



General Palaeontology, Systematics and Evolution (Vertebrate Palaeontology)

Cold-climate rodent indicators for the Late Pleistocene of Central Iberia: New data from the Buena Pinta Cave (Pinilla del Valle, Madrid Region, Spain)



Rongeurs indicateurs de climat froid dans le Pléistocène supérieur de l'Ibérie centrale : nouvelles données de la grotte de la Buena Pinta (Pinilla del Valle, Communauté de Madrid, Espagne)

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ABSTRACT

In the Iberian Peninsula, the Late Pleistocene record of small mammal indicators of cold climates is largely restricted to two sets of sites at the eastern and western ends of the Pyrenees. Some assemblages from other sites at the Peninsular centre have, however, recently yielded such taxa. This work describes the remains of three such rodent species from the Buena Pinta Cave, a site in the Sierra de Guadarrama mountains in the Spanish Central System. Excavation campaigns in the cave have taken place every summer since 2003. Thermoluminescence analyses of sediments from levels 2–5 of the site suggest an age corresponding to the middle of the Late Pleistocene, within Marine Isotope Stage 4 or the beginning of Marine Isotope Stage 3. Sieve-washing and picking out of the small fossils contained in the sediments of levels 2–5 yielded several thousand small mammal teeth and other remains, dominated by *Microtus arvalis*. Smaller numbers of remains belonging to other rodents typical of cold climates were also identified, such as *Microtus oeconomus*, *Microtus gregalis* and *Chionomys nivalis*. Thus, the small mammal record of the Buena Pinta Cave shows that rodent indicators of cold climates reached the centre of the Iberian Peninsula during the mid-Late Pleistocene, i.e., well before the Last Glacial Maximum. These findings represent one of the southernmost Pleistocene records for *M. oeconomus* in Europe, and the most southerly for *M. gregalis*.

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R É S U M É

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Dans la Péninsule ibérique, le registre Pléistocène supérieur de petits mammifères indicateurs de climats froids est principalement restreint à deux ensembles de sites localisés aux extrémités orientale et occidentale des Pyrénées. Quelques assemblages d'autres gisements du centre de la péninsule ont néanmoins délivré récemment de tels taxons. Ce travail décrit les restes de trois de ces espèces de rongeurs de la grotte de la Buena Pinta, un site des montagnes de la Sierra de Guadarrama dans le Système central espagnol. Les campagnes de fouilles dans la grotte ont lieu chaque été depuis 2003. Les analyses de thermoluminescence réalisées sur les sédiments, des couches 2 à 5 ont fourni des datations correspondant à la partie moyenne du Pléistocène supérieur, dans un intervalle comprenant le stade isotopique marin 4 et le commencement du stade isotopique marin 3. Le lavage-tamassage et le tri des petits fossiles contenus dans les sédiments des niveaux 2–5 ont fourni plusieurs milliers de dents et autres restes de petits mammifères, où domine l'espèce *Microtus arvalis*. Un petit nombre d'ossements appartenant à d'autres rongeurs typiques de climats froids ont aussi été identifiés, comme *Microtus oeconomus*, *Microtus gregalis* et *Chionomys nivalis*. Par conséquent, le registre de petits mammifères de la grotte de la Buena Pinta montre que les rongeurs indicateurs de climats froids ont atteint le centre de la péninsule Ibérique au milieu du Pléistocène supérieur, c'est-à-dire bien avant le dernier maximum glaciaire. Ces découvertes représentent l'un des registres pléistocènes les plus méridionaux pour *M. oeconomus* en Europe, et le plus méridional pour *M. gregalis*.

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1. Introduction

During the Pleistocene, the distribution of mammals in Eurasia was strongly conditioned by the climatic changes that characterised this period (Kahlke, 2014; Kurtén, 1968; Lister, 1997; Pushkina, 2007; Sommer and Nadachowski, 2006; Von Koenigswald, 2003). During cold intervals, those species that until then had lived in the centre and north extended their range towards the west and south. In southwestern Europe, the arrival of northern and eastern mammal species was particularly strong during the Late Pleistocene. At this time, and after a long period of stability in the mammalian faunas of the Iberian Peninsula that began at the end of the Mid-Pleistocene Revolution (Rodríguez et al., 2011), a wide set of mammalian species were able to cross the Pyrenees, and species typical of cold climates began to appear in this region (Álvarez-Lao and García, 2010; Sesé and Sevilla, 1996). Most of their records are from two areas, one on either side of the Pyrenees (Álvarez-Lao and García, 2011; Sesé, 2005). In the rest of the Peninsula, records of these species are much more scarce.

This work reports the presence of three rodent indicators of cold climates – *Microtus oeconomus*, *Microtus gregalis* and *Chionomys nivalis* – in the Late Pleistocene levels of a site at the centre of the Iberian Peninsula: the Buena Pinta Cave. The site provides one of the most southerly Pleistocene records for *M. oeconomus*, and the most southerly for *M. gregalis*. The biogeographical significance of the presence of these taxa at such southerly latitudes is discussed.

2. Geographical and geological context

The Buena Pinta Cave lies some 80 km north of Madrid in the upper reaches of the Lozoya Valley, a depression of tectonic origin in the Sierra de Guadarrama, a mountain

range forming part of the Spanish Central System (Fig. 1). To the west of the valley lies the Peñalara Massif, which reaches an altitude of 2428 m – the highest in the Sierra de Guadarrama. The valley itself lies between the altitudes of 1000 and 1100 m. With at least 41 mammal species it has a high biological diversity (Prieto Cana and de Lucio, 1995), a consequence of the many habitats resulting from its steep altitude gradient and varied geomorphology, climate, soil and hydrology. Indeed, the upper reaches of the valley were designated a National Park in 2013.

