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Note on the taxonomy of the *Microtus* (*Iberomys*) (Arvicolinae, Rodentia) from the Late Pleistocene of Gruta do Caldeirão (Tomar, Portugal) and paleoclimatic interpretation of the rodent assemblage

Nota sobre la taxonomía de Microtus (Iberomys) (Arvicolinae, Rodentia) del Pleistoceno superior de la Gruta do Caldeirão (Tomar, Portugal) e interpretación paleoclimática de la asociación de roedores

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ABSTRACT

Gruta do Caldeirão is an archaeological cave site located in Tomar (Portugal, western Iberian Peninsula), which contains an important Late Pleistocene sequence from Middle Paleolithic (Mousterian) to Upper Paleolithic (Solutrean-Magdalenian), including lithic tools, human remains, and other large- and small-vertebrate remains. Our revision and interpretation of the rodent assemblage previously published in the 1990s leads to three important conclusions: 1) the only species of the subgenus *Iberomys* present in the sequence is the current endemic Iberian vole species *Microtus* (*Iberomys*) *cabrerae* (Cabrera's vole); 2) the rodent assemblage is dominated throughout by open-forest species, such as the long-tailed field mouse (*Apodemus sylvaticus*), and species associated with open-humid areas such as the Mediterranean and Lusitanian pine voles (*Microtus* (*Terricola*) spp.), with the notable presence of an extinct hamster (*Allocricetus bursae*) in layer K, and three vole species not currently found in the vicinity of the cave (*Microtus arvalis* [the common vole], *M. agrestis* [the field vole], and *Chionomys nivalis* [the European snow vole]) also in the assemblage; 3) the bioclimatic model, which is used to reconstruct climatic parameters on the basis of the rodent association, corroborates the proposal that the Solutrean occupation from layers H to Fa took place during a cold period equated to the Last Glacial Maximum (LGM), as indicated by the available radiocarbon dates and supported by the magnetic susceptibility data.

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Keywords: *Microtus* (*Iberomys*) *cabrerae*; Middle to Upper Paleolithic; Paleoclimatic reconstruction; Last Glacial Maximum; Western Iberia.

RESUMEN

Gruta do Caldeirão es un yacimiento arqueológico en cueva situado en Tomar (Portugal, oeste de la península Ibérica), que contiene una importante secuencia perteneciente al Pleistoceno superior, adscrita culturalmente al Paleolítico medio (Musteriense) y Paleolítico superior (Solutrense-Magdaleniense), que incluye industria lítica, restos humanos y restos de grandes y pequeños vertebrados. La revisión e interpretación de la asociación de roedores de la secuencia, previamente publicada en los años 90 del siglo pasado, nos ha permitido remarcar tres importantes conclusiones: 1) la única especie del subgénero *Iberomys* presente en la secuencia es la especie endémica actual de topillo *Microtus* (*Iberomys*) *cabrerae* (topillo de Cabrera); 2) la asociación de roedores está dominada en toda la secuencia por especies relacionadas con bosques abiertos, como el ratón de campo (*Apodemus sylvaticus*) y especies relacionadas con espacios abiertos-húmedos como los topillos mediterráneo y lusitánico (*Microtus* (*Terricola*) spp.), remarcando la presencia de un hámster extinto (*Allocricetus bursae*) en el nivel K y tres especies de topillos que no tienen representación actual en la zona circundante a la cavidad (*Microtus arvalis* - topillo campesino, *Microtus agrestis* – topillo agreste y *Chionomys nivalis* - topillo nival); 3) Finalmente, el método del Modelo Bioclimático, aplicado a la asociación de roedores, otorga resultados acordes con que la ocupaciones solutrenses situadas entre los niveles H y Fa están relacionadas con un periodo frío equiparado con el Último Máximo Glacial (LGM), indicado por las dataciones de radiocarbono y anteriores estudios de susceptibilidad magnética de la secuencia.

Palabras clave: *Microtus* (*Iberomys*) *cabrerae*; Paleolítico Medio-Superior; Reconstrucción paleoclimática; Último Máximo Glacial; Iberia occidental.

Introduction

Gruta do Caldeirão (39° 30’ 11” N; 8° 24’ 32” W) is an archaeological site located about 140 km northeast of Lisbon (Portugal) at an altitude of 123 m a.s.l., 8 km north of the city of Tomar (Fig. 1A). The cave opens in calcareous dolomites of the Lower Jurassic, and its entrance, which faces south, is located in the northern slope of a valley in the right bank of River Nabão. The excavations carried out by one of us (J. Zilhão) between 1979 and 1988 (Zilhão, 1992, 1997) showed a 6.2 m stratigraphic sequence divided into 15 layers, containing Late Pleistocene (Middle and Upper Paleolithic) and Early Holocene (Neolithic) archaeological material (Fig. 1B). A zooarchaeological study of the large vertebrates showed that, during the Middle Paleolithic and the early Upper Paleolithic, the cave functioned in part as a large carnivore den; hyenas were the main bone accumulator, with contributions from leopards and the bearded vulture. In the later Upper Paleolithic, the bones were mainly accumulated by humans (Davis, 2002; Davis *et al*., 2007). Human remains have been identified in the Solutrean and Magdalenian layers (Trinkaus *et al*., 2001). Regarding the climatic reconstruction, and in agreement with the radiocarbon dates (ca. 22.5 -25.5 ka cal BP; Zilhão, 1997), the magnetic susceptibility (MS) of the Gruta do Caldeirão sedimentary sequence is lowest in Solutrean layers H to Fc, indicating a cold period related to the Last Glacial Maximum (LGM) (Ellwood *et al*., 1998), which includes, according to Rasmussen *et al*. (2014), Greenland Stadials (GS) GS 2.1, GS 2.2 and GS 3.

