C. R. Palevol 11 (2012) 31–40

Contents lists available at SciVerse ScienceDirect

Comptes Rendus Palevol

www.sciencedirect.com

General palaeontology, systematics and evolution (Vertebrate palaeontology)

Climate and landscape during the Last Glacial Maximum in southwestern Iberia: The small-vertebrate association from the Sala de las Chimeneas, Maltravieso, Extremadura

Climat et paysage durant le Dernier Maximum Glaciaire dans le Sud-Ouest de l'Ibérie: l'association des petits vertébrés de la Sala de las Chimeneas, Maltravieso, Estrémadure

Sandra Bañuls Cardona [a,*,b], Juan Manuel López-García [a,b], Hugues-Alexandre Blain [a,b], Antoni Canals Salomó [a,b,c]

[a] *IPHES, Institut Català de Paleoecologia Humana i Evolució Social, C/Escorxador s/n, 43003 Tarragona, Spain*
[b] *Area de Prehistoria, Universitat Rovira i Virgili (URV), Avinguda de Catalunya 35, 43002 Tarragona, Spain*
[c] *Equipo "Primeros Pobladores de Extremadura", Casa de la Cultura Rodríguez Moñino. Avda. Cervantes s/n. 10003, Cáceres, Spain*

ARTICLE INFO

Article history:
Received 18 March 2011
Accepted after revision 11 October 2011
Available online 13 December 2011

Presented by Philippe Taquet

Keywords:
Small mammals
Herpetofauna
Palaeoenvironment
Palaeoclimate
LGM
Late Pleistocene
Spain

ABSTRACT

Here we present the first palaeoenvironmental and palaeoclimatic analysis based on a study of the microvertebates of the Sala de las Chimeneas (Maltravieso Cave, Cáceres). The fauna is ascribed to the end of the Late Pleistocene, as indicated by the presence of *Microtus* (*Iberomys*) *cabrerae*, *Microtus agrestis* and *Arvicola terrestris* and by absolute datings of ~ 17 ka BP. The palaeoenvironmental analysis points to a setting within the early part of the Last Glacial Maximum (LGM), with a habitat dominated by woods and humid meadows, a climate (mean annual temperatures) colder than at present (−4 °C), and mean annual precipitation markedly higher (+700 mm) than is currently the case in the area around Cáceres. These data provide new information on the impact of the last cold spells of Marine Isotope Stage 2 (MIS 2) in the Southwest of Europe, in a region where no studies of the microvertebrates of this period had previously been undertaken.

© 2011 Académie des sciences. Published by Elsevier Masson SAS. All rights reserved.

Mots clés :
Micro-mammifères
Herpétofaune
Paléoenvironnement
Paléoclimat
LGM
Pléistocène supérieur
Espagne

RÉSUMÉ

Nous présentons ici la première analyse paléoenvironnementale et paléoclimatique à partir de l'étude des petits vertébrés de la Sala de las Chimeneas (Cueva de Maltravieso, Cáceres). La faune est rapportée au Pléistocène supérieur final, comme l'indiquent la présence de *Microtus* (*Iberomys*) *cabrerae*, *Microtus agrestis* et *Arvicola terrestris,* ainsi que les datations absolues (~ 17 Ka BP). La reconstruction paléoenvironnementale intéresse le début du LGM (Dernier Maximum Glaciaire), avec un paysage dominé par des forêts et des prairies humides, un climat (températures moyennes annuelles) plus froid (−4 °C) et des précipitations moyennes annuelles beaucoup plus importantes (+700 mm) qu'actuellement dans

* Corresponding author.
E-mail addresses: sanbac82@hotmail.com (S. Bañuls Cardona), jmlopez@iphes.cat (J.M. López-García), hablain@iphes.cat (H.-A. Blain), acanals@iphes.cat (A. Canals Salomó).

1631-0683/$ – see front matter © 2011 Académie des sciences. Published by Elsevier Masson SAS. All rights reserved.
doi:10.1016/j.crpv.2011.10.001

la région de Caceres. Ces données apportent une information inédite sur l'impact des dernières pulsations froides du Stade Isotopique Marin 2 (MIS 2), dans le Sud-Ouest de l'Europe, dans une région où, jusqu'à présent, aucune étude sur les petits vertébrés de cette époque n'avait été réalisée.