The cave itself, of reduced dimensions, is developed in Cretaceous carbonatic rocks, and was discovered in 2003 during surveys performed as part of a project on human occupation of the Peninsular centre during the Pleistocene (Arsuaga et al., 2011; Baquedano et al., 2014; Pérez-González et al., 2010). The cave has an external chamber where excavation work has been focused since 2003 (Fig. 2). The limestone roof in this area has been eroded and has fallen away. To the east of this area a narrow gallery (about 1.5 m wide) opens that continues some 10 m into the Cretaceous limestones and dolostones in a NNE direction. The sediments in the external chamber and this gallery show stratigraphic continuity. In grid squares M49 and M50 (Fig. 2) at the mouth of the gallery, excavation work has revealed a stratigraphic section with five distinguishable levels (Pérez-González et al., 2010) (Fig. 3). Level 1 is formed from Holocene colluvium some 1.80 m thick. It has a clay sand texture and contains grey-brown and dark grey carbonate clasts. Lying below is a 1.70 m thick layer of yellow, silt-clay sands containing disperse carbonate clasts measuring up to 40 cm along their longest axis. This layer can be divided into four levels (numbered 2–5 from top to bottom) distinguishable by the colour and texture of their sediments. Levels 2–5 are rich in macro- and microvertebrate remains, that have been dated to the middle of the Late Pleistocene (see Section 4.3). These levels lie discordantly over a much eroded speleothem. Beneath

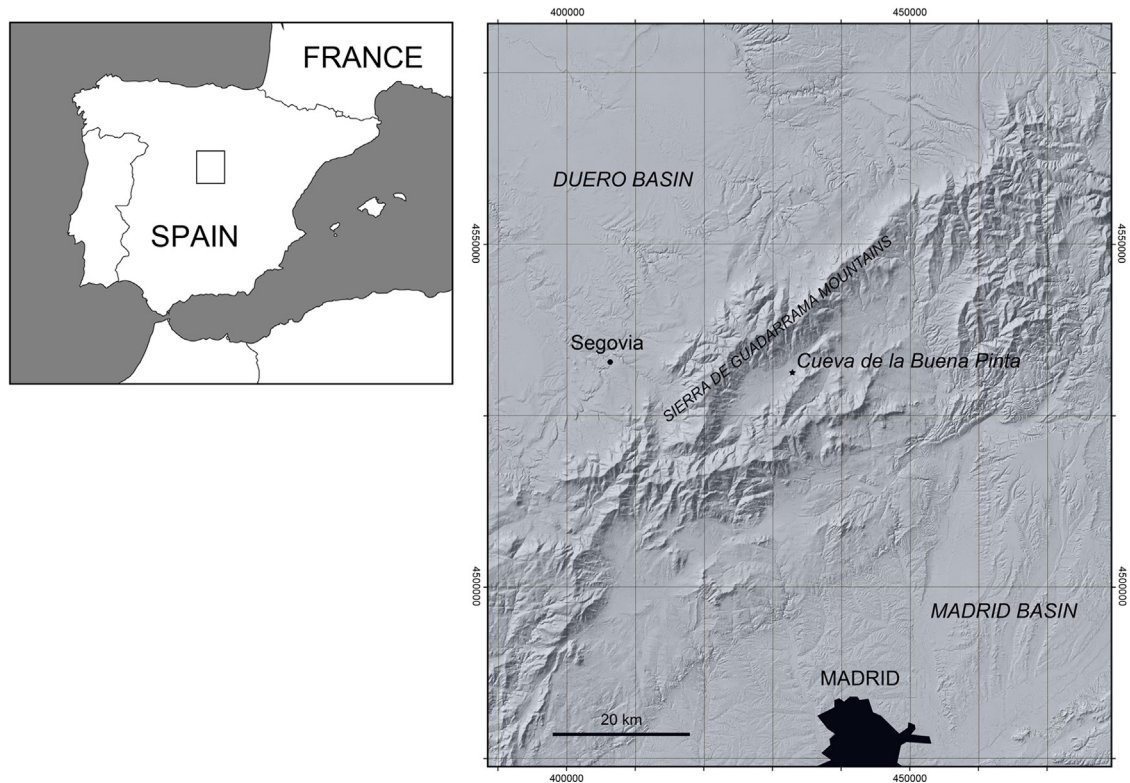


Fig. 1. Geographic location of the Buena Pinta Cave in the Spanish Central System.

Fig. 1. Situation géographique de la grotte de la Buena Pinta dans le Système central espagnol.

this speleothem lie conglomerates and carbonate breccias of limestone and dolomite boulders that make up one of the first stages of infilling of the cave; they also crop out on the northwestern wall forming the boundary of the external chamber. This unit shows continuity to the northeast and completely fills another gallery, the roof of which has disappeared through erosion. A survey of this gallery (known as the Galería Pit) returned a wide range of microvertebrates. The presence and evolutionary stages of the detected species *Microtus vaufreyi* and *Microtus brecciansis* allow the materials of this gallery to be dated to the end of the Middle Pleistocene (Laplana et al., 2013a).

The remains of the cold-climate rodents examined in the present work all come from levels 2–5 of the external chamber of the cave.

3. Methodology

Since its discovery, the Buena Pinta Cave has been the object of annual excavation campaigns. All the archaeological and palaeontological remains found were spatially referenced on an excavation grid. Samples of sediment were taken at 10 cm depth intervals in each 1 × 1 m grid square. For the detection of microvertebrate remains, the collected samples were washed through a series of fine-mesh sieves (down to 0.5 mm). The vertical and horizontal variations in the microvertebrate assemblages therefore became appreciable as work progressed.

The nomenclature used to describe the arvicoline dental elements recovered is that proposed by Van der Meulen (1973) and Nadachowski (1991) (Fig. 4a). The systematic taxonomy followed is that proposed by Musser and Carleton (2005). Measurements of the first lower molars (m1 onwards) were taken following the procedure shown in Fig. 4b. The measurements L (maximal length of the occlusal surface), W1 (width of the posterior part of the anteroconid complex), a (length of the anteroconid complex), b (shortest distance between BRA3 and LRA4), and c (shortest distance between BRA3 and LRA3) are those proposed by Van der Meulen (1973). W2 is the width across T2 and T3. The variables La1 and La2 are similar to those proposed by Cuenca-Bescós et al. (1995). The morphometric ratios A/L, B/W1 and C/W1 are those proposed by Van der Meulen (1973). The ratio L/W was also calculated, as were two others reflecting transversal asymmetry: La1/W1 and La2/W2. The morphotypes identified in the description of the variability of the first lower molars of *Chionomys nivalis* are those proposed by Nadachowski (1991), and in this work they are used with the same meaning.

