblages coming from archaeological sites of this region and belonging to the late Upper Pleistocene (end MIS 3, MIS 2, and first part of MIS 1) the main characteristic is the strong dominance of one species over the others. The dominant species sometimes reaches 90% of the assemblage and it generally is *Microtus arvalis* or *Microtus* (*Terricola*) *savii*. The low percentages of forest species such as *Apodemus* gr. *sylvaticus-flavicollis*, *Clethrionomys glareolus* and *Glis glis* and the relative abundance of *Eliomys quercinus* also characterize these assemblages (Berto, 2013).

In Southern Apulia, *Microtus* (*Terricola*) *savii* is always dominant even during the cold phases, as shown at Grotta delle Cipolliane (Bon and Menon, 2000), Grotta del Cavallo layers B (Benazzi et al., 2011; Dalla Valle, 2008) and Grotta dei Cervi di Porto Badisco (Cason, 2012) (Fig. 1A). In Abruzzo and Molise, north of Grotta

Paglicci, the situation differs depending on site setting. At Grotta Reali (G.I. 8, 7 and 6; De Curtis, 2012; Lembo et al., 2012; Sala et al., 2012) *Microtus* gr. *arvalis-agrestis* is always dominant and *Microtus* (*Terricola*) *savii* is absent. This is probably due to the particular geographic position of this site in inland Molise region. In Abruzzo, Riparo Ermanno de Pompeis (Pescara) contains a sequence dated to the Late Glacial (between the first part of the Late Glacial and the Bølling-Allerød Interstadial) with *Microtus* (*Terricola*) *savii* as the dominant species (Bon and Boschian, 2006). For the Eastern side of the Italian Peninsula, this is the northernmost Late Pleistocene assemblage where such species is dominant and the northernmost site where it is attested. In this context, Grotta Paglicci is a sort of passage point between the southernmost (mediterranean) and the northernmost biocoenoses of this particular region. During the last phases of the Late Pleistocene (Late Glacial) the climatic change from continental to mediterranean caused a return of the southern species to the Gargano area and, more generally, to northern Apulia, coastal Molise and Abruzzo regions. The expansion of *Microtus* (*Terricola*) *savii* probably continues during the Holocene in the whole of the Italian Peninsula also fostered by agricultural activities and deforestation that created a suitable habitat for this species.

On the western side of the Italian Peninsula, there exist three main sequences contemporary to Grotta Paglicci: Grotta della Cala (Bambini, 1996; Bartolomei and Broglio, 1976; Benini et al., 1997; Sala, 1983), Riparo del Romito (López-García et al., 2014; Malavasi, 2006) and Grotta della Serratura (Bertolini et al., 1996). Even considering the differences between these sites (for position and chronology) the main characteristic of this area is the relative high percentage of the forest component (*Apodemus* gr. *sylvaticus-flavicollis* and *Glis glis*) which during the Bølling-Allerød Interstadial became dominant at Riparo del Romito (layers D) and abundant at Grotta della Serratura (layers 8f and 8e).

The differences between the eastern and western side of the Southern Italian Peninsula are mainly attributable to the presence of the Apennines chain which sits in between these two areas. The small mammal assemblage from Grotta Paglicci fits into the eastern side biocoenones confirming that even during the Upper Palaeolithic strong aridity was the main characteristic of south-eastern Italy.

5. Conclusions

The small mammal record from Grotta Paglicci is one of the most complete of the Italian Peninsula and it greatly contributes to the study of climate during the Upper Paleolithic in Southern Italy.

This assemblage can be divided into two parts. In the first one (layers 24 to 17) *Microtus arvalis* is always dominant. This first part ranges from the end of MIS 3 (Greenland Interstadial 7/8) to the beginning of Late Glacial (MIS 2, shortly after the GI 2). *Microtus* (*Terricola*) *savii* and *Arvicola amphibius* dominate the second part (from layer 16 to 3a) which is correlated to the beginning of Late Glacial and Bølling-Allerød Interstadial (GI 1).

The change in the small mammal assemblage reflects a change in climate and environment. During the accumulation of the first part of the sequence, the landscape surrounding the cave was mainly open with dry meadows and scarce forest areas. Climate was continental with low temperatures and precipitations were well distributed over the year. Even if this part of the sequence is monotonous, Heinrich Events 3 (layers 22b to 21c) and 2 (LGM, layers 20b and 20a) are well visible and characterized by temperatures often 9 °C below the current means.

A major climatic and environment change has been individuated within the Epigravettian (Late Glacial). The climate becomes Mediterranean with temperatures close to the present-day means and precipitations are concentrated within few months. It is possible that water streams, lakes and ponds were present during this period along the alluvial fan and on the underlying plain.

This change was gradual and it probably started during the first part of the Late Glacial, after the GI 2. Unfortunately, such a gradual change cannot be described in detail because the layers which accumulated during this period have a low MNI. The climatic switch came to an end during the Bølling-Allerød Interstadial (GI 1) when forest environments developed along the Gargano area in a Mediterranean climate similar to the present-day one.

The comparison with other Southern Italian small mammal sequences confirms that the climate in Apulia was more arid than in the western side of the Italian Peninsula. After the Last Glacial Maximum, *Microtus* (*Terricola*) *savii* may have started to become dominant in northern Apulia before its spread in the northern regions of the Italian Peninsula which took place during the Holocene.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.quascirev.2017.05.004.

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Climate and landscape in Italy during Late Epigravettian. The Late Glacial small mammal sequence of Riparo Tagliente (Stallavena di Grezzana, Verona, Italy)

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ABSTRACT

The site of Riparo Tagliente (north-eastern Italy) contains one of the main Upper Pleistocene archaeological sequences of south-western Europe. It also represents a key site for the study of human adaptation to Late Glacial environmental changes in the southern Alpine area. These climatic and environmental conditions are here reconstructed based on small mammal assemblages, using the Bioclimatic model and Habitat Weighting methods. Climate proxies indicate a rise in temperature during the transition between HE1 and the Bølling-Allerød interstadial, while the landscape surrounding the shelter was still dominated by open grasslands. By comparing the data obtained from Riparo Tagliente with other coeval small mammal faunas from the Italian Peninsula and Europe we contribute to the reconstruction of the processes of faunal renewal registered during the Late Glacial across the continent and of the climatic and environmental context in which the Late Epigravettian hunter-gatherer groups lived.

1. Introduction

The late Upper Pleistocene is characterized by several climatic oscillations which correspond to the Marine Isotopic Stage 2 (MIS 2) and to the beginning of MIS 1 (ca 14.7 ka cal BP) (Lisiecki and Raymo, 2005). After the end of the Last Glacial Maximum (LGM), the final phase of MIS 2 is characterized by three different climatic events. Heinrich Event 1 (H1, Bond et al., 1993) is an arid phase, resulting across the Alpine region in a series of dramatic glacial collapses and periglacial rearrangements (Ravazzi et al., 2014, 2007a). Then, a rapid increase in the temperatures and the development of forest environments is recorded. This marks the beginning of the Bølling-Allerød Interstadial (corresponding roughly to Greenland Interstadial 1 – GI-1), a relatively warm period with several minor oscillations, which have been observed in particular in the northern Alps region (Ravazzi et al., 2007a). Finally, the Upper Pleistocene ends with the cold oscillation called Younger Dryas, broadly equivalent to the Greenland Stadial 1 (GS-1, Rasmussen et al., 2014), the beginning of which is dated at around 12,800 years cal BP (Andersen et al., 2006; Rasmussen et al., 2014; Svensson et al., 2006).

In this climatic context, the faunal assemblages of the Italian Peninsula are characterized by a strong regionalism, which is already evident before the end of Upper Pleistocene (Gliozzi et al., 1997; Masini and Sala, 2011, 2007; Sala, 2007; Sala et al., 1992; Sala and Masini, 2007). Differences between the assemblages of the northern and southern areas of the peninsula are clearly visible (Sala, 2007), especially during the Late Glacial (Sala, 2007, 1990a). However, a variability related to the site's geographic settings (i.e. mountains, valleys, coastal areas) must also be considered. These faunal discontinuities are mainly the effect of relevant geographical features: the Alpine chain, which is considered as a barrier especially for gregarious ungulates (i.e. *Rangifer tarandus* and *Saiga*

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tatarica), the Apennines, which divide the peninsular area into two regions, the East and the West, and the Mediterranean sea with its climatic influence on the central and southern areas of the Italian Peninsula (Berto, 2013; Sala, 2007, 1990b).

We present here the palaeoclimatic and palaeo-environmental data which have been inferred from the small mammal sequence of Riparo Tagliente. A special focus is kept on the variations of rodent communities in the Italian Peninsula during the Late Glacial, through comparisons with other major sites of this territory.

The Late Glacial sequence of Riparo Tagliente has vastly contributed to the knowledge of the technological and subsistence strategies of Late Epigravettian hunter-gatherers in the Southern Alps (Bartolomei et al., 1982; Bertola, 2015; Fontana et al., 2011, 2009; Ravazzi et al., 2007b). This study will help to reconstruct the local climatic and environmental conditions that the human groups inhabiting this region faced in a period of great climatic fluctuations (Bartolomei et al., 1982; Fontana et al., 2009; Pini et al., 2010a).

2. The site

Riparo Tagliente (Stallavena di Grezzana, Verona) is considered to be a key site for the Middle and Upper Palaeolithic in Italy (Bartolomei et al., 1982; Fontana et al., 2009; Thun Hohenstein and Peretto, 2005). It is located on the left slope of Valpantena, one of the main valleys of the Pre-alpine massif of Monti Lessini, at 226 m a.s.l. (Fig. 1, A).

The site was discovered in 1958 (Zorzi, 1962). It was initially investigated by the Museo Civico di Storia Naturale di Verona, and, from 1967, by the University of Ferrara. The research was initially focused on two trenches (called internal and external), in order to investigate the whole sequence (Bartolomei et al., 1982). Starting from the late ’70s, excavations in the Late Epigravettian deposit were extended over an area of about 80 m^2 (Fig. 1, B).

The stratigraphy of this site is characterized by two main deposits that are separated by a river erosion: (Fig. 1, C). The lower deposit (Mousterian and a thin Aurignacian layer detected only in the internal area) has been referred to ancient Würm or MIS 4-3 (Arnaud et al., 2016; Bartolomei et al., 1982). The small mammal assemblage of this part of the sequence is dominated by *Microtus arvalis*, with the presence of cold indicators, especially in the lower layers, such as *Microtus gregalis*, *Microtus oeconomus* and *Ochotona* sp. (Bartolomei et al., 1982).

The upper part of the deposit (Late Epigravettian) is irregular, thinner in the inner part of the shelter (about 50 cm) and thicker in the external one (over 2 m). This is due to the different uses of the two areas by the Epigravettian groups, and to a medieval excavation that destroyed most of the inner parts of the sequence (Bartolomei et al., 1982; Fontana et al., 2009). The Epigravettian deposit is divided into two sub-units, both set in a loess matrix. The lower one (cuts 18-15) is marked by debris, and is closed by a collapse (Bartolomei et al., 1982). Both sub-units (cuts 14-5) are characterized by an intense human occupation, testified not only by lithic industries and faunal remains, but also by spatial organization, ornaments, mobile art objects, and a burial (Bartolomei et al., 1982, 1974; Fontana et al., 2009).

Two different phases have been recognized from the analysis of the Epigravettian lithic assemblages: phase I (layers 17 to 12) is characterized by four different reduction sequences, each one aimed at obtaining a specific type of blank, and phase II (layers 11 to 6) is marked by a simplification of the reduction sequences (Bertola et al., 2007; Fontana et al., 2015). The radiometric dates of the Late Epigravettian sequence show that the formation of the deposit took place between GS-2.1a and GI-1c1 (Rasmussen et al., 2014), during the latest part of the Older Dryas and the first half of the Bølling-Allerød Interstadial, 17,219 to 13,472 years cal BP (Fig. 2). However, results from the recent ^{14}C dates of the lower part of the inner Epigravettian sequence (SUs 13aα, 13a and 300) appear older than the dates from the lowermost layers of the outer series (SUs 15–16). This suggests to consider with caution the latter radiometric dates (SUs 15–16 and 10) that were performed in the early ‘80s on charcoal samples from the trench area.

The large mammal remains, both from the external trench and from the extensive excavation (Bartolomei et al., 1982; Capuzzi and Sala, 1980; Fontana et al., 2009), testify to a change in the trophic community over time especially among ungulates. In the lower layers (18-13), *Capra ibex* is the most represented ungulate, while in the upper ones, starting from layer 10, *Cervus elaphus*, *Capreolus capreolus*, and *Sus scrofa* dominate the assemblage. This variation is also visible in the pollen diagrams and in the malacological assemblages recovered in the external trench (Bartolomei et al., 1982; Capuzzi and Sala, 1980). It has been linked (Bartolomei et al., 1982; Fontana et al., 2009) to the advance of the broadleaf forests in the eastern Prealps during the Bølling-Allerød Interstadial. A brief cold event, related to the Older Dryas (Greenland Interstadial 1c2), has also been detected from ungulates in layers 7b-5, where an increase in *Capra ibex*, *Alces alces*, and *Marmota marmota* is recorded.

3. Materials and methods

From the three investigated areas (Fig. 1, B) only the external one, excavated during the last thirty years, has been considered in this study. This choice derives from the presence in this area of a higher MNI with respect to the other two. In this area, 48 Stratigraphical Units/sedimentological layers have yielded small mammals. The Units have been grouped into six Macrounits following the stratigraphic reconstruction proposed in previous works (Bartolomei et al., 1982; Berto, 2013; Fontana et al., 2009; Scoz, 2007).

The sample is made of disarticulated bone fragments collected by water-screening during the last forty years of excavation campaigns and using 2 and 1 mm mesh sieves.

The assemblage includes a total of 1431 identified remains, corresponding to a minimum number of 839 individuals (Table 1; Fig. 3). The specific attribution of this material was based on the best diagnostic elements: mandible, maxilla and isolated teeth for rodents, mandible and maxilla for shrews, mandible, maxilla, isolated teeth and postcranial bones for *Talpidae*.

The taxonomic classification follows Wilson and Reeder (2005), except for *Clethrionomys glareolus* (for the priority over *Myodes*, see Tesakov et al. (2010)). Data on the distribution and habitat of the species were taken from Amori et al. (2008), Boitani et al. (2003), and Mitchell-Jones et al. (1999).

Biodiversity has been calculated using the Simpson index of Evenness $= 1-\sum(pi^2)$, where pi is the proportion of individuals in the ith species (Harper, 2005; Magurran, 2004). The evenness index is constrained between 0 and 1. The index has been calculated using PAST 3.04 avoiding redundant determinations (i.e., for *Arvicola amphibius*, the individuals determined as *Arvicola* cf. *amphibius* and *Arvicola* sp. have not been included) (Hammer et al., 2001).

3.1. Palaeoenvironmental and climatic reconstruction

In order to propose a palaeoenvironmental reconstruction for the Late Glacial sequence of Riparo Tagliente we used the Habitat Weighting method (Andrews, 2006; Evans et al., 1981), assigning each small mammal taxon to the habitat(s) where it can be presently found in Europe. For this purpose, habitats have been divided into six types (Cuenca-Bescós et al., 2009; López-García et al., 2014, 2010): open land with either dry and wet meadows (OD and OH,

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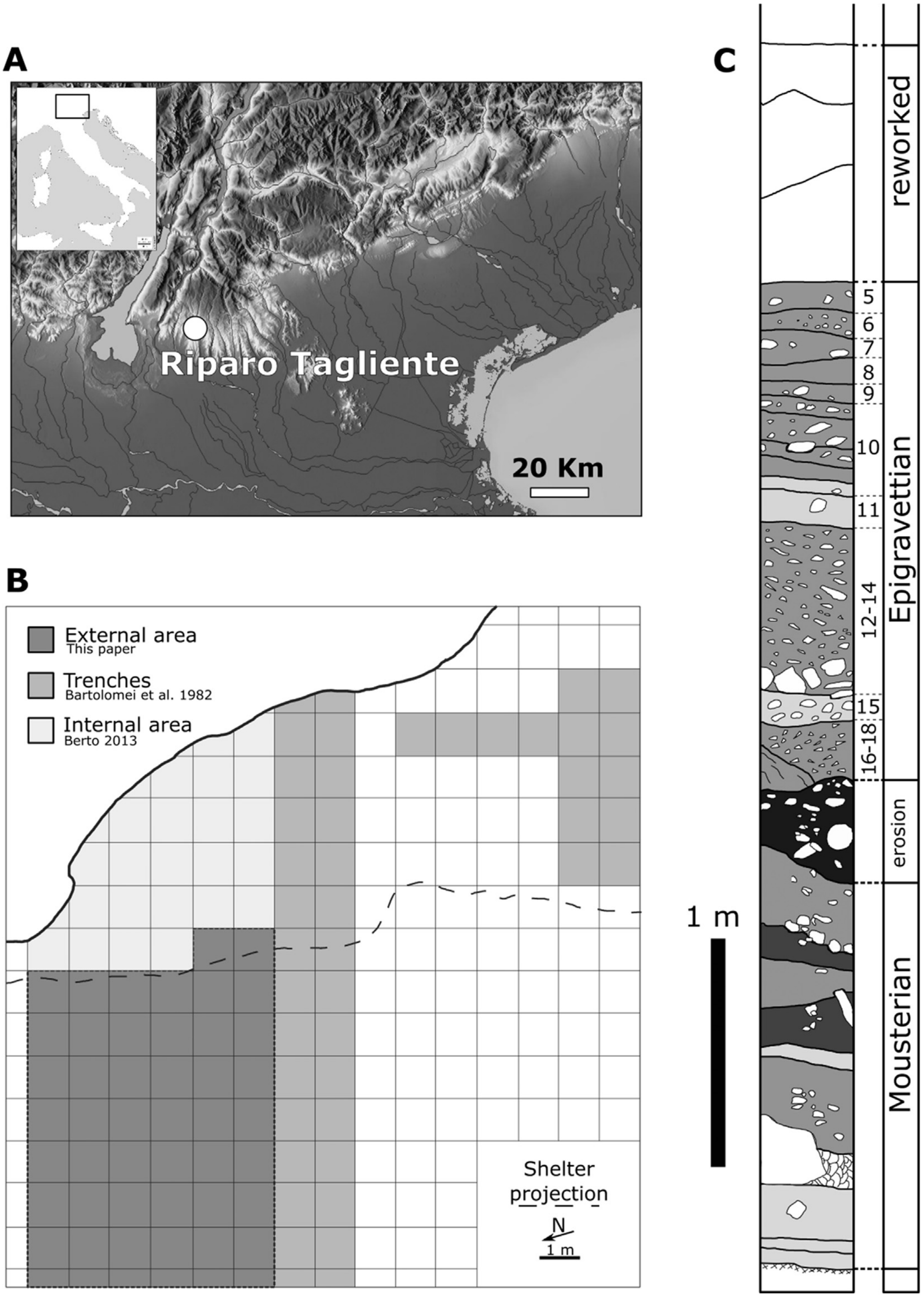

Fig. 1. Riparo Tagliente site location (A), planimetry with the investigated area (B) and stratigraphy (C), external trench, in this area Aurignacian layers are absent, modified from Bartolomei et al. (1982).

respectively); woodland environments, divided into open woodland, woodland margins and forest patches (OW) and woodland and mature forest habitat (W); water areas along streams, lakes and ponds (Wa); and habitats with a suitable rocky or stony substratum (R).

Palaeoclimatic data from Riparo Tagliente have been calculated using the Bioclimatic model described by Hernández Fernández (2001a, 2001b). First, each mammal species has been assigned to climatic types described in Hernández Fernández (2001b) and Walter (1970) following the values established in Hernández Fernández and Peláez-Campomanes (2005): IV Subtropical with winter rains and summer droughts; VI Typical temperate; VII Arid-temperate; VIII Cold-temperate (boreal) and IX Polar. The assemblage of each unit has been analysed using the Climatic Restriction

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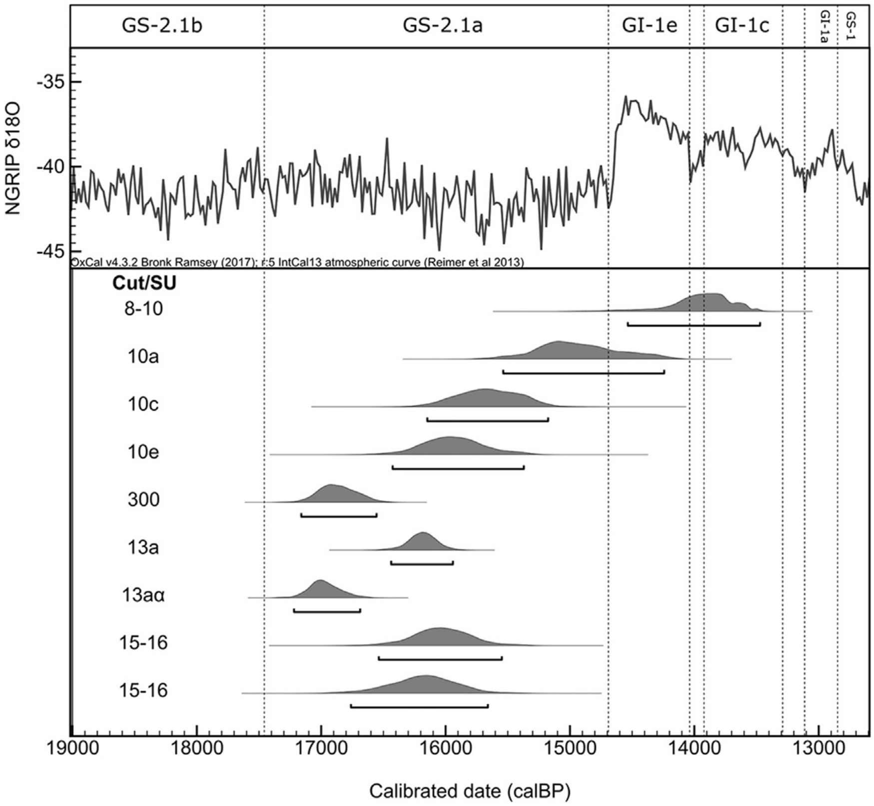

Fig. 2. Radiocarbon dates for the Units of Riparo Tagliente. Ages are calibrated with the OxCal 4.2 software (Bronk Ramsey, 2009) using the IntCal13 curve (Reimer et al., 2013).

Table 1
Small mammals NISP and MNI from Macrounit 5–7 to 13–14 of Riparo Tagliente.

	5–7			8–9			10			11			12			13–14		
	NISP	MNI	%MNI	NISP	MNI	%MNI	NISP	MNI	%MNI	NISP	MNI	%MNI	NISP	MNI	%MNI	NISP	MNI	%MNI
Arvicola amphibius	8	4	18.2	7	2	4.9	48	20	8.5	38	13	11.7	32	12	8.3	44	20	7.0
Clethrionomys glareolus							5	4	1.7	2	2	1.8	4	2	1.4	5	5	1.7
Chionomys nivalis	1	1	4.5	5	5	12.2	20	14	6.0	12	8	7.2	13	7	4.9	18	14	4.9
Microtus agrestis				3	2	4.9	16	14	6.0	2	2	1.8	3	2	1.4	9	8	2.8
Microtus arvalis	20	14	63.6	34	25	61.0	224	133	56.6	66	43	38.7	146	78	54.2	259	153	53.5
Microtus (T.) gr. multiplex-subterraneus	2	1	4.5	4	4	9.8	39	21	8.9	36	24	21.6	63	33	22.9	113	68	23.8
Dinaromys bogdanovi																1	1	0.3
Cricetus cricetus							4	3	1.3	2	2	1.8	1	1	0.7	12	4	1.4
Apodemus sp.				1	1	2.4	7	3	1.3	12	5	4.5	5	3	2.1	5	3	1.0
Apodemus cf. *flavicollis*							2	2	0.9									
Apodemus flavicollis							4	3	1.3	6	4	3.6	1	1	0.7			
Apodemus cf. *sylvaticus*										2	2	1.8						
Apodemus sylvaticus							4	4	1.7	3	2	1.8	3	2	1.4	3	3	1.0
Rattus rattus				1	1	2.4												
Glis glis							1	1	0.4									
Sorex ex gr. *araneus*							2	2	0.9							2	2	0.7
Sorex alpinus													1	1	0.7			
Crocidura cf. *leucodon*	1	1	4.5															
Talpa sp.				1	1	2.4	3	2	0.9									
Talpa caeca							1	1	0.4									
Talpa europaea	1	1	4.5				16	7	3.0	7	4	3.6	8	2	1.4	7	4	1.4
Erinaceus europaeus							1	1	0.4							1	1	0.3
Total	33	22		54	41		397	235		188	111		280	144		479	286	

Index ($CRI_i = 1/n$, where "n" is the number of climatic zones where the species are represented and "I" is the climatic zone where the species appears). Afterwards, the Bioclimatic Component (BC) has been calculated by the following formula: $BCi = (\Sigma\ CRI_i) \times 100/S$, where S is the number of species by unit at Riparo Tagliente. From the BC, climatic parameters have been estimated with the Multiple Linear Regression Method using the values given by Hernández Fernández and Peláez-Campomanes (2005). Mean Annual Temperatures (MAT), Mean Temperatures of the Coldest and Warmest month (MTC and MTW respectively) and Mean Annual Precipitation (MAP) have been obtained. Data thus acquired have been compared to the present conditions registered at Villafranca meteorological station (Verona, 45°23'N, 15°52'E, 68 m a.s.l.), approximately 20 km SW of the site. The current data are:

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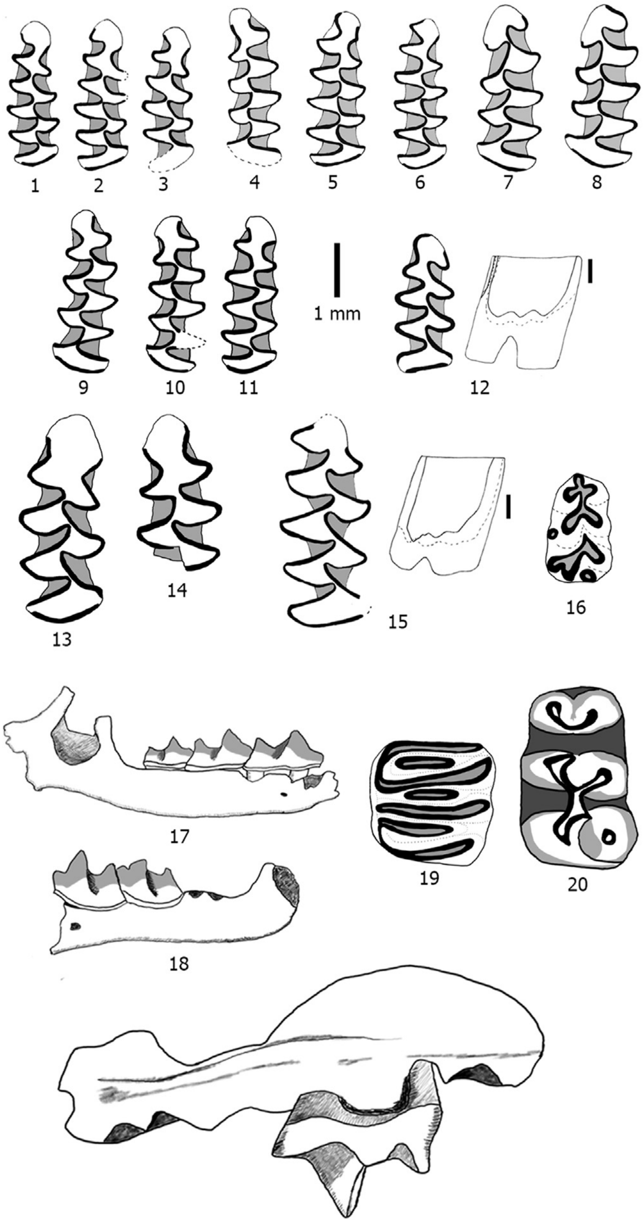

Fig. 3. Selected small mammals from Riparo Tagliente: 1: *Microtus* (*Terricola*) gr. *multiplex-subterraneus*, right m/1, Unit 10 g; 2: *Microtus* (*Terricola*) gr. *multiplex-subterraneus*, right m/1, Unit 10d; 3: *Microtus* (*Terricola*) gr. *multiplex-subterraneus*, right m/1, Unit 10b; 4: *Microtus agrestis*, left m/1, Unit 10; 5: *Microtus agrestis*, right m/1, Unit 10d; 6: *Microtus agrestis*, right m/1, Unit 365; 7: *Chionomys nivalis*, left m/1, Unit 10b; 8: *Chionomys nivalis*, left m/1, Unit 14; 9: *Microtus arvalis*, left m/1, Unit 7; 10: *Microtus arvalis*, left m/1, Unit 6; 11: *Microtus arvalis*, right m/1, Unit 9; 12: *Clethrionomys glareolus*, right m/1, Unit 14; 13: *Arvicola amphibius*, right m/1, Unit 9; 14: *Arvicola amphibius*, left m/1, Unit 9; 15: *Dinaromys bogdanovi*, right m/1, Unit 14; 16: *Apodemus* gr. *sylvaticus-flavicollis*, left m/1, Unit 10c; 17: *Sorex* gr. *araneus*, right mandible with m/1, m/2 and m/3, Unit 365; 18: *Sorex* ex gr. *araneus*, left mandible with m/1 and m/2, Unit 412; 19: *Glis glis*, right m/1, Unit 10f; 20: *Cricetus cricetus*, right M\1, Unit 10 g; 21: *Talpa europaea*, left maxillary with M\1, Unit 10 g.

MAT = 12,7 °C, MTW = 23,3 °C, MTC = 1,6 °C and MAP = 819.5 mm.

4. Results

The assemblage is dominated by *Microtus arvalis* and *Microtus* (*Terricola*) gr. *multiplex-subterraneus* (Table 1). Biodiversity is relatively poor, except for Macrounit 11 (Table 2). The most evident difference between the various Macrounits is the decrease in the pine vole in the upper part of the sequence, starting from layer 10 (Table 1). This tendency has been already observed in the trench assemblage (Bartolomei et al., 1982; Berto, 2013).

Nevertheless, other variations are visible along the sequence. Macrounits 13–14, and 12 are almost alike, and both are dominated by *Microtus arvalis* and *Microtus* (*Terricola*) gr. *multiplex-subterraneus* (over 75% of the entire assemblage). During the deposition of these two Macrounits, the landscape surrounding the site was a periglacial one, mainly open, with scarce forest patches. MAT, MTW, and MTC (especially the MTW) indicate lower temperatures than today's (Table 2).

The situation slowly changes in Macrounit 11. *Microtus arvalis* decreases and the species are more evenly distributed in the assemblage without a clearly dominant one (Fig. 4). This phase is reflected in the habitat by the increase in woodland and water components.

Macrounit 10 can be considered as a turning point in the sequence. *Microtus* (*T.*) gr. *multiplex-subterraneus* strongly decreases, and the only glirid occurrence (*Glis glis*) in the whole sequence is recorded. The climate proxies indicate the first slight increase in MAT, and, in particular, MTC (from 0.4 °C to 1.7 °C), while MTW does not change. In addition, the last occurrence for this sequence of the cold climate-related species *Cricetus cricetus* is registered. Even though the two uppermost Macrounits (8–9 and 5–7) have a low MNI (41 and 22 respectively), the same tendency (increase of MAT and MTC), visible in Macrounit 10, continues up to the end of the sequence, with a similar assemblage dominated by *Microtus arvalis*, and, thus, characterized by a low biodiversity.

5. Discussion

5.1. The small mammal series of Riparo Tagliente and climate change in the Southern Alps between GS-2 and GI-1

Climatic and environmental changes and their dynamics between the end of GS-2 and GI-1 in the Southern Alps are well-known thanks to the study of pollen records from lacustrine sites (Pini et al., 2010; Ravazzi et al., 2014, 2007a,b; among others). During the first part of the Late Glacial (GS-2b and GS-2a), no forest increase is recorded in relation to the retreat of the major glaciers from pedemontane amphitheatres. At the same time, the great prealpine lakes, especially in the inner valleys, are still subject to intense periglacial conditions (Ravazzi et al., 2007a). In this context, Riparo Tagliente is considered to be the first and unique evidence of human frequentation along the Prealpine foothills just a few millennia after the retreat of the glaciers and the onset of the Late Glacial. The other Epigravettian sites in the same area postdate the beginning of the Bølling-Allerød Interstadial (Ravazzi et al., 2007a).