© 2011 Académie des sciences. Publié par Elsevier Masson SAS. Tous droits réservés.

1. Introduction

Maltravieso Cave is located in a peri-urban area to the south of the city of Cáceres (Extremadura, Spain). Its UTM coordinates are: timezone 29S, *x*: 0726342, *y*: 4371039 (Fig. 1A). The cave forms part of the Palaeozoic limestone karst that developed in the Early Carboniferous (Gutiérrez Elorza, 1994). The excavation of the cave was begun in 2001 by the team "Primeros Pobladores de Extremadura" (*First Settlers in Extremadura*), headed by Eudald Carbonell and Antoni Canals. This 77 metre-long cave includes our study area, La Sala de las Chimeneas, with a perimeter of 17 metres (Fig. 1B); the archaeological material recovered from the excavation stems from the sedimentary package known as Level A (Fig. 1C), which has a depth of just 20 cm (Canals et al., 2010; Mancha, 2007). This record consists mainly of lithic industry and fauna (Canals et al., 2010; Rodríguez-Hidalgo, 2008; Rodríguez-Hidalgo et al., 2011; Rodríguez et al., 2009), although remains of perforated marine malacofauna and an engraved bone have also been recovered (Rodríguez-Hidalgo et al., 2010), representing the first portable elements of material culture associated clearly with the Upper Palaeolithic of the region of Extremadura. Other cultural artifacts include various panels of parietal art with a variety of motifs, which date to between 33 and 15 ka BP (Ripoll Perelló et al., 1999). Radiocarbon dates (^{14}C AMS) were obtained on the basis of two pieces of charcoal from *Pinus*, providing an absolute chronology of between 19500 to 18700 cal. BP and 19700 to 18750 cal. BP (Fig. 1C), which corresponds chronoculturally with the end of the Solutrean and the beginnings of the Early Magdalenian (Canals et al., 2010).

2. Material and methods

2.1. Palaeontological study

The palaeontological material analysed in this study comes from the excavation carried out during the 2006 campaign at La Sala de las Chimeneas. In order to obtain the small-vertebrate remains, a system of water screening was used with sieves of decreasing mesh size (1 cm, 0.5 cm and 0.05 cm). Once the microfossils were separated from the now dry sediment, we proceeded to identify each species. This was based on both cranial and post-cranial diagnostic elements from the small-vertebrate skeletons. For Bufonidae, the humerus, ilium, scapula and sacrum were used; for Ranidae, the ilium and humerus (Bailon, 1999; Blain, 2005, 2009); for lizards, the dentaries and maxillae; for snakes, the dorsal vertebrae (Blain, 2005, 2009; Szyndlar, 1984); for *Crocidura russula* and *Erinaceus europaeus*, the mandibles and isolated teeth (Reumer, 1984); for bats, the mandibles, isolated teeth and humeri (Bruijn and Rumke, 1974; Menu and Popelard, 1987; Sevilla, 1988); for Arvicolidae, the first lower molars (van der Meulen, 1973); and for *Apodemus sylvaticus* and *Eliomys quercinus* isolated teeth (Damms, 1981; Pasquier, 1974).

2.2. Palaeoenvironmental reconstruction

In order to reconstruct the palaeoenvironment, we employed the method of habitat weightings (Andrews, 2006; modified from Blain et al., 2008; Evans et al., 1981; López-García et al., 2011b), which consists of ascertaining the percentage distribution of the preferred habitat(s) occupied by each taxon (Table 1). This distribution is based on the locations of each species at present, because all of them are still found on the Iberian Peninsula. We have specified five types of habitat, defined according to a series of very concrete environmental features: dry meadow; wet meadow; woodland; rocky; and water. *Dry meadow* consists of meadowland showing seasonal climate changes; *wet meadow* refers to evergreen meadowland with pastures and dense plant cover; *woodland* ranges from leafy forest to woodland margins, with moderate ground cover; *rocky* represents rocky or stony habitats without plant cover; and *water* refers to areas along streams, lakes and ponds.