4. Results

The excavation work performed over the last 12 years at the Buena Pinta Cave has led to the recovery of tens of thousands of small mammal teeth. For instance, grid units M49 and M50, which represent only a small part of the entire site (Fig. 2) have provided 2744 rodent first lower

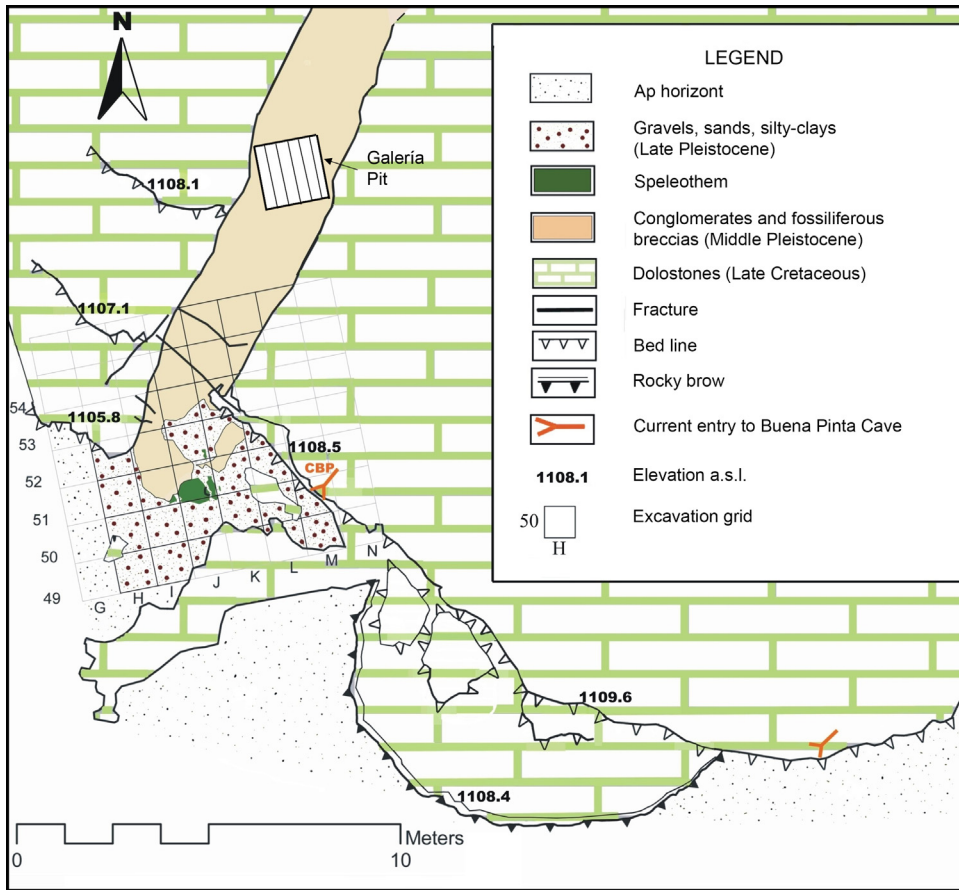


Fig. 2. (Color online). Plan scheme of the Buena Pinta Cave site.

Fig. 2. (Couleur en ligne). Plan de la grotte de la Buena Pinta.

Modified from Pérez-González et al., 2010.

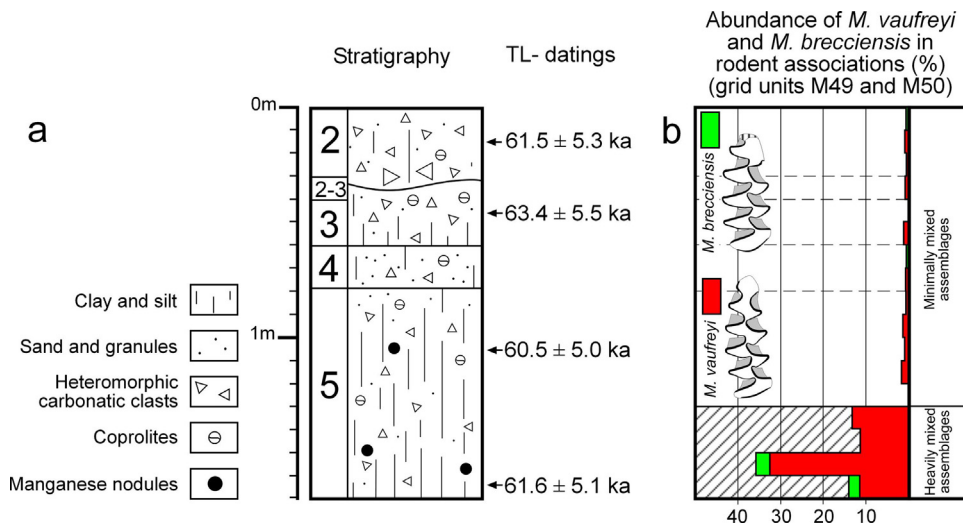


Fig. 3. (Color online). a: Stratigraphy of the external chamber of the Buena Pinta Cave, indicating the provenance of the sediment samples dated by thermoluminescence, and the ages obtained (Dating and Radiochemistry Laboratory, UAM); b: relative abundance of the species *Microtus vaufreyi* and *Microtus brecciensis* (reworked elements) for levels 2–5.

Fig. 3. (Couleur en ligne). a : Stratigraphie de la chambre extérieure de la grotte de la Buena Pinta, avec indication de la provenance des échantillons de sédiment datés par thermoluminescence et des datations obtenues (laboratoire de datation et radiochimie, UAM) ; b : abondance relative des espèces *Microtus vaufreyi* et *Microtus brecciensis* (éléments remaniés) dans les associations de rongeurs de toute la séquence.

Table 1

Rodent species and their abundance by level in grid units M49 and M50 of the Buena Pinta Cave. Middle Pleistocene reworked species are marked with an asterisk. For each species and level, the total number of first lower molars is indicated.

Tableau 1

Liste et abondance des espèces de rongeurs présentes dans les carrés M49 et M50 de la grotte de la Buena Pinta, par couche. Les espèces remaniées du Pléistocène Moyen ont été signalées par un astérisque. Pour chaque espèce et couche, le nombre total de premières molaires inférieures est indiqué.