A preliminary study of the rodent assemblage (Póvoas *et al*., 1992; Brunet-Lecomte & Póvoas, 1993) identified 11 species (Table 1): *Apodemus sylvaticus, Allocricetus bursae, Eliomys quercinus, Microtus arvalis, M. agrestis, M. (Iberomys) brecciensis, M. (Iberomys) cabrerae, M. (Terricola) lusitanicus, M. (Terricola) duodecimcostatus, Chionomys nivalis* and *Arvicola sapidus.* Environmentally, the succession was interpreted as a landscape dominated by open and dry biotopes with forested areas from layers K to Fc (indicated by the presence of *M. arvalis* and *A. bursae),* turning into a more humid and forested biotope in layers Fb and Fa (represented by a high percentage of *A. sylvaticus* and *M. (Terricola)* spp.), and ending in a drier environment in layer Eb (shown by the major presence of *M. arvalis,* the low percentage of *A. sylvaticus,* and the high proportion of *M. (T.) duodecimcostatus* in relation to *M. (T.) lusitanicus).*

Against this background, our present objectives are threefold. Our first aim is to revise the *Microtus*

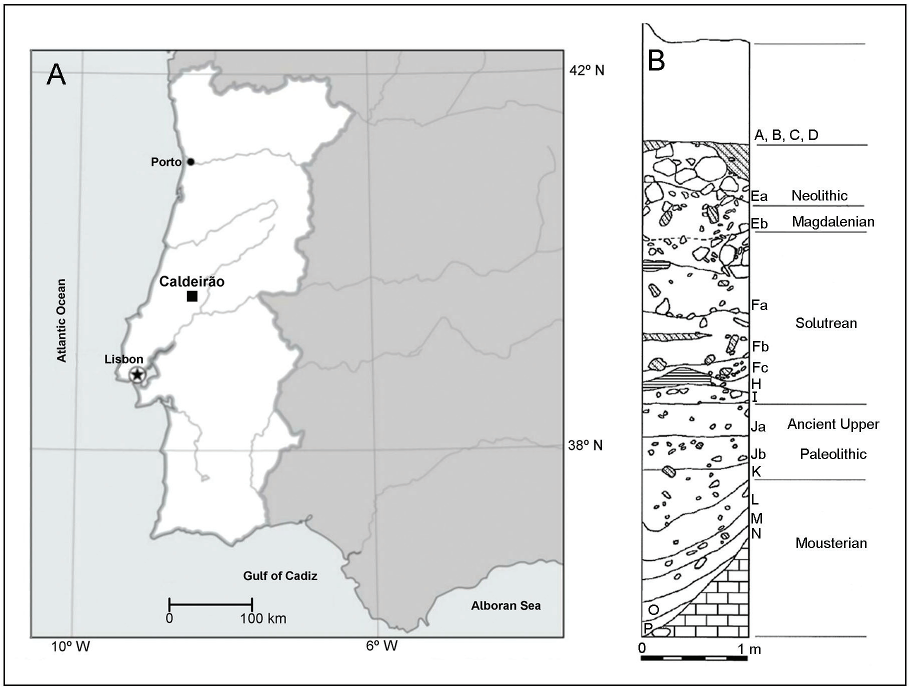

Figure 1.—A: Location of Gruta do Caldeirão (base map: National Geographic Society, modified). B: The stratigraphic sequence of the site (after Póvoas *et al*. 1992 and Ellwood *et al*. 1998, modified).

Table 1.—Minimum Number of Individuals by species and layer from Gruta do Caldeirão. Modified from Póvoas *et al*. (1992).

Species/Layers	**Eb**	**Fa**	**Fb**	**Fc**	**H**	**I**	**Ja**	**Jb**	**K**
Apodemus sylvaticus	251	56	65	9	10	15	21	19	9
Allocricetus bursae	0	0	0	0	0	0	0	0	3
Eliomys quercinus	53	13	16	3	4	6	8	2	4
Microtus arvalis-agrestis	69	11	17	3	4	2	10	13	8
Microtus (*Iberomys*) *cabrerae*	4	1	3	0	2	1	1	1	1
Chionomys nivalis	1	0	1	0	0	0	0	1	0
M. (*T.*) *duodecimcostatus-lusitanicus*	435	65	64	8	12	22	22	15	4
Arvicola sapidus	1	0	0	0	0	0	0	0	0
Total	**814**	**146**	**166**	**23**	**32**	**46**	**62**	**51**	**29**

(Iberomys) material, because current data suggest that the last occurrence of the extinct species *M. (Iberomys) brecciensis* in Iberia was at the end of Marine Isotope Stage (MIS) 6 or the beginning of MIS 5, e.g. at Maltravieso-Sala de los Huesos in Extremadura, dated to between 183–117 ka (Hanquet, 2011), or in layer I of Cova del Rinoceront in Barcelona, dated to ca. 84 ka (López-García *et al*., 2016). Our second aim is to reinterpret the assemblage, focusing on extinct taxa such as *Allocricetus bursae* and on species not currently found in the area, such as *Microtus arvalis, Microtus agrestis and Chionomys nivalis,* using the current distribution and habitat preference of these species (e.g. Paupério *et al*., 2017) as well as their first and last appearance data in Iberia (in the case of *A. bursae)*. Our third aim is to apply the bioclimatic model (in accordance with Hernández-Fernández, 2001a, 2001b) in order to infer various climatic parameters and compare the Gruta do Caldeirão rodent assemblage with the climatic signals obtained by studying the magnetic susceptibility of the sequence (Ellwood *et al*., 1998),

the current climatic parameters for the surrounding area, and the general dynamics of sea surface temperatures (SST) and pollen data from sea cores in the western Iberian margin (Naughton *et al*., 2007; Salgueiro *et al*., 2014; Turon *et al*., 2003).

Material and Methods

Taxonomy

From the revised material, a total of 23 first lower molars (m1) have been identified as *Iberomys*. Although in Cuenca-Bescós *et al*. (2014) we proposed, based on their morphological differences with other microtines species, to consider *Iberomys* as a genus, according to the last phylogenetic studies *Iberomys* species are a sister group to *Microtus agrestis*, ruling out that *Iberomys* be elevated to genus status (Barbosa *et al*. 2018). The nomenclature used in the description of this subgenus (only the first lower molars are considered) is that of Van der Meulen (1973) and Martin (1987) (Fig. 2). Length (L), width (W) and parameter a (Fig. 2) are those proposed by Van der Meulen (1973), and parameters Li and La (Fig. 2) are those proposed by Cuenca-Bescós *et al*. (1995). A/L is the ratio between parameter a and length, and La/Li is the ratio between parameters La and Li. The measurements were compared with the fossil populations of *M.* (*Iberomys*) *brecciensis* from Gruta da Aroeira (López-García *et al*., 2018) and *M.* (*Iberomys*) *cabrerae* from Gruta da Oliveira (unpublished material), both located in the Almonda karst system, some 25 km SW of Gruta do Caldeirão. Also, the measurements were compared with other Iberian fossil populations of *M.* (*I.*) *brecciensis* from Galeria, TD10 and TE18-19 (Cuenca-Bescós *et al*. 1999; López-García *et al*. 2008; 2011c; 2015) and *M.* (*I.*) *cabrerae* from Abric Romaní, Cova del Gegant and Gorham's cave (López-García *et al*. 2008; 2011; 2015).