2.3. Palaeoclimatic reconstruction

We used the Mutual Climate Range (MCR) method in order to study the palaeoclimate by means of the micromammals (Agustí et al., 2009; Blain, 2005, 2009; Blain et al., 2007, 2009, 2010; López-García et al., 2010). Of these micromammals, *Microtus* (*Iberomys) cabrerae* and the chiropterans were excluded. In the case of *Microtus* (*Iberomys) cabrerae*, this was because its present-day distribution has been modified by anthropic activities, above all by the cultivation and drainage of the wetland areas with which this taxon is associated (Palombo and Gisbert, 2005). In the case of the chiropterans, it was because their mobility frequently makes it impossible to pinpoint their current geographical distribution, which could falsify our data.

The method consists of ascertaining the current distribution area of the faunal association under study. This is done by superimposing the maps from atlases of current distribution, divided into 10×10 km UTM squares (Palombo and Gisbert, 2005). The resulting intersection will indicate an area with climate conditions similar to those of the association under study. On the basis of this intersection, we calculated the mean annual temperature (MAT), mean temperature of the coldest month (MTC) and mean temperature of the warmest month (MTW), as well as the mean annual precipitation (MAP). These climate conditions were obtained using maps of present-day temperatures

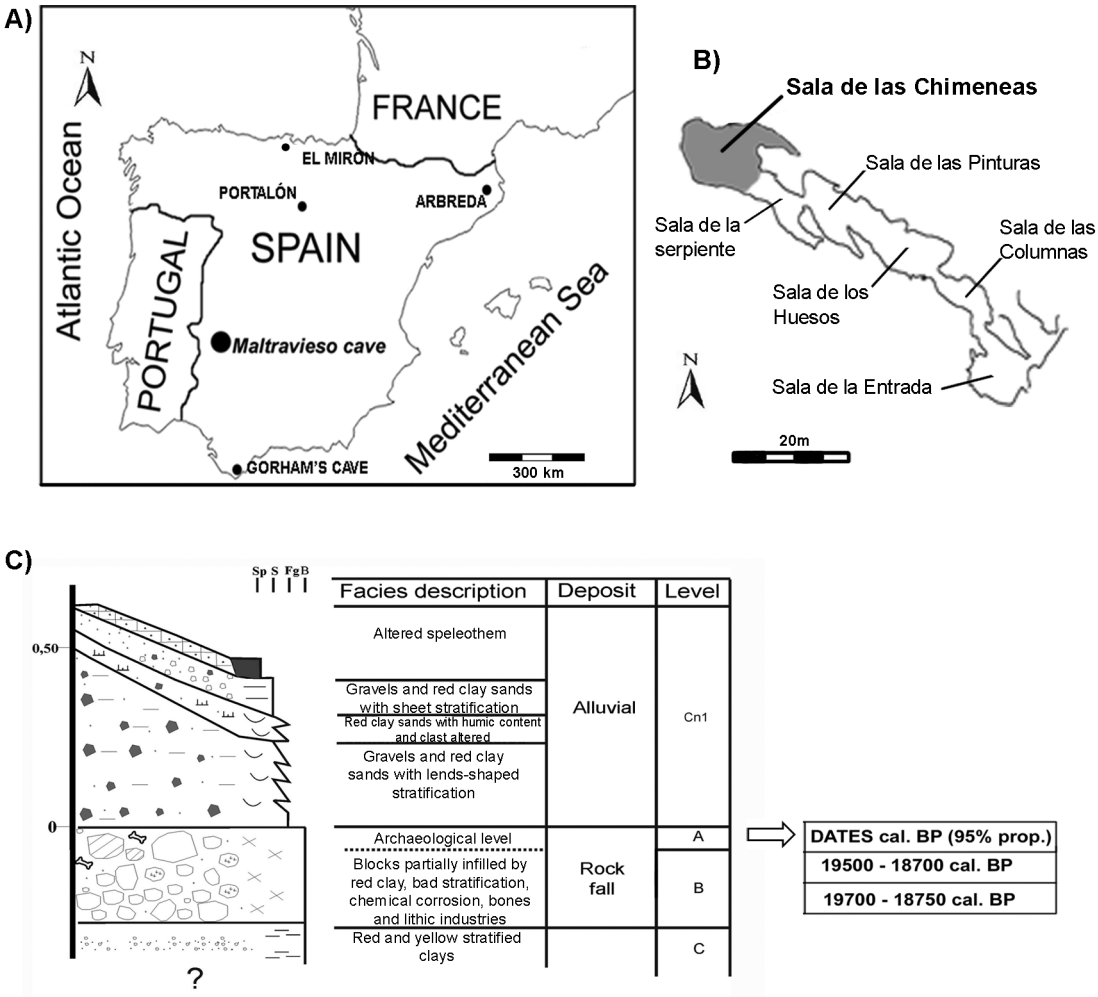

Fig. 1. A. Geographical location of Maltravieso Cave. B. Position of study area within the cave. C. Stratigraphy of La Sala de las Chimeneas (Mancha, 2007), and the recent radiocarbon datings of level A (Canals et al., 2010).

Fig. 1. A. Localisation géographique de la Grotte Maltravieso. B. Position de la zone étudiée dans la grotte. C. Stratigraphie de La Sala de las Chimeneas (Mancha, 2007) et récentes datations radiocarbone du niveau A (Canals et al., 2010).

and precipitation figures (Font Tullot, 2000). Finally, the results were compared to data from the weather station of the city of Cáceres (Extremadura, Spain) over the last 30 years.

3. Taphonomic remarks

The accumulation of microvertebrates is produced by the activity of other animals, primarily birds of prey and small carnivores. These accumulations would have been brought to our study area through the "chimneys" that connect the cave with the outside. In this case, having analysed the micromammals in their entirety, we established that they form an assemblage of great taxonomic