	Levels				
	2	2–3	3	4	5
Family Sciuridae					
<i>Sciurus vulgaris</i>	0	0	0	0	0
<i>Marmota marmota</i>	0	1	0	0	0
Family Gliridae					
<i>Elimomys quercinus</i>	18	3	15	20	9
Family Castoridae					
<i>Castor fiber</i>	0	0	0	0	0
Family Cricetidae					
<i>Arvicola sapidus</i>	21	3	24	14	6
<i>Arvicola amphibius</i> s. l.	13	0	2	0	0
<i>Myodes glareolus</i>	0	0	0	0	0
<i>Chionomys nivalis</i>	4	1	0	0	0
<i>Microtus gr. agrestis</i>	138	16	127	83	26
<i>Microtus arvalis</i>	690	73	433	223	39
<i>Microtus brecciensis</i> *	2	0	0	3	2
<i>Microtus cabreræ</i>	0	1	0	0	1
<i>Microtus cf. gregalis</i>	0	0	0	0	0
<i>Microtus gr. lusit.-duodecimcostatus</i>	127	42	141	143	49
<i>Microtus oeconomus</i>	0	0	0	1	1
<i>Microtus vaufreyi</i> *	8	0	5	5	21
<i>Pliomys lenki</i>	1	0	4	7	1
<i>Allocricetus bursæ</i>	3	4	14	15	9
Family Muridae					
<i>Apodemus</i> sp. gr. <i>A. sylv.-flavicollis</i>	45	4	29	34	20
Total number of first lower molars by level	1070	148	794	548	184

molars (Table 1). Indeed, the site is home to one of the most species-rich assemblages for the entire Iberian Late Pleistocene [see provisional list in Baquedano et al. (2010)]. From levels 2–5, 18 rodent species were identified, mostly arvicolines (Table 1). Their abundance was estimated from the total number of first lower molars recovered for each.

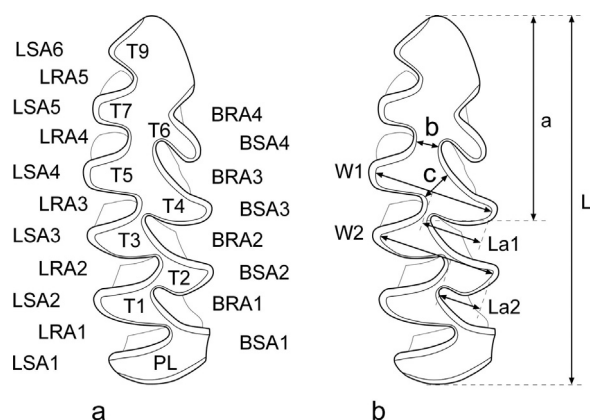


Fig. 4. a: terminology for the occlusal surface elements of the first lower molar (m1) according to Van der Meulen (1973) and Nadachowski (1991). BRA: buccal re-entrant angle; BSA: buccal salient angle; LRA: lingual re-entrant angle; LSA: lingual salient angle; PL: posterior lobe; b: measurements taken on the occlusal surface of m1.

Fig. 4. a : terminologie des éléments de la surface occlusale de la première molaire inférieure (m1) selon Van der Meulen (1973) et Nadachowski (1991) ; b : schéma des mesures prises sur la superficie occlusale des m1 des arvicolinés.

4.1. Preliminary taphonomic context

The remains of at least two species recovered from levels 2–5, *M. vaufreyi* and *M. brecciensis*, are reworked elements from Middle Pleistocene sediments that crop out at the base of the site's sedimentary infilling and at the north-western wall of the external chamber. These species are characteristic of the Middle Pleistocene (Brunet-Lecomte, 1988; Laplana and Sevilla, 2013) and have never been cited for younger sediments. Their presence in levels 2–5 is incongruent with their dating, and with the presence in the same levels of *Microtus cabreræ*, a descendent of *M. brecciensis*. The teeth of these species were often seen to be extensively impregnated with manganese oxide; those of other species were much less commonly affected, and when they were, smaller areas were involved. *M. brecciensis* and *M. vaufreyi* are plentiful in the lower part of level 5, reaching abundance values of 10–30% (Fig. 3b). These proportions can be explained in that, during the deposition of this level, the Middle Pleistocene conglomerates and breccias situated under the eroded speleothem at the base of the site's sedimentary infilling outcropped extensively in an area adjacent to grid units M49 and M50 and became eroded too. The microvertebrate remains they contained were thus incorporated into the younger level 5 as reworked elements. The onlap arrangement of levels 2–5 over the older units led to the rapid disappearance of the exposed surface of the latter as the sediments of levels 2–5 were deposited. From that moment onwards, the only available source of Middle Pleistocene microvertebrate remains were the breccias and conglomerates that

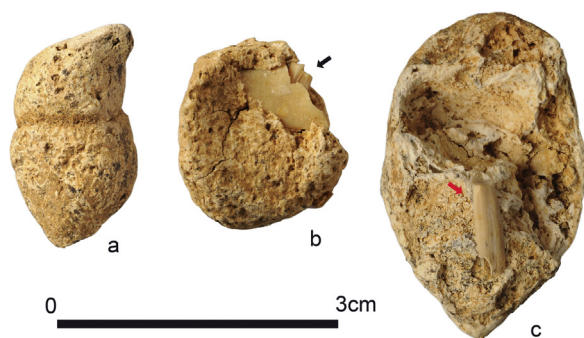


Fig. 5. (Color online). Medium to small size carnivore coprolites from levels 2–5 of the Buena Pinta Cave. Arrows point to bone remains of small mammals.

Fig. 5. (Couleur en ligne). Coprolithes produits par un carnivore de taille moyenne et provenant des couches 2–5 de la grotte de la Buena Pinta. Les flèches signalent des fragments d'os de petits mammifères.

ocropped at the northwestern wall of the external chamber and at its base, which were 2–3 m far from grid units M49 and M50. Thus, from the beginning of the upper third of level 5, the remains of these species become much less abundant in grid units M49 and M50 (Fig. 3b), with values of just 0–3%.

It is possible that some remains of other species in the Late Pleistocene levels are reworked since, in the Middle Pleistocene conglomerates and breccias exposed in the Galería Pit, a relatively large number of species have been found (Laplana et al., 2013a). *M. vaufreyi* dominates this Middle Pleistocene assemblage, accounting for some 70% of all rodent remains encountered. Its abundance in levels 2–5 can be considered an indicator of the proportion of reworked elements the sequence contains. Where the frequency of *M. vaufreyi* in levels 2–5 is low, that of the other rodents in the same Middle Pleistocene conglomerates and breccias is virtually nil. None of the cold-climate micro-mammalian species identified in levels 2–5 were seen in the Galería Pit Middle Pleistocene assemblage.

The large concentration of microvertebrate remains in levels 2–5 represents the activity of a small-middle sized predator, as shown by the numerous small coprolites (2–4 cm maximum length) (Fig. 5). These coprolites appear both intact and fragmented, and contain the remains of the same microvertebrates.