Large and small mammals from the lower Epigravettian layers of Riparo Tagliente (14–12) reflect the climate and environmental setting attested in the southern Alpine and Prealpine pollen records. This, in a general periglacial climate, was characterized by open environments, with bushes, herbs, xerophytes, and a scarce tree component, represented mainly by conifers. These landscapes were occupied by Alpine ibexes, aurochs, and bisons (Bartolomei et al., 1982; Capuzzi and Sala, 1980; Ravazzi et al., 2007a). The presence of a molar attributed to *Dinaromys bogdanovi* suggests the persistence of continental conditions (Krystufek et al., 2007) during the deposition of Macrounit 13–14. During the Upper Pleistocene, this species slowly withdraws to the Balkan region, and in the Late Glacial, it constitutes a relict in northern Italy (Bartolomei et al., 1982; Berto, 2013; Berto and Rubinato, 2013; López-García et al., 2015).

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Table 2
Biodiversity, Climate and Landscape values. Number of taxa in each layer; values obtained for evenness: Simpson diversity index; Relation of temperature and precipitation for Riparo Tagliente sequence: MAT: Mean Annual Temperature, MTW: Mean Temperature of the Warmest month, MTC: Mean Temperature of the Coldest month, MAP: Mean Annual Precipitation; Percentage representation of small mammal taxa associated with open dry meadows (OD, Mediterranean and continental), open humid meadows (OH), open woodland environments (OW), woodland environments (W), rocky environments (R) and landscapes constituted by river, lakes and ponds (Wa).

Macrounits	Biodiversity		Climate				Landscape					
	Taxa	Simpson 1-D	MAT	MTW	MTC	MAP	OD	OH	OW	W	R	Wa
5–7	7	0.535	10.1	17.2	4.1	1418	38.9	5.6	18.5	7.4	3.7	14.8
8–9	7	0.5601	9.2	17.5	2.8	1373	46.9	11.3	21.9		12.5	5.0
10	14	0.5901	8.5	16.4	1.7	1547	41.3	12.1	20.2	7.2	6.4	8.2
11	10	0.7215	8.0	16.5	0.4	1445	30.0	14.4	22.7	13.1	8.1	11.7
12	11	0.5817	8.0	16.5	0.4	1445	40.4	13.5	25.7	5.5	5.3	8.2
13–14	12	0.5869	8.7	17.4	0.6	1525	40.3	15.7	26.3	3.6	5.5	6.9

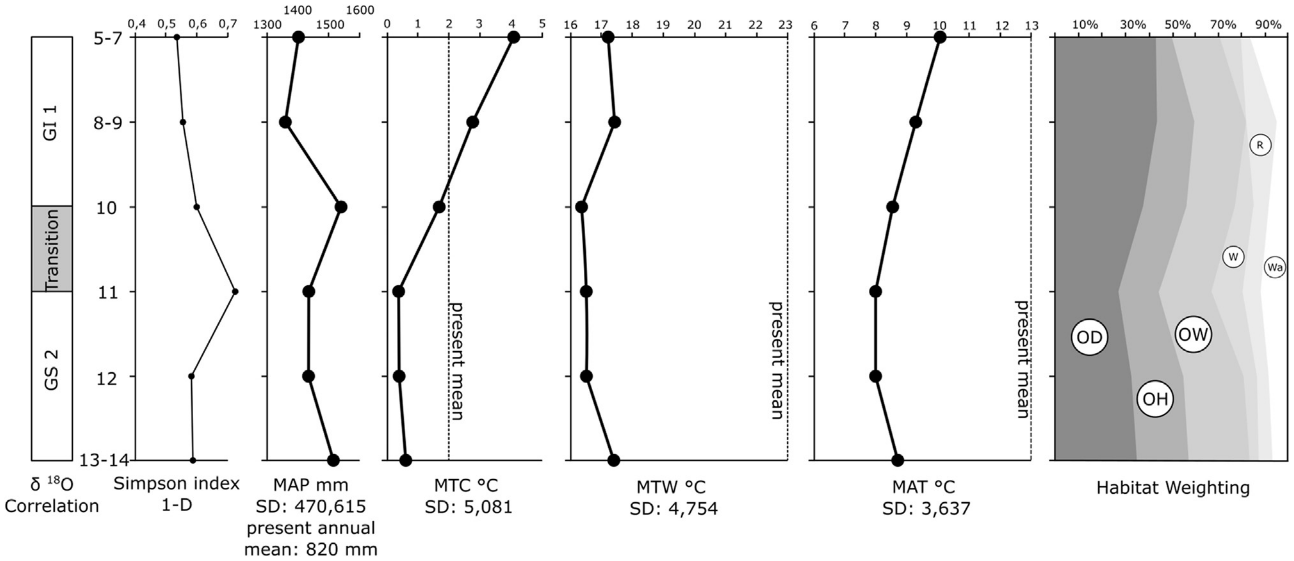

Fig. 4. Representation of the small mammal Simpson diversity index (1-D), the mean annual precipitation (MAP), the mean annual temperature of the coldest month (MTC), the mean annual temperature of the warmest month (MTW), the mean annual temperature (MAT), and the landscape percentages (OD: open dry meadows; OH: open humid meadows; OW: open woodland, woodland-edge; W: woodlands; R: rocky areas; Wa: areas along streams, lakes and ponds); SD: Standard Deviation, from Hernández Fernández (2001b).

The faunal record starts to change in Macrounit 11, where an increase in biodiversity and water component is suggested by the presence of *Arvicola amphibius*. The presence of water-related species is also attested in the large mammal record of layers 12-11 (internal trench, corresponding to Macrounits 11 and 12), where *Alces alces* has a relatively high percentage (Bartolomei et al., 1982; Capuzzi and Sala, 1980). Even if these layers are not dated yet, it is probable that they accumulated before GI-1, in a wet phase following the “Ragogna oscillation”. The latter is a dry, cold and continental moment recorded in the Garda Lake and related to Heinrich Event 1, prior to the Bølling-Allerød onset (Monegato et al., 2007; Ravazzi et al., 2014).

The recorded increase in temperatures (MAT and MTW), starting from Macrounit 10, attests to the beginning of GI 1. In the Southern Alps, this interstadial is characterized by a quick increase in forest density, even at altitudes up to 1350 m a.s.l. (Ravazzi et al., 2007a). The small mammal assemblage from the upper part of the sequence of Riparo Tagliente (Macrounits 10, 8–9 and 5–7) does not reflect such an increase in forest. This might suggest a persistence of the periglacial conditions during the beginning of the Bølling-Allerød in the Pantena Valley. However, it might also be a consequence of a bias in the microfauna record, due to the intense anthropic occupation recorded in these horizons, or to the selection by predators. The strong decrease of *Microtus* (*Terricola*) gr. *multiplex-subterraneus* and the increase of *Chionomys nivalis* can be related to a transitional moment when the landscape of the Pantena valley was changing from a dense grassland to a degraded environment. This change can be interpreted as an effect of the strong deglaciation process that took place in the Southern Alps during the Late Glacial period. Nevertheless, the presence of *Glis glis* and *Erinaceus europaeus* in Macrounit 10 and the disappearance of *Cricetus cricetus* in Macrounits 8–9 and 5–7 indicate an influence, even if a mild one, of the general climate warming which is registered during GI-1.

5.2. *Rodent communities’ adaptations to the Late Glacial climate change*

The study of rodent communities' variations, especially where the small mammals are collected in archaeological sites, contribute to analyse the dynamics of climatic and environmental modifications that led the major changes in settlement strategies and behaviours of prehistoric hunter-gatherer groups. In particular, small mammal communities' response to the Late Glacial climate changes mostly follows a same trend: the demise of cold indicator taxa and the increase of forest-related species. Nonetheless, differences due to sites’ geographic position and geomorphology must be taken into account.

In the Iberian Peninsula, a decline in the species diversity is observable during the Bølling-Allerød Interstadial. The percentage

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of woodland rodents faunas, such as *Apodemus*, *Glis*, *Clethrionomys*, and *Eliomys* starts to rise within rodent assemblages (Cuenca-Bescós et al., 2010a; Lopez-Garcia et al., 2013), even if tree cover seems to increase widely only during the mid-Holocene. At the same time, *Pliomys lenki* (= *coronensis*), which was present only in the Cantabrian region during MIS 2, becomes extinct shortly after the Bølling-Allerød Interstadial, during the Younger Dryas (Cuenca-Bescós et al., 2010a, 2010b).

In south-western France, the shift from rodent communities of mostly cold-climate species to communities dominated by temperate species is observable during the HE1 and Bølling events. In particular, species related to cold environments, like *Dicrostonyx torquatus*, *Microtus oeconomus*, *Microtus gregalis*, and *Spermophilus* sp., disappear from this region between the Bølling-Allerød Interstadial and the Younger Dryas (Royer et al., 2016).

In the Italian peninsula, very few well-dated sites have yielded sediments with small mammals accumulated between HE1 and the Bølling-Allerød Interstadial (Fig. 5): Riparo Tagliente in northern Italy, Grotta del Romito (López-García et al., 2014) and Grotta della Serratura (Bertolini et al., 1996) in south-western Italy, and Grotta Paglicci in Apulia (Berto et al., 2017). The other sites are mainly “spots”, showing a situation before, during, or after the Bølling-Allerød Interstadial, sometimes with doubtful chronological attributions. Nevertheless, the general responses to such climate changes can be observed within each region.

In northern Italy, in particular at Biarzo and Grotta del Clusantin (Bartolomei, 1996; Peresani et al., 2008), *Microtus* gr. *arvalis-agrestis* dominated assemblages appear to be replaced by rodent communities dominated by forest-related species, in particular, *Clethrionomys glareolus*.

The cold-climate related species that characterize MIS 3 and the LGM disappear during the Late Glacial (Berto, 2013). *Microtus oeconomus*, which is not present in the Epigravettian layers of Riparo Tagliente, seems to be the first species to disappear during this period, probably shortly after the LGM. Its last appearance is attested at Grotta Paina, in the ancient Epigravettian layers (Bartolomei et al., 1988). The presence of *Cricetus cricetus* in the Epigravettian layers of Riparo Tagliente is one of the last occurrences of this species in the Italian Peninsula, together with that from Unit 5 of Riparo di Biarzo, dated shortly after the Bølling-Allerød Interstadial (Bartolomei, 1996; Vai et al., 2015). *Sicista* sp. was widespread in northern Italy during MIS 3 (Berto, 2013), and it is present in the Mousterian layers of the same age also at Riparo Tagliente (Bartolomei et al., 1982). During the Late Glacial, this genus is reported only at Grotta Paina (layer 6, Bartolomei et al., 1988) and Grotta della Ferrovia (Bartolomei, 1966; Berto, 2013) in the Epigravettian layers related to a period prior to GI 1, while findings related to the Bølling-Allerød Interstadial (Late Epigravettian layers) at Grotte Verdi di Pradis can be considered as its last attested presence in Italy (Gurioli et al., 2011).

Excluding Caverna degli Orsi, which is related more to the Balkan biocoenosis than to the western European one, Riparo Tagliente can be considered as the site with the last occurrence of *Dinaromys bogdanovi* in the Italian Peninsula (Berto and Rubinato, 2013; Boschian et al., 1996). Therefore, it seems that in northern Italy, the response of rodent communities to the abrupt climatic change of MIS 1 consists only of a change of dominant species, and, in some cases, in an increase in biodiversity.

On the contrary, eastern and northern European species rarely reach southern Italy during MIS 3 and 2 (Berto, 2013; Berto et al., 2017). *Chionomys nivalis* disappears from this region during the Bølling-Allerød Interstadial, moving northward and becomes progressively attested in the Alpine chain (Jeaneau and Aulagnier, 1997). On the eastern side of the Italian Peninsula, rodent communities are characterized by a low biodiversity and dominated by *Microtus* gr. *arvalis-agrestis* during the HE1 and *Microtus* (*T.*) *savii* - *Arvicola amphibius* after the GS1, thus testifying a change in climate, from continental conditions to Mediterranean ones (Berto, 2013; Berto et al., 2017). On the western side, the rodent communities attributed to HE1 are dominated by *Microtus* gr. *arvalis-agrestis*, and, in a single case, at Grotta della Serratura, by *Apodemus* gr. *sylvaticus-flavicollis*. The Bølling-Allerød Interstadial is characterized by the rise of *Microtus* (*Terricola*) *savii* and *Glis glis*, the latter dominant at Grotta del Romito (López-García et al., 2014) and at Grotta della Cala (Bambini, 1996).

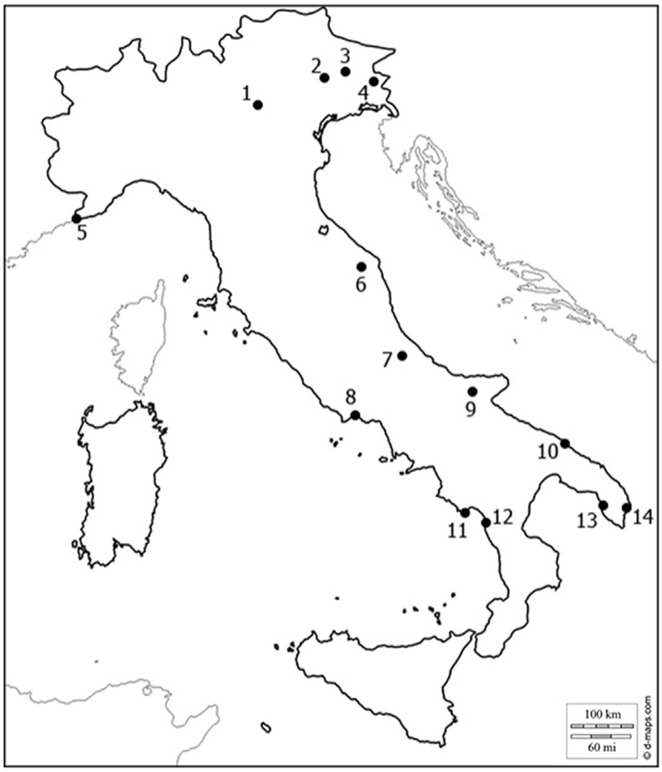

Fig. 5. Location of the most important sites with Epigravettian layers in Italy: 1: Riparo Tagliente; 2: Barcis; 3: Clusantin; 4: Riparo di Biarzo; 5: Riparo Mochi; 6: Grotta Ferrovia; 7: Riparo Ermanno de Pompeis; 8: Riparo Salvini; 9: Grotta Paglicci; 10: Grotta delle Mura; 11: Grotta della Serratura; 12: Grotta del Romito; 13: Grotta del Cavallo; 14: Grotta delle Cipolliane.

In this context of abrupt changes that occurred in climate, environments and biota during the transition between MIS 2 and 1, the rodent community from the Epigravettian series of Riparo Tagliente follows the faunal renewal which is recorded in northern Italy for the Late Glacial.

5.3. *Environmental context and Upper Palaeolithic hunter-gatherers' adaptations*

The adaptations of hunter-gatherer groups to the environmental change and the faunal renewal of the Late Glacial have been extensively studied, especially in south-western Europe (Broglio et al., 2009; Duches et al., 2015; Fontana et al., 2011; Naudinot et al., 2016; Tomasso, 2015; Tomasso et al., 2014; among others). Changes in settlement patterns and a gradual shift within lithic technology are highlighted by archaeological records. The improvement of climatic conditions during the Bølling-Allerød Interstadial made new territories available along the Alpine valleys, where glaciers and periglacial environments were present until the end of MIS 2. Riparo Tagliente yields the most ancient evidence of

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this reoccupation of the southern Alpine fringe after the end of the LGM, whereas innermost and upland Alpine territories were gradually colonized by the Late Epigravettian groups both during and after the Bølling-Allerød interstadial (Fig. 6) (Ravazzi et al., 2007a).

The closing of the environments with the rise of the forest, attested by the pollen and faunal records, could have somehow affected the mobility of the hunter-gatherer groups. Hunting weapons made of Apennine cherts are attested in north-eastern Italy and, in particular, at Grotta Paina in the Berici area. This points to a large-scale mobility during the LGM around 25,000 years cal BP, when the Po plain was a steppe area reaching southwards as far as the city of Ancona (Bertola, 2015; Bertola et al., 2017; Broglio et al., 2009). The contacts with these southern areas continued at least until the second part of the Oldest Dryas, as testified by the lower layers of the series of Riparo Tagliente. On the other hand, such evidence is not recorded in the uppermost layers of the same site and at the other southern Alpine sites. The latter are dated to or after the Bølling-Allerød Interstadial, when woodlands and forests become widespread (Bertola, 2015; Bertola et al., 2017). Further changes in the mobility of human groups seem to have characterized the following period (Youngest Dryas) (Duches et al., 2014) which is not attested in Riparo Tagliente.

As far as lithic technology is concerned, a gradual and progressive modification has been observed in reduction sequences within Late Epigravettian assemblages. These modifications occur from GS-2.1a (only documented at Riparo Tagliente) to the end of the YD. Several rather well-dated sites are attested in the south-eastern Alpine area (Montoya, 2008) during the same period. Moreover, any attempt to demonstrate a connection between climate changes and technology for this temporal span have apparently failed so far even in neighbouring areas, such as France, where technological changes within the contemporary Magdalenian-Azilian-Laborian sequence are much more clear-cut than in the Late Epigravettian (Naudinot et al., 2016).

6. Conclusions

The climate reconstruction based on small mammals from Riparo Tagliente indicates an increase in temperatures (especially MAT and MTW) during the first part of the Bølling-Allerød Interstadial. However, throughout this warming-up phase, the

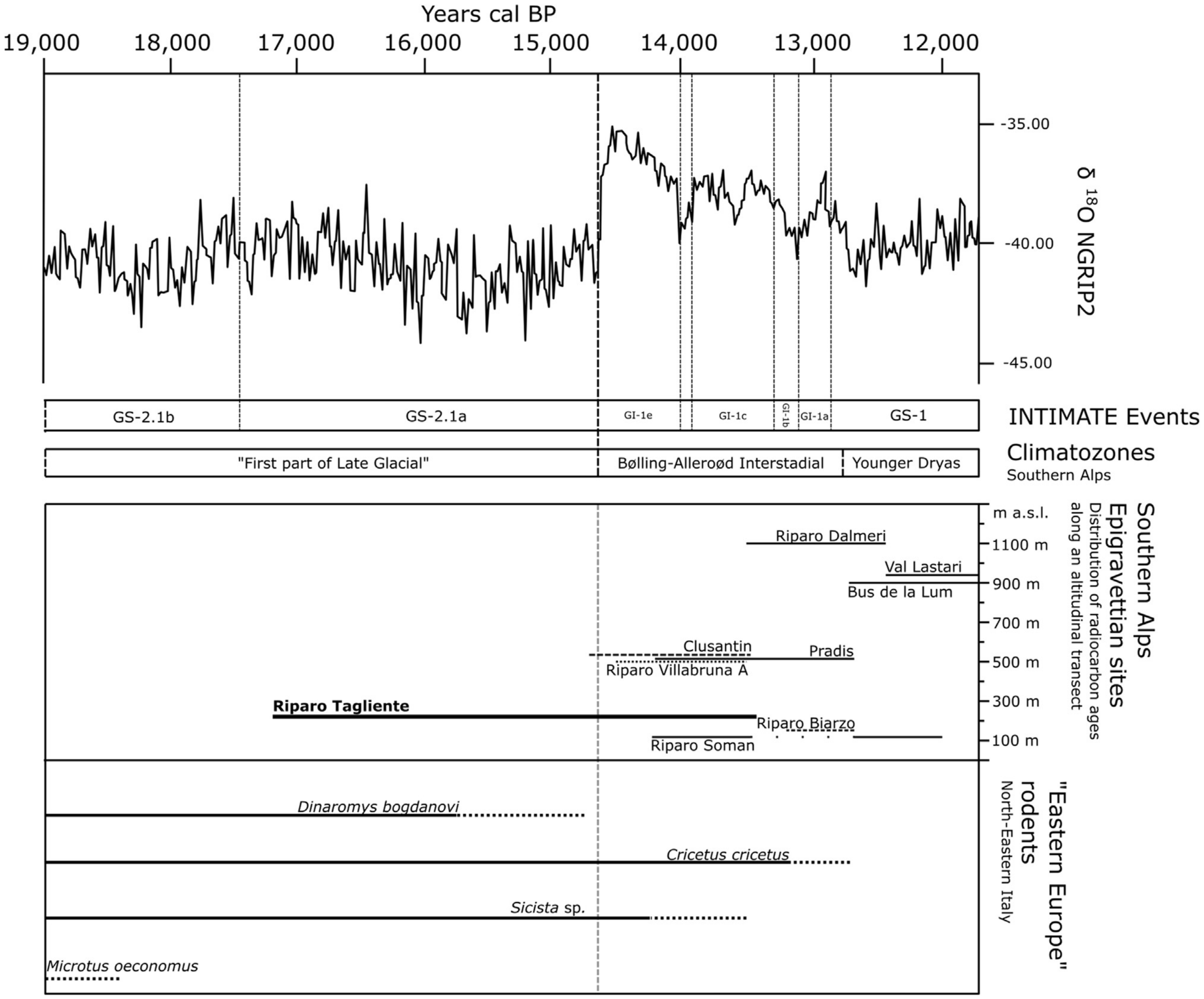

Fig. 6. Major changes visible in the Southern Alps during the Late Glacial related to δ^{18}O NGRIP, INTIMATE Events (Rasmussen et al., 2014) and Climatozones (Ravazzi et al., 2007a,b). A progressive occupation of highest sites is visible after the Bølling-Allerød interstadial. During the Late Glacial rodents related to Eastern Europe biocoenoses progressively disappear from north-eastern Italy.

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assemblage continues to be dominated by *Microtus arvalis* and to record a relative stability of the open environments in Valpantena, along the southern Alpine fringe.

The absence of *Cricetus cricetus* and *Dinaromys bogdanovi* in the uppermost Macrounits matches the general faunal renewal recorded in Western Europe and in the Italian Peninsula, shortly after the beginning of MIS 1. Among the rodent communities, this faunal renewal comprises a progressive demise of cold related species (*Cricetus cricetus*, *Microtus oeconomus*, *Sicista* sp., *Dinaromys bogdanovi*), and an increase in the percentage of forest-related taxa in north-eastern Italy.

In the Southern Alps, this trend is mostly shown by the change in settlement and mobility patterns: starting from the Bølling-Allerød warming phase, Alpine valleys are colonized up to around 1700 m a.s.l. At the same time the diffusion of woodlands in the south-eastern Alps, previously characterized by open environments, probably caused the end of the settlement strategy of Late Epigravettian groups, which had been based since the LGM on high mobility between the central Adriatic area and the south-eastern Alpine fringe.

The data inferred from the small mammal assemblage of Riparo Tagliente show that the colonization of the Southern Alps by Late Epigravettian hunter-gatherer groups took place well before the Bølling-Allerød interstadial, at a time when cold climatic conditions were still prevailing and open grasslands dominated the landscape. Even if the area surrounding the shelter was still characterized by open environments, the general forest growth, registered by the pollen sequences during the beginning of the Bølling-Allerød interstadial at Riparo Tagliente, is confirmed by an increase in the forest-related large mammals, and indirectly suggested by the change in mobility patterns of the hunter-gatherer groups.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.quascirev.2017.07.022.

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Middle to Late Pleistocene environmental and climatic reconstruction of the human occurrence at Grotta Maggiore di San Bernardino (Vicenza, Italy) through the small-mammal assemblage

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ABSTRACT

Grotta Maggiore di San Bernardino, located at an altitude of 135 m a.s.l. in the Berici Hills in northeastern Italy, is an archaeological site with a discontinuous sedimentary sequence dating from Marine Isotope Stage 7 (MIS 7) to MIS 3. In this paper we present for the first time a palaeoenvironmental and palaeoclimatic reconstruction of the sequence based on small-mammal (insectivore, bat and rodent) assemblages. Coupled with biochronological data and absolute dating together with previous studies on large mammals, birds and other studies on small mammals and pollen from comparable time-spans in Italy, the results enable us clearly to identify distinct climatic periods: the end of MIS 7 (7c to 7a) in units VIII-VII, MIS 5d in unit V, and probably MIS 5b in unit IV and an indeterminate MIS 3 interstadial in units III-II. Finally, the study shows that the early Middle Palaeolithic human occupation in Italy occurs during mild and temperate sub-stages of MIS 7 and that human groups with the same techno-cultural background (Mousterian) were well adapted to the changing environmental and climatic conditions of the Middle to Late Pleistocene in this part of southern Europe.

1. Introduction

The late Middle Pleistocene and the Late Pleistocene were two periods of great climatic fluctuations. The three marine isotope stages (MIS) that are important for this manuscript range from MIS 7 to MIS 3.

MIS 7 is an isotopic interglacial dated to ca. 246–186 ka. According to pollen analyses of marine and terrestrial sequences in Europe, it is characterized by a marked alternation of three warm (MIS 7e, MIS 7c and MIS 7a) and two cold periods (MIS 7d and MIS 7b) (Despart et al., 2006; Rouchoux et al., 2006, 2008). Terrestrial records with small-mammal studies from the late Middle Pleistocene are scarce in Italy and are limited to two or three sites: the lower layers of Grotta del Broion (Berici Hills, Vicenza) (Sala, 1980; Colamussi, 2002), Torre in Pietra 2 (Latium) (Caloi and Palombo, 1978) and probably Sossano 2 (Berici Hills, Vicenza) (Bartolomei, 1980; Bon et al., 1991). In terms of cultural attribution, it seems that MIS 7 is the period when the Middle Palaeolithic culture was established in Italy, appearing for the first time in the Torre in Pietra site (Villa et al., 2016).

MIS 5 corresponds to the early Late Pleistocene, which is characterized by a minimum ice volume lasting from ca. 130 to 75 ka and has been divided into five substages, warm episodes (MIS 5e, MIS 5c and MIS 5a) alternating with two cold episodes (MIS 5d and MIS 5b) (Kukla et al., 2002; Sánchez-Goñi et al., 2012; Sánchez-Goñi, 2007; among others). As occurs with MIS 7, the terrestrial record for MIS 5 based on small-mammal studies in the Italian Peninsula is poor and may be limited to two recently studied sites: Ciota Ciara cave (Borgosesia) (Berto et al., 2016) and Caverna degli Orsi (Trieste) (Berto and Rubinato, 2013).

Finally, MIS 3 falls chronologically between ca. 57 and 27 ka and records intense cyclicity and instability in the climate (Bond et al., 1993; Dansgaard et al., 1993). In the North Atlantic, repeated abrupt climatic changes called Dansgaard/Oeschger (D/O) events have been detected during this period (Bond et al., 1993). The high

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peaks visible in the oxygen isotope curve are the Greenland interstadials (GI), corresponding to exceptional atmospheric and marine warming. The stadial phases are indicated by a general increase in the proportion of Arctic planktonic foraminifera such as *Neogloboquadrina pachyderma*, as well as the appearance of IRD (iceberg-rafted detritus) (Bond et al., 1993). These stadial phases are known as Heinrich Events (H events) (Heinrich, 1988). During MIS 3, approximately ten Dansgaard/Oeschger cycles (GI 14 to 3) and three Heinrich Events (H5 to H3) have been identified. The extreme variability of these periods and the questions raised by archaeological research into the extinction of the Neanderthals (Middle Palaeolithic) and their substitution by Anatomically Modern Humans (AMH) (Upper Palaeolithic) (Stewart, 2005; Finlayson and Carrión, 2007; Higham et al., 2014; among others) have stimulated particular interest in MIS 3. Fortunately, for MIS 3 there are recently studied sequences with small-mammal assemblages in Italy with which to compare our data, such as Riparo Mochi (Ventimiglia) (Berto, 2013), the upper layers of Grotta del Broion (Berici Hills, Vicenza) (Colamussi, 2002), Grotta Paglicci (Foggia) (Berto, 2013) or Fumane Cave (Verona) (López-García et al., 2015).

Such is the cultural and climatic context of the late Middle Pleistocene to Late Pleistocene (Middle Palaeolithic) discontinuous archaeological sequence of Grotta Maggiore di San Bernardino in the northeastern region of Italy. This site provides a continental stratigraphic succession spanning the interval from MIS 7 to MIS 3, culturally represented by the Mousterian, a Middle Palaeolithic ensemble of Neanderthal-related techno-complexes in Europe in all the stratigraphic units (Peresani, 1995–1996, 1996; Picin et al., 2013). In this context, the present paper aims to undertake an environmental and climatic reconstruction of the MIS 7, MIS 5 and MIS 3 stages represented at Grotta Maggiore di San Bernardino on the basis of the small-mammal assemblages (insectivores, bats and rodents), framing our results within the ecological context previously defined on the basis of palaeontological data (large mammals and birds; Cassoli and Tagliacozzo, 1994; Fiore et al., 2004). In addition, these ecological reconstructions will be discussed within a broader scenario incorporating other sources such as pollen studies undertaken at continental lakes in Italy (Follieri et al., 1988; Allen and Huntley, 2009; Pini et al., 2009, 2010) and the above-mentioned Italian sites with similar chronology and comparable small-mammal associations (Caloi and Palombo, 1978; Sala, 1980; Bartolomei, 1980; Bon et al., 1991; Colamussi, 2002; Berto, 2013; Berto and Rubinato, 2013; Berto et al., 2016; López-García et al., 2015).

2. Grotta Maggiore di San Bernardino in the north-east of Italy

Grotta Maggiore di San Bernardino (Mossano, Berici Hills, Vicenza), located at 135 m a.s.l. (Fig. 1), lies in the foreland of the eastern Italian Alps, which represent a physical and environmental threshold where ice fields and alpine glaciers developed during cold stages of the late Middle Palaeolithic and temperate vegetation was restored during warm phases. The Alpine foreland is a large alluvial plain that was produced mainly during the Middle and Late Pleistocene by major rivers such as the Po and the Adige and the rivers of the Venetian-Friulian Plain. This region also includes hills of different origins, such as the Berici karst plateau and the cone-shaped volcanic reliefs of the Euganean Hills, which are separated by the spreading outwash of the aggrading plain.

The morphological evolution of this part of the Po Valley has been assessed in several works (Antonioli, 2012; Fontana et al., 2008; Mozzi, 2005; Zecchin et al., 2008). Before the last glacial-interglacial cycle, the penultimate glacial maximum (150 to ca. 140 ka) severely impacted the landscape of the eastern southern Alps and the Piedmont Plain (Monegato et al., 2011; Pini et al., 2009), which at the time was steppe and dry meadows with scattered pine, birch and larch trees. This period was followed by the last interglacial, when the Tyrrhenian transgression in the northern Adriatic reached the border of the Euganean Hills (Ferranti et al., 2006), leading to water table elevation along the western part of the plain and, supported by rainfall, favouring the development of wetlands and temperate oceanic forests in the lower plain. Persistent afforestation with temperate trees, notably Tilia and Abies, has been recorded throughout the entire early and middle part of the last glaciation, with only moderate forest withdrawals during early DO events (Pini et al., 2010). The Middle Würm records prevailing zonal vegetation on the plain that includes open birch-conifer forests, xerophytic scrubs and steppe, and phases of contraction of conifer forests and expansion of steppic communities alternating with mixed conifer (Pinus and Picea) – Betula forests (Pini et al., 2009). Soil formation affected aeolian deposits (Cremaschi, 1987, 1990). During a late phase of this period (about 38.2 ± 1.45 cal ka BP according to Pini et al., 2010), aggradation of the alluvial fans in the western Venetian Plain occurred, in coincidence with the establishment of long-lasting marshes in the Venetian–Friulian Plain (Fontana et al., 2008).

The cave opens along the eastern slope of the karst plateau of the Berici Hills on a carbonate sandstone cliff from the Middle Eocene, facing the alluvial plain of the Bacchiglione River and the south-western sector of the Euganean Hills. The cave is 41 m long, 7 m wide and 9 m high and was produced by thermoclastic processes and chemical dissolution, which widened deep, SE-NW-oriented fractures. In the western side of the same slope, a second, shorter cave named Grotta Minore di San Bernardino is situated. The area around the cave is characterized by the karstic plateau with dolines at the top of the hill (300–400 m), dissected by valleys with concave bottoms and delimited by the slope where the caves open. The foot of this slope is covered by clayey slope-waste deposits, which connect it to the alluvial lowlands that were occupied by marshes and swamps during the Pleistocene and earlier phases of the Holocene (Cassoli and Tagliacozzo, 1994). Like the San Bernardino caves, other caves open along this side of the Berici Hills, such as Grotta del Broion (Sala, 1980), the De Nadale Cave (Jéquier et al., 2015) or Covolo Fortificato di Trene (Romandini and Nannani, 2011), yielding Middle and Upper Palaeolithic archaeological evidence.

The first archaeological excavations were carried out by Prof. P. Leonardi in the 1960s in the area facing the medieval wall, uncovering a Pleistocene sequence with faunal remains and knapped stones (Leonardi and Broglio, 1961–62). A second cycle of research, between 1986 and 1995, allowed a more detailed reexamination of the stratigraphic series of the different facies between the inner and outer zones of the cave (Peresani, 1995–96).