variety, indicating that it was the work of an opportunistic hunter, but moreover, the remains present slight modification (soft wear). Taking these factors into account, it can be surmised that the main animal responsible for the accumulation of these microvertebrates in the cave was a category 1 predator, in other words a nocturnal bird of prey that displays an opportunistic trophic pattern and produces slight modifications of the bones it ingests (Andrews, 1990).

Furthermore, within the association, we also found remains of chiropterans, whose dentition we analysed in accordance with the methodology expounded by Sevilla (1986). This stipulates four categories of wear: (0) without wear, (1) slight wear, (2) cusps and crests worn, and (3) cusps and crests very worn. Applying these criteria to the association under study, it was seen that this only contains adult individuals, and that all of these display wear of the latter three levels, both in the individuals we classified as *Myotis* sp. and in those classified as *Myotis myotis-blythii* (Fig. 2). Accordingly, the accumulation of chiropterans in the cave may well differ from that of the rest of the association, involving a hibernation colony in which the most adult individuals died a natural death. As happens with amphibians and squamates, whose contribution to the cave may be for predation, this might also be due to mortality during hibernation or aestivation in the cave.

Table 1
Numbers of identified specimens (NISP), minimum number of individuals (NMI) and distribution by habitat of the small vertebrates represented in the Sala de las Chimeneas (Maltravieso cave).
Tableau 1
Nombre de restes identifiés (NISP), nombre minimum d'individus (NMI) et distribution par habitat des petits vertébrés représentés dans la Sala de las Chimeneas (grotte de Maltravieso).

TAXA	NISP	MNI	Open-dry meadow	Open-humid meadow	Woodland and woodland margin	Rocky	Watre edge
Crocidura russula	2	2	0.5		0.5		
Erinaceus europaeus	2	2		0.5	0.5		
Myotis myotis-blythii	7	6		0.25	0.75		
M. (Iberomys) cabrerae	12	10		0.5	0.5		
Arvicola sapidus	5	4					1
Arvicola terrestris	2	2		1			
M. (Terricola) duodecimcostatus	8	6		0.5	0.5		
Microtus agrestis	4	3		0.5	0.5		
Microtus arvalis	6	5	0.5		0.5		
Apodemus sylvaticus	15	12			1		
Eliomys quercinus	4	3			0.5	0.5	
Bufo bufo	14	11	0.1	0.3	0.4		0.2
Bufo calamita	13	10	0.75			0.25	
Pelophylax perezi	3	2					1
Timon lepidus	7	6		0.5		0.5	
Coronella girondica	16	13	0.25	0.25	0.25	0.25	
cf. Natrix maura	1	1					1
Vipera latasti	4	3	0.375		0.25	0.375	