The Late Pleistocene layers also contain the remains of bony fish, sharks, rays and marine reptiles as reworked elements from the Late Cretaceous carbonate rock forming the walls and ceiling of the cave (Hontecillas et al., 2015).

4.2. Preliminary palaeoenvironmental context

Palynological studies performed on the Late Pleistocene layers of the cave (Ruiz-Zapata et al., 2008, 2012) indicate a low diversity of flowering plants, with just 24 identifiable taxa, and with just six of these being trees. Open landscapes appear to have dominated at this time, with a largely herbaceous vegetation made up mostly of members of Chenopodiaceae and Asteraceae. *Pinus* was the most common of the impoverished tree list, accompanied by the odd representative of deciduous *Quercus* and *Ulmus*. Such

pollen profiles are indicative of cold, dry conditions that prevented the development of greater floral complexity.

The extensive mixing of faunas of different chronology in the lower part of level 5 prevents any reliable environmental conclusions for this part of the stratigraphic series being drawn from the rodents present. In the remaining levels, however, this mixing is much less intense, and the different rodents identified can provide a palaeoenvironmental picture. Excluding the lower part of level 5, the rodent assemblages of the remainder of the stratigraphic series are dominated (in decreasing order) by *M. arvalis*, *M. gr. lusitanicus-duodecimcostatus* and *M. gr. agrestis*. At the base of the series these species appear in similar proportions (20–30% each). Towards the top, however, *M. arvalis* increases in abundance and becomes dominant, reaching a frequency of around 75% in level 2. The net predominance of vole species (which together account for some 75–90% of all rodents in the different levels), and the reduced abundance of forest species such as *Apodemus* sp. gr. *A. sylvaticus*–*A. flavicollis* or *Eliomys quercinus*, indicate – in agreement with the pollen data – the predominance of open spaces.

4.3. Chronological context

Pérez-González et al. (2010) published two datings for levels 1 and 3 in the external chamber of the Buena Pinta Cave. For level 1, C^{14} dating returned a result of 4940 ± 40 BP (5740–5600 cal BP), while for level 3, thermoluminescence dating returned a result of 63.4 ± 5.5 ka. New datings performed on samples of sediment from levels 2–5 have provided very similar dates (Fig. 3a). Taking into account the similarity between the whole set of datings, it would therefore appear that these levels were deposited over a brief period of time.

From a biochronological standpoint (leaving out *M. vaufreyi* and *M. brecciensis*, the remains of which, as indicated above, are reworked from older sediments), the rodent assemblage of levels 2–5 is characteristic of the Late Pleistocene. *Arvicola amphibius* s. l., *M. Cabrerae*, *M. oeconomicus* and *C. nivalis* are all exclusive to this period in the Iberian Peninsula; in earlier periods they are completely absent (Sesé and Sevilla, 1996).

At the Peninsular centre, the assemblages of the start of the Late Pleistocene are characterised by the abundance of *M. Cabrerae*, a thermophilic species. At the PRERESA site, which has been dated to 84 ± 5.6 ka, it is the most abundant rodent species (71% of the minimum number of individuals [NMI] for rodents) (Sesé et al., 2011), and in the northern sector of the Cueva del Camino site (90.9 ± 7.8 ka) it is the third most abundant (9% of the NMI) (Laplana et al., 2013b). In this latter site there appears to be a reduction in the abundance of this species over the last moments of MIS5, with values falling to 1% in the central sector, and even 0% in the southern sector (74.5 ± 6.3 ka; Arsuaga et al., 2012). The scarcity of this species in levels 2–5 of the Buena Pinta Cave (never above 1% NMI) can be interpreted as their being younger than the northern sector of the Cueva del Camino site (a site situated just 130 m away), but more similar in age to its central sector and even closer in age to its southern sector. This also agrees with the presence of *C. nivalis*

Table 2

Measurements made on the m1 of *M. oeconomus* (L and W in mm; ratios are dimensional and are expressed as percentages, except L/W).

Tableau 2

Mesures faites sur la m1 de *M. oeconomus* (L et W en mm ; les rapports sont adimensionnels et sont donnés en pourcentages, à l'exception de L/W).

	n	Min	Mean	Max	SD
L	5	2.62	2.82	2.92	0.12
W1	5	1.16	1.30	1.39	0.09
A/L	5	44.3	46.3	48.1	1.52
B/W1	3	15.2	20.0	24.3	4.53
C/W1	3	2.91	3.78	4.63	0.86
AS1	3	34.3	36.4	37.9	1.87
AS2	3	32.7	34.5	35.7	1.56
L/W1	3	2.64	2.70	2.81	0.09

only in the southern sector of the Cueva del Camino site (Laplana et al., 2013b) (this species is present throughout levels 2–5 in the Buena Pinta Cave). *M. cabreræ* is absent in the Peninsular centre from sites corresponding to MIS3 and MIS2. Such is the case of the Jarama VI site (dated to some 30 ka [MIS3]) (Lorenzo et al., 2012), the Abrigo del Monte site (dated to 14 ka [MIS2]) (Sevilla et al., 2009), and the Peña de Estebanvela site (the sequence at which has been dated to 10–14 ka) (Cacho et al., 2012). Although this species has been cited for the Cueva de la Zaramora site (dated to 44 ka) (Sala et al., 2011), the more recent chalcolithic disturbance of the site's stratigraphy through its use as a burial ground (Sala et al., 2013) poses serious concerns regarding the age of the microvertebrate assemblage recovered. Indeed, the remains of some species might be Holocene in age, including those of *M. cabreræ*.

Thus, the rodent assemblage of the Buena Pinta Cave is congruous with the datings available for the site. These datings, plus the biochronological interpretation of the faunal assemblage of levels 2–5, suggest the latter sequence to be Late Pleistocene in age (between MIS4 and the start of MIS3); the palaeoclimatic context inferred from the palynological data and micromammal assemblage places it within a cold interval during this period. New dating sampling currently underway may allow a more precise dating within the stated period.

4.4. Description of the materials

Three of the rodent species identified – *M. oeconomus*, *M. gregalis* and *C. nivalis* – are of particular importance from a climatic point of view. The following lines describe the recovered material attributable to these species, and discuss the climatic and biogeographic significance of their presence. The stratigraphic distribution of these species is shown in Table 1 (for grid units M49 and M50).