The deposit at Grotta Maggiore di San Bernardino is a complex sedimentary body shaped like an elongated prism, extending from inside the cave to partly outside it, where it becomes a detritic talus coalescing with that of the Grotta Minore. The deposit, which was still visible before the first excavation at the site, comprises the lower part of the sediments that originally filled the cave. At present, the sedimentary sequence is 4.5 m thick and includes eight stratigraphic units with sub-horizontal bedding, which tilt progressively outside the cave (Fig. 1). Excavations from 1986 to 1994 confirmed that all the units contained Mousterian industries except unit I, which contained a few Upper Palaeolithic artifacts.

The stratigraphic succession is currently visible in the longitudinal section exposed at the entrance to the cave during the most recent excavations and consisting of eight lithological units from the base to the top (Fig. 1):

Unit VIII. This unit is characterized by an alternating centimetric

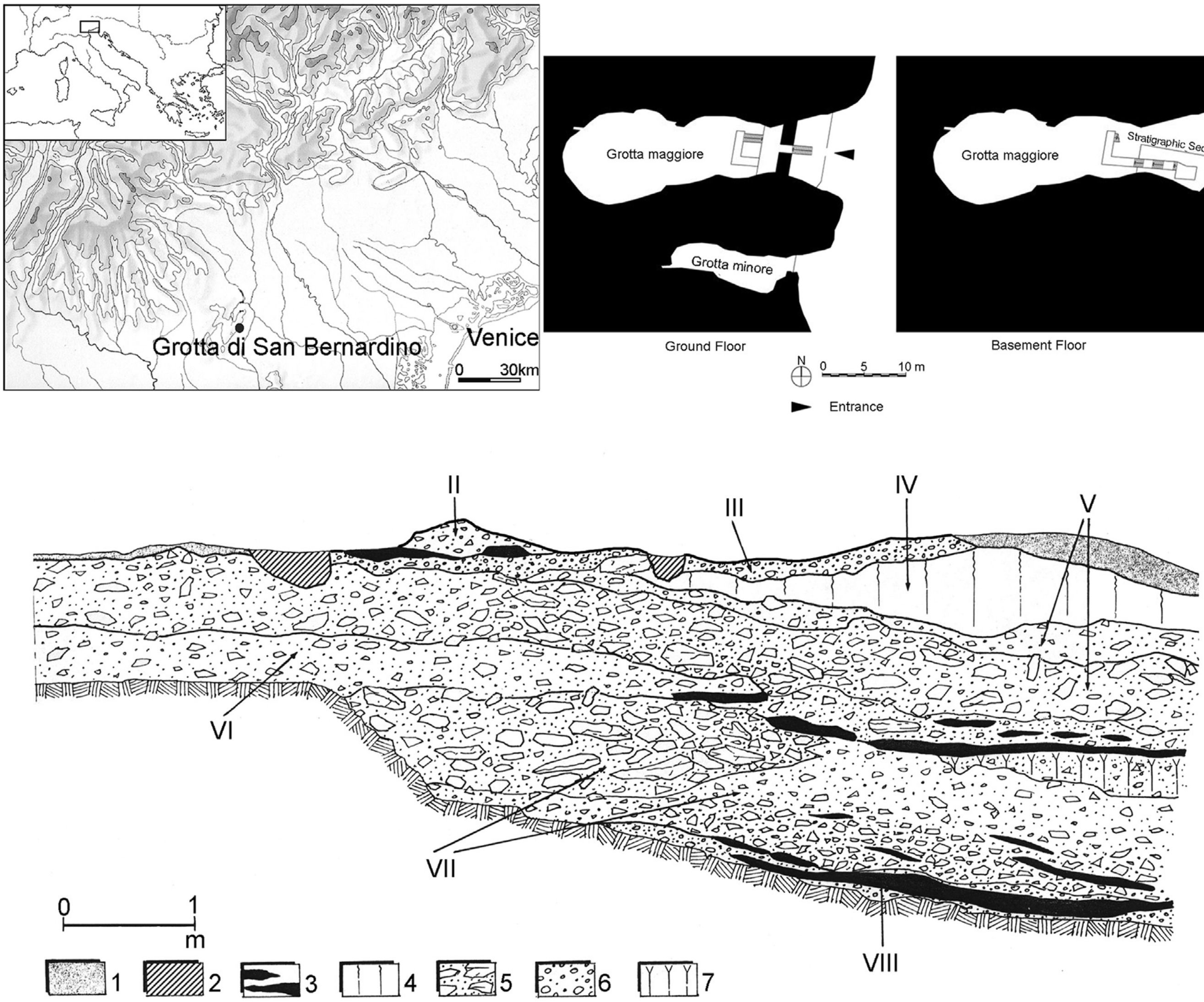

Fig. 1. Above-left: location of Grotta Maggiore di San Bernardino; Above right: plan of Grotta di San Bernardino with the stratigraphic section marked; Below: stratigraphic section from Grotta Maggiore di San Bernardino: 1. disturbed deposit with medieval finds; 2. bioturbation; 3. main palaeo-living floors; 4. loess; 5. thermoclastic breccia; 6. limestone gravel; 7. palaeosoil.

anthropogenic layer with abundant faunal remains and lithic tools and a selected gravel carbonate colluvium. The faunal remains record the predominance of cervids, mainly *Cervus elaphus* (Cassoli and Tagliacozzo, 1994), and the lithic assemblage is characterized by the Levallois method (Picin et al., 2013).

Unit VII. This is a thermoclastic breccia with aeolian fine fraction, poor in faunal remains, which are mostly cervids (Cassoli and Tagliacozzo, 1994) and with lithic tools, which are mainly Levallois flakes (Picin et al., 2013).

The lower archaeological units of San Bernardino (units VIII and VII) may be contemporaneous with the very end of MIS 7 and the beginning of MIS 6, as shown by the mean age, with a minimum age range of between 214 and 154 ka (Picin et al., 2013).

Unit VI. This is included in the whole excavation surface. It is an anthropogenic unit with hearths composed of sub-rounded stones of medium size associated with dark, silty-sand fine fraction, more reddish and clayey in the inner zone; the exterior zone shows evidence of a palaeosoil. The faunal remains are dominated by roe deer over other cervids (Cassoli and Tagliacozzo, 1994), and the stone tools are typically Mousterian (Peresani, 1995–96). Its chronological position in the very late MIS 6 and at the onset of MIS 5 is provided by the averaged ESR dates specifying 133 ± 43 ka BP (Gruppioni, 2003).

Unit V. This is a cryoclastic breccia with large angular stones on aeolian matrix, with few lithic and faunal remains. The stones corresponding to the entrance area show a horizontal arrangement whereas in the more exterior area they assume chaotic arrangements due to cryoturbation and solifluction; the lower limit is clear. Mousterian stone tools and faunal remains are few, but record the maximum spread of Caprinae, mainly *Capreolus capreolus* (Cassoli and Tagliacozzo, 1994). Averaged ESR dates place this unit at 108 ± 15 ky BP, in middle-late MIS 5.

Unit IV. Situated at the front of the cave entrance, this deposit is composed of light-dark loess layers, devoid of stones and highly calcareous. Faunal remains and lithics are scarce. The lower limit is gradual. This unit has been ESR-dated to 83 ± 18 ka, covering the late MIS 5 to MIS 4 (Gruppioni, 2003).

Unit III. This unit is made up of carbonate pebbles and lithic artifacts, rounded by water dripping. It lies on an undulating erosion surface.

Unit II. This is situated at the entrance to the cave and below the medieval wall that lay above it. This layer is made up of medium-sized sub-rounded stones and a brownish sandy-silty soil, numerous faunal remains with a prevalence of cervids and a few wild boar (Cassoli and Tagliacozzo, 1994), knapped stones (Peresani, 1995–96) and few combustion structures. Medieval human teeth, previously attributed to *Homo neanderthalensis*, were also found in this unit as a result of post-depositional introduction after a massacre occurred in 1509 (Benazzi et al., 2014). This unit has been dated to between 38 ± 5 ka and 35 ± 4 ka (Gruppioni, 2003).

Unit I: This is only visible in the northern wall of the cave. It is composed of thermoclastic breccia and loess matrix with large angular stones, and with few lithic and faunal remains; the lower limit is abrupt.

Human occupations in units VIII, VI and II are recorded from palaeo-living floors with dense concentrations of bones, flint and charcoal, in addition to some preserved hearths. By contrast, units VII, V and IV record only sporadic occupations, as documented by their poor archaeological content. Levallois is the dominant flaking method in units VIII and VII, marking the oldest numerically dated appearance of this technology in northern Italy (Picin et al., 2013); the recurrent centripetal modality is most used in unit VIII, and the unidirectional modality in unit VII. Further details on the lithic economy and the features of some categories of tools have been provided by Peresani et al. (2015) and Picin et al. (2010).

3. Material and methods

3.1. Small-mammal sorting and the palaeontological and taphonomic study

The small-mammal fossil remains used for this study are disarticulated bone fragments and isolated teeth collected by water-screening the sediments from the excavation campaigns performed in two phases, one in 1959 (thus including the assemblages briefly described in a note by Bartolomei, 1960) and the other one from 1986 to 1994 (unpublished), using a 2-mm mesh screen. The material was processed, sorted and classified in the research institution Institut de Paleoecologia Humana i Evolució Social (IPHES, Tarragona, Spain). The assemblage includes a total of 2641 identified specimens, corresponding to a minimum of 1399 individuals, representing at least 31 taxa (Table 1; Fig. 2).

The fragments were identified following the general criteria given by Berto (2013) and López-García (2008, 2011) for insectivores and rodents, and Felten et al. (1973), López-García et al. (2009) and Sevilla (1988) for bats. The specific attribution of this material is principally based on the best diagnostic elements: mandible, maxilla and isolated teeth for shrews; mandible, isolated teeth and humerus for Talpidae; first lower molars for Arvicolinae; and mandible, maxilla and isolated teeth for *Apodemus* spp., *Eliomys quercinus*, *Glis glis*, *Dryomys nitedula*, *Muscardinus avellanarius*, *Sicista betulina*, *Cricetus cricetus*, *Sciurus* sp. and *Marmota marmota*. Moreover, the fossils were grouped using the minimum-

Table 1
Representation of the percentage of the MNI (%) for the small mammals from the Grotta Maggiore di San Bernardino sequence and the small-mammal distribution by habitat. OD, open dry; OH, open humid; OW, open woodland; Wo, woodland/woodland-edge; Ro, rocky; Wa, water. NISP: total number of identified specimens by level; MNI: Minimum number of individuals by units.

	Unit II	Unit III	Unit IV	Unit V	Unit VI	Unit VII	Unit VIII	OD	OH	OW	Wo	Ro	Wa
Erinaceus cf. *E. europaeus*	0.00	0.00	0.00	0.15	0.46	1.11	0.00				1		
Talpa cf. *T. europaea*	5.88	5.56	1.26	3.07	4.61	6.67	14.29		0.5	0.5			
Crocidura gr. *leucodon-suaveolens*	0.00	2.78	0.00	0.00	0.00	3.33	0.00	0.25	0.25	0.5			
Sorex gr. *araneus-samniticus*	2.94	11.11	3.15	7.47	8.76	6.67	4.76		0.75	0.25			
Sorex minutus	0.00	0.00	0.00	0.44	0.46	1.11	0.00		0.25		0.75		
Neomys cf. *N. fodiens*	5.88	0.00	0.00	0.73	0.46	0.00	0.00		0.25				0.75
Neomys cf. *N. anomalus*	0.00	2.78	0.32	1.17	0.00	0.00	0.00		0.75				0.25
Myotis sp..	0.00	0.00	0.00	0.29	0.46	3.33	4.76				0.5		0.5
Plecotus gr. *auritus-austriacus*	0.00	0.00	0.00	0.00	0.92	0.00	0.00				0.75	0.25	
Nyctalus cf. *N. lasiopterus*	0.00	0.00	0.00	0.15	0.00	0.00	0.00			0.5	0.5		
Pipistrellus sp.	0.00	0.00	0.00	0.00	0.46	0.00	0.00			0.25	0.25	0.5	
Hypsugo/Vespertilio sp.	2.94	0.00	0.00	0.00	0.00	0.00	0.00			0.25	0.25	0.5	
Arvicola amphibius	14.71	8.33	8.20	8.93	11.06	0.00	0.00						1
Arvicola mosbachensis	0.00	0.00	0.00	0.00	1.38	14.44	14.29						1
Dinaromys cf. *D. bogdanovi*	0.00	0.00	0.00	0.00	2.30	8.89	4.76					1	
Chionomys nivalis	0.00	2.78	0.63	0.29	0.00	0.00	0.00					1	
Clethrionomys glareolus	0.00	5.56	5.36	9.66	7.37	3.33	9.52				1		
Microtus arvalis	14.71	22.22	41.64	27.96	26.27	8.89	14.29	0.75		0.25			
Microtus agrestis	20.59	19.44	24.92	21.52	18.89	10.00	14.29		0.5	0.5			
Microtus arvalis-agrestis	0.00	0.00	0.32	0.15	0.00	0.00	0.00						
Microtus gregalis	2.94	2.78	3.15	2.34	0.00	0.00	0.00		0.25	0.25		0.25	0.25
Microtus oeconomus	0.00	0.00	0.95	0.59	0.00	0.00	0.00		0.5	0.5			
M. (T.) gr. *multiplex-subterraneus*	2.94	2.78	7.89	9.08	6.91	2.22	0.00		0.5	0.5			
Cricetus cricetus	0.00	5.56	1.26	1.76	1.38	4.44	0.00	0.5				0.5	
Apodemus gr. *sylvaticus-flavicollis*	20.59	5.56	0.63	3.66	6.91	23.33	4.76				1		
Marmota marmota	0.00	0.00	0.00	0.15	0.00	0.00	0.00						
Sciurus sp.	0.00	0.00	0.00	0.00	0.00	1.11	0.00				1		
Sicista betulina	0.00	0.00	0.32	0.15	0.00	0.00	0.00		0.5	0.5			
Muscardinus avellanarius	0.00	0.00	0.00	0.15	0.00	0.00	0.00				1		
Eliomys quercinus	0.00	0.00	0.00	0.00	0.00	0.00	4.76				0.75	0.25	
Glis glis	0.00	0.00	0.00	0.00	0.46	1.11	9.52				1		
Dryomys nitedula	5.88	2.78	0.00	0.15	0.46	0.00	0.00				1		
Total	**100**	**100**	**100**	**100**	**100**	**100**	**100**	**1.5**	**5**	**4.75**	**10.75**	**4.25**	**3.75**
MNI	**34**	**36**	**317**	**683**	**217**	**90**	**21**						
NISP	**53**	**62**	**595**	**1314**	**418**	**163**	**36**						

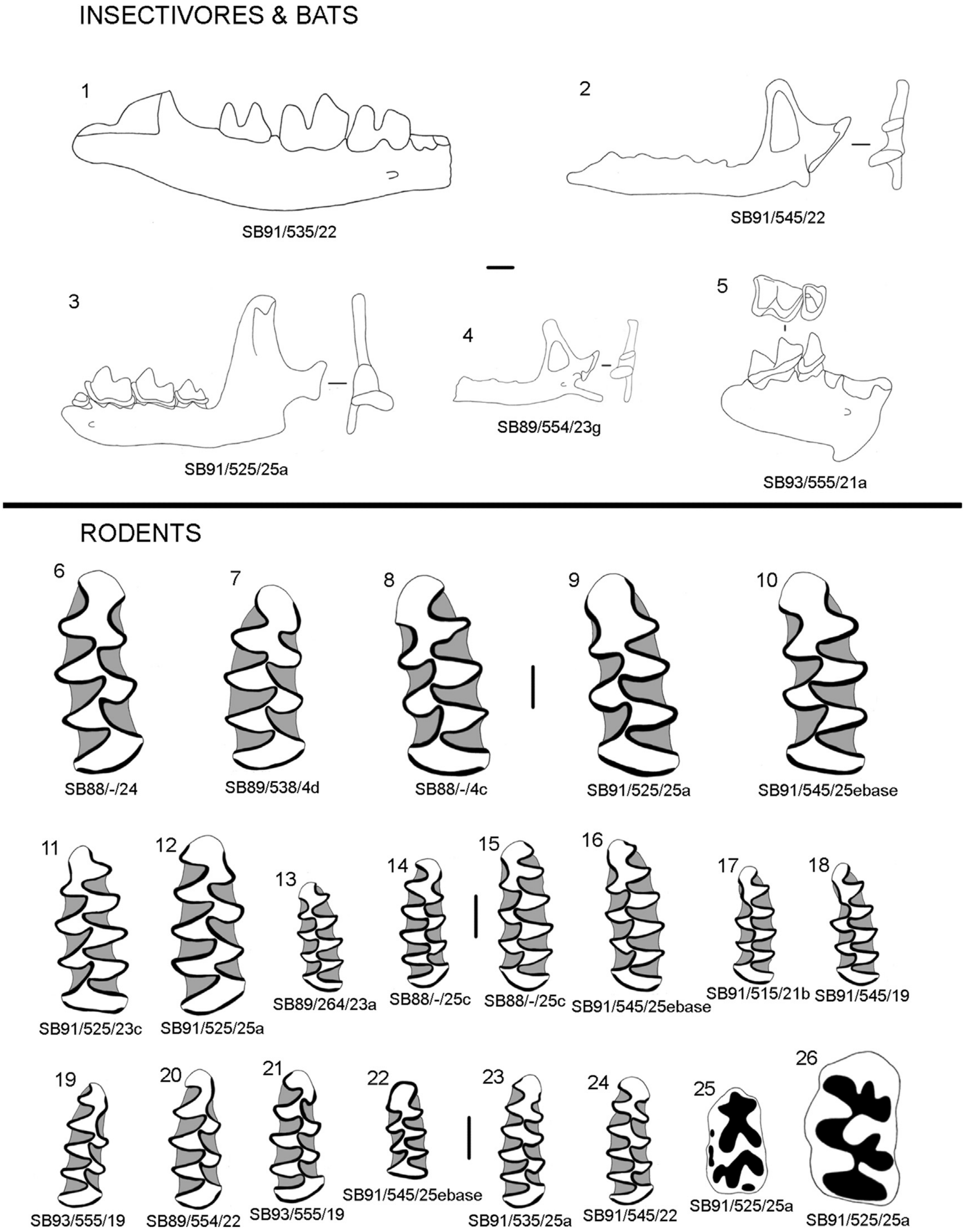

Fig. 2. Some of the small mammals identified at Grotta Maggiore di San Bernardino. 1: right mandible *Talpa* cf. *T. europaea* (labial view); 2: right mandible *Neomys* cf. *N. anomalus* (lingual and posterior views); 3: left mandible *Crocidura* gr. *leucodon-suaveolens* (labial and posterior views); 4: right mandible *Sorex minutus* (lingual and posterior views); 5: right mandible *Nyctalus* cf. *N. lasiopterus* (occlusal and labial views); 6–8: m1 *Arvicola amphibius* (6–7 right: 8 left-occlusal view); 9–10: m1 left *Arvicola mosbachensis* (occlusal view); 11–12: m1 *Dinaromys* cf. *D. bogdanovi* (11 left: 12 right-occlusal view); 13–14: m1 *Microtus arvalis* (13 left: 14 right-occlusal view); 15–16: m1 left *Microtus agrestis* type *jansoni* (occlusal view); 17–18: m1 left *Microtus gregalis* (occlusal view); 19–20: m1 right *Microtus oeconomus* (occlusal view); 21: m1 right *Chionomys nivalis* (occlusal view); 22: m1 left *Clethrionomys glareolus* (occlusal view); 23–24: m1 right *Microtus* (*Terricola*) *multiplex-subterraneus* (occlusal view); 25: m1 left *Apodemus* gr. *sylvaticus-flavicollis* (occlusal view); 26: M1 left *Cricetus cricetus* (occlusal view). Scales 1 mm.

number-of-individuals (MNI) method, by means of which we determined the sample (i.e. from each level) by counting the most-represented diagnostic elements.

The preliminary taphonomic study of the small mammals is based on the descriptive and systematic method for studying the changes resulting from predation (Andrews, 1990; Fernández-Jalvo et al., 2016). For this preliminary study, the alterations caused by digestion present in the first lower molars of the arvicoline rodent species have been observed and described (Table 2), allowing us to identify and recognize the action of predation.

Table 2
Percentages of arvicoline lower first molars from the Grotta Maggiore di San Bernardino sequence showing different degrees of digestion.

		Arvicola amphibius	*Arvicola mosbachensis*	*Dinaromys* cf. *D. bogdanovi*	*Chionomys nivalis*	*Clethrionomys glareolus*	*Microtus arvalis*	*Microtus agrestis*	*Microtus arvalis-agrestis*	*Microtus gregalis*	*Microtus oeconomus*	*M. (Terricola)* gr. *multiplex-subterraneus*	**Total**	**%**
Unit II	absent	2	0	0	0	0	7	7	0	1	0	2	**19**	**67.86**
	light-moderate	0	0	0	0	0	1	2	0	0	0	0	**3**	**10.71**
	severe	2	0	0	0	0	0	1	0	0	0	0	**3**	**10.71**
	extreme	1	0	0	0	0	1	1	0	0	0	0	**3**	**10.71**
	Total	5	0	0	0	0	9	11	0	1	0	2	**28**	**100**
Unit III	absent	3	0	0	1	2	8	8	0	1	0	1	**24**	**61.54**
	light-moderate	1	0	0	0	0	5	4	0	1	0	0	**11**	**28.21**
	severe	0	0	0	0	0	2	2	0	0	0	0	**4**	**10.26**
	Total	4	0	0	1	2	15	14	0	2	0	1	**39**	**100**
Unit IV	absent	25	0	0	1	29	166	76	0	11	4	30	**342**	**63.45**
	light-moderate	8	0	0	0	0	55	45	0	5	0	9	**122**	**22.63**
	severe	4	0	0	0	0	20	25	0	4	1	6	**60**	**11.13**
	extreme	0	0	0	1	2	4	7	1	0	0	0	**15**	**2.78**
	Total	37	0	0	2	31	245	153	1	20	5	45	**539**	**100**
Unit V	absent	66	0	0	3	117	234	150	0	16	0	71	**657**	**64.29**
	light-moderate	27	0	0	0	0	91	62	0	5	5	34	**224**	**21.92**
	severe	10	0	0	0	1	33	54	0	1	2	16	**117**	**11.45**
	extreme	3	0	0	0	0	6	13	1	0	0	1	**24**	**2.35**
	Total	106	0	0	3	118	364	279	1	22	7	122	**1022**	**100**
Unit VI	absent	29	1	9	1	25	80	46	0	0	0	16	**207**	**69.23**
	light-moderate	6	1	0	0	2	22	17	0	0	0	9	**57**	**19.06**
	severe	3	1	0	0	3	8	8	0	0	0	3	**26**	**8.70**
	extreme	2	1	0	0	1	2	3	0	0	0	0	**9**	**3.01**
	Total	40	4	9	1	31	112	74	0	0	0	28	**299**	**100**
Unit VII	absent	0	17	15	0	3	12	15	0	0	0	3	**65**	**92.86**
	light-moderate	0	3	0	0	0	1	1	0	0	0	0	**5**	**7.14**
	Total	0	20	15	0	3	13	16	0	0	0	3	**70**	**100**
Unit VIII	absent	0	3	1	0	2	5	5	0	0	0	0	**16**	**88,889**
	light-moderate	0	2	0	0	0	0	0	0	0	0	0	**2**	**11,111**
	Total	0	5	1	0	2	5	5	0	0	0	0	**18**	**100**

3.2. Palaeoenvironmental reconstruction

In order to reconstruct the environment at Grotta Maggiore di San Bernardino, we used the method of habitat weightings (see Evans et al., 1981; Andrews, 2006), distributing each small-mammal taxon in the habitat(s) where it can be found at present in the Italian Peninsula. Habitats are divided into six types, five of them in accordance with Cuenca-Bescós et al. (2005, 2009), Blain et al. (2008) and López-García et al. (2010): open land in which dry and wet meadows are distinguished, woodland and woodland margin areas, rocky areas and areas surrounding water; finally, a new habitat type has been included: open woodlands (López-García et al., 2014a). These types are detailed as follows (Table 1): open dry denotes meadows under seasonal climate change; open humid, evergreen meadows with dense pastures and suitable topsoil; open woodland, woodland margins and forest patches, with moderate ground cover; woodland, mature forest; water, areas along streams, lakes and ponds; and rocky, areas with a suitable rocky or stony substratum.

3.3. Palaeodiversity reconstruction

Among the large number of indexes proposed for evaluating the biodiversity of a sample, species evenness is fundamental for assessing the homogeneity of an environment (Magurran and McGill, 2011). Evenness is a diversity index that is used to quantify how equal the various communities are numerically. The evenness of a community can be represented by the Simpson index of diversity, which is also equivalent to the probability of interspecific encounter (Simpson, 1949; Blois et al., 2010; López-García et al., 2013): i.e., the Simpson index of diversity = $1 - \sum(pi^2)$, where pi is the proportion of individuals in the ith species. The evenness index is constrained between 0 and 1. The index will be close to 0 if there is a single dominant species. To avoid the statistical problems of high sample-size dependence, we have standardized the absolute values by dividing by total sample abundances, expressed as percentages of MNI. This standardization allows the taxon evenness to be compared in samples of different size. This index of evenness was obtained using the Paleontological Statistics Program (PAST) (Hammer et al., 2001).

3.4. Palaeoclimatic reconstruction

The Italian Peninsula extends between the parallels 35° and 47° N, in the range of a humid-temperate mesothermal climate. Italy is one of the most mountainous areas in Europe, and these mountains play a major role in the characterization of its climatic diversity. Climatic conditions can change abruptly over a few tens of kilometres, from the mildness of the marine coast to the harshness of coastal mountain summits, and from the temperate semi-continental conditions of the Po Plain to the harshness of the inner Alps, resulting in a great variety of climates. As a result, the taxonomic composition of the rodent assemblage allows us to evaluate the climatic conditions. In order to assess the palaeoclimatic data from Grotta Maggiore di San Bernardino, we used the bioclimatic model established by Hernández-Fernández (2001a and b). This method is based on the hypothesis that a significant correlation exists between climate and mammal communities. According to Hernández-Fernández (2001a and b), Hernández-Fernández and Peláez-Campomanes (2005) and Hernández-Fernández et al. (2007), mammal assemblages can be assigned to ten climate types, five of which are represented by the rodent assemblage of Grotta Maggiore di San Bernardino. This assemblage has been analysed using the Climatic Restriction Index ($CRI_i = 1/n$, where "n" is the number of climatic zones where the species are represented and "i" is the climatic zone where the species appears) (Table 3). The climate types in question are: IV Subtropical with winter rains and summer droughts; VI Typical temperate; VII Arid-temperate; VIII Cold-temperate (boreal) and IX Polar. After obtaining this distribution, the Bioclimatic Component (BC; representation by level of each of the five available climates) has been calculated using the following formula: $BC_i = (\sum CRI_i) \times 100/S$, where S is the number of species per unit at Grotta Maggiore di San Bernardino (Appendix A1). From the BC, a mathematical model has been elaborated using a multiple linear regression (Hernández-Fernández and Peláez-Campomanes, 2005); by means of a series of functions, this allows various climatic parameters to be estimated (Appendix A2). On the basis of this method, two climatic factors are estimated: the mean annual temperature (MAT) and the mean annual precipitation (MAP). These parameters are compared with the present-day data of the meteorological station (over a period of 30 years) of Mossano (45° 25′ N, 11° 33′ E) situated at 92 m a.s.l. For the area around Grotta Maggiore di San Bernardino, the current data show that MAT = 13.1 °C and MAP = 906 mm (Blasi et al., 2007).

4. Results and discussion

4.1. Taphonomic remarks

A total of 2015 arvicoline first lower molars from the seven archaeo-palaeontological units (II-VIII) have been studied, which represents 76.3% of the total NISP in the entire sequence. A significant percentage of the analysed molars (i.e. 34%) show an abnormal morphology due to digestion, indicating that the accumulation is associated with predation (Table 2). The degree of alteration enables us to identify the presence of several predators in the sequence. The high percentage of remains with no alteration in the lower units (VIII and VII) shows that the main agent responsible for the accumulation of these units was probably a category 1 or 2 predator, with a light to intermediate capacity for modification. According to Andrews (1990), several nocturnal birds of prey could be included within these categories, such as *Tyto alba* or *Strix aluco*. Unfortunately, there is no information available pertaining to the bird assemblage recovered in these units, and for the moment it is

Table 3
Distribution of the rodent species identified at Grotta Maggiore di San Bernardino according to their climate preferences, in accordance with Hérnandez-Fernández (2001b) and Hérnandez-Fernández et al. (2007). IV Subtropical with winter rains and summer droughts; VI Typical temperate; VII Arid-temperate; VIII Cold-temperate (boreal) and IX Polar.

	IV	VI	VII	VIII	IX
Arvicola amphibius	0.25	0.25	0.25	0.25	
Arvicola mosbachensis	0.25	0.25	0.25	0.25	
Dinaromys cf. *D. bogdanovi*		0.50	0.50		
Chionomys nivalis	0.25	0.25		0.25	0.25
Clethrionomys glareolus		0.50		0.50	
Microtus arvalis		1.00			
Microtus agrestis		0.50		0.50	
Microtus gregalis			0.33	0.33	0.33
Microtus oeconomus		0.33		0.33	0.33
M. (Terricola) gr. *multiplex-subterraneus*		1.00			
Cricetus cricetus		0.50	0.5		
Apodemus gr. *sylvaticus-flavicollis*	0.50	0.50			
Marmota marmota		0.50	0.50		
Sciurus sp..	0.33	0.33		0.33	
Sicista betulina		0.50		0.50	
Muscardinus avellanarius		1.00			
Eliomys quercinus	0.50	0.50			
Glis glis		1.00			
Dryomys nitedula	0.33	0.33	0.33		

not possible to ascribe the small-mammal accumulation to a specific predator. However, in general these kinds of predator do not display a specific prey consumption pattern (Andrews, 1990). Thus, palaeoecological interpretations based on the relative abundances of small-mammal taxa for these units are reliable indicators of the habitat where the hunting predators consumed their prey. By contrast, the variation in the represented percentages of absent to extreme digestion in units VI to II suggests that several agents from categories 1 to 5 were probably responsible for the accumulation. Various predators were identified, such as the nocturnal bird of prey *Athene noctua* (unit VI), the diurnal birds of prey *Buteo buteo* (unit V-IV), *Aquila chrysaetos* and *Falco subbuteo* (both in unit VI) and the small carnivores *Vulpes vulpes* and *Martes* sp. (both in units VI to II) (Cassoli and Tagliacozzo, 1994). Although some of these predators may not be opportunistic, the relatively high diversity in small mammals detected from units VI to II (Table 4) leads us to suggest that the small-mammal assemblages are representative of the environment surrounding the cave at the moment of the accumulation of the remains.

4.2. Biochronological remarks

On the basis of the occurrence and disappearance of taxa throughout the sequence and the morphological characters of single species, it is possible to observe remarkable differences between the rodent assemblages of units II-V and those of units VII-VIII. There are several indications that the accumulation might have taken place in two very different biochronological periods.

1) The transition between the early and the late Toringian small-mammal age is marked by the progressive disappearance of *Arvicola mosbachensis* and the first occurrence of *A. amphibius* with modern morphology. The most distinctive character that allows these two species to be separated is the thickness of the enamel of the tooth walls. *Arvicola* from the lower units (VII-VIII) clearly presents the *Mimomys*-like enamel pattern typical of *A. mosbachensis*, while in the upper units (II to V) *A. amphibius* displays an evident *Microtus*-like pattern. Even though geographical variability exerts a large influence on the time and conditions of this transition in the Italian Peninsula (Maul et al., 1998), in the northeastern region the transition *A. mosbachensis* – *A. amphibius* is completed before the end of MIS 5e (Sala and Masini, 2007). Therefore, the late Toringian units II-V can be assigned to the Late Pleistocene (dating from MIS 5e onwards), while the early Toringian units VII-VIII should be assigned to the Middle Pleistocene (older than MIS 5e).