Paleoclimatic reconstruction

The taxonomic composition of the rodent assemblage allows us to evaluate the paleoclimatic conditions prevalent in the area around Gruta do Caldeirão. We used the bioclimatic model developed by Hernández-Fernández (2001a, 2001b), which is based on the hypothesis that a significant correlation exists between climate and mammal communities (see also Hernández-Fernández & Peláez-Campomanes, 2005; Hernández- Fernández *et al*., 2007). According to this model, mammal

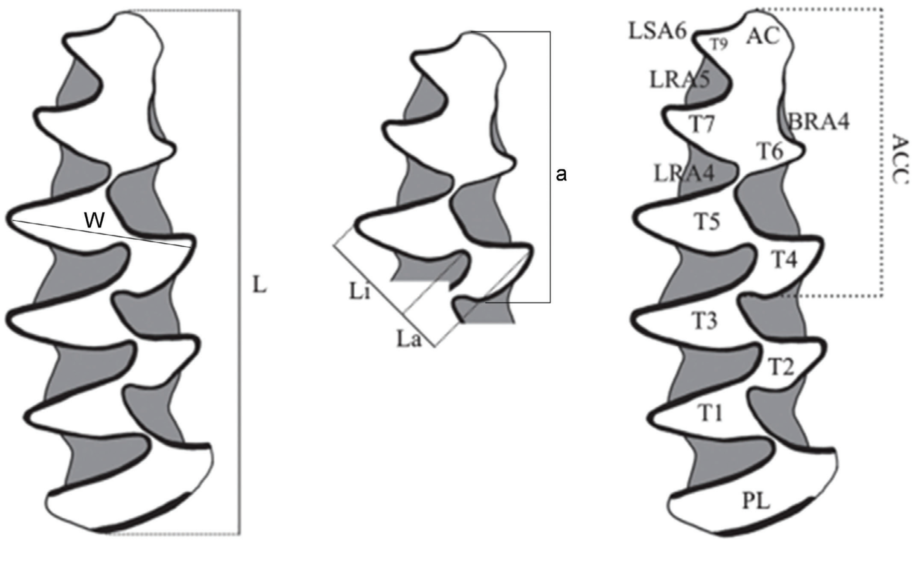

Figure 2.—Nomenclature and measurement methods used for the description of the m1 of arvicolines. Abbreviations: a: length of anteroconid complex; L: total length; La: width of T4; Li: width of T5; W: width; ACC: anteroconid complex; AC: anterior cap; BRA: buccal re-entrant angle; LRA: lingual re-entrant angle; T4-T9: triangles 4–9 (after Luzi & López-García 2019, modified).

assemblages can be assigned to ten climate types, five of which are represented in the Gruta do Caldeirão rodent assemblage. On the basis of these, a climatic restriction index can be calculated (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 appear) (Table 2). 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. The bioclimatic component (BC; representation of each of these five climate types per stratigraphic unit) is also calculated, using the following formula: BCi = (∑CRIi) × 100 / S), where S is the number of species per unit at Gruta do Caldeirão (Table 2). From the BC, a multiple linear regression mathematical model (Hernández-Fernández & Peláez-Campomanes, 2005) allows various climatic parameters to be estimated (Table 3): mean annual temperature (MAT), mean temperature of the coldest month (MTC), mean temperature of the warmest month (MTW) and mean annual precipitation (MAP). These parameters are compared with the present-day data (from over a period of 30 years) from the meteorological station of Tomar (39° 36′ N, 8° 25′ E), situated at an altitude of 54 m a.s.l. The figures for Tomar are as follows: MAT = 16.4 °C, MTC = 10.5 °C, MTW = 22.9 °C and MAP = 773 mm (Climate-Data.org).

Taxonomy

Family Cricetidae Fischer, 1817
Subfamily Arvicolinae Gray, 1821
Genus ***Microtus*** Schrank, 1798
Subgenus ***Iberomys*** Chaline, 1972
Microtus (***Iberomys***) ***cabrerae*** Thomas, 1906
(Fig. 3: 1–15)

Table 2.—Distribution of the rodent species identified at Gruta do Caldeirão according to their climate preferences, in accordance with Hernández-Fernández (2001b) and Hernández-Fernández *et al*. (2007). IV Subtropical with winter rains and summer droughts; VI Typical temperate; VII Arid-temperate; VIII Cold-temperate (boreal); IX Polar.

	IV	VI	VII	VIII	IX
Apodemus sylvaticus	0.5	0.5			
Allocricetus bursae	0.333	0.333	0.333		
Eliomys quercinus	0.5	0.5			
Microtus arvalis		1			
Microtus agrestis		0.5		0.5	
Microtus (Iberomys) cabrerae	1				
Chionomys nivalis	0.25	0.25		0.25	0.25
Microtus (Terricola) lusitanicus	1				
Microtus (*Terricola*) *duodecimcostatus*	1				
Arvicola sapidus	0.5	0.5			

Table 3.—Multiple linear regressions for each studied climatic factor as a function of the bioclimatic components in the Gruta do Caldeirão rodent fauna. b: intercept; aIV-aIX slopes of the different bioclimatic components; r^2: coefficient of determination; SE: standard error of the estimate. Modified from Hernández-Fernández (2001b) and Hernández-Fernández & Peláez-Campomanes (2005).