4.4.1. *Microtus oeconomus* (Pallas, 1776) – Root vole

Eight first lower molars (m1) were recovered from levels 2–5. Table 2 shows their dimensions.

The occlusal surface of the first lower molars shows the basic model for the genus *Microtus*, with triangles T4 and T5 being non-confluent, plus the diagnostic characteristics of a wide neck communicating triangle T5 with the anterior lobule, and a usually absent or little apparent triangle

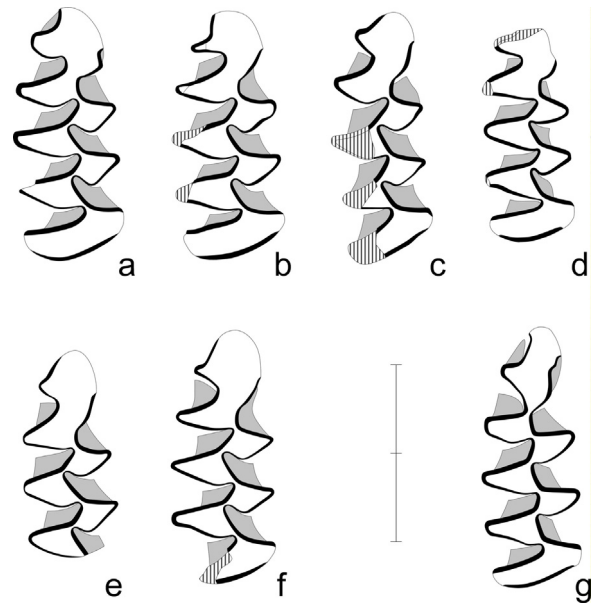


Fig. 6. Morphology of the occlusal surface of m1 of *M. oeconomus* (a–f) and *M. cf. gregalis* (g) from the Buena Pinta Cave (all are represented as though they were from the right side, even if they are not). a: CBP'03 M49 N1–2 (m1 d); b: CBP'07 M49 L2 150–155 (right); c: CBP'10 K52 L3 210–220 (right); d: CBP'13 M50 L5 270–280 (left); e: CBP'06 M49 L5 280–290 (right); f: CBP'08 L50 L3 230–240 (right); g: CBP'04 L49 L3 180–190 (left). Scale bar = 2 mm.

Fig. 6. Morphologie de la surface occlusale des m1 de *M. oeconomus* (a–f) et *M. cf. gregalis* (g) de la grotte de la Buena Pinta (toutes les molaires sont représentées comme si elles étaient droites, même lorsqu'elles ne le sont pas). a : CBP'03 M49 N1–2 (m1 d) ; b : CBP'07 M49 L2 150–155 (droite) ; c : CBP'10 K52 L3 210–220 (droite) ; d : CBP'13 M50 L5 270–280 (gauche) ; e : CBP'06 M49 L5 280–290 (droite) ; f : CBP'08 L50 L3 230–240 (droite) ; g : CBP'04 L49 L3 180–190 (gauche). L'échelle graphique mesure 2 mm.

T6. Triangle T7 is always present, although it is less developed than the other triangles of the molar, and limited in its anterior area by a shallow LRA5 with or without cement in its interior (Fig. 6).

4.4.2. *Microtus cf. gregalis* (Pallas, 1779) – Narrow-headed vole

Two m1 were recovered from level 2. Table 3 shows the dimensions for the only complete m1.

The occlusal surfaces of all the recovered m1 show morphological characteristics of the species: five closed triangles, a hardly apparent T6 (present only as a slight wave on the perimeter of the enamel), and a well developed T7 (Fig. 6).

Little material belonging to this species was found, and even then, that which was found might be argued to

Table 3

Measurements made on the m1 of *M. cf. gregalis* (L and W in mm; ratios are dimensional and are expressed as percentages, except L/W).

Tableau 3

Mesures faites sur la m1 de *M. cf. gregalis* (L et W en mm ; les rapports sont adimensionnels et sont donnés en pourcentages, à l'exception de L/W).

L	W1	A/L	B/W1	C/W1	AS1	AS2	L/W1
2.96	0.95	52.74	3.87	3.87	40.31	36.62	0.95

Table 4

Measurements made on the m1 of *C. nivalis* (L and W in mm; ratios are adimensional and are expressed as percentages, except L/W).

Tableau 4

Mesures faites sur la m1 de *C. nivalis* (L et W en mm ; les rapports sont adimensionnels et sont donnés en pourcentages, à l'exception de L/W).

	n	Min	Med	Max	SD
L	14	2.73	3.00	3.21	0.08
W1	15	0.99	1.13	1.24	0.06
A/L	14	47.6	48.7	50.3	0.74
B/W1	15	6.36	18.4	29.3	6.96
C/W1	15	3.64	4.79	5.79	0.87
AS1	15	31.3	38.5	43.0	3.19
AS2	15	30.2	33.8	36.3	1.88
L/W1	13	2.45	2.66	2.80	0.11

correspond to extreme variants of *M. arvalis*, the dominant species. The same was noted by Pemán (1994) at the Iberian Laminak II site. However, at the nearby Cueva del Camino, which is slightly older and represents a warm context across most of its stratigraphy (end of MIS5 and transition to MIS4) (Blain et al., 2014; Laplana et al., 2013b), the abundant *M. arvalis* remains show no sign of “gregalis” morphology. Thus, the possible *M. gregalis* material collected probably does represent this species at the Buena Pinta Cave.

4.4.3. *Chionomys nivalis* (Martins, 1842) – Snow vole

Twenty-two m1 were recovered from levels 2–5. Table 4 shows their dimensions. The occlusal surface of these molars (Fig. 7) shows a posterior lobe, four closed triangles (T1–T4), and a T5 generally in communication with the anterior lobe, although in one case (1/22; 0.45%) these elements were separate. These molars appear symmetrical, although the lingual triangles are somewhat more developed than the buccal triangles. The anterior lobe reveals the scant or null development of LRA5, while that of BRA4 is more variable: it may be completely absent, appear as a shallow wave, or one that reaches a considerable depth, although always smaller than the rest of the buccal re-entrant angles. T6, when it is present, is small and pointed, unlike T7, which is more open and rounded (Fig. 7).