2) The presence of the genus *Dinaromys* in northeastern Italy is well documented from the Early Pleistocene on, with the occurrence of *D. allegranzii* at Rivoli Veronese (Sala, 1996) and *D. dalmatinus* at Monte la Mesa (Marchetti et al., 2000), Monrupino (Kormos, 1931), Slivia, Bristie II, and San Giovanni Duino (the former as archaic *Dolomys* sp. – recte *Dinaromys* sp. – and the latter as *Dinaromys* cf. *dalmatinus*, Bartolomei, 1980). Fossil forms of the recent species *D. bogdanovi* are signalled starting from the Middle Pleistocene (Kovalsky, 2001), as in Fontana Marella Cave (Zanalda, 1994; Bona et al., 2008), and its last occurrence in Italy is reported at Riparo Tagliente (Berto, 2013) at the end of the Late Pleistocene. *Dinaromys* from Grotta Maggiore di San Bernardino has been assigned to *D.* cf. *D. bogdanovi*, although it presents some archaic features. In fact, characters such as the large size of m1, the strong alternation of T6-T7, and the abundance of cement in juveniles (according to Bartolomei, 1969) are not fully developed here as in Late Pleistocene individuals, e.g. at Fumane Cave (MIS 3, López-García et al., 2015) or Caverna degli Orsi (MIS 5–3, Berto and Rubinato, 2013). This suggests that the population of *Dinaromys* of Grotta Maggiore di San Bernardino belongs to an earlier evolutionary stage, prior to MIS 5.

3) *Dinaromys bogdanovi* and *Chionomys nivalis* share a preference for continental climates and open habitat with rocky exposures. Therefore, when and where sympatric, they are direct competitors. Kryštufek and Bužan (2008) suspect that the r-selected strategy of *C. nivalis* eventually led the relatively K-selected *D. bogdanovi* to local extinction, forcing *D. bogdanovi* to retire to its current distribution range. In the fossil record of northeastern Italy it is possible to observe a shift in the assemblages: where these two species occur together, *Dinaromys* is either dominant over *Chionomys* or equal to it until the onset of MIS 5 (Bona et al., 2008; Berto and Rubinato, 2013). From the end of the Eemian, however, *Chionomys* slowly but surely becomes dominant over *Dinaromys*, sometimes achieving a complete substitution (Berto, 2013; López-García et al., 2015; Jéquier et al., 2015). Given the fact that climatic and environmental conditions over the time-span covered by the sequence of Grotta Maggiore di San Bernardino seem suitable for both species, the presence of *Dinaromys* alone in the lower units and of *Chinomys* in the upper units might be taken to suggest that the former date to before MIS 5e, while the latter are younger.

4) *Microtus agrestis* from units VIII-VII presents a morphology described by Chaline (1972) and ascribed by the author to *M. agrestis* type *jansoni* (Figs. 2-15). There are no direct comparisons with other sites in the Italian Peninsula, but populations of this rodent have been identified in other late Middle Pleistocene sites in Mediterranean western Europe (Cuenca-Bescós et al., 1999; Mourer-Chauviré et al., 2003; Brunet-Lecomte and Paunesco, 2004; Cuenca-Bescós et al., 2010; Galindo-Pellicena et al., 2011; López-García et al., 2014b, 2016; among others). Furthermore, the peculiar morphology displayed in Fig. 2-15 has never been found in Italian Late Pleistocene or Holocene populations of *M. agrestis*.

5) The occurrence in the Italian Peninsula of *M. oeconomus*, *Sicista betulina* and *Dryomys nitedula* has been reliably documented only during the Late Pleistocene (Kovalsky, 1991). The arrival of this species was probably supported by the deteriorating climatic and environmental conditions that followed the Eemian interglacial.

Table 4
Values obtained for evenness. Simpson diversity index = $1 - \sum(pi^2)$ obtained using standardized values; relation of temperature and precipitation for the Grotta Maggiore di San Bernardino sequence; MAT, mean annual temperature; MAP, mean annual precipitation; Δ: difference between the values obtained by analysing the small mammals from Grotta Maggiore di San Bernardino and the present mean of Mossano meteorological station over the last 30 years; and percentage representation of small-mammal taxa associated with open dry meadows and rocky areas (O. dry + rocky) and open woodland and woodland environments (O. wood + wood).

	Simpson Index			Climate				Landscape	
	n	Indiv.	1-D	MAT	Δ	MAP	Δ	O.dry + rocky	O.wood + wood
Unit II	11	100	0.8581	7.75	−5.35	1210	304	13.24	47.79
Unit III	14	100	0.8765	6.48	−6.62	1140	234	23.61	38.19
Unit IV	15	100	0.7462	4.35	−8.75	1139	233	33.91	35.65
Unit V	23	100	0.8409	5.90	−7.20	1220	314	23.61	41.03
Unit VI	19	100	0.8571	8.89	−4.21	1366	460	23.85	41.13
Unit VII	16	100	0.8837	8.58	−4.52	1439	533	20.83	47.50
Unit VIII	11	100	0.8889	9.17	−3.93	1383	477	16.67	48.81

All this evidence suggests that units VIII-VII can be assigned to the late Middle Pleistocene, while units V-II belong to the Late Pleistocene, as previously pointed out by Sala (1980) and Cassoli and Tagliacozzo (1994).

4.3. Small-mammal composition of Grotta Maggiore di San Bernardino

There are taxonomic differences between the small-mammal associations from the lower units (VIII-VII) and the upper units (V to II) of the sequence. The small-mammal distribution in the lower units (VIII-VII) is characterized by the relative abundance of *Arvicola mosbachensis*, *Dinaromys* cf. *D. bogdanovi*, *Microtus arvalis* and *Microtus agrestis* type *jansoni*. From a quantitative point of view, in unit VIII the European mole (*Talpa* cf. *T. europaea*), the extinct water vole (*A. mosbachensis*), the bank vole (*Clethrionomys glareolus*), the common vole (*M. arvalis*), the field vole (*M. agrestis* type *jansoni*) and the fat dormouse (*Glis glis*) are the most abundant species (Table 1). These six taxa represent 76.2% (16 individuals) of the total MNI for this unit (= 21). In unit VII, although it is very similar to unit VIII, there are quantitative differences in the assemblage, the most abundant species being *A. mosbachensis*, *D.* cf. *D. bogdanovi* (the Balkan snow vole), *M. arvalis*, *M. agrestis* type *jansoni* and *Apodemus* gr. *sylvaticus-flavicollis* (the wood/yellow-necked mouse group) (Table 1). These five taxa represent 65.5% (59 individuals) of the total MNI for this unit (= 90). No one species dominates over the others, but the small-mammal assemblage seems typical of the late Middle Pleistocene in Italy (Sala and Masini, 2007). As previously pointed out by Sala (2013), there are few late Middle Pleistocene sites in Italy where the small mammals have been studied. The lower units of Grotta Maggiore di San Bernardino are comparable with the lower layers (S and R) of Grotta del Broion (Berici Hills, Vicenza) (Sala, 1980), where *T. europaea*, *A. amphibius*, *M. arvalis*, *M. agrestis*, *C. glareolus*, *A. sylvaticus* and *G. glis* are present, and with Torre in Pietra 2 (Latium) (Caloi and Palombo, 1978), where *Arvicola* sp., *M.* gr. *arvalis-agrestis*, *C. glareolus*, *A.* gr. *sylvaticus-flavicollis* and *G. glis* are present, though with the absence in both sites of *D. bogdanovi* (Caloi and Palombo, 1978; Colamussi, 2002). They are probably also comparable with Sossano 2 (Monte Mason, Berici Hills, Vicenza), where *T. europaea*, *A.* gr. *praeceptor*, *D.* gr. *bogdanovi*, *M. agrestis*, *C. glareolus*, *A. sylvaticus* and *G. glis* are present, though with the absence of *M. arvalis* (Bon et al., 1991). Although the most abundant species are *M. arvalis* (26.3%) and *M. agrestis* (18.9%), unit VI is characterized by a mixture of taxa from the Middle and Late Pleistocene, as exemplified by *A. mosbachensis* (11.1%) and *A. amphibius* (1.4%), making the interpretation of this unit problematic. By contrast, the small-mammal assemblages of units V to II clearly pertain to the Late Pleistocene. The small-mammal distribution is characterized by the relative abundance throughout these units of *M. arvalis* and *M. agrestis* (576 individuals). From a quantitative point of view, the northern water vole (*A. amphibius*), the common vole (*M. arvalis*) and the field vole (*M. agrestis*) are the most abundant species, representing 62.7% (671 individuals) of the total MNI for these units (= 1070) (Table 1). *M. arvalis* is the most abundant species in all these units with the exception of unit II, where the dominant species is *M. agrestis* (20.6%) and *A.* gr. *sylvaticus-flavicollis* (20.6%), although the MNI is low in this unit (= 34) (Table 1), indicating a relative increase in humidity and forest cover. *M. arvalis* is commonly abundant in Late Pleistocene sites across the Italian Peninsula, as evidenced in the MIS 5 layers of Caverna degli Orsi (Berto and Rubinato, 2013) and Ciota Ciara (Berto et al., 2016) and in the MIS 3 layers of Grotta del Broion (Colamussi, 2002), Grotta Minore di San Bernardino (Bartolomei and Broglio, 1964) and Grotta Fumane (López-García et al., 2015), Riparo Mochi in the Ligurian Alps (Berto, 2013), and Grotta di Castelcivita (Masini and Abbazzi, 1997), Grotta Paglicci (Berto, 2013) and Grotta Reali (Sala et al., 2012) in the southern Apennines. The abundance of *M. arvalis* is currently reported to be higher in open areas and relatively drier regions of north Italy (Amori et al., 2008).

4.4. Palaeoenvironmental and palaeoclimatic reconstruction

The bioclimatic model used to reconstruct the palaeoclimatic conditions shows that the temperatures are generally lower and the precipitation is higher than today (Table 4; Fig. 3). The mean annual temperatures (MAT) in units VIII to II vary between −8.7 °C and −3.4 °C with respect to the current mean ($MAT_{Mossano}$ = 13.1 °C), reaching their minimum values in unit IV (MAT_{IV} = 4.3 °C) and maximum values in unit VIII (MAT_{VIII} = 9.2 °C) (Table 4; Fig. 3). The mean annual precipitation (MAP) varies between +233 mm and +533 mm in relation to the present ($MAP_{Mossano}$ = 906 mm), reaching its minimum values in unit IV (MAP_{IV} = 1139 mm) and its maximum in unit VII (MAP_{VII} = 1439 mm) (Table 4; Fig. 3).

A direct comparison of the evenness diversity index with the temperatures and precipitation shows that changes in small-mammal diversity follow a reverse trend in relation to the mean annual precipitation (MAP) in units VIII-VII and III-II and in relation to mean annual temperatures (MAT) in units III-II and follow a direct trend in relation to MAT in units VIII-VI and in relation to MAT and MAP in units V-IV (Fig. 3).

As for the evolution of the environment at Grotta Maggiore di San Bernardino, this shows a habitat alternating between open dry meadows (including open dry and rocky; mean 22.2%) and woodland landscape (including open woodland and woodland; mean 42.9%) through the sequence (Table 4; Fig. 3). The evenness diversity index also varies in accordance with the relation between the evolution of open dry and woodland habitats (Fig. 3).

4.4.1. MIS 7 (Units VIII-VII)

Units VIII and VII show a high diversity index (0.88 in both), high percentages of woodland formations (VIII = 48.8%; VII = 47.5%), and high values for MAT (VIII = 9.1 °C; VII = 8.5 °C) and MAP (VIII = 1383 mm; VII = 1439 mm) (Table 4; Fig. 3), indicating that these units originated during a temperate and moist climatic period, when the landscape was dominated by woodland formations. Taking into account these results, the stratigraphic position and the biochronological placement for these units are consistent with an assignation to the later partd of MIS 7 (~220–190 ka), probably 7c or 7b, and partially agree with the age proposed for these units (ca. 214–154 ka; Picin et al., 2013). This proposal conforms with the data previously set forth by Cassoli and Tagliacozzo (1994) on the basis of the large-mammal assemblages, where the abundance of cervids suggests a forest environment and temperate humid climatic conditions. Also, the climatic data inferred by the cenogram method on the basis of arvicoline species from the previous faunal list of Grotta Maggiore di San Bernardino (Bon et al., 1991) by Montuire and Marcolini (2002) suggest a mean annual temperature (MAT) of 9.17 °C for these lower units, coinciding with our results. Furthermore, our data fit with the Italian terrestrial pollen sequences of the Azzano Decimo core in Friuli (Pini et al., 2009) and Valle di Castiglione in Roma (Follieri et al., 1988), revealing the presence of a continuous tree population associated with a moist temperate climate for the MIS 7c and 7b samples. They thus coincide with the Mediterranean pollen sequences of Ioannina in Greece and the MD01-2443 deep-sea core off Portugal (Roucoux et al., 2006), where MIS 7c is represented by a long forest interval and MIS 7b by a slight contraction of the temperate forest with an abundance of tree populations.

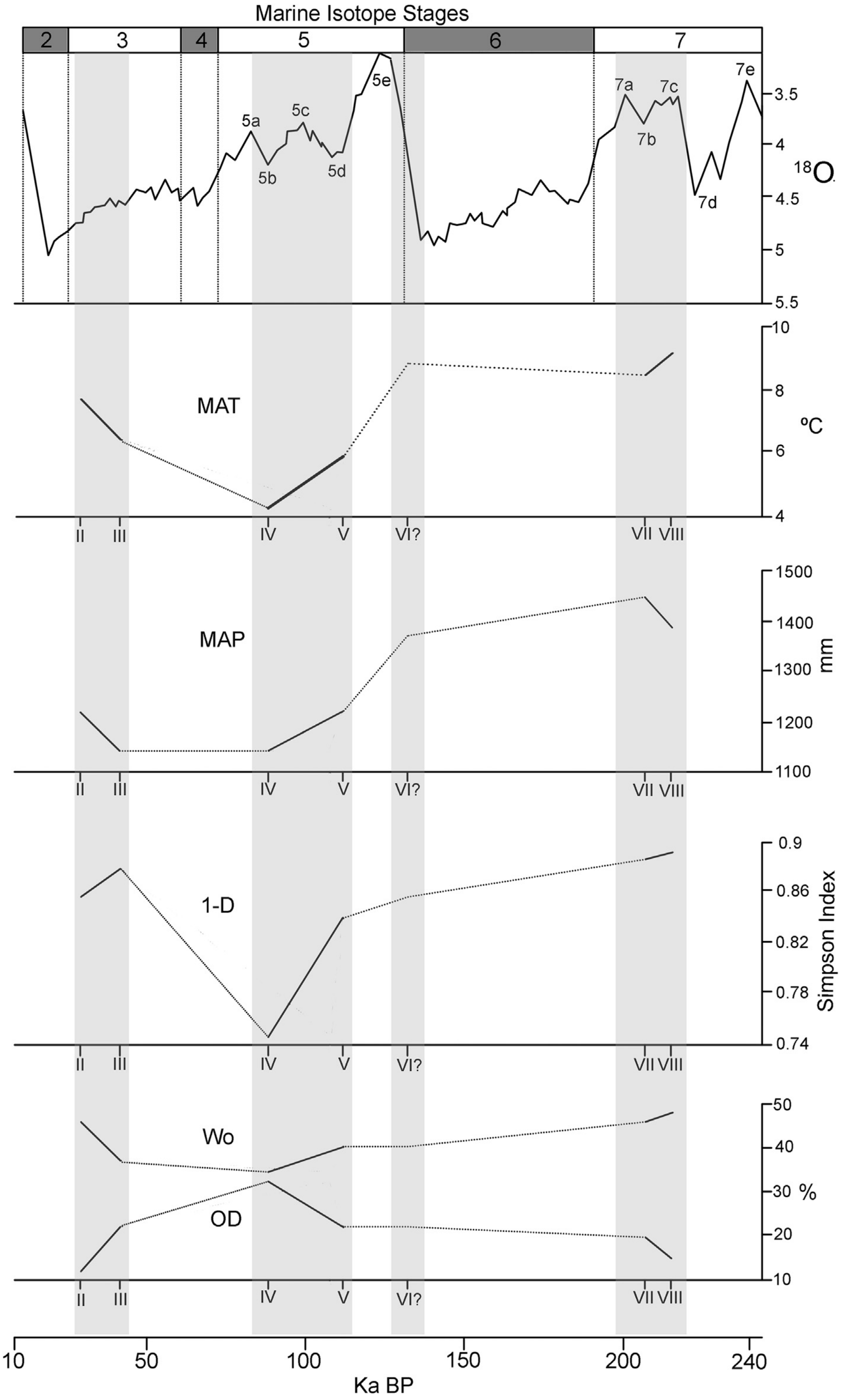

Fig. 3. Representation of mean annual temperature (MAT), mean annual precipitation (MAP), the Simpson small-mammal diversity index (1-D) and the landscape percentages (Wo: woodland + open woodland; OD: open dry + rocky) from the Grotta Maggiore di San Bernardino sequence in relation with the ^{18}O isotope curve.

4.4.2. *MIS 5 (Units V-IV)*

Unit V is biochronologically positioned in the early Late Pleistocene and dated to middle-late MIS 5 (Gruppioni, 2003). It shows lower values for the diversity index (V = 0.84), high percentages of open dry meadows (V = 23.6%), and low values for MAT (V = 5.9 °C) and MAP (V = 1220 mm) in comparison to the older units (Table 4; Fig. 3). These parameters indicate that this unit could be associated with cool and dry climatic conditions, and that the landscape was dominated by open meadows. The stratigraphic and biochronological position support the assignation of unit V to MIS 5d (~116–107 ka).

Unit IV is chronologically positioned at the end of MIS 5 and beginning of MIS 4 (Gruppioni, 2003). Like the previous unit, it shows low values for the diversity index (IV = 0.74), high percentages of open dry meadows (IV = 33.9%) and low values for MAT (IV = 4.3 °C) and MAP (IV = 1139 mm). Indeed, it shows even lower values than the previous unit (Table 4; Fig. 3). Again, these parameters indicate that this unit could be associated with cool and dry climatic conditions, and that the landscape was dominated by open meadows. The stratigraphic and the biochronological position support the assignation of unit IV to MIS 5b (~87–82 ka), although it cannot be ruled out that part of this unit belongs to MIS 4, since most of the small-mammal specimens identified (around 70%) belong to the lower part of this unit.

These proposals fit with the palaeontological data revealed by Cassoli and Tagliacozzo (1994) and Fiore et al. (2004), where the decline of cervids in concomitance with the diffusion of caprines, the increase in cave bears and the presence of marmots are indicative of a cool and relatively arid climate with open habitats, but also humid zones as shown by the presence of the otter (*Lutra lutra*) and the mallard (*Anas platyrhynchos*). Our environmental and climatic data are also compatible with the few data known for MIS 5 on the basis of studies of small-mammal assemblages across Italy. Units V-IV of Grotta Maggiore di San Bernardino are compatible with US 14 of Ciota Ciara, where the assemblage is dominated by *M. arvalis*, *Microtus* (*Terricola*) and *C. glareolus* species, with the cold climate indicators *Cricetus cricetus*, *M.* cf. *gregalis* and *C. nivalis* indicating colder and more open climatic and environmental conditions with respect to the layer underneath (US 13) (Berto et al., 2016). Furthermore, our data are also comparable with levels 126–124 of Caverna degli Orsi, where the assemblage is dominated by *M. arvalis* and *M. agrestis* with a high representation of *D. bogdanovi*, indicating cold and dry climatic and environmental conditions (Berto and Rubinato, 2013). In Italy, moreover, our reconstruction reflects the terrestrial pollen sequences of the Azzano Decimo core (Pini et al., 2009), Lake Fimon (Pini et al., 2010) and Lago Grande di Monticchio (Allen and Huntley, 2009), which record a moderate reduction of forest cover, high representation of *Pinus* and an abundance of herbaceous plants such as *Artemisia* during MIS 5d and 5b, in a context of cold and dry climatic and environmental conditions. Finally, the sporadic traces of human occupation expressed by the decrease in Mousterian lithic artifacts can be ascribed to the above-described harsher environmental and climatic conditions.

4.4.3. MIS 3 (Units III-II)

Units III-II are chronologically positioned in MIS 3, as shown by the dates 52 ± 5 ka BP, 38 ± 5 ka BP and 33 ± 5 ka BP for unit II (Peresani, 2001). They show high values for the diversity index (III = 0.87; II = 0.85), high percentages of woodland landscape, especially for unit II (III = 38.2%; II = 47.8%), high values for MAT (III = 6.5 °C; II = 7.7 °C) and similar values for MAP (III = 1140 mm; II = 1210 mm) in comparison with the older units (Table 4; Fig. 3). These values can be considered an expression of mild and humid climatic conditions, in a woodland context. The stratigraphic and chronometric position are consistent with assignation to an interstadial (IS) (~50–30 ka) within MIS 3. This is in agreement with the data previously set forth by Cassoli and Tagliacozzo (1994) and Fiore et al. (2004) on the basis of large-mammal and bird assemblages, which show an increase in cervids, the first appearance of wild boar, and the presence of *Alces alces*, *Marmota marmota* and of birds (*Pyrrhocorax graculus*, *Nucifraga caryocatactes* and *Tetrao tetrix*) ascribable to woodland environments in association with alpine grasslands and humid conditions in the context of a temperate-cold climate. On the other hand, the wide chronological range prevents us from specifying which interstadial is recorded by the accumulation of small-mammal remains. As observed by Pini et al. (2009, 2010) on the basis of their pollen data, moreover, the correlation of individual Mediterranean interstadials with their respective Greenland interstadials (GI) is problematic due to the lack of biological similarities between them. However, some data are known for these interstadials based on small-mammal records across Italy, at Fumane (López-García et al., 2015), Grotta del Broion (Sala, 1980; Colamussi, 2002) and Grotta Paglicci (Berto, 2013). These studies suggest that Interstadial 12 (IS 12) at Fumane (represented in the complex A5-A6 and in layer A4) and Grotta del Broion (layers O-15) is characterized by open woodland formations in a temperate and relatively moist climatic period. By contrast, IS7 at Grotta Paglicci (layer 24) is characterized by open woodland formations in a temperate and relatively dry period. At Grotta Maggiore di San Bernardino the human occupation increases in unit II, as indicated by the large number of Mousterian lithics, bones and fire-places (Peresani, 1995–96, 1996), tallying with the mild environmental and climatic conditions.

5. Conclusions

The discontinuous sequence of the Grotta Maggiore di San Bernardino constitutes one of the most important small-mammal records with environmental and climatic data, increasing our knowledge of the late Middle Pleistocene and Late Pleistocene of the Italian Peninsula. On the basis of an assemblage composed of insectivores, bats and rodents, our analysis enables the following conclusions to be drawn:

1) The assemblage includes a total of 2641 identified specimens, corresponding to a minimum of 1399 individuals, representing at least 31 taxa: 7 insectivores (*Erinaceus* cf. *E. europaeus*, *Talpa* cf. *T. europaea*, *Crocidura* gr. *leucodon-russula*, *Sorex* gr. *araneus-samniticus*, *Sorex minutus*, *Neomys* cf. *N. fodiens* and *Neomys* cf. *N. anomalus*); 5 bats (*Myotis* sp., *Plecotus* gr. *auritus-austriacus*, *Nyctalus* cf. *N. lasiopterus*, *Pipistrellus* sp. and *Hypsugo*/*Vespertilio* sp.); and 19 rodents (*Arvicola amphibius*, *Arvicola mosbachensis*, *Dinaromys* cf. *D. bogdanovi*, *Chionomys nivalis*, *Clethrionomys glareolus*, *Microtus arvalis*, *Microtus agrestis*, *Microtus gregalis*, *Microtus oeconomus*, *Microtus* (*Terricola*) gr. *multiplex-subterraneus*, *Cricetus cricetus*, *Apodemus* gr. *sylvaticus-flavicollis*, *Marmota marmota*, *Sciurus* sp., *Sicista betulina*, *Muscardinus avellanarius*, *Eliomys quercinus*, *Glis glis* and *Dryomys nitedula*)
2) From the preliminary taphonomic data based on the digestive alterations present in 2015 first lower molars of arvicoline rodent species, the intervention of various predators can be inferred. The high incidence of unaltered specimens in the lower units (VIII and VII) suggests that the main agent responsible for the bone accumulation was probably a category 1 or 2 predator with a light to intermediate capacity of modification. Moreover, the variation in the represented percentages of absent to extreme digestion in units VI to II shows that various agents from categories 1 to 5 probably contributed to the accumulation.
3) The biochronological record, mostly based on rodents, suggests that units VIII-VII, with the presence of *Arvicola mosbachensis*, *Dinaromys* cf. *D. bogdanovi* and *Microtus agrestis* type *jansoni*, can be assigned to late Middle Pleistocene, while units V-II, with the presence of *Arvicola amphibius*, *Chionomys nivalis*, *Micrtous agrestis*, *M. oeconomus*, *Sicista betulina* and *Dryomys nitedula*, belong to the Late Pleistocene.
4) The palaeoenvironmental and palaeoclimatic data identify three discontinuous climatic phases in the sequence: i) MIS 7c or 7b in units VIII-VII, associated with a temperate and moist climatic period and a landscape dominated by woodland formations; ii) MIS 5d in unit V, and probably MIS 5b in unit IV, associated with a cool and dry climatic period and a landscape dominated by

open meadows; and iii) an indeterminate interstadial from MIS 3 in units III-II, associated with mild and humid conditions, with a landscape dominated by woodland formations.

5) The studies carried out on the small mammals of Grotta Maggiore di San Bernardino thus seem to support the hypothesis that the ancient Middle Palaeolithic human occupation in this part of northern Italy occurred during mild and temperate substages of MIS 7. It also shows that the more intense human occupation phases occurred in a mild climate and in forest environments (units VIII-VII and units III-II). Finally, our study shows that Neanderthals were well adapted to the changing environmental and climatic conditions of the Middle to Late Pleistocene in northeastern Italy.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.quascirev.2017.05.005

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Environmental and climatic reconstruction of MIS 3 in northwestern Europe using the small-mammal assemblage from Caverne Marie-Jeanne (Hastière-Lavaux, Belgium)

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ABSTRACT

Marine Isotope Stage 3 (MIS 3, ca. 60–30 ka) is characterized by dynamic alternations of forest expansion with semi-arid area expansion in accordance with the warming and cooling, respectively, of the sea-surface temperatures in Northern Europe. It was in this context of rapid fluctuations that the terrestrial sequence of Caverne Marie-Jeanne (Hastière-Lavaux, Belgium) in northwestern Europe was formed. The habitat weighting method and the bioclimatic model, as well as the Simpson diversity index, are applied to the small-mammal assemblage of Caverne Marie-Jeanne in order to reconstruct the environmental and climatic fluctuations that are reflected in the MIS 3 sequence of the cave. Revision of the small-mammal fossil material deposited in the collections of the Royal Belgian Institute of Natural Sciences (RBINS, Brussels, Belgium) shows that the lower layers (6 to 4) of the cave, pertaining to MIS 3 (ca. 50–40 ka), underwent cold, dry environmental and climatic conditions for these layers. This is indicated by temperatures lower than at present and precipitation slightly higher than at present, together with an environment dominated by open woodland formations and open dry meadows. Our results are consistent with the available chronological, large-mammal, herpetofaunal and mollusc datasets for this lower part of the sequence. They are also consistent with regional loess studies in Belgium and with previous work performed on small mammals from MIS 3 in Belgium and elsewhere in Europe.

1. Introduction

Interest in Marine Isotope Stage 3 (MIS 3) (ca. 60–30 kyr B.P.) has been stimulated by the extreme variability of the period, as displayed by ice-core and marine records (e.g. Cacho et al., 1999; Sánchez-Goñi and d'Errico, 2005; van Meerbeeck et al., 2009, among others). On the basis of pollen analysis, MIS 3 is in general characterized by a dynamic that alternates between phases of forest development and the expansion of semi-arid areas in accordance with the warming and cooling, respectively, of sea-surface temperatures (Huntley et al., 2003; Fletcher and Sánchez-Goñi, 2008, among others). Much of the terrestrial climatic information from this period in northwestern Europe comes from loess deposits, which provide an excellent high-resolution terrestrial archive of climate evolution (Pirson et al., 2009; Haesaerts et al., 2011, 2016, among others). In this context, small-mammal studies can provide new terrestrial data to enrich our palaeoenvironmental and palaeoclimatic knowledge of the region. However, studies of Pleistocene small mammals have been relatively scarce in Belgium. To our knowledge, there are some studies of sites from the second half of the Late Pleistocene and the Early Holocene, such as Trou des Blaireaux (Cordy and Peuchot, 1983), Trou Jadot (Cordy and Toussaint, 1993), Caverne du Bois de la Saute (Toussaint et al., 1979), Grotte du Coléoptère (Dewez et al., 1983), Grotte Walou (see review in Stewart and Parfitt, 2011) and Trou Al'Wesse (Miller et al., 2012). However, only a few stratigraphic sequences studied from a small-mammal point of view contain deposits from the first half of the Late Pleistocene (MIS 3). Examples are Grotte Scladina (Cordy, 1992; López-García et al., 2017), Trou du Diable (Toussaint, 1988), Trou Magrite (Cordy, 1995), Grotte Walou (Stewart and Parfitt, 2011) and Trou Al'Wesse (Brace et al., 2012).

The first studies of the small-mammal assemblage from Caverne Marie-Jeanne were undertaken by A. Gautier (Ballmann et al., 1980), revealing 29 different small-mammal taxa (including insectivores, bats and rodents) (Appendix A1). The recent revision of the small-mammal collections deposited in the Royal Belgian Institute of Natural Sciences (RBINS) has permitted us to add to the previous list two vole species,

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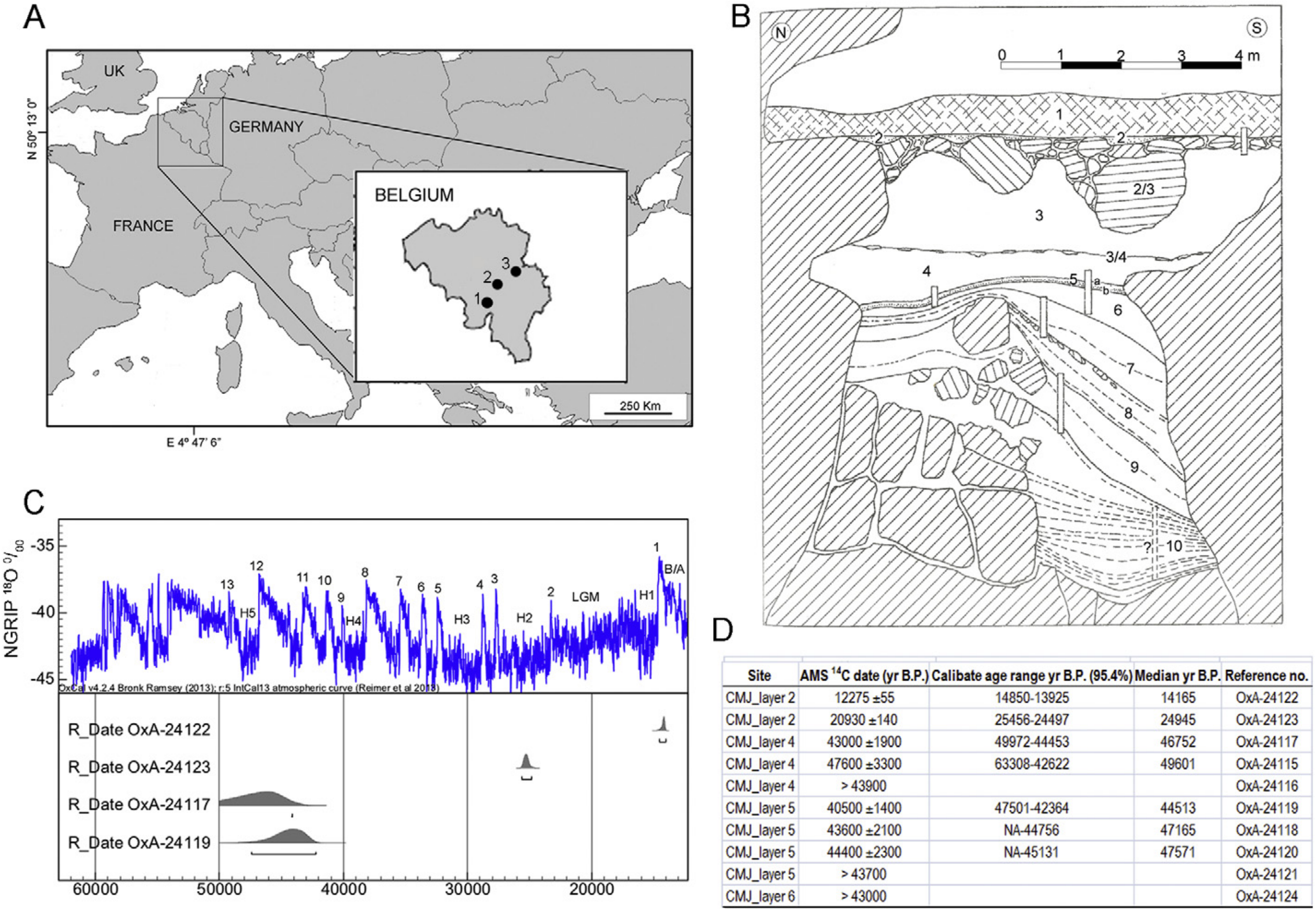
the steppe lemming (*Lagurus lagurus*) and the European pine vole (*Microtus* (*Terricola*) *subterraneus*) (Appendix A1), and to undertake a new palaeoenvironmental and palaeoclimatic reconstruction based on alternative methods from those previously used for the MIS 3 sequence of Caverne Marie-Jeanne. It was thus possible to compare and correlate our results with the chronological dating available for the Caverne Marie-Jeanne sequence (Brace et al., 2012); with previous interpretations of the site based on archaeobotanical studies (including pollen and charcoal) and faunal studies (including molluscs, large mammals, birds, amphibians, reptiles and fishes) (Ballmann et al., 1980); with the other two Late Pleistocene sites in Belgium where small-mammal studies have recently been carried out (Stewart and Parfitt, 2011; López-García et al., 2017); and with the study of regional loess in Belgium (see review in Haesaerts et al., 2016). This enabled us to put our results into context with the environmental and climatic fluctuations that occurred during MIS 3 in western Europe.