Climatic Parameters	b	aIV	aVI	aVII	aVIII	aIX	r^2	SE
MAT in °C	26.686	-0.074	-0.135	-0.217	-0.404	-0.386	0.93	3.637
MTW in °C	26.219	0.031	-0.113	-0.037	-0.121	-0.287	0.746	4.754
MTC in °C	27.538	-0.175	-0.141	-0.418	-0.710	-0.465	0.932	5.081
MAP in mm	2978.195	-32.648	-5.076	-28.400	-33.109	-25.980	0.746	470.615

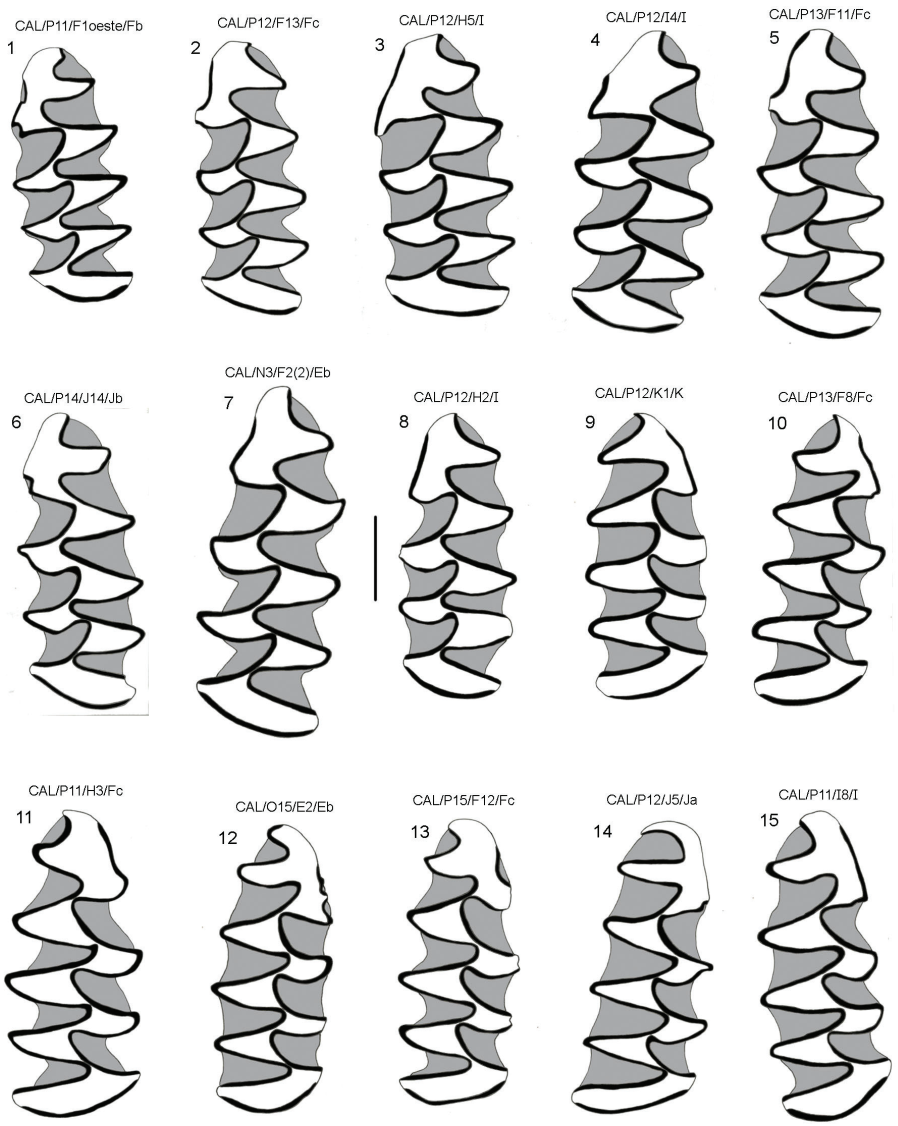

Figure 3.—First lower molars (m1) of *Microtus* (*Iberomys*) *cabrerae* from Gruta do Caldeirão. 1-7: left m1; 8-15: right m1. All teeth are in occlusal view. Scale 1 mm.

Material: nine left lower m1 (CAL/P11/F11oeste/Fb, CAL/P12/F13/Fc, CAL/P12/H5/I, CAL/P12/H2/I, CAL/P12/I4/I, CAL/P12/K1/K, CAL/P13/F11/Fc, CAL/P14/J5/Jb and CAL/N13/E2(2)/Eb), and 14 right lower m1 (CAL/P11/H3/Fc, CAL/P11/I8/I, CAL/P11/K2/K, CAL/P12/F15/Fc(1), CAL/P12/F15/Fc(2), CAL/P12/K1/K, CAL/P12/J5/Ja(1), CAL/P12/J5/Ja(2), CAL/P13/F8/Fc, CAL/P13/F10/Fc, CAL/O15/E2/Eb, CAL/L15/E1(1)/Eb, CAL/L15/E1(2)/Eb and CAL/N13/E2(2)/Eb).

Description: In terms of the description by Chaline (1972), modified by Ayarzagüena & López-Martínez (1976) and Cuenca-Bescós *et al*. (2014), the first lower molars (m1) recovered from Gruta do Caldeirão are characterized by clear labio-lingual asymmetry, more pronounced than in other microtines; on the labial side of the m1 there are only three re-entrants filled with cement; in some specimens there is a fourth, greatly reduced re-entrant (BRA4), allowing these specimens to be distinguished from other species of the genus *Microtus* and subgenus *Terricola*. Moreover, except for three juveniles (CAL/P11/K2/K, CAL/P12/F15/Fc(2) and CAL/P12/K1/K), all the identified teeth are large and feature the following: very marked labio-lingual asymmetry (mainly observed between triangles T4 and T5); a labial re-entrant angle 5 (LRA5); a scarcely to very pronounced angle between triangle T7 and the anterior cusp (AC); and a non-visible to well-developed double angle in triangle T6. The specimens from Caldeirão differs from *M.* (*I.*) *brecciensis* because in this fossil species the m1 are smaller and less asymmetrical than in *M.* (*I.*) *cabrerae*, and in general the LRA5 and the double angle of triangle T6 are nonexistent or variably developed. All these features lead us to ascribe our material morphologically to the species *M.* (*I.*) *cabrerae*. This conclusion can be metrically corroborated by drawing a comparison between 17 measurable m1 (Table 4; excluding the juvenile or fragmented teeth CAL/P12/J5/Ja(2) and CAL/L15/E1(2)/Eb) and the extinct *M.* (*I.*) *brecciensis* from the Middle Pleistocene sites of Gruta da Aroeira (Torres Novas, Portugal) (López-García *et al*., 2018), Galeria, TD10 and TE 18–19 (all three from Sierra de Atapuerca, Burgos, Spain) (Cuenca-Bescós *et al*. 1999; López-García *et al*. 2008; 2011c; 2015) and the *M.* (*I.*) *cabrerae* from the Late Pleistocene sites of Gruta da Oliveira (Torres Novas, Portugal) (unpublished material), A. Romaní (Capellades, Barcelona, Spain), C. Gegant (Sitges, Barcelona, Spain) and Gorham's cave (Gibraltar, UK) (López-García *et al*. 2008; 2011c; 2015) (Table 5; 6; Fig. 4).