In the Buena Pinta Cave sample the “nivalis” morphotype [sensu Nadachowski (1991), in which T5 and T6 are separate, T6 and T7 are well developed, and BRA4 and LRA5 only incipient] is very scarce. In current and fossil populations of *C. nivalis* it is usually the most common, with proportions of over 50%. However, Nadachowski (1991) indicates that in *C. nivalis abulensis*, a subspecies that today lives in the mountain ranges of the Peninsular centre, this morphotype is represented in relatively low proportion (18.7%). The same occurs in other populations of *C. nivalis* in southwestern Europe, where the morphotype “lebrunii” is generally dominant. The length and relative development of the anterior part of the molars from the cave are similar to those recorded for current and fossil populations of *C. nivalis* (Nadachowski, 1991). This, in conjunction with the morphological similarities discussed, suggests the recovered material belongs to *C. nivalis*.

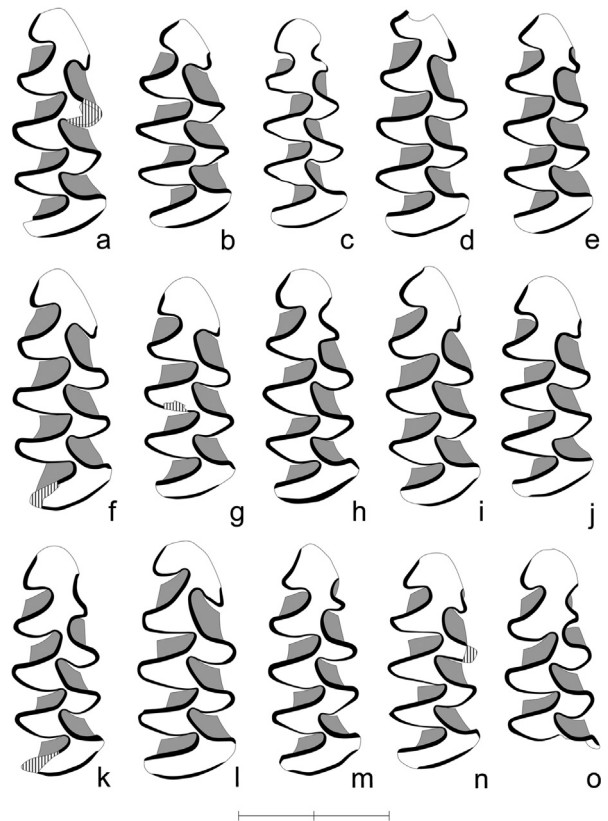


Fig. 7. Morphology of the occlusal surface of m1 of *C. nivalis* (all are represented as though they were from the right side, even if they are not). a: CBP'03 M49 L1–2 150–160 (right); b: CBP'03 M49 L1–2 150–160 (right); c: CBP'03 M49 L1–2 150–160 (left); d: CBP'05 J50 L2 160–170 (left); e: CBP'03 M49 L2 150–155 (right); f: CBP'05 M51 L1–2 190–200 (left); g: CBP'06 M50 L2 170–180 (left); h: CBP'06 L50 L2 180–190 (left); i: CBP'06 L50 L2 190–200 (left); j: CBP'06 M50 L3 190–200 (right); k: CBP'06 M50 L2 180–190 (left); l: CBP'06 M49 L4 245–255 (right); m: CBP'04 M49 L2 (left); n: CBP'06 M50 L3 190–200 (right); o: CBP'04 K50 L2 140–150 (right). Scale bar = 2 mm.

Fig. 7. Morphologie de la superficie occlusale des m1 de *C. nivalis* de la grotte de la Buena Pinta (toutes les molaires sont représentées comme si elles étaient droites, même lorsqu'elles ne le sont pas). a : CBP'03 M49 L1–2 150–160 (droite) ; b : CBP'03 M49 L1–2 150–160 (droite) ; c : CBP'03 M49 L1–2 150–160 (gauche) ; d : CBP'05 J50 L2 160–170 (gauche) ; e : CBP'03 M49 L2 150–155 (droite) ; f : CBP'05 M51 L1–2 190–200 (gauche) ; g : CBP'06 M50 L2 170–180 (gauche) ; h : CBP'06 L50 L2 180–190 (gauche) ; i : CBP'06 L50 L2 190–200 (gauche) ; j : CBP'06 M50 L3 190–200 (droite) ; k : CBP'06 M50 L2 180–190 (gauche) ; l : CBP'06 M49 L4 245–255 (droite) ; m : CBP'04 M49 L2 (gauche) ; n : CBP'06 M50 L3 190–200 (droite) ; o : CBP'04 K50 L2 140–150 (droite). L'échelle graphique mesure 2 mm.

5. Biogeographical significance of the identified rodents

During the coldest moments of the Pleistocene, ice sheets spread across the North of Europe (Ehlers and Gibbard, 2004). The expansion of steppe-tundra ecosystems towards the south and west led to important modifications in the distributions of the animals and plants that inhabited the continent. The large mammals that became displaced south and westward are together known

as the Mammuthus-Coelodonta faunal complex (Kahlke, 1999). They reached their most southerly and westerly distribution during the Late Pleistocene (Kahlke, 2014); indeed, many large species penetrated the peninsulas of the Mediterranean, including the Iberian Peninsula (Álvarez-Lao and García, 2010, 2011; García and Arsuaga, 2003) where remains of *Mammuthus primigenius*, *Coelodonta antiquitatis*, *Rangifer tarandus*, *Gulo gulo*, *Alopex lagopus*, *Ovibos moschatus* and *Saiga tatarica* have all been discovered. Some of these species, such as the woolly mammoth, reached as far as Granada in southern Spain (Aguirre et al., 1973; Álvarez-Lao et al., 2009). These large animals were accompanied in their displacement by a wide range of smaller ones, including some rodents and lagomorphs. Among them, *M. oeconomus*, *M. gregalis*, *S. betulina*, *Sp. superciliosus*, *Sp. major*, *L. timidus* and *O. pusilla* have all been recorded for the Late Pleistocene of the Iberian Peninsula (Arribas, 2004; Laplana et al., 2009; López-García et al., 2010; López-García, 2011; Rofes et al., 2012). Currently, however, they are not found there, but much further to the north and east of Europe, where the climate is colder. Most of the palaeontological sites where these have been found are in the northern third of the Peninsula, especially in the Cantabrian Mountains and Catalonia (Álvarez-Lao and García, 2011). Only a few pieces of evidence exist that suggest they reached any more southerly latitudes; the Buena Pinta Cave is one of these. The record for *M. oeconomus* at this site is one of the most southerly for the species in Europe. Indeed, it is known from only one more southerly location, the Abrigo del Monte site (Sevilla et al., 2009) some 25 km to the south of the Buena Pinta Cave, where it appears in a somewhat more modern Magdalenian setting (MIS2). A citing for *M. aff. ratticeps* (a synonym of *M. oeconomus*) from further south at the Las Yedras site in Granada (Ruiz Bustos, 1978) may be the result of an erroneous identification. An inspection of these materials revealed many to show a partial confluence of T4 and T5, which does not occur in *M. oeconomus*. The materials thus identified may in fact belong to *Microtus huescarensis* (see Figs. 8 and 9 in Plate 1 of Ruiz Bustos, 1978) and perhaps to *Microtus chalinei* (see Figs. 10 and 11 in Plate 1 of Ruiz Bustos, 1978).