2. Caverne Marie-Jeanne

Caverne Marie-Jeanne, located at 50°13′0″ N/4°47′6″ E, is an archaeological site situated in the southeast of Belgium, in the Ardennes region (Fig. 1A). The cave, which is formed from Tournaisian (Early Carboniferous) calcareous deposits, is located 25 m above the right bank of a small tributary (Féron) of the River Meuse, near the town of Hastière-Lavaux (Ballmann et al., 1980; Brace et al., 2012). The excavations at this site began in 1943, conducted by M. Gilbert of the Royal Belgian Institute of Natural Sciences. During this field campaign, about 40 m^3 of sediment was extracted and sifted, recovering a large collection of bones and several plant, mollusc and archaeological remains (Ballmann et al., 1980). These remains are housed at the RBINS under the General Inventory number 14138 from September 4th 1943. The excavated deposits evidenced ten Quaternary layers (Fig. 1B). Layers 10 to 7, which do not contain any faunal or artefact remains, suggest that the cave was closed during its formation. Layers 6 to 2, which contain the large collection of faunal remains and some lithic tools (some Mousterian artefacts have been identified mainly in Layer 3), are principally composed of silt sands. Among the large mammals, the most frequently, according to Ballmann et al. (1980), in these layers are the carnivore *Crocuta crocuta spelaea* and the herbivores *Coleodonta antiquitatis*, *Equus* cf. *remagensis*, *Cervus elaphus*, *Bison priscus* and *Bos primigenius*. The interpretation of these layers is that the cave was connected with the outside from Layer 6 onward; the scarcity of the lithic tool remains, which suggests that the tools were accidentally introduced, and the vertebrates and terrestrial molluscs recovered, indicate that the cave probably functioned as a hyena den or hibernation place. Layer 1 is composed of clayey soil mixed with organic remains where fossil and modern faunal remains have been identified (Ballmann et al., 1980). The recent dating of the stratigraphic sequence at Caverne Marie-Jeanne shows that the lower layers (6 to 4) have a chronological range pertaining to MIS 3, i.e. between ca. 50–40 kyr B.P.; the upper Layer 2 has a chronological range pertaining to MIS 2, but the datings diverge (14,850–13,925 and 25,456–24,497 cal yr B.P.) (Fig. 1C and D) (Brace et al., 2012).



Site	AMS ^{14}C date (yr B.P.)	Calibate age range yr B.P. (95.4%)	Median yr B.P.	Reference no.
CMJ_layer 2	12275 ±55	14850-13925	14165	OxA-24122
CMJ_layer 2	20930 ±140	25456-24497	24945	OxA-24123
CMJ_layer 4	43000 ±1900	49972-44453	46752	OxA-24117
CMJ_layer 4	47600 ±3300	63308-42622	49601	OxA-24115
CMJ_layer 4	> 43900			OxA-24116
CMJ_layer 5	40500 ±1400	47501-42364	44513	OxA-24119
CMJ_layer 5	43600 ±2100	NA-44756	47165	OxA-24118
CMJ_layer 5	44400 ±2300	NA-45131	47571	OxA-24120
CMJ_layer 5	> 43700			OxA-24121
CMJ_layer 6	> 43000			OxA-24124

Fig. 1. A. Location of Caverne Marie-Jeanne (1), Scladina cave (2) and Walou cave (3) in Belgium; B. Stratigraphic sequence of Caverne Marie-Jeanne (modified from Ballmann et al., 1980); C. Calibrated dating of Caverne Marie-Jeanne correlated with IntCal13 curve (Reimer et al., 2013) and compared with the NGRIP (North Greenland Ice Core Project) ^{18}O isotope curve [Prepared using OxCal v. 4.1.7; Bronk Ramsey and Lee, 2013]; D. ^{14}C dating performed for Caverne Marie-Jeanne layers (taken from Brace et al., 2012).

3. Material and methods

3.1. Small-mammal sorting and palaeontological and taphonomic study

The small-mammal fossil remains used for this study come from the excavations undertaken at Caverne Marie-Jeanne during the 1940s. These allow us to identify six layers with archaeo-palaeontological material (Fig. 1B)·This material consists mainly of disarticulated bone fragments and isolated teeth probably collected (we lack information on the samples recovered) by water-screening with a 1-mm mesh screen, to judge by the dimensions of the bone remains. The fossil material was processed, sorted, classified and deposited in the collections of the Royal Belgian Institute of Natural Sciences (RBINS, Brussels, Belgium). The small-mammal material was partially studied by A. Gautier (in Ballmann et al., 1980). Our studied fossil assemblage includes 9897 identified specimens, corresponding to a minimum of 4980 individuals, representing at least 31 taxa (Table 1; Fig. 2). This is a representative statistical sample of all the material deposited in the RBINS collections that has not been fully studied. The fossil fragments were identified following the palaeontological criteria given by Chaline (1972), Nadachowski (1984), Sevilla (1988) and López-García (2008, 2011). The specific attribution of this material is based principally on the best diagnostic elements: mandible, maxilla and isolated teeth for shrews; isolated teeth and humeri for Talpidae; isolated teeth, humeri and mandibles for bats; first lower molars for Arvicolinae; and mandibles and isolated teeth for *Sciurus vulgaris*, *Apodemus* spp., *Eliomys quercinus*, *Glis glis*, *Cricetulus migratorius*, *Cricetus cricetus* and *Sicista betulina.* Moreover, the fossils were grouped using the minimum number of individuals (MNI) method, by means of which we determined the sample (i.e. from each Layer) by counting the most represented diagnostic elements and taking laterality into account where appropriate. The small-mammal remains recovered from layers 1 and 3 are too scarce to reconstruct their palaeoenvironment and palaeoclimate with confidence (Table 1). The data inferred from these layers will be displayed (in tables and figures in this manuscript) but not used for further interpretation.

The taphonomic study of small mammals is based on a descriptive and systematic method that studies the changes resulting from predation (Andrews, 1990). For this, the alterations caused by digestion present in the first lower molars were observed and described in accordance with Andrews (1990) for the arvicoline rodent species (Table 2), allowing us to identify and recognize the action of the predators that accumulated the small-mammal remains.

3.2. Reconstruction of palaeodiversity

Among the many indices proposed for evaluating the biodiversity of a sample, species evenness is fundamental for assessing the homogeneity of an environment (Magurran and McGill, 2011). Evenness is a diversity index that is used to quantify how equal the various communities are numerically. The evenness of a community can be represented by the Simpson index of diversity, which is also equivalent to the probability of interspecific encounter (Simpson, 1949; Blois et al., 2010; López-García et al., 2013): i.e. Simpson's index of diversity $= 1 - \Sigma (p_i^2)$, where p_i is the proportion of individuals in the ith species to the total number of individuals. The evenness index is constrained between 0 and 1. It will be close to 0 if there is a single dominant species and close to 1 when the diversity is highest. To avoid the statistical problems of high sample-size dependence, we standardized the absolute values of the MNIs by dividing by total sample abundances, expressed as percentages of the MNI. This standardization allows taxon evenness to be compared in samples of different size. The evenness index was obtained using the Paleontological Statistics Program (PAST) (Hammer et al., 2001).

Table 1

Representation of the percentage of the MNI (%) for the small mammals from the Caverne Marie-Jeanne sequence and the small-mammal distribution by habitat: OD, open dry; OH, open humid; Wo, woodland/woodland-edge; Ro, rocky; Wa, water. NISP: total number of identified specimens by layer; MNI: Minimum number of individuals by layer.

	Layer 2	Layer 3	Layer 4	Layer 5	Layer 6	OD	OH	Wo	Ro	Wa
Talpa europaea	17.53	6.35	1.20	1.71	0.83		0.5	0.5		
Crocidura gr. *leucodon-russula*	0.18	0.00	0.05	0.26	0.18	0.5		0.5		
Sorex gr. *araneus*	10.20	0.00	0.96	5.46	2.02		0.5	0.5		
Sorex minutus	1.25	0.00	0.48	1.53	0.46		0.5	0.5		
Neomys cf. *N. fodiens*	0.00	0.00	0.24	1.19	0.18		0.25			0.75
Myotis gr. *myotis-blythii*	0.00	0.00	0.05	0.17	0.18	0.5			0.5	
Myotis cf. *nattereri*	0.00	0.00	0.05	0.09	0.09	0.25	0.25	0.25		0.25
Myotis bechsteinii	0.00	0.00	0.00	0.09	0.09			1		
Myotis type *daubentoni*	0.00	0.00	0.05	0.17	0.09			0.25		0.75
Myotis mystacinus s.l	0.00	0.00	0.14	0.09	0.00			0.5	0.25	0.25
Plecotus gr. *auritus-austriacus*	0.54	0.00	0.10	0.85	0.37			0.75	0.25	
Eptesicus nilssonii	0.00	0.00	0.34	0.34	0.18	0.25	0.25	0.25	0.25	
Dicrostonyx torquatus	6.62	15.87	15.08	15.52	17.57	0.75		0.25		
Lemmus lemmus	1.07	0.00	2.07	0.68	0.55	0.75		0.25		
Lagurus lagurus	0.18	1.59	0.24	0.60	0.55	1				
Arvicola amphibius	10.02	34.92	3.27	6.31	5.61					1
Microtus arvalis	25.76	19.05	27.95	10.14	23.64	0.5		0.5		
Microtus agrestis	3.58	4.76	4.13	2.81	1.93		0.5	0.5		
Microtus arvalis-agrestis	0.00	0.00	0.86	0.34	0.18					
Microtus oeconomus	3.58	1.59	3.84	1.02	3.13		0.5	0.25		0.25
Microtus gregalis	14.13	12.70	35.93	46.63	36.43		0.25	0.25	0.25	0.25
Microtus (*Terricola*) *subterraneus*	0.00	0.00	0.05	0.09	0.37	0.25	0.25	0.25	0.25	
Chionomys nivalis	0.54	3.17	1.83	0.43	1.93				1	
Clethrionomys glareolus	2.33	0.00	0.53	0.60	0.18			1		
Sciurus vulgaris	0.00	0.00	0.00	0.00	0.09			1		
Cricetus cricetus	0.72	0.00	0.14	0.17	0.18	0.5			0.5	
Cricetulus migratorius	0.00	0.00	0.05	0.43	0.09	1				
Apodemus gr. *sylvaticus-flavicollis*	1.61	0.00	0.14	0.77	1.20			1		
Sicista betulina	0.00	0.00	0.05	0.77	0.09		0.5	0.5		
Eliomys quercinus	0.00	0.00	0.00	0.17	0.37			0.75	0.25	
Glis glis	0.18	0.00	0.19	0.60	1.20			1		
Total	100	100	100	100	100	6.25	4.25	12.5	3.5	3.5
MNI	559	63	2082	1173	1098					
NISP	1300	101	4081	2302	2108					

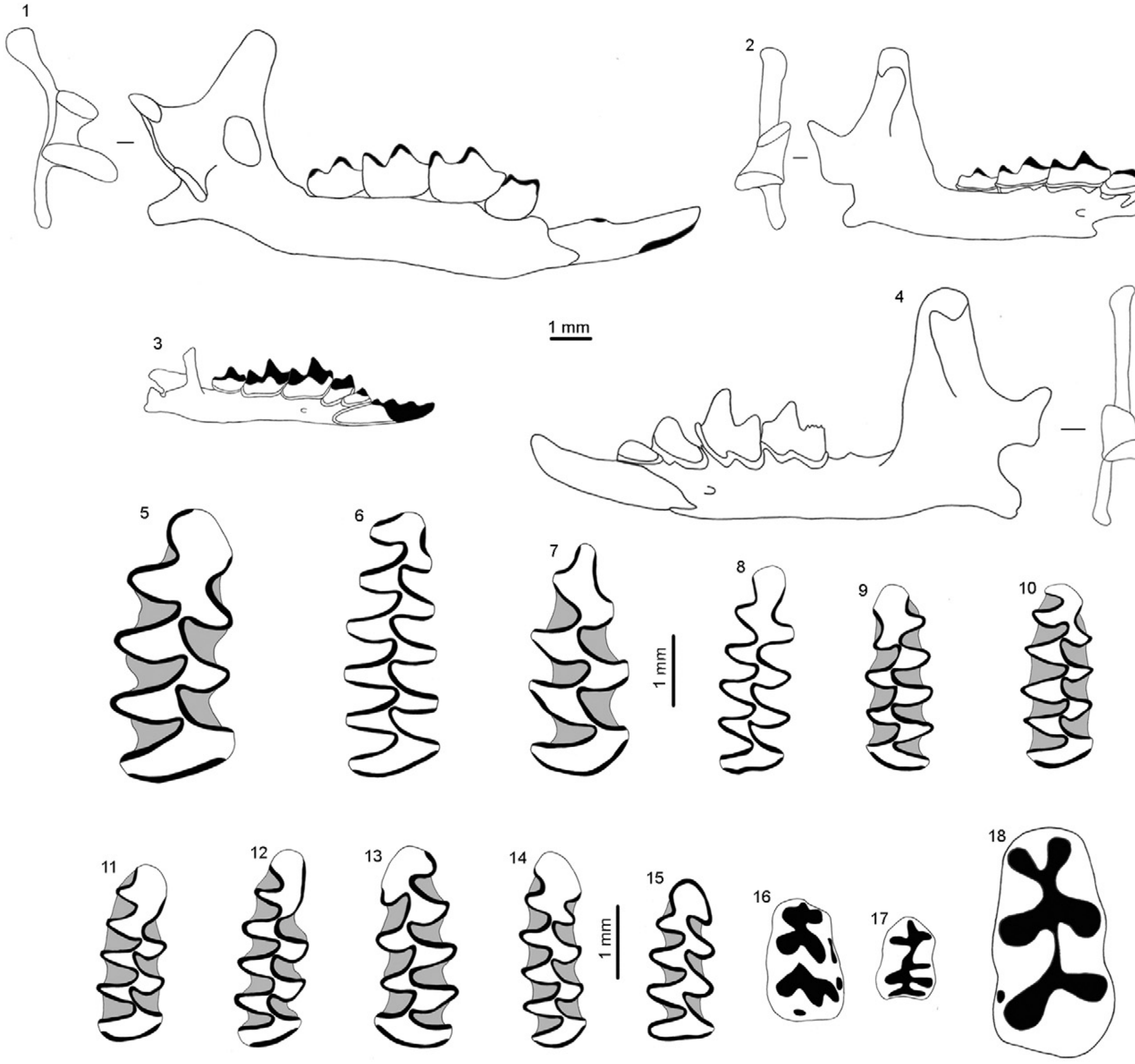


Fig. 2. Some small-mammal remains identified from Caverne Marie-Jeanne. 1. Left mandible *Neomys* cf. *N. fodiens* (posterior and lingual views) from Layer 5 a + b (IRSNB M 2281); 2. Right mandible *Sorex* gr. *araneus* (posterior and buccal views) from Layer 5 a + b (IRSNB M 2282); 3. Right mandible *Sorex minutus* (buccal view) from Layer 5 sup-a (IRSNB M 2283); 4. Left mandible *Crocidura* gr. *leucodon-russula* (posterior and buccal views) from Layer 5 a + b (IRSNB M 2284); 5. First lower right molar (m1) *Arvicola amphibius* (occlusal view) from Layer 5 sup-a (IRSNB M 2285); 6. Right m1 *Dicrostonyx torquatus* (occlusal view) from Layer 5 sup-a (IRSNB M 2286); 7. Right m1 *Lemmus lemmus* (occlusal view) from Layer 5 a + b (IRSNB M 2287); 8. Right m1 *Lagurus lagurus* (occlusal view) from Layer 6 (IRSNB M 2288); 9. Left m1 *Microtus arvalis* (occlusal view) from Layer 4 (IRSNB M 2289); 10. Right m1 *Microtus agrestis* (occlusal view) from Layer 4 (IRSNB M 2290); 11. Right m1 *Microtus oeconomus* (occlusal view) from Layer 5 a + b (IRSNB M 2291); 12. Right m1 *Microtus gregalis* (occlusal view) from Layer 3 (IRSNB M 2292); 13. Left m1 *Chionomys nivalis* (occlusal view) from Layer 5 a + b (IRSNB M 2293); 14. Right m1 *Microtus* (*Terricola*) *subterraneus* (occlusal view) from Layer 5 sup-a (IRSNB M 2294); 15. Right m1 *Clethrionomys glareolus* (occlusal view) from Layer 5 sup-a (IRSNB M 2295); 16. Right m1 *Apodemus* gr. *sylvaticus-flavicollis* (occlusal view) from Layer 5 sup-a (IRSNB M 2296); 17. Left m1 *Sicista betulina* (occlusal view) from Layer 5 sup-a (IRSNB M 2297); 18. Left m1 *Cricetus cricetus* (occlusal view) from Layer 4 (IRSNB M 2298). Scales 1 mm.

3.3. Biochronology

Rodents, and particularly arvicolines, evolved rapidly during the Quaternary, so their record provides an important basis for stratigraphical divisions and correlations between distant areas in Europe. The rapid evolutionary radiation of the 'Microtus group' and the changes along the *Mimomys*–*Arvicola* lineage constitute very useful tools for correlating European Pleistocene faunas (Fejfar and Heinrich, 1980; Heinrich, 1978, 1982, 1987; van Kolfschoten, 1990; Rekovets, 1994). The different stages in the evolution of arvicolid species present problems in determining the exact age of a site (Martin, 2014), but can prove highly valuable in suggesting relative or similar chronologies between different sites (Lozano-Fernández et al., 2014, 2015), as in the case of *Arvicola amphibius* in this paper.

To evaluate our biochronological inferences, we make a morphological and biometric comparison of the remains of *A. amphibius* from layers 2, 4 and 6 with those from other European sites. As the evolution of the *Arvicola* genus entails an increase in the length of m1 and a decrease in the SDQ index (enamel differentiation index; Heinrich, 1978, 1982, 1987; van Kolfschoten, 1990; Maul et al., 2013; Maul and Markova, 2007; Rekovets, 1994), these are the features on which the biochronological evaluation was based.

A total of 228 remains of adult *A. amphibius* were studied: 63 from Layer 2, 102 from Layer 4, and 63 from Layer 6. For each item, the m1 length was estimated as the occlusal mesiodistal length, and the SDQ index was calculated as: $\sum(\text{teet} \times 100 / \text{leet}) / \text{N}$, where N corresponds to the number of dentine fields of the studied tooth; teet refers to the maximum thickness of the posterior enamel band; and leet refers to

Table 2
Percentages of arvicoline lower first molars from the Caverne Marie-Jeanne sequence showing the different degrees of digestion.

		Dicrostonyx torquatus	*Lemmus lemmus*	*Lagurus lagurus*	*Arvicola amphibius*	*Microtus arvalis*	*Microtus agrestis*	*Microtus arvalis-agrestis*	*Microtus oeconomus*	*Microtus gregalis*	*Microtus (Terricola) subterraneus*	*Chionomys nivalis*	*Clethrionomys glareolus*	Total	%
Layer 2	Absent	25	8	1	104	203	35	0	35	74	0	4	26	515	73.99
	Light-moderate	24	3	0	4	32	2	0	4	48	0	0	0	117	16.81
	Severe	13	1	1	1	15	0	0	3	17	0	0	0	51	7.33
	Extreme	4	0	0	0	3	0	0	0	6	0	0	0	13	1.87
		66	**12**	**2**	**109**	**253**	**37**	**0**	**42**	**145**	**0**	**4**	**26**	**696**	**100**
Layer 3	Absent	7	0	0	31	7	4	3	1	5	0	2	0	60	61.86
	Light-moderate	1	0	0	6	3	0	0	0	5	0	1	0	16	16.49
	Severe	3	0	1	1	4	1	0	0	5	0	0	0	15	15.46
	Extreme	2	0	0	1	3	0	0	0	0	0	0	0	6	6.19
		13	**0**	**1**	**39**	**17**	**5**	**3**	**1**	**15**	**0**	**3**	**0**	**97**	**100**
Layer 4	Absent	283	46	5	88	765	87	30	100	645	2	49	16	2116	55.39
	Light-moderate	104	14	0	14	201	24	0	32	385	0	10	1	785	20.55
	Severe	134	15	0	13	135	40	1	15	287	0	15	2	657	17.20
	Extreme	73	3	0	3	37	16	2	6	120	0	2	0	262	6.86
		594	**78**	**5**	**118**	**1138**	**167**	**33**	**153**	**1437**	**2**	**76**	**19**	**3820**	**100**
Layer 5	Absent	197	10	8	114	163	37	5	17	551	1	9	11	1123	59.20
	Light-moderate	60	1	2	17	28	7	0	4	285	0	0	0	404	21.30
	Severe	69	1	0	1	26	8	0	1	171	0	1	0	278	14.65
	Extreme	22	1	0	0	4	10	0	0	55	0	0	0	92	4.85
		348	**13**	**10**	**132**	**221**	**62**	**5**	**22**	**1062**	**1**	**10**	**11**	**1897**	**100**
Layer 6	Absent	228	21	12	92	388	19	2	46	429	4	27	3	1271	65.41
	Light-moderate	68	9	0	18	69	1	0	7	195	0	6	0	373	19.20
	Severe	58	1	0	11	34	7	0	4	106	0	0	0	221	11.37
	Extreme	28	1	0	0	7	4	0	0	36	1	1	0	78	4.01
		382	**32**	**12**	**121**	**498**	**31**	**2**	**57**	**766**	**5**	**34**	**3**	**1943**	**100**

The bold numbers in table are the sum of arvicoline degrees of digestion by species and layers.

the maximum thickness of the anterior enamel band for each dentine field (Heinrich, 1978, 1987; von Koenigswald and van Kolfschoten, 1996; modified by Cuenca-Bescós et al., 2010).

All the measurements were taken with the image-treatment software Adobe Photoshop CS5, using photographs from a Dino-Lite Digital Microscope. This software ensures highly reliable measurements made on flat surfaces.

3.4. Palaeoenvironmental reconstruction

To reconstruct the palaeoenvironment at Caverne Marie-Jeanne, we used the method of habitat weightings (see Evans et al., 1981;Andrews, 2006), distributing each small-vertebrate taxon in the habitat(s) where it can be found at present in Belgium. The habitats are divided into five types (in accordance with Cuenca-Bescós et al., 2005;Blain et al., 2008; López-García et al., 2010). These types are defined as follows (Table 1): *open dry*, meadows under seasonal climate change; *open humid*, evergreen meadows with dense pastures and suitable topsoil; *woodland*, mature forest, including woodland margins and forest patches, with moderate ground cover; *water*, areas along streams, lakes and ponds; and *rocky*, areas with a suitable rocky or stony substratum.

3.5. Palaeoclimatic reconstruction

In order to assess the palaeoclimatic data from Caverne Marie-Jeanne, we used the bioclimatic model established by Hernández-Fernández (2001, b). This method is based on the hypothesis that there exists a significant correlation between climate and mammal communities. According to Hernández-Fernández (2001, b), Hernández-Fernández and Peláez-Campomanes (2005) and Hernández-Fernández et al. (2007), mammal assemblages fall into ten climatic types, five of which are represented by the rodent assemblage of Caverne Marie-Jeanne: (IV) Subtropical with winter rains and summer droughts; (VI) Typical temperate; (VII) Arid-temperate; (VIII) Cold-temperate (boreal) and (IX) Polar (Table 3). The latter was distributed according to the climatic restriction index (CRIi = 1/ n, where "n" is the number of climatic zones where the species are represented and "i" is the climatic zone where the species appears). After obtaining this distribution, the bioclimatic component (BC; representation by level of each of the five available climates) was calculated using the following formula: BCi = (ΣCRIi) × 100 / S, where S is the number of species by unit (Appendix A2). From the BC, a mathematic model has been elaborated using a multiple linear regression (Hernández-Fernández and Peláez-Campomanes, 2005); by means of a series of functions, this makes it possible to estimate various climatic parameters (Appendix A3). Based on this method, two climatic factors are estimated: the mean annual temperature (MAT) and the mean annual precipitation (MAP). These climatic parameters are compared with the modern climatic data (over a period of 30 years) from the meteorological station of Hastière-Lavaux (50°4′ N, 4°49′ E), situated at 98 m.a.s.l. For the area around Caverne Marie-Jeanne, the current data show that MAT = 9.9 °C, and MAP = 840 mm.

4. Results and discussion

4.1. Remarks on the small-mammal taphonomy

A total of 8453 arvicoline first lower molars from the entire sequence of Caverne Marie-Jeanne have been analysed, representing 85.4% of the total NISP. The scarcity of the remains recovered from Layer 3 (97 first lower molars) makes taphonomic interpretation difficult (Table 2). However, the alteration produced by digestion on the molars in the other layers reaches values between 26% and 40.8%, indicating that the accumulation is indeed associated with predation (Table 2). This degree of alteration allows us to identify, at the least, the presence of three main predators in the sequence. The largely moderate alterations (between 19 and 21%) and the severe alterations (between 11 and 17%) in the lower layers (6 to 4) indicate that the agents responsible for the accumulation were probably: 1) a predator with an intermediate capacity for modification (according to Andrews, 1990) such as the strigiform *Bubo bubo* (Eurasian eagle-owl), which is present in Layer 4 (Ballmann et al., 1980); and 2) a category 3 predator (according to Andrews, 1990) such as the falconiform *Falco tinnunculus* (common kestrel), which is present in Layer 4 (Ballmann et al., 1980). On the other hand, the high values for the absence of digestion (about 74%) detected in the first lower molars in Layer 2 indicate that the agent responsible for this accumulation is a category 1 predator (according to Andrews, 1990) such as an indeterminate strigiform, as no bird of prey has been identified for this layer (Ballmann et al., 1980). The main potential predators identified, such as the category 1 predator, *Bubo bubo* or *Falco tinnunculus*, suggest that open or semi-open palaeoecological conditions prevailed in the area around the site of Caverne Marie-Jeanne. Thus, palaeoecological interpretations based on the relative abundances of small-mammal taxa for these layers reliably show the habitat where the hunting predators consumed their prey. However, the diurnal and moderately selective habits of the falconiforms (Andrews, 1990; Gil-Delgado et al., 1995;Aparicio, 2000) suggest that the relative abundances of the taxa present in the association from layers 6 to 4 should be treated with caution.

4.2. The small-mammal assemblage from Caverne Marie-Jeanne

Although there are no relevant taxonomic differences from the base to the top of the sequence, there are changes in the small-mammal percentage distribution in the sequence between the lower layers (6 to 4) pertaining to MIS 3 and Layer 2, pertaining to MIS 2. The small-mammal distribution from the lower layers (6 to 4) is characterized by the predominance of the narrow-headed vole (*M. gregalis*), the common vole (*M. arvalis*), and the Arctic lemming (*Dicrostonyx torquatus*), which are from a quantitative point of view the most abundant species (Table 1). These three taxa represent between 72% and 79% (3336 individuals) of the total minimum number of individuals from these layers ($\text{MNI}_{\text{Layers 6 to 4}} = 4342$). Among the fossil material analysed by taxon from these layers, *M. gregalis* corresponds to 1691 individuals (i.e. 35.9% to 46.6%), *M. arvalis* to 958 individuals (i.e. 10.1% to 28%), and *D. torquatus* to 687 individuals (i.e. 15.1% to 17.5%). *M. gregalis* is the most abundant species in these studied layers (6 to 4) (Table 1). Although *M. gregalis* is a species not currently present in Belgium, during the Late Pleistocene and more specifically during MIS 3 it is relatively abundant, as evidenced by recent studies at Scladina cave in Namur (López-García et al., 2017) and Walou cave in Trooz (Stewart and Parfitt, 2011), both located in the Wallonia region. The abundance of *M. gregalis* is currently reported to be higher in grass steppes and alpine and water meadows (Batsaikhan et al., 2008). On the other hand, the small-mammal distribution from Layer 2 is characterized by the prevalence of the common vole (*M. arvalis*), the common mole (*T. europaea*), the narrow-headed vole (*M. gregalis*), the common shrew group (*S.* gr. *araneus*), the European water vole (*A. amphibius*) and the Arctic lemming (*D. torquatus*), which are from a quantitative point of view the most abundant species (Table 1). These six taxa represent 84.2% (471 individuals) of the total minimum number of individuals from this layer ($\text{MNI}_{\text{Layer 2}} = 559$). Among the fossil material analysed by taxon from this layer, *M. arvalis* corresponds to 144 individuals (i.e. 25.8%), *T. europaea* to 98 individuals (i.e. 17.5%), *M. gregalis* to 79 individuals (i.e. 14.1%), *S.* gr. *araneus* to 57 individuals (10.2%), *A. amphibius* to 56 individuals (i.e. 10%) and *D. torquatus* to 37 individuals (i.e. 6.6%). *M. arvalis* is the most abundant species in this studied layer (Table 1). An abundance of *M. arvalis* is relatively common in the MIS 2 sites of western Europe, as evidenced by recent studies in Belgium from Walou cave in Trooz (Stewart and Parfitt, 2011), France (Royer et al., 2016), the Italian peninsula (Berto, 2013; López-García et al., 2014, 2015) and the Iberian peninsula (Fernández-García et al., 2016; López-García, 2011). In its wide distribution across Eurasia, *M. arvalis* is currently found in a great variety of open habitats, including moist meadows, forest steppe, moist forest and agricultural areas (Yigit et al., 2016). In Belgium the species inhabits non-humid, open, herbaceous meadows, open areas and forest edges, as well as cultivated fields and gardens (Frechkop, 1981).

Table 3
Distribution of the rodent species identified at Caverne Marie-Jeanne according to their climate preferences, according to Hernández-Fernández (2001) and Hernández-Fernández et al. (2007). IV Subtropical with winter rains and summer droughts; VI Typical temperate; VII Arid-temperate; VIII Cold-temperate (boreal) and IX Polar.

	IV	VI	VII	VIII	IX
Dicrostonyx torquatus					1
Lemmus lemmus				0.5	0.5
Lagurus lagurus			1		
Arvicola amphibius	0.25	0.25	0.25	0.25	
Microtus arvalis		1			
Microtus agrestis		0.5		0.5	
Microtus oeconomus		0.333		0.333	0.333
Microtus gregalis			0.333	0.333	0.333
Microtus (*Terricola*) *subterraneus*		1			
Chionomys nivalis	0.25	0.25		0.25	0.25
Clethrionomys glareolus		0.5		0.5	
Sciurus vulgaris	0.333	0.333		0.333	
Cricetus cricetus		0.5	0.5		
Cricetullus migratorius	0.333	0.333	0.333		
Apodemus gr. *sylvaticus-flavicollis*	0.5	0.5			
Sicista betulina		0.5		0.5	
Eliomys quercinus	0.5	0.5			
Glis glis		1			

4.3. Biochronological remarks

In the course of its evolution in Europe, the *Arvicola* lineage undergoes an increase in the length of m1 and a decrease in its SDQ index (Heinrich, 1978, 1982, 1987; van Kolfschoten, 1990; Rekovets, 1994). However, recent works such as Escudé et al. (2008a, 2008b) have shown that in certain cases the use of SDQ and m1 length as biochronological indicators is not reliable, suggesting that the evolution of arvicolid molars is more complex than was previously thought. According to Maul et al. (2013), these recent studies have highlighted methodological problems, notably differences in measurement protocols and the importance of regional variation, particularly in species with large geographical ranges (Maul and Markova, 2007). However, the results of Maul et al. (2013), which take into account the length of the chronological range, have generally confirmed the known patterns of change in SDQ and m1 length. The m1 length increases, this process starting in the older species of the *Mimomys-Arvicola* lineage, and SDQ undergoes a process of reduction that starts before the *Mimomys-Arvicola* transition at around 600 ka, with values of around 150 in the older samples falling to values as low as 50–60 at the youngest sites.

In the light of the previous considerations, we can deduce that the features of *Arvicola amphibius* from different sites with similar chronologies will be similar.