Table 4.—Measurements and indices of the m1 of *Microtus* (*Iberomys*) *cabrerae* from Gruta do Caldeirão. Linear data (L, W, a,Li, La) are in mm. Abbreviations: n, number of m1 measured; 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.

	n	mean	max	min	SD
L	17	3.49	3.98	3.05	0.23
W	17	1.36	1.54	1.22	0.10
Li	17	0.95	1.11	0.84	0.08
La	17	0.41	0.51	0.30	0.06
a	17	1.92	2.15	1.72	0.12
A/L	17	55.00	57.01	53.29	1.12
La/Li	17	42.90	51.32	30.27	6.47

Remarks: M. (*I.*) *cabrerae* (Cabrera's vole) is currently endemic to the Iberian Peninsula, where it is widely distributed, with well-documented populations in the foothills of the Pyrenees, the southern Iberian System, the Baetic Sierras and the Central System, also extending the length of Portugal from SW to NE in a limited and patchy manner (Palomo *et al*., 2007; Paupério *et al*., 2017) (Fig. 5). It exclusively inhabits areas with a Mediterranean climate, a high water table, and all-year-round herbaceous cover (Pita *et al*., 2017). At present, the first appearance datum of *M.* (*I.*) *cabrerae* in the Iberian Peninsula occurs in the Marine Isotope Stage 5 (MIS 5) sites of Cueva de las Pinturas (Sesé & Ruiz-Bustós, 1992), Cova Bolomor (Guillem-Calatayud. 1995, 2001), Cueva del Camino (Laplana *et al*., 2013), Preresa (Sesé *et al*. 2011), Figueira Brava (Jeannet, 2000; Zilhão *et al*., 2020), and Gruta da Oliveira (unpublished material) (Fig. 5). During MIS 3 and MIS 2 *M.* (*I.*) *cabrerae* is represented outside its current range (Fig. 5), e.g. at Gorham's cave (López-García *et al*., 2011a), Boquete de Zafarraya (Barroso Ruiz *et al*., 2006), El Portalón (López-García *et al*. 2010a), Cueva de la Zarzamora (Sala *et al*. 2011), Cueva de los Moros de Gabasa (Gil & Lanchares, 1988), Cueva de Aguilón-P7 (Cuenca-Bescós *et al*., 2010a), Cova dels Xaragalls (López-García *et al*., 2012a), Cova de Teixoneres (López-García *et al*., 2012b), Cova del Toll (Fernández-García & López-García, 2013),

Table 5.—Measurements of Length (L) of the different Iberian sites with presence of *M.* (*I.*) *brecciensis* (Aroeira, Galeria, TD10 and TE18-19) and *M.* (*I.*) *cabrerae* (Romaní, Gegant and Gorham's) including Gruta do Caldeirão. Abbreviations: n, number of m1 measured; 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.

	n	mean	max	min	SD
Aroeira	7	2,78	2,90	2,43	0,16
Galeria	10	2,97	3,47	2,42	0,29
TD10	28	2,88	3,20	2,57	0,16
TE18-19	12	2,91	3,04	2,64	0,12
Oliveira	84	3,22	3,85	2,60	0,24
Romaní	25	3,35	3,72	3,00	0,19
Gegant	7	3,31	3,45	3,05	0,15
Gorham's	5	3,40	3,64	3,16	0,18
Caldeirão	17	3,49	3,98	3,05	0,23

Table 6.—Measurements of Length (L) and Width (W) used for the comparison of Middle Pleistocene *M. (I.) brecciensis* from Gruta da Aroeira (ARO) and Late Pleistocene *M. (I.) cabrerae* from Gruta do Caldeirão (CAL).

	L	W
ARO_Xc_1	2.82	0.896
ARO_Xc_2	2.76	1.165
ARO_Xc_3	2.88	0.963
ARO_Xc_4	2.43	1.025
ARO_Xc_5	2.88	0.934
ARO_Xc_6	2.9	0.947
ARO_Xc_7	2.82	0.949
CAL_P11_F11oeste_Fb_1	3.054	1.261
CAL_P11_H3_Fc_2	3.837	1.532
CAL_P11_I8_I_3	3.801	1.291
CAL_P12_F13_Fc_4	3.396	1.264
CAL_P12_F15_Fc_5	3.406	1.334
CAL_P12_H5_I_6	3.429	1.495
CAL_P12_H2_I_7	3.482	1.381
CAL_P12_I4_I_8	3.561	1.491
CAL_P12_K1_K_9	3.47	1.405
CAL_P12_J5_Ja_10	3.62	1.388
CAL_P13_F8_Fc_11	3.393	1.267
CAL_P13_F10_Fc_12	3.462	1.319
CAL_P13_F11_Fc_13	3.544	1.344
CAL_P14_J5_Jb_14	3.482	1.298
CAL_O15_E2_Eb_15	3.247	1.224
CAL_L15_E1(1)_Eb_16	3.222	1.294
CAL_N3_E2 (2)_Eb_17	3.981	1.537

Abric Romaní (Fernández-García *et al*., 2018), Cova del Gegant (López-García *et al*., 2012b), Cova de Valdavara-1 (López-García *et al*., 2011b), El Salt (Fagoaga *et al*., 2018) and Cova Colomera (López-García *et al*., 2010b)

The Gruta do Caldeirão rodent assemblage

According to Póvoas *et al*. (1992), the long-tailed field mouse (*Apodemus sylvaticus*) represents more than 30% of the individuals in all the layers of the Gruta do Caldeirão sequence. The relative abundance of *A. sylvaticus* indicates that the landscape surrounding the cave featured good shrub cover and forest margins (Paupério *et al*., 2017). Moreover, the pine vole species *M.* (*T.*) *duodecimcostatus* and *M.* (*T.*) *lusitanicus* represent more than 30% of the individuals in all the layers, except K (13.8 %) and Jb (29.4 %). The relative abundance of these species indicates open landscapes and humid environmental conditions (Paupério *et al*., 2017). Worthy of note is also the presence of the extinct hamster *Allocricetus bursae* and of three vole taxa currently absent in the area: the European snow vole (*Chionomys nivalis*), the common vole (*Microtus arvalis*), and the field vole (*Microtus agrestis*).