The record for *M. gregalis* at the cave is the southernmost for Europe. Until now, the most southerly citations were those for Erralla (Pemán, 1985), El Mirón (Cuenca-Bescós et al., 2008), Sopena (Pinto-Llona et al., 2012) and perhaps the Laminak II (Pemán, 1994) sites, all in the Cantabrian region to the north.

The chronology of the sediments at the cave is important in understanding the biogeographical significance of *M. oeconomus* and *M. gregalis*. Levels 2–5 have been dated to an interval ranging from MIS4 to the beginning of MIS3. Although some northern European rodent species colonised the Iberian Peninsula during the beginning of the Late Pleistocene, as shown by the presence of *S. betulina* in MIS5 levels at the Lezetxiki II site (Rofes et al., 2012), most northern rodent records are for sites corresponding to MIS3 and (especially) MIS2, which includes the Last Glacial Maximum (LGM) (López-García, 2011; Sesé, 2005). Until now, the oldest records for *M. oeconomus* inhabiting the centre

of the Peninsula were from the Magdalenian (MIS2) levels of the Peña de Estebanvela site, some 30 km to the north of the Buena Pinta Cave (Sesé, 2006, 2013), and the Abrigo del Monte site, some 20 km to the south (Sevilla et al., 2009). The finding of *M. oeconomus* and *M. gregalis* remains in the Buena Pinta Cave confirms these species arrived well before MIS2.

Whereas the latter species no longer live in the Iberian Peninsula, *C. nivalis* still does, although only in mountainous regions, especially at altitudes of between 1000 and 2600 m (depending on the mountains in question) (Luque-Larena and Gosálbez, 2002). Although temperatures are usually low at this altitude, the species is not as well adapted to the cold as *M. oeconomus* or *M. gregalis* (Nappi, 2002; Pérez-Aranda Serrano, 2009). Its link with mountainous areas lies in that these produce the petricolic environments that provide the species its microhabitat. *Chionomys nivalis* lives in the spaces between rocks (normally of periglacial origin) in open areas, where the conditions of thermal stability upon which the species depend are found (Krystufek and Kovacic, 1989; Luque-Larena et al., 2002). Indeed, *C. nivalis* still lives not too far from the Buena Pinta Cave, at altitudes of over 1800 m (Pérez-Aranda Serrano, 2009). The presence of its remains at the site, which is at 1105 m, indicates that during the Late Pleistocene the conditions it requires were available at lower altitude, i.e., there must have been periglacial scree available and open spaces. For this to have been the case, the temperature must have been lower than it is today. The presence of *C. nivalis* at the cave is therefore an indication of a colder climate having reigned during the Late Pleistocene.

Along with the remains of *M. gregalis*, *M. oeconomus* and *C. nivalis*, the single remain (a jaw fragment) belonging to *O. pusilla* found in level 3 (Laplana et al., 2009) is also indicative of a colder climate during the Late Pleistocene. This lagomorph is no longer found in the Iberian Peninsula, but on the steppes of central Asia. Like *M. gregalis* and *M. oeconomus* the abundance of *O. pusilla* is under 1%. Its identification was in part due to the concerted sampling effort undertaken and the richness of the site in terms of microvertebrate remains. Less intense sampling at other Central System sites of similar age may be the reason why they have not been noticed there – which may have affected the palaeoclimatic interpretations made for these sites. Nonetheless, the small number of remains recovered does indicate a low density of individuals for these species in the area during the Late Pleistocene. The Buena Pinta Cave now marks the second most southerly known Pleistocene site for *M. oeconomus*, and the southwesternmost limit for both *M. gregalis* and *O. pusilla*, and it is well known that population density tends to decrease away from the centre of a species' distribution (Brown, 1984). For *C. nivalis*, the site does not mark its known limit of distribution; it has been cited for the Carihuela Cave in Granada, 400 km to the south (Ruiz Bustos and García Sánchez, 1977; Ruiz Bustos, 2000), in levels chronologically similar to those of the Buena Pinta Cave. This may explain why it is more common than the other cold-climate indicators, although it never surpasses an abundance of 1% in any level.

6. Conclusions

The Buena Pinta Cave provides the southernmost European record of *M. gregalis*, and one of the most southerly (along with those of the Abrigo del Monte [Sevilla et al., 2009] and Peña de Estebanvela [Sesé, 2006, 2013] sites) for *M. oeconomicus*. Thermoluminescence datings of levels 2–5, where these species were found, place them within a time interval ranging from MIS4 to the beginning of MIS3. This confirms that these species were present in the centre of the Iberian Peninsula before the LGM. Neither is currently found in the Peninsula, but farther north and east in Europe and Asia (and indeed in North America in the case of *M. oeconomicus*). They may therefore be considered indicators that the climate was cold when the site formed.

C. nivalis, which still survives in the Peninsula, is also a marker of cold conditions during the Late Pleistocene at the site; it now lives at altitudes of over 1800 m (Pérez-Aranda Serrano, 2009). Since the site is located at 1100 m, the periglacial phenomena that produce the scree among which this animal lives must have been active at this lower altitude during the Late Pleistocene. Such a cold-climate would have produced the more open environments suitable to the species.

The relative and absolute rarity of *M. oeconomicus* and *M. gregalis* at the site may be the result of their lying far from the centres of their distributions – indeed, at the southernmost edge of their ranges. This may explain why they have not been cited from sites of similar age and geographical location; they may not have been common enough for their remains to have been detected.

The presence at the cave of these three rodent species indicates that the climatic conditions of the surrounding region during the middle of the Late Pleistocene were colder than they are today. This agrees with conclusions drawn from the types of pollen found at the site (Ruiz-Zapata et al., 2008, 2012).

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