The different SDQ values for *A. amphibius* measured in Caverne Marie-Jeanne range from 69.3–87.1 for Layer 2; 72.3–95.9 for Layer 4; to 81.5–92.1 for Layer 6. The mean SDQ values by layer are 75.7 in Layer 2; 82.9 in Layer 4; and 87.6 in Layer 6 (Appendix A4). The values from layers 4 and 6 are close to the values of populations of *A. amphibius* (cited as *A. terrestris*) from the Euerwanger Bühl H locality (Germany; SDQmean = 83.029); the Kemathenhöhle locality (Germany; SDQmean = 89.23); the Krockstein/Rübeland locality (Germany; SDQmean = 89.08); the Istállóskö locality (Hungry; SDQmean = 89.54) and the Peskö locality (Hungary; SDQmean = 89.31), all of them with an age between 30 and 60 ka (Heinrich, 1982; Maul et al., 2013).

The mean length of *A. amphibius* m1s from Caverne Marie-Jeanne is 4.04 mm for layers 4–6, and 4.1 mm for Layer 2. As occurs with SDQ, the length values from layers 4–6 are close to the values from the localities of Euerwanger Bühl H, Kemathenhöhle, Krockstein/Rübeland, Istállóskö and Peskö, all of them with a mean length of m1 between 4 and 4.07 mm (Heinrich, 1982; Maul et al., 2013).

In the light of the above, we can thus assume that layers 4–6 from Caverne Marie-Jeanne correspond to a chronology between 30 and 60 ka (MIS 3); the lower SDQ value from Layer 2 in conjunction with the greater length of m1 from *A. amphibius* in Layer 2 indicates that this layer is younger than layers 4–6. These observations are coherent with the results previously obtained by Brace et al. (2012).

According to the ^{14}C AMS data obtained directly from the specimens of Arctic lemming (*D. torquatus*) from the different layers of Caverne Marie-Jeanne (Brace et al., 2012), the lower layers (6 to 4) have a chronological range pertaining to MIS 3, i.e. between ca. 50–40 kyr B.P. On the other hand, the upper Layer 2 has a chronological range pertaining to MIS 2, although the disparate datings for this layer (14,850–13,925 and 25,456–24,497 cal yr B.P.) hamper its environmental and climatic reconstruction.

4.4. Palaeoenvironmental and palaeoclimatic reconstruction

4.4.1. MIS 3

In the MIS 3 layers (6 to 4), the mean annual temperature (MAT) varies between −6.6 °C and −5.7 °C with respect to the current mean ($\text{MAT}_{\text{Hastière-Lavaux}} = 9.9$ °C), reaching its minimum values in Layer 4 ($\text{MAT}_{\text{Layer 4}} = 3.3$ °C) and its maximum values in Layer 6 ($\text{MAT}_{\text{Layer 6}} = 4.2$ °C) (Table 4; Fig. 3). The mean annual precipitation (MAP) varies between +160 mm and +180 mm in relation to the present ($\text{MAP}_{\text{Hastière-Lavaux}} = 840$ mm), reaching its minimum values in Layer 6 ($\text{MAP}_{\text{Layer 6}} = 1000$ mm) and its maximum values in Layer 5 ($\text{MAP}_{\text{Layer 5}} = 1022$ mm) (Table 4; Fig. 3).

The Simpson index shows relatively low values for diversity in these layers (between 0.73 and 0.77), a consequence of the dominance of the one species (*M. gregalis*). These values follow the opposite pattern to MAT and MAP (Table 4; Fig. 3).

As regards the evolution of the environment in the MIS 3 layers of Caverne Marie-Jeanne, this shows a mixed habitat dominated by open woodland formations (between 30.2% and 32.7%) and open dry meadows (between 18.6% and 27.3%); there is also a high component of open humid meadows, but in no layer does this exceed a representation of 20% (Table 4; Fig. 3).

These data partially coincide with the palaeoenvironmental and palaeoclimatic interpretations previously proposed for these layers (Ballmann et al., 1980). Although the pollen, charcoal, fish and bird samples recovered and identified from these layers have not provided conclusive environmental and climatic results, the other faunal proxies (molluscs, amphibians, squamate reptiles and large mammals) can be taken to support our environmental and climatic interpretation (Ballmann et al., 1980). Firstly, the mollusc studies broadly indicate an environment that is relatively dry for Layer 5 and relatively more humid for Layer 4, with generally cool climatic conditions. For Layer 5 the mollusc association indicates interstadial conditions, exemplified by the presence of the three species with southern affinities, *Pyramidula rupestris* (rock snail), *Abida secale* (bulin snail family) and cf. *Helicella profuga* (land snail). However, the presence of just one southern species (*P. rupestris*) out of the total of eight identified in Layer 4 shows a probable decrease in temperatures for this layer in relation to Layer 5 (Ballmann et al., 1980). In addition, a previous study of the herpetofaunal assemblages from Caverne Marie-Jeanne (Ballmann et al., 1980) also suggested environmental conditions becoming progressively wetter, typified by a progression from assemblages where the common frog (*Rana temporaria*) dominates (layers 5 and 6) to assemblages where the more hygrophilous common toad (*Bufo bufo*) becomes most abundant (especially in layers 1 and 2). Finally, the large-mammal assemblage shows cold climatic conditions for the lower layers (6 to 4), with the presence of species such as *Mammuthus primigenius* (woolly mammoth), *Rangifer tarandus* (reindeer), *Vulpes lagopus* (Arctic fox) and *Ochotona pusilla* (steppe pika), and generally dry environmental conditions, though slightly wetter in Layer 6 and slightly drier in layers 5 and 4 (Ballmann et al., 1980).

At a regional scale, the loess-based palaeoenvironmental interpretations for the chronological time span where the lower layers (6 to 4) are included (ca. 50–40 ka) coincide with the data expounded above for the small-mammal assemblage of Caverne Marie-Jeanne. These show that the period in question is dominated by cold climatic conditions, with boreal climatic conditions for interstadial 12 (IS 12; ca. 47 ka) and two polar climatic peaks (ca. 40 ka and 48 ka) between IS8 and IS 12 (probably associated with Heinrich event 4, H4) and between IS 12 and IS 17 (probably associated with H5) (Haesaerts et al., 2016).

4.4.2. Indeterminate MIS 2

MIS 2 is represented by Layer 2 at Caverne Marie-Jeanne. As pointed out above, the disparate dating obtained for this layer, 14,850–13,925 cal yr B.P. (coinciding with the Bølling/Allerød interstadial) and 25,456–24,497 cal yr B.P. (coinciding with H2) (Brace et al., 2012), make the palaeoenvironmental and palaeoclimatic reconstruction of this layer difficult. However, the data obtained from the small-mammal assemblage of this layer are expounded below.

In Layer 2 the mean annual temperature (MAT) is −7.7 °C with respect to the current mean ($\text{MAT}_{\text{Hastière-Lavaux}} = 9.9$ °C) and the mean annual precipitation (MAP) is +81 mm in relation to the present ($\text{MAP}_{\text{Hastière-Lavaux}} = 840$ mm) (Table 4; Fig. 3).

The Simpson index shows a relatively high value for diversity in this layer (1-D = 0.85), a consequence of the equal representation of six species, two insectivores (*T. europaea* and *S.* gr. *araneus*) and four arvicolines (*D. torquatus*, *A. amphibius*, *Microtus arvalis* and *M. gregalis*) (Table 4; Fig. 3).

As regards the environment, Layer 2 of Caverne Marie-Jeanne shows a habitat dominated by woodland formations (i.e. 40.1%) and open humid meadows (i.e. 21.6%); there is also a high component of open dry meadows, but this does not exceed a representation of 20% (Table 4; Fig. 3).

Accordingly, the previous faunal studies of this layer suggest the same results as those expounded above (Ballmann et al., 1980). For example, the mollusc association shows an increase in species richness in Layer 2 from eight to thirteen in relation to the lower layers (5 and 4), though without the presence of southern species. The previous study of the mammalian assemblage suggests an increase in forest formations in Layer 2 with respect to the earlier layers (6 to 4) (Ballmann et al., 1980).

The stratigraphic interpretation of Layer 2 shows that it is a residual layer that is difficult to interpret because it has little sediment matrix, which lies on the depressions of a stalagmitic plate (Ballmann et al., 1980), in addition to the chronological data set forth above (Brace et al., 2012). Layer 2 is formed from a mixture of at least two different climatic moments, one probably before (H2 event) and one after (Bølling/Allerød interstadial) the Last Glacial Maximum (LGM).

4.5. Comparison with other Late Pleistocene sites with small-mammal studies

There are only a few sites in Belgium containing Late Pleistocene (MIS 3) sequences with small mammals that have been studied from a palaeoenvironmental point of view. Besides Caverne Marie-Jeanne, only Trou Magrite (Cordy, 1995), Grotte Walou (Stewart and Parfitt, 2011) and Grotte Scladina (López-García et al., 2017) have been analysed in such a way. In the case of Trou du Diable (Toussaint, 1988), a small-mammal study by G. Brochet may be mentioned, but the faunal list is not published and the number of remains is too low, preventing any palaeoenvironmental interpretation. Taking into

Table 4
Values obtained for evenness. Simpson diversity index = 1 − Σ(pi^2) obtained using standardized values; relation of temperature and precipitation for the Caverne Marie-Jeanne sequence; MAT, mean annual temperature; MAP, mean annual precipitation; Δ:difference between the values obtained by analysing the small mammals from Caverne Marie-Jeanne and the present mean of Hastière-Lavaux meteorological station over the last 30 years; and percentage representation of small-mammal taxa associated with open dry meadows (OD); open humid meadows (OH); woodland environments (Wo); rocky environments (Ro) and landscapes beside running water (Wa).

	Simpson index			Climate				Landscape				
	n	Indiv.	1-D	MAT	Δ	MAP	Δ	OD	OH	Wo	Ro	Wa
Layer 2	18	100	0.8544	2.16	−7.74	921	81	19.28	21.60	40.12	4.56	14.45
Layer 3	9	100	0.7926	0.33	−9.57	752	−88	23.02	9.52	22.62	6.35	38.49
Layer 4	28	100	0.7646	3.35	−6.55	1018	178	27.35	14.48	32.77	11.06	13.47
Layer 5	30	100	0.7392	4.10	−5.80	1023	183	18.67	18.73	30.33	12.64	19.29
Layer 6	30	100	0.7746	4.22	−5.68	1000	160	26.48	13.54	32.49	11.54	15.73

account that the small-mammal studies from Trou Magrite (Cordy, 1995) are rather old and difficult to compare with our data, a comparison of the environmental results of our studies will be with the recent studies of Grotte Walou (Stewart and Parfitt, 2011) and Grotte Scladina (López-García et al., 2017).

Layers CII-6 and CII-7 from Cycle II of Grotte Walou, related to the early part of MIS 3 (according to Pirson, 2011 and Pirouelle, 2011), show a predominance of *M. arvalis-agrestis*, with the presence of *D. torquatus*, *M. gregalis* and *L. lemmus*. This led to the palaeoenvironmental conditions being interpreted as relatively cool and dry (Stewart and Parfitt, 2011), coinciding with the data for pollen, which is dominated by herbaceous steppe and meadowland (Damblon et al., 2011). Although the predominant small mammals in the lower layers (6 to 4) of Caverne Marie-Jeanne are quite different from layers CII-6 and CII-7 of Grotte Walou, the general pattern, with the dominance of *M. gregalis*, *M. arvalis* and *D. torquatus*, the relatively low values for the diversity index and MAT and the environment dominated by open woodland formations with a high percentage of open dry meadows, are comparable with the data obtained for layers CII-6 and CII-7 of Grotte Walou.

Similar environmental and weather conditions are detected from the small-mammal assemblage of Layer I in Grotte Scladina (López-García et al., 2017). According to Pirson (2007) and Pirson et al. (2008), Layer I of Grotte Scaldina ranges between ca. 43.1 and 40.2 kyr B.P. In general, the small-mammal assemblage shows that Scladina Layer I could be located in a cold and dry phase of MIS 3 (López-García et al., 2017). Analysing the data obtained with the small-mammal assemblage in the two cases (Grotte Scladina and Caverne Marie-Jeanne), the environmental results obtained for the species with strictly dry requirements (*L. lemmus*, *D. torquatus*, *M. arvalis* and *C. nivalis*) show similar values for Layer I of Grotte Scladina (33.3%) and the lower layers (6 to 4) of Caverne Marie-Jeanne (between 26.2% and 47%). However, the MAT obtained for Grotte Scladina ($MAT_{Layer\ I} = -10.7$ °C with respect to the present) is slightly lower than the values obtained for Marie-Jeanne ($MAT_{Layers\ 6\ to\ 4} = -5.7$ °C to −6.6 °C with respect to the present). These differences can be explained by the percentage representation of species with strictly cold requirements (*L. lagurus*, *L. lemmus* and *D. torquatus*), which represent 19.03% in Layer I of Grotte Scaldina, but do not reach 18% in any of the lower layers (6 to 4) studied from Caverne Marie-Jeanne.

5. Conclusions

The present analysis of the data from the Caverne Marie-Jeanne sequence allows us to draw the following conclusions on the basis of the small-mammal assemblage (comprising insectivores, bats and rodents):

1) Revision of a significant part of the collection deposited in the RBINS (Brussels, Belgium) allowed us to identify 9897 specimens, corresponding to a minimum of 4980 individuals, adding two new vole taxa (making a total of 31 taxa) to the previous studies: the steppe lemming (*Lagurus lagurus*) and the European pine vole (*Microtus* (*Terricola*) *subterraneus*).

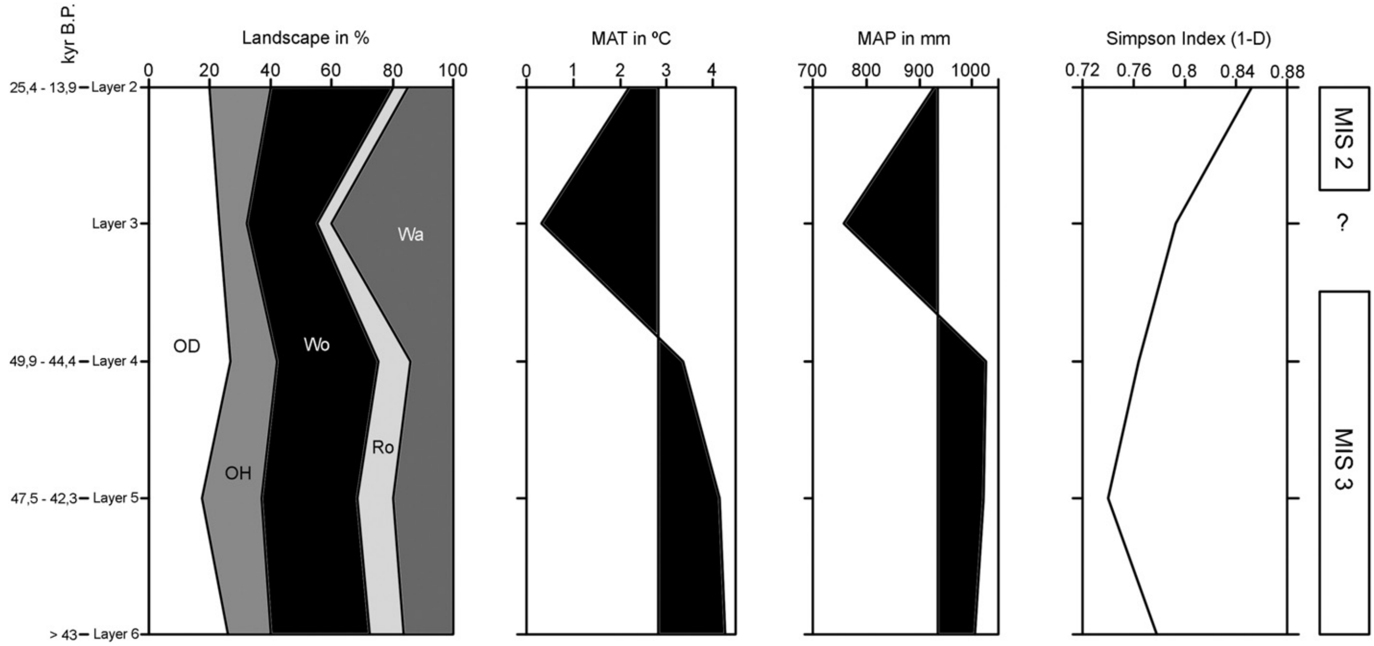


Fig. 3. Representation of landscape percentages, mean annual temperature (MAT), mean annual precipitation (MAP) and the small-mammal Simpson diversity index (1-D), from the Caverne Marie-Jeanne sequence. OD: Open Dry; OH: Open Humid; Wo: Woodland: Ro: Rocky; Wa: Water.

2) The preliminary taphonomic study performed on 8453 arvicoline first lower molars from the entire sequence of Caverne Marie-Jeanne shows that in the lower layers (6 to 4) the agents responsible for the accumulation were probably predators with an intermediate capacity for modification such as *Bubo bubo* (Eurasian eagle-owl) or *Falco tinnunculus* (common kestrel) and an indeterminate category 1 predator in Layer 2.
3) The small-mammal assemblages show that while *M. gregalis* is the most abundant species in the lower layers (6 to 4) of the sequence, in Layer 2 there is an equal representation of the species *M. arvalis*, *T. europaea*, *M. gregalis*, *S.* gr. *araneus*, *A. amphibius* and *D. torquatus*.
4) From a palaeoclimatic and palaeoenvironmental point of view, the lower layers (6 to 4) of the Caverne Marie-Jeanne sequence, located chronologically in MIS 3 (ca. 50–40 kyr B.P.), show a MAT that is lower than at present (by between −5.7 °C and −6.6 °C) and a MAP that is slightly higher than now (by between +160 mm and +180 mm). The palaeoenvironment is dominated by open woodland formations (between 30.2% and 32.7%) and open dry meadows (between 18.6% and 27.3%), generally indicating cold and dry environmental and climatic conditions for these layers, also coinciding with previous faunal studies and regional loess-based palaeoenvironmental interpretations.
5) On the other hand, the environmental and climatic data obtained with the small-mammal assemblage for Layer 2, together with previous faunal and stratigraphical studies and the chronological position of this layer, show that Layer 2 is formed from a mixture of at least two different climatic moments during MIS 2, one probably before (Heinrich event 2) and one after (Bølling/Allerød interstadial) the Last Glacial Maximum (LGM); a more accurate palaeoenvironmental and palaeoclimatic interpretation is not possible.
6) Finally, comparison of the small-mammal results for Caverne Marie-Jeanne with other recent studies performed on small-mammal assemblages in this area shows that, although there are differences between the studied sites and although there are a lot of climatic fluctuations around ca. 50–40 kyr B.P., in general this period of MIS 3 in the region is characterized by cold, dry environmental and climatic conditions, coinciding too with other proxies, such as pollen and regional loess.

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.palaeo.2017.07.017.

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General Palaeontology, Systematics and Evolution (Palaeoecology)

Small and large mammals from the Ciota Ciara cave (Borgosesia, Vercelli, Italy): An Isotope Stage 5 assemblage

Les petits et grands mammifères de la grotte Ciota Ciara (Borgosesia, Vercelli, Italie) : un assemblage du stade isotopique 5

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ABSTRACT

The Ciota Ciara cave is located within the Monte Fenera karst system (Borgosesia, Vercelli, Italy) at 670 m a.s.l. The cave entrance presents a deposit with Mousterian quartz and flint industry. The faunal remains from Stratigraphic Units 13, 14 and 103 are the subject of this work and are presented here as a whole for the first time. The large mammal assemblage is dominated by *Ursus spelaeus*. In addition, a few remains of carnivores such as *Panthera leo spelaea*, *Panthera pardus*, *Meles meles* have been found together with ungulates such as *Cervus elaphus* and *Rupicapra rupicapra*. The small mammal assemblage is characterized by a high biodiversity, especially in bats, by the dominance of *Clethrionomys glareolus* and by a relatively large number of *Pliomys coronensis*, a species that seems to disappear from the Italian Peninsula at the end of Marine Isotope Stage 5 or during the beginning of MIS 4. The changes in frequency of the small and large mammals between the two S.U. suggest a change from a relatively cold-humid (S.U. 14) to a warmer-still humid climate (S.U. 13). Although no radiometric dates are available yet, the small and large mammal assemblages, the presence of *Pliomys coronensis* and the climate change inferred by the variation of the small mammal frequencies allow us to correlate these two units of the Ciota Ciara cave to a relatively warm moment of Marine Isotope Stage 5.

RÉSUMÉ

Mots clés :
Grands mammifères
Petits mammifères

La grotte Ciota Ciara est située dans le complexe karstique du Monte Fenera (Borgosesia, Vercelli, Italie) à 670 m a.s.l. Les nombreuses campagnes de fouilles ont permis de mettre en évidence des dépôts à industries moustériennes sur quartz et silex à l'entrée de la

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MIS 5
Péninsule italienne

grotte. Ce travail se base sur l'étude des restes fauniques de ces dépôts, et particulièrement des unités stratigraphiques 13, 14 et 103. Ces unités se caractérisent par la présence d'un large assemblage de grands mammifères dominé par *Ursus spelaeus* et quelques restes de carnivores tels que *Panthera leo spelaea*, *Panthera pardus*, *Meles meles*, ainsi que des ongulés comme *Cervus elaphus* et *Rupicapra rupicapra*. Les assemblages de grands mammifères de la péninsule Italique du stade isotopique 5 sont relativement bien connus, ce qui n'est pas le cas des assemblages à petits mammifères. En effet, seulement quelques sites datés du MIS 5, principalement dans le Sud de la péninsule, ont révélé la présence de quelques espèces de micromammifères. Dans le site de Ciota Ciara, l'assemblage de micromammifères se caractérise par une grande biodiversité, particulièrement chez les chauves-souris, et une dominance de *Clethrionomys glareolus* et un relativement grand nombre de *Pliomys coronensis*, une espèce qui semble disparaître de la péninsule Italique à la fin du stade isotopique 5 ou au début du stade 4. Le changement dans la fréquence de petits et grands mammifères entre les unités stratigraphiques 13 et 14 suggère un passage d'un climat relativement humide (US 14) à un climat humide plus tempéré (US 13). Bien qu'aucune datation radiométrique ne soit encore disponible, les assemblages de macro- et micro-mammifères, la présence de *Pliomys coronensis* et le changement climatique déduit de la variation dans la fréquence de micromammifères permettent de corréler les deux unités stratigraphiques 13 et 14 de Ciota Ciara à un épisode relativement tempéré du stade isotopique 5.

1. Introduction

The records of small and large mammals during Marine Isotope Stage 5 (MIS 5) of the Italian Peninsula are relatively scarce and not well dated. In general, the faunal assemblages during this period often reflect a more temperate climate than the following Isotopic Stages, with species that would disappear or be strongly reduced in frequency during MIS 4 and 3 up to the Bølling–Allerød interstadial.

Among large mammals, MIS 5 is characterized by the occurrence of *Dama dama dama* (Palombo, 2009), a species that, however, already appears in MIS 9 (Gliozzi et al., 1997). The fallow deer lives in temperate climates and disappears in the north-eastern Italian Peninsula during MIS 4 (Mazza, 2006). Another chronologically important species is *Stephanorhinus kirchbergensis*, which occurs mainly in interglacial conditions (Sala et al., 1992). Finally, *Hippopotamus* seems to disappear in Italy during the last phases of MIS 5 (Sala et al., 1992) and *Palaeoloxodon antiquus* during MIS 4 (Palombo, 2009).

Among the small mammals, *Pliomys coronensis* (=*Pliomys lenki*, priority discussed by Terzea, 1983) seems to be a good chronological indicator for Italian Peninsula, because it is relatively widespread during MIS 5 (Bartolomei et al., 1975; Berto, 2013), while it seems to strongly decrease during the MIS 4, taking refuge in particular areas such as the Lessini Mountains (Verona province). Only one specimen of *Pliomys coronensis* is signaled at Fumane Cave, in levels correlated to the MIS 3 (Bartolomei et al., 1992).

The MIS 5 is characterized by the transition from *Arvicola mosbachensis* to *Arvicola amphibius* (Koenigswald von, 1994; Koenigswald von and Kolfschoten van, 1996; Maul et al., 1998). In central and northern Europe, the SDQ (*Schmelzband Differenzierungs Quotient* or enamel thickness differentiation quotient) analysis of *Arvicola* has allowed to distinguish these voles (basing on the enamel thickness) and to recognize a pattern of progressive decrease of this quotient.

In this context, the small and large mammals from Ciota Ciara cave represent one of the most complete examples of MIS 5 mammal assemblage in the Italian Peninsula and contribute to the knowledge of mammal association dynamics during this period.

1.1. The site

The Ciota Ciara cave is located at 670 m a.s.l. in the karst complex of Monte Fenera (Borgosesia, Vercelli, Fig. 1) which stands upon an Ercinic basement of effusive rocks, surmounted by carbonatic and arenithic lithological units of Mesozoic age with angular unconformity (Fantoni and Decarlis, 2005). It is an 80 m-long, still active karst cavity and was investigated several times during the second half of the XXth century (Fedele, 1988, 1974, 1968, among others), and it represents an example of the first human occupation of north-western Italy.

Starting from 2009, the University of Ferrara, in collaboration with the *Soprintendenza per i Beni Archeologici del Piemonte*, has carried out six excavation campaigns that primarily focussed on the three main Stratigraphic Units with faunal remains and lithic assemblage: 13, 14 and 103 (Arnaud et al., 2014; Arzarello et al., 2013, 2012). Stratigraphic Units 13 and 14 have a horizontal disposition and are characterized by a reddish-brown clay-sand matrix with rare and altered centimetre-sized pebbles, more frequent in S.U. 14. The Stratigraphic Units in question extended over the whole investigated area, with the exception of S.U. 103, which has an almost vertical trend and is localized exclusively in an area of about 50 cm^2, probably as a result of water percolation in the area along the rock wall (Fig. 1) (Daffara et al., 2014).

The lithic assemblage is composed of flakes, retouched tools, cores, hammers and debris. The raw materials were exploited using the direct percussion technique with

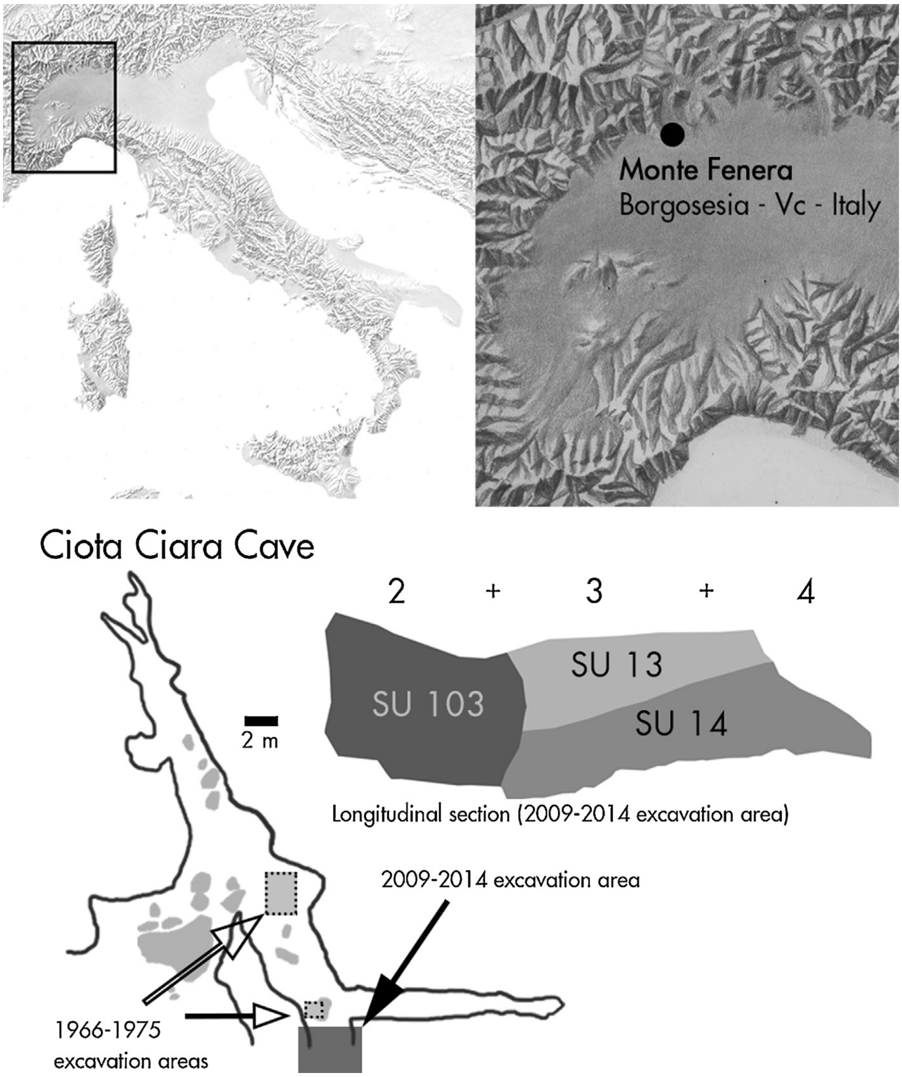

Fig. 1. Location of Ciota Ciara cave (top), simplified stratigraphy of the longitudinal section, cave map and location of excavation areas (bottom).

Fig. 1. Localisation de la grotte Ciota Ciara (en haut), stratigraphie simplifiée de la section longiutudinale, plan de la grotte et zone de fouilles (en bas).

various methods: SSDA (*Système par surface de débitage alterné*, Forestier, 1993), discoid and Levallois (Boëda, 1993, 1988; Daffara et al., 2014). Several lithologies are represented, in different proportions: quartz is the predominantly exploited raw material, followed by spongolite, sandstone, mylonite and opal. The archaeological record consists of various types of quartz: macro-crystalline pegmatite quartz, micro-crystalline pegmatite quartz and hyaline quartz. All these types of raw materials have been found in secondary position in the proximity of the archaeological site, within a 5-km range (Daffara et al., 2014).

The present landscape surrounding the Ciota Ciara cave is characterized by a rich forest dominated by chestnuts, maples and oaks. Among the large mammals, wild boar and roe deer are dominant.

2. Materials and methods

2.1. Large mammals

The large mammal analysis is based on a total of 4904 specimens: 838 from S.U. 13, 120 from S.U. 103 and 3946 from S.U. 14 (Table 1). Forty percent of the specimens was too fragmented for identification. Species determinations were made using the comparative collection from the Large Mammals Laboratory at the Department of Human Studies, University of Ferrara. For each taxon, we calculated the Number of Identified Specimens (NISP) and the Minimum Number of Individuals (MNI). Because the remains of *Ursus spelaeus* had a different mode of accumulation (see par.3.1), this species is considered separately.

Table 1
NISP, MNI and percentages of the NISP for the large mammals from the Ciota Ciara cave.
Tableau 1
NRI, NMI et pourcentages du NRI des grands mammifères de la grotte Ciota Ciara.

	NMI								
	103			13			14		
	MNI	NISP	%NISP	MNI	NISP	%NISP	MNI	NISP	%NISP
Rodents									
Marmota marmota				1	1	0.34	3	68	5.43
Carnivores									
Panthera leo spelaea	1	1	1.89				2	14	1.12
Panthera pardus							1	5	0.40
Lynx lynx				1	1	0.34	1	4	0.32
Canis lupus		1	1.89	1	8	2.74	2	11	0.88
Vulpes vulpes				2	2	0.68	1	3	0.24
Ursus spelaeus	5	33	62.26	9	232	79.45	18	989	78.99
Ursus arctos	1	15	28.30	2	24	8.22	2	17	1.36
Meles meles				1	6	2.05	1	2	0.16
Martes martes							1	1	0.08
Ungulates									
Stephanorhinus sp.							2	4	0.32
Bos primigenius				1	1	0.34	1	1	0.08
Bos vel Bison				1	1	0.34	1	1	0.08
Cervus elaphus				2	8	2.74	5	104	8.31
cf. *Dama*							1	1	0.08
Rupicapra rupicapra	1	3	5.66	2	9	3.08	2	26	2.08
Sus scrofa							1	1	0.08
Total carnivores	7	50	94.34	16	273	93.49	29	1046	83.55
Total ungulates	1	3	5.66	6	19	7	13	138	11.02
Total determined	**8**	**53**		**22**	**292**		**45**	**1252**	
Undetermined		*67*			*546*			*2694*	

Bold is used to highlight the total number of determined sample. NISP: total number of identified specimens by level; MNI: minimum number of individuals by stratum.

2.2. Small mammals

The small mammal remains consist of disarticulated bone fragments collected by water-screening using sieves of 0.5 mm mesh during the excavation campaigns from 2009 to 2013. Part of the material has been previously published in Arnaud et al. (2014) and Arzarello et al. (2012).