Allocricetus bursae has been found only in layer K (Póvoas *et al*., 1992; initially assigned to the Mousterian, this unit has since been recognized as belonging in fact to an undiagnostic early Upper Paleolithic). The biotope preferences of this extinct hamster can be inferred from the present-day species that is phylogenetically closest to it, *Cricetulus migratorius* (the grey hamster). The latter's present range extends from eastern Europe through Russia and central Asia to Mongolia and western China, where it inhabits dry grasslands, steppes and semi-deserts; arid areas with relatively sparse vegetation are preferred, and forests and damp habitats avoided (Kryštufek *et al*., 2016). The fossil record of *A. bursae* in the Iberian Peninsula goes back to the early Middle Pleistocene of Gran Dolina (Cuenca-Bescós *et al*. 2010b), with an age around 600 ka, and it is relatively abundant during the Middle Pleistocene and Late Pleistocene in central-south and eastern Iberia. At present, the most recent occurrence of the species is in the Late Pleistocene site of Cueva Ambrosio, with an age between 17.9–16.5 ka BP (Sesé & Soto, 1988).

Chionomys nivalis is found in layers Jb (early Upper Paleolithic), Fb (Solutrean) and Eb (Magdalenian) (Póvoas *et al*., 1992). It is a species mainly linked to the presence of stony soils with open meadows and herbaceous vegetation in mountainous regions above 1000 m (Paupério *et al*., 2017). In Portugal, it is currently only found in the northeastern Serra de Montesinho, at altitudes above 1340 m (Paupério *et al*., 2017). *C. nivalis* appears in the Iberian Peninsula during the Late Pleistocene (Sesé, 1994; Sesé & Sevilla. 1996), where it is well represented everywhere but the Levant (López-García, 2011).

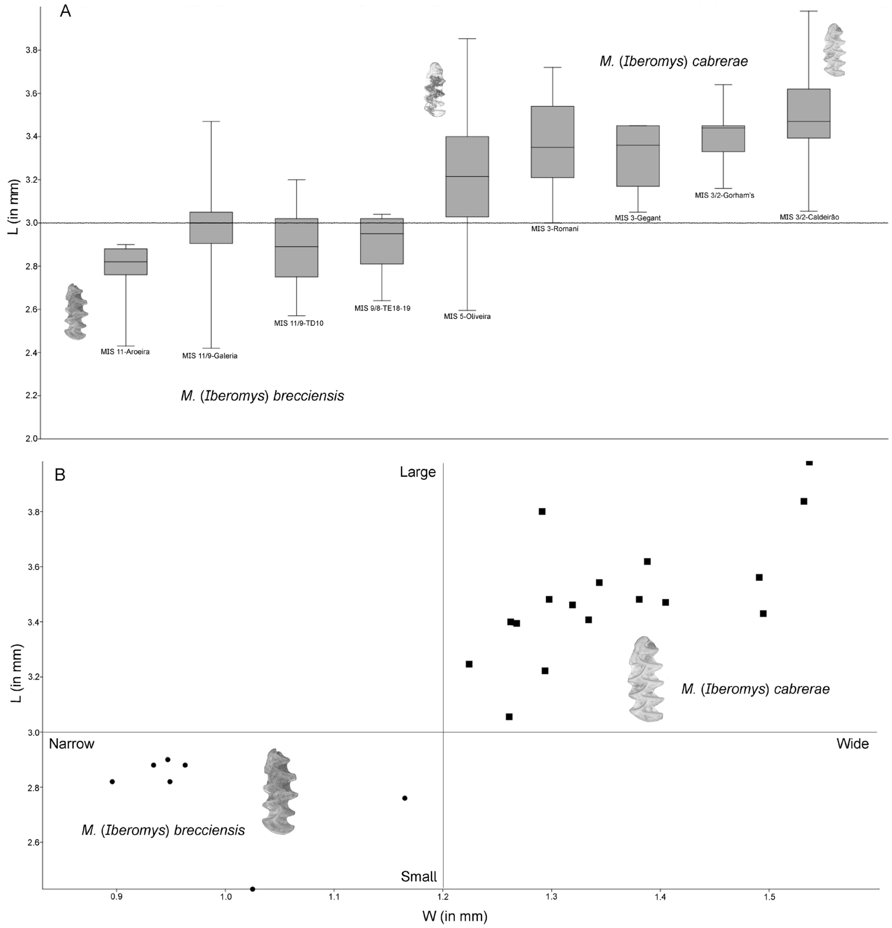

Figure 4.—A: Box plot comparing length (L) of the first lower molars (m1) of *M.* (*Iberomys*) ***brecciensis*** from the Middle Pleistocene sites of Gruta da Aroeira (López-García ***et al***. 2018), Galeria, TD10 and TE18-19 (Cuenca-Bescós ***et al***. 1999; López-García ***et al***. 2008; 2011c; 2015), ***M.*** (***Iberomys***) ***cabrerae*** from the Late Pleistocene sites of Gruta da Oliveira (unpublished data), A. Romaní, C. Gegant and Gorham's cave (López-García ***et al***. 2008; 2011c; 2015) and the identified material from Gruta do Caldeirão. The horizontal lines inside the boxes indicates de median. The boxes limits indicate the 25-75 % quartiles; B: length to width comparison of the Middle Pleistocene *M.* (*Iberomys*) ***brecciensis*** from Gruta da Aroeira with the identified *M.* (*Iberomys*) ***cabrerae*** from Gruta do Caldeirão.