The small mammal assemblage comprises a total of 1187 remains, corresponding to a minimum number of 373 individuals (Table 2). The specific attribution of this material was mainly based on the best diagnostic elements: maxilla and isolated teeth for rodents, mandible and maxilla for shrews, mandible, maxilla, isolated teeth and humeri for bats.

The taxonomic classification follows Wilson and Reeder (2005), except *Clethrionomys glareolus* (for the priority over *Myodes*, see Tesakov et al., 2010). Data on the distribution and habitat of the species were taken from Amori et al. (2008), Boitani et al. (2003) and Mitchell-Jones et al. (1999).

We calculated the palaeodiversity using the Simpson index of Evenness = $1-\sum(p_i^2)$, where p_i is the proportion of individuals in the i^{th} species (Harper, 2005; Magurran, 2004). The evenness index is constrained between 0 and 1. The index has been calculated using PAST 3.04 avoiding redundant determinations (i.e., for *Arvicola amphibius*, the individuals determined as *Arvicola* cf. *amphibius* and *Arvicola* sp. were not included in the Simpson index calculation) (Hammer et al., 2001).

The SDQ index (Heinrich, 1978) quantifies the difference in enamel thickness between the anterior and the posterior wall of each triangle of arvicolid molars. This index was calculated for m1 of *Arvicola amphibius* of Ciota Ciara. SDQ was measured for the three main triangles T1, T2 and T3 of first lower molars (SDQ3, according to Kosciow and Nadachowski, 2002; Lippi et al., 1998; Markova, 2005) in order to include the maximum number of specimens. Higher values for these indices generally correspond to early evolutionary stage of *Arvicola*. However, remarkable differences exist between modern populations, and can be correlated to altitude (Kratochvil, 1981) and/or latitude (Maul et al., 1998; Röttger, 1987). Furthermore, critics have been moved to use SDQ as a strong tool for biochronological reconstruction (Escudé et al., 2008). Although this coefficient cannot provide conclusive evidence of the relative age of a fauna, combined with other data – such as the whole composition of the mammal assemblage – SDQ can give additional information about the chronological position of a site (Maul et al., 2000).

2.3. Palaeoenvironment reconstruction based on small mammals

In order to reconstruct the palaeoenvironment at Ciota Ciara cave, we used the method of habitat weighting (Andrews, 2006; Evans et al., 1981), assigning each small mammal taxon to the habitat(s) where it can be found at present in Europe. For this purpose, habitats were divided into six types (Cuenca-Bescós et al., 2009; López-García et al., 2014, 2010): open land with either dry and wet meadows (OD and OH, respectively); woodland environments,

Table 2
NISP, MNI and percentages of the MNI for the small mammals from the Ciota Ciara cave.
Tableau 2
NRI, NMI et pourcentages du NMI de micromammifères de la grotte Ciota Ciara.

	13			14		
	NISP	MNI	% MNI	NISP	MNI	% MNI
Sciurus vulgaris	1	1	2.27	1	1	0.30
Eliomys quercinus				1	1	0.30
Muscardinus avellanarius	2	1	2.27			
Glis glis	3	1	2.27	14	4	1.22
Arvicola sp.				11	3	0.91
Arvicola cf. *amphibius*	6	2	4.55	37	9	2.74
Arvicola amphibius				1	1	0.30
Cricetus cricetus				1	1	0.30
Chionomys nivalis				1	1	0.30
Microtus gr. *arvalis-agrestis*				15	12	3.65
Microtus arvalis	5	3	6.82	101	53	16.11
Microtus agrestis				13	7	2.13
Microtus cf. *gregalis*				7	5	1.52
Microtus (*Terricola*) sp.	3	2	4.55			
Microtus (*Terricola*) gr. *multiplex-subterraneus*				73	44	13.37
Clethrionomys glareolus	56	9	20.45	395	65	19.76
Pliomys coronensis	6	1	2.27	26	7	2.13
Apodemus sp.	2	1	2.27			
Apodemus (*Sylvaemus*) gr. *sylvaticus-flavicollis*	10	5	11.36	26	11	3.34
Erinaceus sp.				3	2	0.61
Crocidura sp.				2	1	0.30
Crocidura suaveolens	1	1	2.27			
Sorex ex gr. *araneus*				2	1	0.30
Talpa sp.	1	1	2.27	12	3	0.91
Talpa cf. *caeca*				5	3	0.91
Talpa caeca	1	1	2.27	30	6	1.82
Talpa cf. *europaea*				4	3	0.91
Talpa europaea	1	1	2.27	1	1	0.30
Rhinolophus sp.				2	1	0.30
Rhinolophus gr. *euryale-mehelyi*				6	3	0.91
Rhinolophus ferrumequinum	3	1	2.27	16	6	1.82
Rhinolophus cf. *hipposideros*				27	9	2.74
Rhinolophus hipposideros				7	5	1.52
Eptesicus conf. *serotinus*				3	2	0.61
cf. *Nyctalus*				6	5	1.52
cf. *Plecotus*				4	2	0.61
Plecotus gr. *auritus-austriacus*				12	2	0.61
Barbastella barbastellus	4	1	2.27	1	1	0.30
Myotis myotis	3	1	2.27	44	8	2.43
Myotis sp.	16	10	22.73	87	21	6.38
Miniopterus schreibersii	3	1	2.27	62	18	5.47
Pipistrellus sp.				1	1	0.30
	127	44		1060	329	

divided into open woodland, woodland margins and forest patches (OW) and woodland and mature forest habitat (W); water, areas along streams, lakes and ponds (Wa); and habitats with a suitable rocky or stony substratum (R) (Table 3).

2.4. Palaeoclimatic reconstruction based on small mammals

In order to infer the palaeoclimatic data from Ciota Ciara cave assemblage, we applied the Mutual Climatic Range method (Elias, 1997; Pross, 2000 among others, see also Blain et al., 2009 and López-García et al., 2014, 2010). This method assesses potential palaeoclimatic conditions by evaluating the current distribution of all taxa occurring in each level.

Two climatic factors were calculated: the mean annual temperature (MAT) and the mean annual precipitation (MAP), using climatic maps of Italy (Attorre et al., 2008) and data provided by the network of Italian meteorological research stations over a period of 30 years. Then, we could compare them with the modern climatic data from the weather station of Borgosesia (359 m a.s.l.). For the area surrounding Ciota Ciara cave, the current data show an MAT = 10.7 °C and MAP = 1009 mm. Because of the scarce interpolations (only two), we also used the linear regression method (Hernández Fernández and Peláez-Campomanes, 2005; Hernández Fernández, 2006, 2004; Hernández Fernández et al., 2007).

The Italian Peninsula is characterized by different climates, due to its peculiar position in the centre of the Mediterranean Sea and its geography. In Italy, two macrobioclimates are present: the temperate bioclimate, which

Table 3
Small mammal distribution by habitat.
Tableau 3
Distribution des micromammifères par habitat.

	OD	OH	OW	W	R	Wa
Sciurus vulgaris				1		
Eliomys quercinus				0.75	0.25	
Muscardinus avellanarius				1		
Glis glis				1		
Arvicola amphibius						1
Cricetus cricetus	1					
Chionomys nivalis					1	
Microtus arvalis	0.75		0.25			
Microtus agrestis		1				
Microtus cf. *gregalis*	1					
Microtus (*Terricola*) gr. *multiplex-subterraneus*			1			
Clethrionomys glareolus			0.25	0.75		
Pliomys coronensis						
Apodemus(*Sylvaemus*) gr. *sylvaticus-flavicollis*				1		
Erinaceus sp.			0.25	0.75		
Crocidura sp.		0.5	0.5			
Crocidura suaveolens		0.5	0.5			
Sorex ex gr. *araneus*		0.75	0.25			
Talpa caeca		0.25	0.5			
Talpa europaea		0.5	0.5			
Rhinolophus gr. *euryale-mehelyi*				0.5	0.25	0.25
Rhinolophus ferrumequinum				0.8	0.2	
Rhinolophus cf. *hipposideros*				0.6	0.2	0.2
Rhinolophus hipposideros				0.6	0.2	0.2
Eptesicus conf. *serotinus*				0.4	0.6	0.1
cf. *Nyctalus*				1		
cf. *Plecotus*	0.2			0.7	0.1	
Plecotus gr. *auritus-austriacus*	0.2			0.7	0.1	
Barbastella barbastellus				0.8	0.2	
Myotis myotis	0.2			0.6	0.2	
Miniopterus schreibersii	0.2	0.2		0.4	0.2	

OD: open dry; OH: open humid; OW: open woodland; Wo: woodland/woodland-edge; Ro: rocky; Wa: water.

is found in the north-eastern Peninsula up to the Marche region, the Po Valley and part of the Appenines as opposed to the Mediterranean bioclimate found in the Tyrrhenian coast up to the Ligurian region and the southern Adriatic coast. These macro-bioclimates are subdivided into nine different climates, and climatic conditions may change abruptly over a few tens of kilometres, from the mildness of the seashore to the harshness of coastal mountain summits (Stoch, 2009).

3. Results

3.1. Large mammals

The faunal assemblage is composed of *Ursus spelaeus*, *Ursus arctos*, *Canis lupus*, *Vulpes vulpes*, *Meles meles*, *Martes martes*, *Lynx lynx*, *Panthera leo*, *Panthera pardus*, *Rupicapra rupicapra*, *Cervus elaphus*, *Bos* sp., *Bos* vel *Bison*, *Sus scrofa*, *Stephanorhinus* sp. and *Marmota marmota*. A right upper incisor previously determined as *Hystrix* sp. from S.U. 13 (Arnaud et al., 2014; Arzarello et al., 2013, 2012; Daffara et al., 2014) has been revised and assigned to *Marmota marmota* (Fig. 2, no. 5).

Ungulates appear to be underrepresented in S.U. 13 and 103 (3,8% of identifiable remains) but in S.U. 14 there is a clear increase (13,4% of determinable remains).

Ursus is the best represented carnivore in the Ciota Ciara cave, and *Ursus spelaeus* is the most copious species in all the stratigraphic units (S.U. 103: 27.50%; S.U. 13: 40,77%; S.U. 14: 59.04%). *Ursus arctos* is progressively rare from the top to the bottom of the sequence: (S.U. 103: 8.33%; S.U. 13: 4.22%; S.U. 14: 1.01%). *Ursus spelaeus* used caves during dormancy and as a nest for the cubs (Pacher and Stuart, 2009), which probably accounts for this species being overrepresented in the assemblage.

The other taxa are represented by only a few remains, but, especially in S.U. 14, the biodiversity is high. The ungulates are more abundant in the lower part of the stratigraphic sequence: in S.U. 103 and 13, the only herbivores present are *Rupicapra rupicapra*, *Cervus elaphus* and a bovid, while in S.U. 14 *Rupicapra rupicapra*, *Cervus elaphus*, cf. *Dama*, *Bos primigenius*, *Bos* vel *Bison*, *Stephanorhinus* sp., and *Sus scrofa* are present. Fedele (1968) also reported the occurrence of *Capra ibex* and *Castor fiber* but they have not been recovered in modern excavations. In a breach of the site of Ara, near Ciota Ciara cave, a mandible of *Stephanorhinus kirchbergensis* has been found (Giacobini and Strobino, 1978), attesting to the presence of this species in the area of Monte Fenera.

Considering the MNI in S.U. 14, the most abundant taxon is *Ursus spelaeus* (18 specimens), followed by *Cervus elaphus* (five specimens) and *Marmota marmota* (three specimens). All the other taxa are represented by only one or two specimens. The deciduous teeth of bear are abundant (71 specimens); unfortunately, cubs of *U. spelaeus* are not distinguishable from *U. arctos*. Considering the

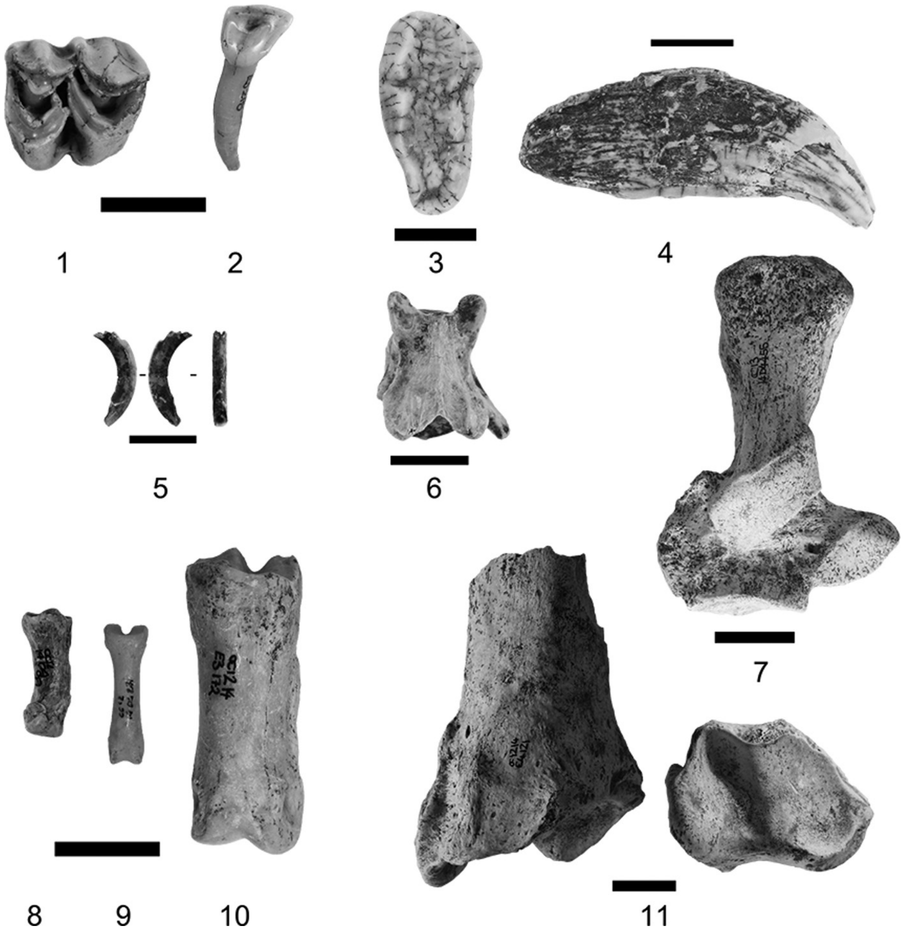

Fig. 2. Some large mammals identified from the Ciota Ciara cave, S.U. 14, all scales are 2 cm long. 1. *Cervus elaphus*, left m2; 2. *Cervus elaphus*, right i3; 3. *Ursus spelaeus*, right M2; 4. *Ursus spelaeus*, right upper C; 5. *Marmota marmota*, right upper I (lingual, labial and occlusal view); 6. *Canis lupus*, third cervical; 7. *Ursus spelaeus*, right calcaneus; 8. *Panthera pardus*, second phalanx; 9. *Vulpes vulpes*, first phalanx; 10. *Cervus elaphus*, first phalanx; 11. *Panthera leo spelaea*, right tibia.

Fig. 2. Quelques exemples de grands mammifères identifiés à Ciota Ciara, U.S. 14 (échelle = 2 cm). *Cervus elaphus*, m2 gauche; 2. *Cervus elaphus*, i3 droite; 3. *Ursus spelaeus*, M2 droite; 4. *Ursus spelaeus*, C supérieure droite; 5. *Marmota marmota*, I supérieure droite (vue linguale, labiale et occlusale); 6. *Canis lupus*, troisième vertèbre cervicale; 7. *Ursus spelaeus*, calcanéum droit; 8. *Panthera pardus*, deuxième phalange; 9. *Vulpes vulpes*, première phalange; 10. *Cervus elaphus*, première phalange; 11. *Panthera leo spelaea*, tibia droit.

different ecology between *U. spelaeus* and *U. arctos*, the deciduous teeth probably could be referred to *U. spelaeus*, *U. arctos* preferring small dens for dormancy, while *U. spelaeus* commonly used large caves (Kurtén, 1976).

The abundance of carnivores in the cave could be the result of selective use of the cave by these taxa, but error sampling due to the limited number of the remains or anthropic selection cannot be excluded until more accurate taphonomic analysis are available.

3.2. Small mammals

Ciota Ciara cave is unique in the Italian Peninsula context because of the relatively high abundance of *Pliomys coronensis*, and the high biodiversity of bats (Fig. 3). The Simpson index of Evenness indicates that in both Units, the biodiversity is high and relatively equally distributed (S.U. 14: 0.88 and S.U. 13: 0.86) (Fig. 4B).

The presence of one sample identified as *Erinaceus* sp. is remarkable. It is a right P4 and, based on the samples present in our collection, falls more into the size range of present *Erinaceus roumanicus* than that of *E. europaeus*. Unfortunately, the lack of specific works on the dental differences (especially on P4 measurements and morphology) between these two species does not allow a specific determination.

In Fedele (1966), only few remains of *Sorex* gr. *araneus*, *Chionomys nivalis*, *Microtus arvalis*, *Arvicola* sp. and *Glis glis* have been signalled in a trench (Trench II) excavated in the interior of the cave, approximately 20 m far from the 2009-2014 investigated area.

In S.U. 103, only two specimens of *Pliomys coronensis* have been found. S.U. 13 and 14 are both dominated by *Clethrionomys glareolus* which, together with *Apodemus* (*Sylvaemus*), *Glis glis*, *Eliomys quercinus* and the bats, contributes to the forest component (W). Thus, the environment surrounding the cave was dominated by

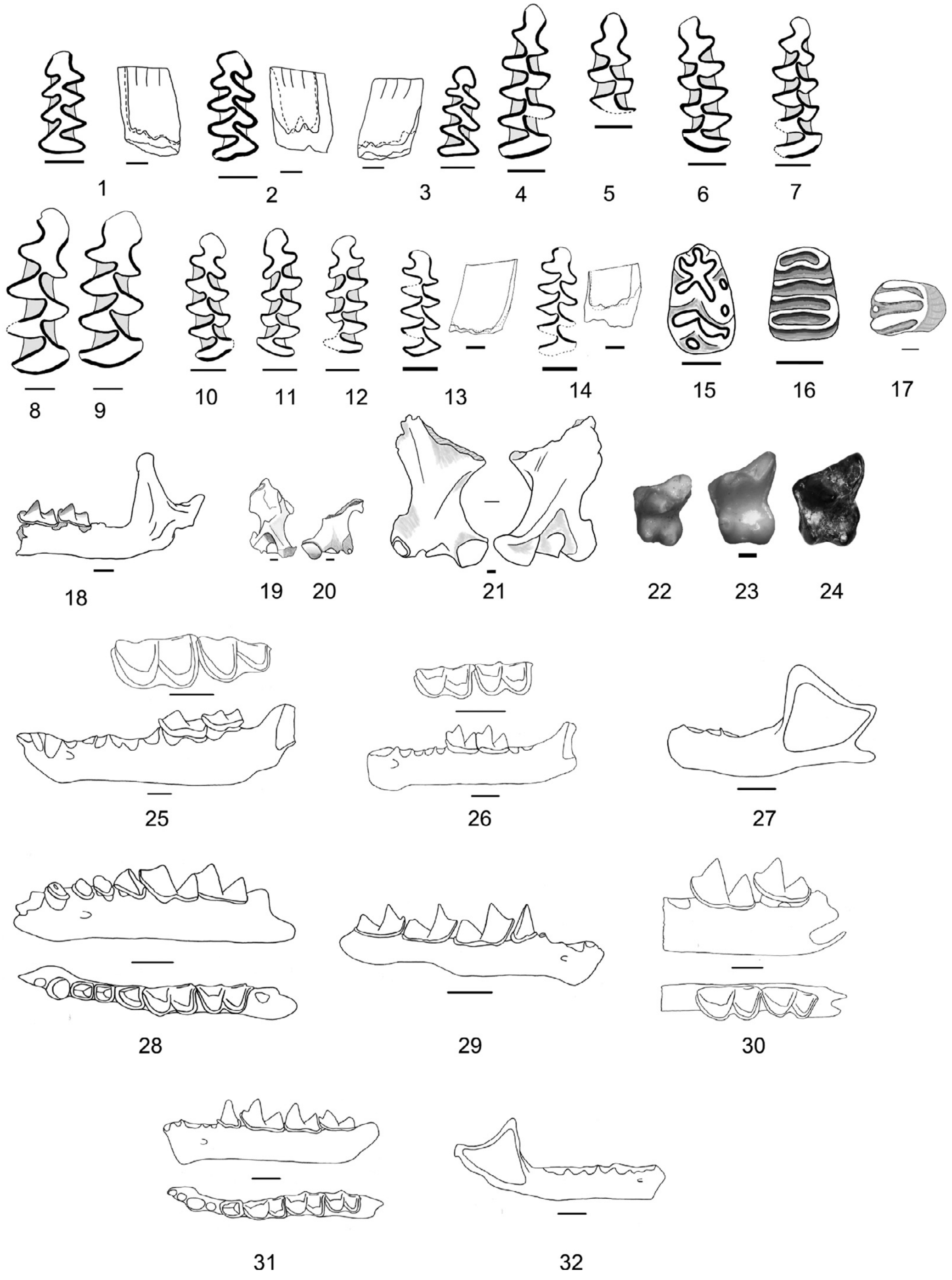

Fig. 3. Some small mammals identified from Ciota Ciara cave, S.U. 14 (excluding numbers 21 and 22 that present specimens coming from the Ferrara University collection), all scales are 1 mm long. 1. *Clethrionomys glareolus*, left m1 (occlusal view and labial view with linea sinuosa); 2. *Clethrionomys glareolus*, right m1 (occlusal view and labial view with linea sinuosa); 3. *Clethrionomys glareolus*, right m1 (occlusal view and labial view with linea sinuosa); 4. *Microtus arvalis*, right m1; 5. *Microtus arvalis*, right m1; 6. *Microtus arvalis*, left m1; 7. *Microtus agrestis*, right m1; 8. *Arvicola amphibius*, right m1; 9. *Arvicola amphibius*, right m1; 10. *Microtus* (*Terricola*) gr. *multiplex-subterraneus*, right m1; 11. *Microtus* (*Terricola*) gr. *multiplex-subterraneus*, left m1; 12. *Microtus* (*Terricola*) gr. *multiplex-subterraneus*, left m1; 13. *Pliomys coronensis*, right m1 (occlusal view and labial view with linea sinuosa); 14. *Pliomys coronensis*, right m1 (occlusal view and labial view with linea sinuosa); 15. *Apodemus* (*Sylvaemus*) gr. *sylvaticus-flavicollis*, right m1; 16. *Muscardinus avellanarius*, right m1; 17. *Sciurus vulgaris*, right M2; 18. *Sorex* ex gr. *araneus*, left mandible with m1 and m2; 19. *Talpa* cf. *caeca*, right humerus; 20. *Talpa* cf. *caeca*, right humerus; 21. *Talpa* cf. *europaea*, left humerus; 22. *Erinaceus europaeus*, left P4; 23. *Erinaceus roumanicus*, left P4; 24. *Erinaceus* sp., left P4; 25. *Myotis* gr. *myotis-blythii*, left mandible with m2 and m3 (labial and occlusal view); 26. *Myotis* sp., left mandible with m1 and m2 (labial and occlusal view); 27. *Myotis* sp., left mandible (labial view); 28. *Minopterus schreibersii*, left mandible (labial and occlusal view); 29. *Rhinolophus* cf. *hipposideros*, left mandible (labial view); 30. *Rhinolophus ferrumequinum*, left mandible with m2 and m3 (labial and occlusal view); 31. *Rhinolophus* gr. *euryale-mehelyi*, left mandible (labial and occlusal view); 32. *Plecotus* gr. *auritus-austriacus*, right mandible (labial view).

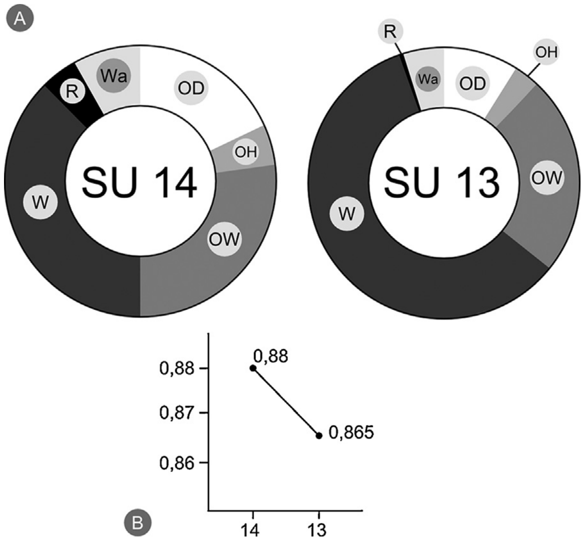

Fig. 4. Top: representation of landscape percentages (OD: Open Dry meadows; OH: Open Humid meadows; OW: Open Woodland, forest patches; W: Woodland; R: Rocky; Wa: Water, areas along streams, lakes and ponds). Bottom: Simpson index of Evenness based on small mammals assemblage.

Fig. 4. En haut : représentation des pourcentages correspondant aux types de paysages (OD : prairies ouvertes sèches ; OH : prairies ouvertes humides ; OW : forêt ouverte, lopin de forêt ; W : forêt ; R : rocheux ; Wa : eau, zone située le long des ruisseaux, des lacs et des étangs). En bas : indice d'égalité de Simpson basé sur l'assemblage de micromammifères.

woodland, woodland margins and forest patches (Fig. 4). These considerations are confirmed by the presence of typical woodland small mammals such as *Glis glis* and *Sciurus vulgaris*, the latter rather rare in Late Pleistocene sequences because of its diurnal habits (Berto, 2012). Also, the chiropters found in Ciota Ciara cave confirm the presence of these kind of habitats. Species as *Rinolophus hipposideros*, *R. ferrumequinum*, *Barbastella barbastellus* and *Plecotus* sp. normally hunt in wooded areas, while *Myotis myotis* prefers grassland environments. Although the chiropters have different habits than the other small mammals, these species are considered sedentary, their areal varies from 15 to 30 km from the nest, even though sporadic migration up to 50 km are registered.

Nevertheless, a climatic change is visible along these two Stratigraphic Units. The environment was more open during the deposition of S.U. 14 and the cave was surrounded by an open woodland environment with exposed

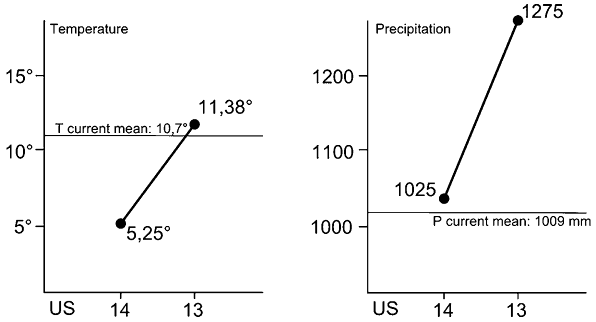

Fig. 5. The mean annual temperature (MAT) and the mean annual precipitation (MAP) from the Ciota Ciara cave (Mutual Climatic Range method).

Fig. 5. Température moyenne annuelle (MAT) et précipitation moyenne annuelle (MAP) de la grotte Ciota Ciara (méthode du *Mutual Climatic Range*).

rocks. In this Unit percentages of *Microtus arvalis* and *M.* (*Terricola*) gr. *multiplex-subterraneus* are high (16,11% and 13,37% respectively) and cold climate indicators, such as *Cricetus cricetus*, *Microtus* cf. *gregalis* and *Chionomys nivalis*, are present, although rare. The change to a more temperate climate is confirmed also by temperatures (MAT) and precipitations (MAP) (Fig. 5), even though this result must be considered with prudence, given the few interpolations found with the Mutual Climatic Range. It is possible to observe an improvement in climatic conditions, but the temperature for S.U. 14 indicates a "pleniglacial" condition that does not entirely reflect the situation visible in the faunal assemblage. *Clethrionomys glareolus* always stands as the most represented arvicolid. This is a strong indicator of a forested environment and the species can be underrepresented in the thanatocoenoses because it lives in bushes and it is considered difficult to pray. In addition, bats related to wooden environments are constantly present. The linear regression method tested on our sample shows that The MAT oscillation is less severe (S.U. 14, MAT = 9.4 °C; S.U. 13, MAT = 11 °C) while the MAP is much higher (S.U. 14, MAP = 1756 mm; S.U. 13, MAP = 1933 mm) but it must be noted that the standard deviation of this method is high (3.367 °C and 470.615 mm respectively, data inferred from Hernández Fernández, 2004).

4. Chronological considerations

Although radiometric dates are not yet available, some chronological considerations can be inferred based on

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Fig. 3. Quelques exemples de micromammifères identifiés à Ciota Ciara, U.S. 14 (excepté les numéros 21 et 22, qui correspondent à des spécimens provenant de la collection de l'université de Ferrare), échelle = 1 mm. 1. *Clethrionomys glareolus*, m1 gauche (vue occlusale et vue labiale avec linea sinuosa) ; 2. *Clethrionomys glareolus*, m1 droite (vue occlusale et vue labiale avec linea sinuosa) ; 3. *Clethrionomys glareolus*, m1 droite (vue occlusale et vue labiale avec linea sinuosa) ; 4. *Microtus arvalis*, m1 droite ; 5. *Microtus arvalis*, m1 droite ; 6. *Microtus arvalis*, m1 gauche ; 7. *Microtus agrestis*, m1 droite ; 8. *Arvicola amphibius*, m1 droite ; 9. *Arvicola amphibius*, m1 droite ; 10. *Microtus* (*Terricola*) gr. *multiplex-subterraneus*, m1 droite ; 11. *Microtus* (*Terricola*) gr. *multiplex-subterraneus*, m1 gauche ; 12. *Microtus* (*Terricola*) gr. *multiplex-subterraneus*, m1 gauche ; 13. *Pliomys coronensis*, m1 droite (vue occlusale et vue labiale avec linea sinuosa) ; 14. *Pliomys coronensis*, m1 droite (vue occlusale et vue labiale avec linea sinuosa) ; 15. *Apodemus* (*Sylvaemus*) gr. *sylvaticus-flavicollis*, m1 droite ; 16. *Muscardinus avellanarius*, m1 droite ; 17. *Sciurus vulgaris*, M2 droite ; 18. *Sorex* ex gr. *araneus*, mandibule gauche avec m1 et m2 ; 19. *Talpa* cf. *caeca*, humérus droit ; 20. *Talpa* cf. *caeca*, humérus droit ; 21. *Talpa* cf. *europaea*, humérus gauche ; 22. *Erinaceus europaeus*, P4 gauche ; 23. *Erinaceus roumanicus*, P4 gauche ; 24. *Erinaceus* sp., P4 gauche ; 25. *Myotis* gr. *myotis-blythii*, mandibule gauche avec m2 et m3 (vues labiale et occlusale) ; 26. *Myotis* sp., mandibule gauche avec m1 et m2 (vues labiale et occlusale) ; 27. *Myotis* sp., mandibule gauche (vue labiale) ; 28. *Minopterus schreibersii*, mandibule gauche (vues labiale et occlusale) ; 29. *Rhinolophus* cf. *hipposideros*, mandibule gauche (vue labiale) ; 30. *Rhinolophus ferrumequinum*, mandibule gauche avec m2 et m3 (vues labiale et occlusale) ; 31. *Rhinolophus* gr. *euryale-mehelyi*, mandibule gauche (vues labiale et occlusale) ; 32. *Plecotus* gr. *auritus-austriacus*, mandibule droite (vue labiale).

Table 4
SDQ and SDQ3 results based on *Arvicola amphibius* from Ciota Ciara cave.
Tableau 4
Résultats de SDQ et SDQ3 basés sur *Arvicola amphibius* de la grotte Ciota Ciara.

	n	Min.	Mean	Max.	SD
SDQ	4	102.68	105.61	111.47	3.99
SDQ3	6	86.67	105	122.35	14.66

the mammal assemblage of this site. Small-mammal assemblages strongly related to woodland or woodland margins environment are rare in sites correlated to more recent chronological periods such as MIS 3 in northern Italy. Generally, these small mammals assemblages are characterized by open environment species with high percentages of *Microtus arvalis* (Berto, 2012). Around 50 km far from Ciota Ciara cave, the Caverna Generosa site (1450 m a.s.l.) displays a typical MIS 3 northern Italian small mammals assemblage. The sequence is dominated by *Microtus arvalis* during stadial oscillations (group III of "Sala Terminale" and "lev. Cun III-II") and by *M.* (*Terricola*) gr. *multiplex-subterraneus* during interstadials (groups II and I of "Sala Terminale" and "lev. Cun VI"). *Sciurus vulgaris* and *Glis glis* are absent and *Clethrionomys glareolus* increases in percentage only during the warmer oscillations, but it never dominates the association (Bona et al., 2009).