Microtus arvalis and *Microtus agrestis* are represented in all layers (Póvoas *et al*., 1992). Both taxa inhabit grassland, but *M. arvalis* prefers open dry terrain with discontinuous herbaceous cover and *M. agrestis* prefers damp areas such as marshes, peatbogs and river banks (Paupério *et al*., 2017). In Portugal, *M. arvalis* is currently only present in the extreme northeast, and *M. agrestis* lives exclusively in the north and north-central area (Paupério *et al*., 2017). Both species are also identified (Moreno-García & Pimenta, 2002) in Portugal outside its nowadays distribution in layers TP06 and TP09 of the Lagar Velho rockshelter (Lapedo valley, Leiria) with an age between 24–27 ka cal BP (Zilhão & Almeida, 2002). The first occurrence of these species in the Iberian Peninsula is in the Middle Pleistocene sites of Sierra de Atapuerca (ca. 400 ka) (Luzi & López-García, 2019; Luzi, 2018); both are well represented all over Iberia throughout the Late Pleistocene (López-García, 2011).

Paleoclimatic reconstruction

By comparison with current data (Table 7), the bioclimatic model characterizes the climate of the area around Gruta do Caldeirão as colder

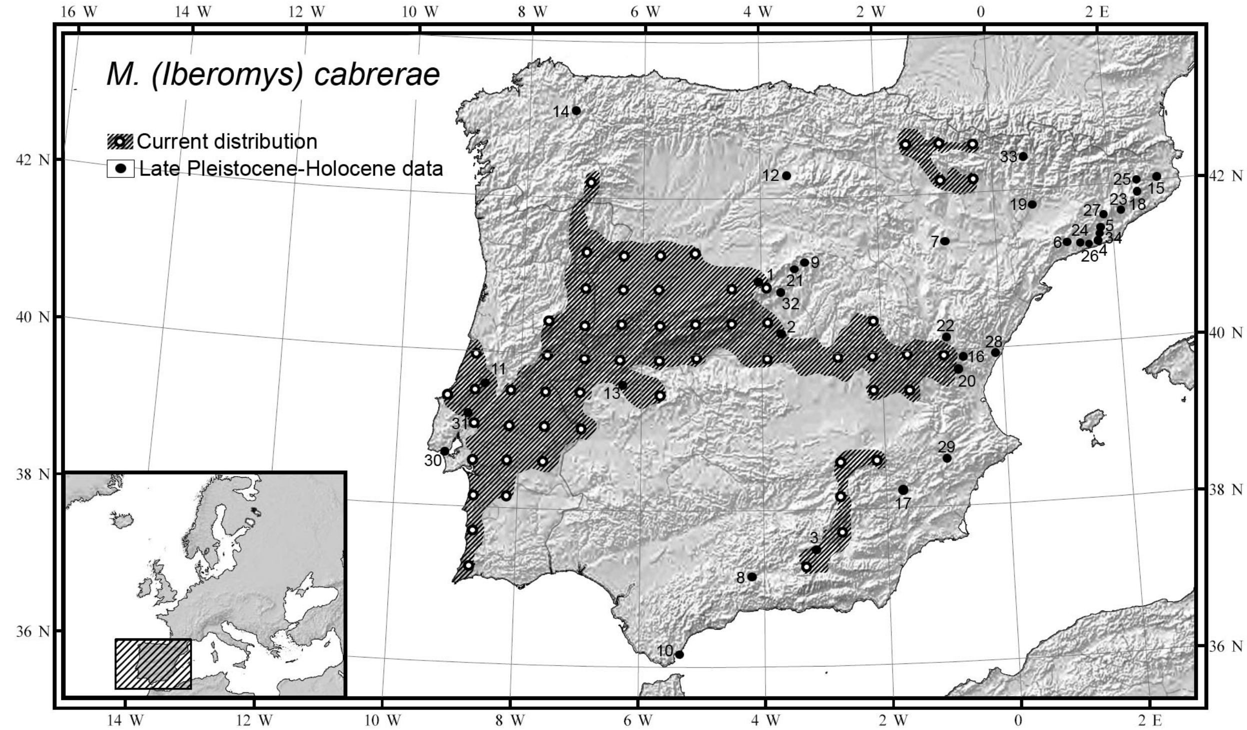

Figure 5.—Current and Late Pleistocene-Early Holocene distribution of *Microtus* (*Iberomys*) *cabrerae* in the Iberian Peninsula (modified and updated from López-García and Cuenca-Bescós 2012, using Laplana and Sevilla 2013, Bañuls-Cardona 2017, and Fagoaga *et al*. 2018). 1. Camino; 2. HAT and Preresa; 3. C. Horá; 4. C. Gegant; 5. A. Romaní; 6. Xaragalls; 7. Aguilón; 8. Zafarraya; 9. Zarzamora; 10. Gorham's; 11. Caldeirao; 12. El Portalón; 13. Chimeneas; 14.Valdavara-1; 15. l'Arbreda; 16. Cendres; 17. Baños de Mula; 18. Cingle Vermell; 19. C. Colomera; 20. La Sarsa; 21. La Ventana; 22. Bolumini; 23. El Frare; 24. Cova Foradada; 25. Cova 120; 26. Alorda Park; 27. Coves del Toll (Teixoneres and Toll caves) and Balma del Gai; 28. C. Bolomor; 29. El Salt; 30. Figueira Brava; 31. Oliveira; 32. C. de las Pinturas; 33. Gabasa; 34. C. Bonica.

Table 7.—Difference (Δ) between the values obtained by analyzing the rodent assemblage from each stratigraphic unit of Gruta do Caldeirão and the present-day values of the same parameters. ΔMAT, difference in mean annual temperature (ºC); ΔMTW, difference in mean temperature of warmest month (ºC); ΔMTC, difference in mean temperature of coldest month (ºC); ΔMAP, difference in mean annual precipitation (mm).

	ΔMAT	ΔMTW	ΔMTC	ΔMAP
Eb	-2.93	-0.93	-4.50	-49.27
Fa	-1.65	0.19	-3.07	-78.18
Fb	-3.28	-0.95	-5.22	-95.30
Fc	-2.41	-0.85	-3.50	85.39
H	-1.65	0.19	-3.07	-78.18
I	-1.65	0.19	-3.07	-78.18
Ja	-1.65	0.19	-3.07	-78.18
Jb	-3.28	-0.95	-5.22	-95.30
K	-1.93	0.09	-3.61	-68.00

(ΔMAT = -3.3 °C to -1.6 °C) and relatively drier (ΔMAP = -95 mm to -49 mm) with the exception of layer Fc, where the precipitation would have been higher than nowadays (ΔMAP_{Fc} = +85 mm). Summers were similar to the present (ΔMTW = -0.9 °C to +0.2 °C), but winters were colder (ΔMTC = -5.2 °C and -3.0 °C). The study of the magnetic susceptibility of the sequence (Ellwood *et al*. 1998) also concluded that layers H to Fb corresponded to the coldest period of the sequence, in agreement with their radiocarbon dating to the Last Glacial Maximum (LGM).

The magnetic susceptibility and the MAT and MAP data derived from the rodent assemblage thus concur that the LGM in the area was characterized by relatively low temperatures and high precipitation (Fig. 6). This inference is consistent with the presence of species that according to López-García *et al*.

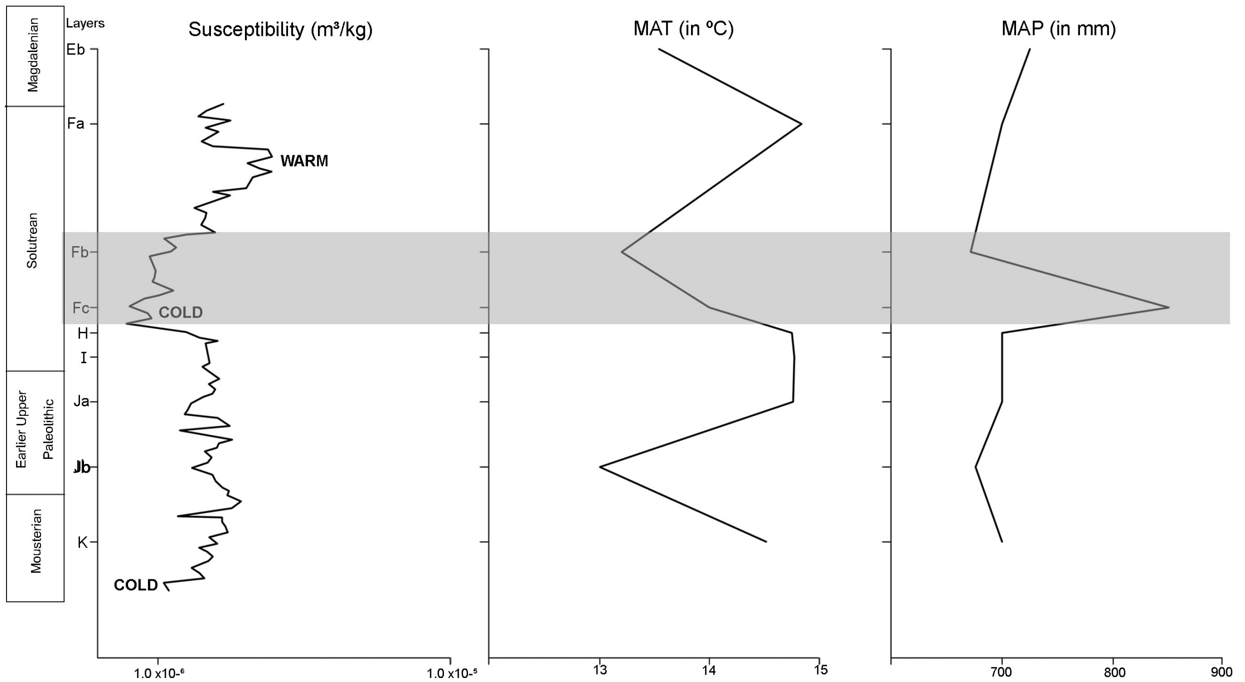

Figure 6.—Comparison of the magnetic susceptibility data for the Gruta do Caldeirão sequence (after Ellwood *et al*. 1998, modified) with the mean annual temperature (MAT) and mean annual precipitation (MAP) derived from the rodent assemblages using the bioclimatic model.

(2010b) have mid-European requirements (e.g. the *C. nivalis* found in level Fb), as well as with the absence in layer Fc of species that have strict Mediterranean requirements (i.e. *M*. (*I*). *cabrerae*); it is also consistent with the suggestion made by Póvoas *et al*. (1992) to the effect that more humid conditions prevailed during the deposition of layers Fa and Fb.

These data coincide with the SST data from the western Iberian margin, which show differences between 1.5 °C and 4 °C for the LGM in relation to present-day temperatures (Salgueiro *et al*., 2014). Also, the LGM was characterized in western Iberia by a predominantly herbaceous environment, with *Pinus* starting to expand and an almost continuous presence of deciduous tree pollen (Naughton *et al*., 2007). In addition, the slight expansion of ericaceous communities detected in western Iberia suggests an increase in humidity near the continent at that time (Turon *et al*., 2003).

All lines of evidence therefore concur in contrasting the paleoclimatic conditions prevalent throughout the accumulation of the Pleistocene Gruta do Caldeirão sequence with those at present. Indeed, the area around Tomar nowadays falls within the temperate Mediterranean zone with warm summers (CSa) of the Köppen-Geiger classification (Beck *et al*., 2018).

Conclusions

Our revision of the rodent assemblage from Gruta do Caldeirão thus leads us to draw the following conclusions:

1. The extinct vole species *Microtus* (*Iberomys*) *brecciensis* is not present. The material previously ascribed to this subgenus can be ascribed in its entirety to the extant vole species *Microtus* (*Iberomys*) *cabrerae*.
2. The extinct hamster *Allocricetus bursae* is present in layer K, and three vole species (*Chionomys nivalis*, *Microtus arvalis* and *Microtus agrestis*) that are not currently found in the area also occur in the sequence.
3. The bioclimatic model agrees with the magnetic susceptibility data in suggesting colder and more humid conditions for the regional LGM climate, in agreement with the SST and pollen data for the western Iberian margin.

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