Reported for the first time in Europe during the Middle Pleistocene (Cuenca-Bescós et al., 2010), *Pliomys coronensis* in Italy is widespread in the north-eastern region during this Age (Bartolomei and Pasa, 1969; Dalla Valle, 2011). In Europe, this species reduces its areal at the beginning of Late Pleistocene to become a relict in Iberian Peninsula until its disappearance during the Last Glacial (Cuenca-Bescós et al., 2010). From the Late Pleistocene in Italy, *Pliomys coronensis* is reported only at Ponte di Veia A (Lessini Mountains, Verona) and Grotta del Vento (Central Italy, Ancona) in sediments dated around the end of MIS 5 (Esu et al., 1990; Pasa, 1950) and only one specimen seems to be present at Fumane Cave in a unit correlated to MIS 3 (Bartolomei et al., 1992). The population of *Pliomys coronensis* found at Ciota Ciara cave is one of the largest in the Italian Peninsula. The relatively strong presence of this species can be considered an indication that the sequence has been accumulated during the MIS 5.

The mean of SDQ3 index, based only on six specimens of *Arvicola amphibius*, is 105 and the index varies, in our assemblage, from 87 (SDQ_{min}) to 122 (SDQ_{max}). The SDQ ($N = 4$) displays a similar mean value, although slightly higher (Table 4). In Europe, the MIS 5 is characterized by the transition from *Arvicola mosbachensis* to *Arvicola amphibius*, with values of SDQ index around 100 characteristic for latest Eemian and earliest Weichselian localities (Koenigswald von, 1994; Koenigswald von and Heinrich, 1999; Koenigswald von and Kolfschoten van, 1996). In this context, considering altitude, latitude and the probability of immigration events during Eemian (and the consequent increase of SDQ), the SDQ and SDQ3 Ciota Ciara sample values could be considered as transitional. This data alone could not provide strong evidence for precise dating, but they can concur with others to support the chronological hypothesis proposed of an accumulation occurred during a final phase of MIS 5.

5. Conclusions

The small and large mammal association of Units 13 and 14 of Ciota Ciara cave (Borgosesia, Vercelli) is one of the most complete of the Piedmont region. The environment surrounding the cave during the deposition of the S.U. was dominated by woodland, woodland margins and forest patches and it seemed to be more open during the deposition of S.U. 14. The climate was similar to the present one in S.U. 13 and colder in S.U. 14.

Among the small mammals, *Pliomys coronensis* is relatively abundant, and has a higher contribution than at any of the other Italian Peninsula sites where this species has been reported. This species, together with the SDQ analyses and the general mammal association seems to indicate that the deposition of S.U. 13 and 14 happened during the MIS 5 (after the Eemian interglacial).

This makes Ciota Ciara cave one of the few sites for MIS 5 in northern Italy. It gives precious insight into palaeoclimatic and palaeoenvironmental conditions of an area that is otherwise poorly known in the context of Upper Pleistocene mammal assemblages.

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BIOCHRONOLOGICAL DATA FOR THE MIDDLE PLEISTOCENE SITE OF GROTTE DE LA CARRIÈRE (LACHAMBRE KARSTIC COMPLEX, CORNEILLA-DE-CONFLENT, EASTERN PYRENEES, SOUTHERN FRANCE) INFERRED FROM THE SMALL-MAMMAL ASSEMBLAGE

■

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ABSTRACT

The Embullà Mountain, located between the municipalities of Ria and Corneilla-de-Conflent (Eastern Pyrenees), possesses a large karstic complex with more than 20 caves situated at different altitudinal levels. Lachambre Cave, with more than 26 km of galleries, is the largest of these. The research carried out by the authors since 2011 has led to the discovery of several Middle to Late Pleistocene sites. Grotte de la Carrière is one of these newly discovered sites. The first paleontological survey, undertaken in May 2015, led to the unearthing of more than 2000 large- and small-vertebrate remains in eight different stratigraphical layers. The small-mammal assemblage from the richest layer of the sequence (layer 4) includes at least two insectivores (*Talpa europaea* and *Sorex* sp.) and eight rodents (*Microtus arvalis*, *Microtus agrestis jansoni*, *Iberomys brecciensis*, *Clethrionomys glareolus*, *Pliomys coronensis*, *Apodemus* gr. *sylvaticus-flavicollis*, *Allocricetus bursae* and *Sciurus* sp.). This association is very similar to other Middle Pleistocene sites in southern France, such as Caune de l'Arago and Grotte du Lazaret, as well as being similar to other Iberian Middle Pleistocene sites, such as Gran Dolina (TD10), Galeria and Sima del Elefante (TE18-19) in the Sierra de Atapuerca. These data suggest an approximate age for Grotte de la Carrière - layer 4 of between 220 and 450 ka. The chronology proposed on the basis of the micromammal assemblage also coincides with the large mammals recovered and identified from this layer, mainly composed of the species *Ursus deningeri*, *Panthera fossilis* and *Canis mosbachensis*.

Keywords: biochronology, Arvicolinae, Middle Pleistocene, Eastern Pyrenees

RÉSUMÉ

DONNÉES BIOCHRONOLOGIQUES POUR LE SITE PLÉISTOCÈNE MOYEN DE LA GROTTE DE LA CARRIÈRE (COMPLEXE KARSTIQUE LACHAMBRE, CORNEILLA-DE-CONFLENT, PYRÉNÉES-ORIENTALES, SUD DE LA FRANCE) À PARTIR DE L'ASSOCIATION DE MICROMAMMIFÈRES

La montagne d'Embullà, située entre les municipalités de Ria et Corneilla-de-Conflent (Pyrénées-Orientales) possède un grand complexe karstique avec plus de 20 grottes disposées sur plusieurs niveaux, la Grotte de Lachambre étant la plus grande avec plus de 26 km de galeries. Les recherches faites par les auteurs depuis 2011 ont permis la découverte de plusieurs sites du Pléistocène moyen et supérieur. La Grotte de la Carrière est un de ces nouveaux sites. La première reconnaissance menée en mai 2015 a permis de collecter plus de 2000 restes de grands et petits vertébrés dans huit couches stratigraphiques différentes. L'assemblage de petits mammifères du niveau le plus riche (couche 4) comprend au moins deux insectivores (*Talpa europaea* et *Sorex* sp.) et huit rongeurs (*Microtus arvalis*, *Microtus agrestis jansoni*, *Iberomys brecciensis*, *Clethrionomys glareolus*, *Pliomys coronensis*, *Apodemus* gr. *sylvaticus-flavicollis*, *Allocricetus bursae* et *Sciurus* sp.). Cette association est très similaire à celles des autres sites du Pléistocène moyen du sud de la France, comme la Caune de l'Arago ou la Grotte du Lazaret, et est aussi similaire à celles d'autres sites ibériques du Pléistocène moyen, comme Gran Dolina (TD10), Galeria ou Sima del Elefante (TE18-19) dans la Sierra d'Atapuerca. Ces données suggèrent un âge approximatif pour la Grotte de la Carrière - couche 4 entre 220 et 450 ka . De plus, la chronologie proposée à partir de l'assemblage des petits mammifères coïncide avec celle des grands mammifères découverts dans ce niveau, qui incluent principalement les espèces *Ursus deningeri*, *Panthera fossilis* et *Canis mosbachensis*.

Mots-clés : biochronologie, Arvicolinae, Pléistocène moyen, Pyrénées-Orientales

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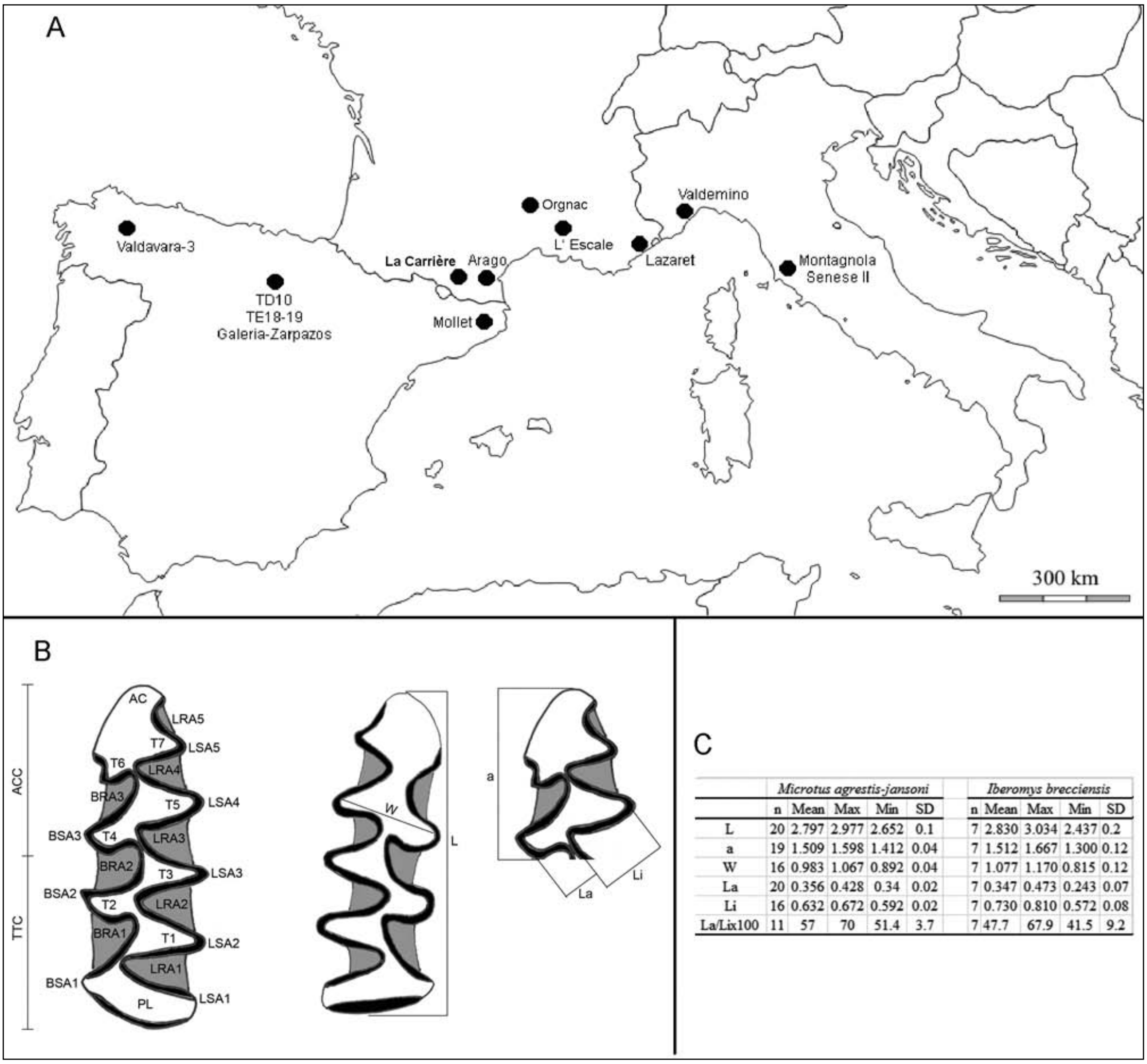
1 - INTRODUCTION

Rodents are one of the stratigraphically most significant groups of mammals in the European Pleistocene, because they have diversified more than other taxa over this relatively short geological time span. Arvicolines (voles) are particularly useful for biochronological correlation, because of the abundance of their remains and their rapid evolutionary rates. In addition, some voles undertook rapid, long-range migrations and may have had extensive geographical distributions, making inter-regional correlations possible (Minwer-Barakat *et al.*, 2011). For these reasons, arvicolines have been used to establish the biostratigraphic subdivisions of the Quaternary (Chaline, 1972; van der Meulen, 1973; Agustí, 1986; Sala & Masini, 2007; Cuenca-Bescós *et al.*, 2010; Agustí *et al.,* 2015; among many others).

Grotte de la Carrière is a newly discovered site in the Embullà Mountain, located between the municipalities of Ria and Corneilla-de-Conflent (Eastern Pyrenees) (fig. 1A). This mountain chain possesses a large karstic complex with more than 20 caves situated at different altitudinal levels. Réseau Lachambre Cave, with more than 26 km of galleries, is the largest of these.



	Microtus agrestis-jansoni					*Iberomys brecciensis*				
	n	Mean	Max	Min	SD	n	Mean	Max	Min	SD
L	20	2.797	2.977	2.652	0.1	7	2.830	3.034	2.437	0.2
a	19	1.509	1.598	1.412	0.04	7	1.512	1.667	1.300	0.12
W	16	0.983	1.067	0.892	0.04	7	1.077	1.170	0.815	0.12
La	20	0.356	0.428	0.34	0.02	7	0.347	0.473	0.243	0.07
Li	16	0.632	0.672	0.592	0.02	7	0.730	0.810	0.572	0.08
La/Lix100	11	57	70	51.4	3.7	7	47.7	67.9	41.5	9.2

Fig. 1: A/ Location of Grotte de la Carrière and the main Middle Pleistocene sites mentioned in the text. B/ Nomenclature and measuring methods used for the first lower molars in the description of Arvicolinae. C/ Measurements and indices of m1 of *Microtus agrestis jansoni* and *Iberomys brecciensis* from Grotte de la Carrière. Linear data (L, W, a) are in mm.
Abbreviations for B: a. length of the anteroconid complex; ACC. anteroconid complex; AC. anterior cap; BRA. buccal re-entrant angle; BSA. buccal salient angle; L. length; LRA. lingual re-entrant angle; LSA. lingual salient angle; PL. posterior lobe; TTC. trigonid-talonid complex. T1-T7. triangles 1-7; W. width. Abbreviations for C: n. number of m1 measured for each species; mean. mean of the obtained values; max. maximum of the obtained values; min. minimum of the obtained values; SD. standard deviation of the obtained values.
Fig. 1 : A/ Localisation de la Grotte de la Carrière et des principaux sites du Pléistocène moyen mentionnés dans le texte. B/ Nomenclature and mesures utilisées pour les premières molaires inférieures dans la description des Arvicolinae. C/ Mesures et indices des m1 de Microtus agrestis jansoni et Iberomys brecciensis de la Grotte de la Carrière. Les mesures linéaires (L, W, a) sont en mm. Abréviations pour B : a : longueur du complexe anteroconide ; ACC. complexe anteroconide ; AC. anterior cap ; BRA. buccal re-entrant angle ; BSA. buccal salient angle ; L. longueur ; LRA. lingual re-entrant angle ; LSA. lingual salient angle ; PL. lobe postérieur ; TTC. trigonid-talonid complex. T1-T7. triangles 1-7 ; W. largeur. Abréviations pour C : n. nombre de m1 mesurées pour chaque espèces ; mean. moyenne ; max. maximum ; min. minimum ; SD. déviation standard.

The research carried out by the authors since 2011 has led to the discovery of several Middle to Late Pleistocene sites (Madurell-Malapeira *et al.*, 2015). The first paleontological survey of Grotte de la Carrière, undertaken in May 2015, resulted in the unearthing of more than 2000 large- and small-vertebrate remains in eight different stratigraphical layers. The small-mammal material recovered comes mainly from layer 4, a five-centimetre-thick layer composed of brown clays with boulders some centimetres in size comprising quartzes and calcareous schists.

This paper aims to provide a study of the small-mammal (insectivore and rodent) faunas from Grotte de la Carrière. Particularly interesting is the correlation and chronological position of Grotte de la Carrière in relation to other Middle Pleistocene sites from southern France, Spain and Italy, based mainly on a study of their vole species. This study thus offers a good opportunity for adding to our knowledge of the small-mammal assemblages of the Middle Pleistocene of Western Europe.

2 - MATERIAL AND METHODS

During the excavation of Grotte de la Carrière, sediments from each layer were screen-washed in order to obtain the small-vertebrate fossil remains. Most of the material comes from layer 4. The specimens under study were sorted at the Institut Català de Paleontologia Miquel Crusafont (ICP, Barcelona, Spain). The Grotte de la Carrière - layer 4 assemblage includes a total of 91 identified small mammals corresponding to a minimum number of 42 individuals, representing at least ten taxa: *Talpa europaea*, *Sorex* sp., *Microtus arvalis*, *Microtus agrestis jansoni*, *Iberomys brecciensis* (= *mediterraneus*; priority discussed by Cuenca-Bescós *et al.* 2014), *Clethrionomys glareolus*, *Pliomys coronensis* (= *lenki*; priority discussed by Terzea, 1983), *Apodemus* gr. *sylvaticus-flavicollis*, *Allocricetus bursae* and *Sciurus* sp.

The nomenclature for the description of the arvicoline teeth (only first lower molars are considered) used for the chronological inferences is that from van der Meulen (1973) and Martin (1987). Length, width, and parameter a are those proposed by van der Meulen (1973), and parameters Li and La are those proposed by Cuenca-Bescós *et al.* (1995). Index La/Li is the ratio between parameters Li and La (fig. 1B et C).

3 - BIOCHRONOLOGICAL REMARKS

Small mammals, and particularly arvicolines, evolved rapidly during the Quaternary, so their record provides an important basis for stratigraphic divisions and correlations between distant areas. In particular, the quick evolutionary radiation of the '*Microtus* group' (which includes forms ascribed to *Microtus*, *Allophaiomys*, *Stenocranius*, *Terricola*, *Iberomys* and *Pallasiinus*) constitutes a very useful tool for correlating European Pleistocene faunas. In our case, the most diagnostic species from a chronological point of view are the voles *Microtus agrestis jansoni* and *Iberomys brecciensis* (fig. 2A).

3.1 - *MICROTUS AGRESTIS JANSONI* (CHALINE, 1972)

Microtus agrestis morphotype *jansoni* was first described by Chaline (1972) on the basis of material from Grotte de l'Escale (Saint-Estève-Janson, Bouches-du-Rhône, France) as a vole with *agrestis*-like morphology: m1 that presents a posterior loop, 5 closed triangles with a clear labio-lingual asymmetry, alternatingly confluent T6 and T7, and an asymmetric anterior cap. In particular, the *jansoni*-type is characterized by a middle-large size, a deep LRA4, the presence of T9 in the ACC and a broad LRA5. In some cases, the populations of the late Middle Pleistocene develop a small BRA4 on T6, resulting in a T8 that recalls the mimomyan-fold. This archaic character is rare in Late Pleistocene populations (1/1000). Chaline (1972) and Cuenca-Bescós *et al.* (1999) suggest a trend toward a decrease in size for this sub-species during the Middle Pleistocene.

Other populations of *M. agrestis jansoni* have been identified in the Middle and Late Pleistocene sites of Caune de l'Arago (Brunet-Lecomte & Paunesco, 2004), La Fage (Mourer-Chauvire *et al.*, 2003), Grotte des Cèdres (Defleur *et al.*, 1990) and Combe Grenal (Chaline, 1972) in France, and in the Middle Pleistocene sites of Galeria, Zarpazos, Gran Dolina TD10, Sima del Elefante TE18-19 (Cuenca-Bescós *et al.*, 1999, 2010; Galindo-Pellicena *et al.*, 2011; López-García *et al.*, 2011), Mollet (López-García *et al.*, 2014) and Valdavara-3 in Spain.

The specimens from Grotte de la Carrière identified as *Microtus agrestis jansoni* present all the morphological characters proper to this sub-species. One specimen also shows a T8 which, taking into account the number of remains recovered, suggests a Middle Pleistocene age. From a biometric point of view, the mean length of m1 (2.796 mm) is lower than those from the type-population of L'Escale (2.87 mm) and from TE 18-19 (2.886 mm) and Zarpazos (2.849 mm), and it is close to those from Mollet (2.775 mm), TD10 (2.776 mm) and Valdavara-3 (2.801 mm). The labio-lingual asymmetry is more pronounced in Grotte de la Carrière (La/Li = 57) than in the samples from Mollet, TD10, Zarpazos, Valdavara-3 and TE 18-19 (La/Li = 41.5, 51.5, 51.6, 52.5 and 54 respectively). The population of *M. agrestis* from layer IIb of Teixoneres Cave (López-García *et al.*, 2012) (Late Pleistocene, Spain) is smaller and more symmetrical (L = 2.662 mm; La/Li = 64.1) than those of the Middle Pleistocene (fig. 2B). Thus, a morphometric comparison between these populations indicates that Grotte de la Carrière has an age close to Valdavara-3 and TD10 and younger than Zarpazos (Falguères *et al.*, 2013; Demuro *et al.*, 2014), ranging from 360 to 250 ka.

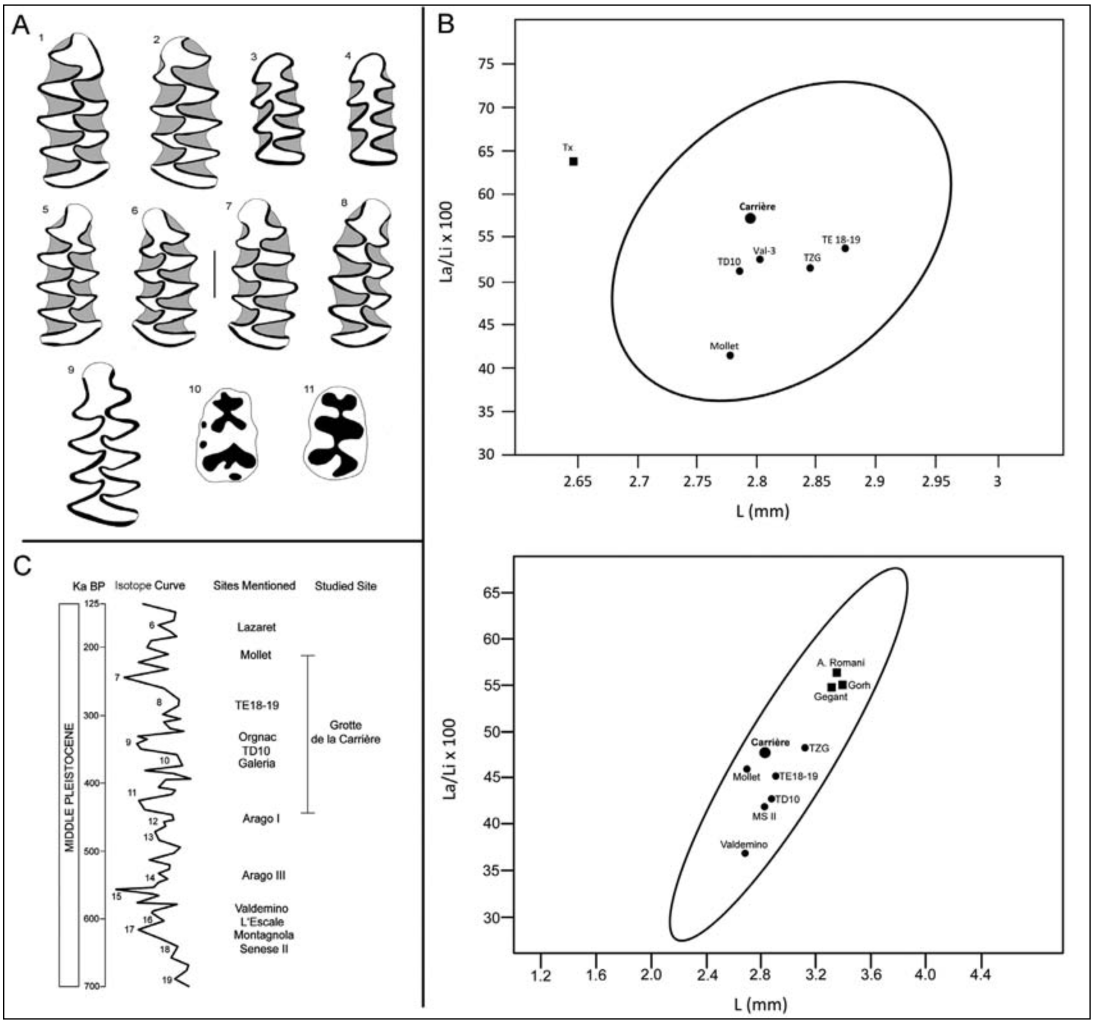


Fig 2: A/ Some small-mammal remains identified from layer 4 of Grotte de la Carrière. B/ Distribution of the species *Microtus agrestis jansoni* (above) and *Iberomys brecciensis* (below) from several Middle Pleistocene sites and some Late Pleistocene sites with *Microtus agrestis* (Tx) and *Iberomys cabrerae* (Abric Romaní, Gegant and Gorh), including Grotte de la Carrière, for the mean of variables La/Li and L. C/ Chronological position for Grotte de la Carrière in relation to the other Middle Pleistocene sites cited in the text and the oxygen isotope curve for this chronological period.

A/ 1-2. right and left m1 *Iberomys brecciensis* (C1-N4-D6-8 and C4-N4-D6-23); 3-4. left m1 *Clethrionomys glareolus* (C2-N4-D6-15 and C5-N4-D6-29); 5-6. right and left m1 *Microtus agrestis jansoni* (C2-N4-D6-12 and C2-N4-D6-13); 7-8. left and right m1 *Microtus arvalis* (C2-N4-D6-10 and C1-N4-D6-1); 9. left m1 *Pliomys coronensis* (C1-N4-D6-4); 10. left m1 *Apodemus* gr. *sylvaticus-flavicollis* (C6-N4-D6-31/1); 11. right m1 *Allocricetus bursae* (C1-N4-D6-9). All teeth are oriented in occlusal view. Scale 1 mm. B/ For abbreviations of the ratios see Material and Methods. TE: Atapuerca Sima del Elefante layers TE18-TE19; TD: Atapuerca Gran Dolina layer TD10; TZG: Atapuerca Trinchera Zarpazos-Galeria; MSII: Montagnola Senese II; Val-3: Valdavara-3; Gorh: Gorham's cave; Tx: Teixoneres cave.

Fig. 2 : A/ *Quelques petits mammifères identifiés dans la couche 4 de la Grotte de la Carrière. B/ Distribution des espèces Microtus agrestis jansoni* (*en haut) et Iberomys brecciensis (en bas) de plusieurs sites du Pléistocène moyen et plusieurs sites du Pléistocène supérieur avec Microtus agrestis (Tx) et Iberomys cabrerae* (*Abric Romaní, Gegant and Gorh), incluant la Grotte de la Carrière, pour la moyenne des variables La/Li et L. C/ Position chronologique de la Grotte de la Carrière en relation avec d'autres sites du Pléistocène moyen cités dans le texte et des courbes isotopiques de l'oxygène pour cette période. A/ 1-2. m1 droite et gauche d'Iberomys brecciensis (C1-N4-D6-8 et C4-N4-D6-23) ; 3-4. m1 gauche de Clethrionomys glareolus (C2-N4-D6-15 et C5-N4-D6-29) ; 5-6. m1 droite et gauche de Microtus agrestis jansoni (C2-N4-D6-12 and C2-N4-D6-13) ; 7-8. m1 gauche et droite de Microtus arvalis (C2-N4-D6-10 and C1-N4-D6-1) ; 9. m1 gauche de Pliomys coronensis (C1-N4-D6-4) ; 10. m1 gauche d'Apodemus* gr. *sylvaticus-flavicollis (C6-N4-D6-31/1) ; 11. m1 droite d'Allocricetus bursae (C1-N4-D6-9). Toutes les dents sont orientées en vue occlusale. Échelle 1 mm. B/ Pour les abréviations des indices voir Matériel et Méthodes. TE- Atapuerca Sima del Elefante couches TE18-TE19 ; TD-Atapuerca Gran Dolina couche TD10 ; TZG- Atapuerca Trinchera Zarpazos-Galeria ; MSII-Montagnola Senese II ; Val-3-Valdavara-3 ; Gorh-Grotte de Gorham ; Tx-Grotte de Teixoneres.*

3.2 - IBEROMYS BRECCIENSIS (= *MEDITERRANEUS*) (GIEBEL, 1847)

Microtus (*Iberomys*) *brecciensis* was described by Chaline in 1972 as a subgenus of *Microtus* species. Chaline proposed a specimen drawn by Cuvier (1823) as the holotype, and Sète as the type locality, a karst fissure of imprecise location where lagomorphs have been found.

The distinctive morphological traits of *I. brecciensis* are the T4 and T5 that are closed in all specimens. In some specimens, BRA4 forms a reduced re-entrant angle, and in most m1, T6 is clearly separated from the anterior cusp due to the strong development of the re-entrant angle LRA4. These characteristics allow our material to be attributed to the species *I. brecciensis*, thus distinguishing it, moreover, from the present-day species *I. cabrerae* and from the fossil species from the Early Pleistocene *I. huescarensis*.

Other populations of *I. brecciensis* have been identified in Middle Pleistocene sites such as Caune de l'Arago, Orgnac and Le Lazaret (Hanquet, 2011; Hanquet &

Desclaux, 2011) in France, Valdemino or Montagnola Senese II in Italy (López-García *et al.*, 2015), and Galeria, Zarpazos, Gran Dolina TD10, Sima del Elefante TE18-19 (Cuenca-Bescós *et al.*, 1999, 2010; Galindo-Pellicena *et al.*, 2011; López-García *et al.*, 2011) and Mollet (López-García *et al.*, 2014) in Spain.

The specimens from Grotte de la Carrière identified as *Iberomys brecciensis* present all the morphological characters proper to this species, suggesting a Middle Pleistocene age for layer 4. From the biometric point of view, m1 (mean length 2.830 mm) is longer than those from the sites of Valdemino (2.69 mm) and Mollet (2.7 mm), shorter than those from Orgnac (2.96 mm), Lazaret (3.15 mm), TE 18-19 (2.91 mm) and Galeria (3.12 mm), and similar to those from Arago I (2.89 mm), L'Escale (2.89 mm), Montagnola Senese II (2.83 mm) and TD10 (2.88 mm). The labio-lingual asymmetry is less pronounced in Grotte de la Carrière (La/Li = 47.6) than in Galeria (La/Li = 48.2), but more pronounced than in Valdemino, Montagnola Senese II, TD10, TE18-19 and Mollet (36.8, 41.8, 42.7, 45.2 and 45.9 respectively). The populations of *I. cabrerae* from the Late Pleistocene sites of Cova del Gegant (L = 3.31 mm; La/Li = 54.7), Abric Romaní (L = 3.35 mm; La/Li = 56.9) and Gorham's cave (L = 3.40 mm; La/Li = 55.07) (López-García *et al.*, 2008; López-García, 2011) are larger and more asymmetrical than those of the Middle Pleistocene (fig. 2B). Thus, morphological and biometric comparisons between these populations indicate that Grotte de la Carrière has an age close to TD10, Galeria and TE18-19, older than Mollet, and younger than Valdemino and Montagnola Senese II (López-García *et al.*, 2011; Maroto *et al.*, 2012; Falguères *et al.*, 2013; Demuro *et al.*, 2014; ; de Lombera-Hermida *et al.*, 2015; López-García *et al.,* 2015), ranging from 450 to 215 ka.

In summary, the small-mammal association from layer 4 of Grotte de la Carrière fits within the range of typical associations from the Middle Pleistocene faunas of the southwestern Mediterranean and can be included in FU6 (ranging from 600 to 125 ka) as defined by Cuenca-Bescós *et al.* (2010), where the characteristic species of this Faunal Unit are *I. brecciensis*, *M. arvalis*, *M. agrestis jansoni*, *Pliomys coronensis* and *Allocricetus bursae*. Thus, the Grotte de la Carrière association is also very similar to other Middle Pleistocene sites from the south of France, such as Caune del Arago or Grotte du Lazaret (Hanquet, 2011; Hanquet & Desclaux, 2011), and Spain, such as Gran Dolina (TD10), Galeria and Sima del Elefante (TE18-19) from the Sierra de Atapuerca (Cuenca-Bescós *et al.*, 1999, 2010; Galindo-Pellicena *et al.*, 2011; López-García *et al.*, 2011). All these data, together with the morphological and biometric studies of the species *Iberomys brecciensis* and *Microtus agrestis jansoni*, suggest a rough age for layer 4 of between 450 and 220 ka (fig. 2C). The chronology proposed on the basis of the micromammal assemblage is in accordance with the large mammals recovered and identified from this layer, *Ursus deningeri*, *Panthera fossilis* and *Canis mosbachensis* being the most characteristic species.

4 - CONCLUSIONS

Our study of the small-mammal assemblage from layer 4 of Grotte de la Carrière allows the following conclusions to be drawn:

– 1/ Ten small-mammal (insectivore and rodent) species are currently known to be present in Grotte de la Carrière - layer 4: *Talpa europaea*, *Sorex* sp., *Microtus arvalis*, *Microtus agrestis jansoni*, *Iberomys brecciensis*, *Clethrionomys glareolus*, *Pliomys coronensis*, *Apodemus* gr. *sylvaticus-flavicollis*, *Allocricetus bursae* and *Sciurus* sp.

– 2/ Within the context of the small- and large-mammal assemblages from layer 4 of Grotte de la Carrière, the evolutionary states of the vole species *Microtus agrestis jansoni* and *Iberomys brecciensis* are indicative of a chronological age within the range of 450 and 220 ka .

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