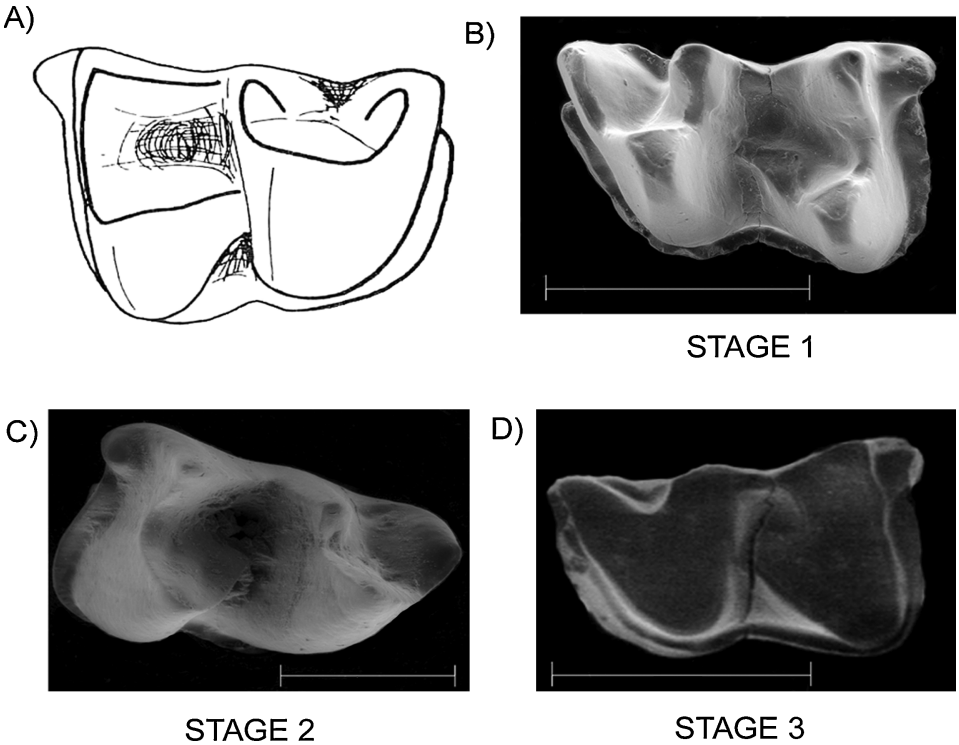

Fig. 2. Diagram of the different degrees of dental wear in the m1 of chiropterans from La Sala de las Chimeneas. A. Original morphology right m1 of *Myotis* (Sevilla, 1988). B. Left m1 of *Myotis* sp. C. Right m1 of *Myotis myotis-blythii*. D. Left m1 of *Myotis* sp. Scale 1 mm.
Fig. 2. Diagramme des différents degrés d'usure dentaire dans la m1 de chiroptères de La Sala de las Chimeneas. A. Morphologie originelle de la m1 droite de *Myotis* (Sevilla, 1988). B. M1 gauche de *Myotis* sp. C. M1 droite de *Myotis myotis-blythii*. Échelle : 1 mm.

4. Results

4.1. Small vertebrate assemblage

The sample under study consists of 343 remains (NR), from which 150 individuals (MNI) have been calculated. Twelve taxa of micromammals have been identified: *Crocidura russula*, *Erinaceus europaeus*, *Myotis* sp., *Myotis myotis-blythii*, *Microtus (Iberomys) cabrerae*, *Arvicola sapidus*, *Arvicola terrestris*, *Microtus (Terricola) duodecimcostatus*, *Microtus arvalis*, *Microtus agrestis*, *Apodemus sylvaticus* and *Eliomys quercinus* (Fig. 3), and 9 taxa of anurans and squamates: *Bufo bufo*, *Bufo calamita*, *Pelophylax perezi*, *Timon lepidus*, Lacertidae indet, *Coronella girondica*,

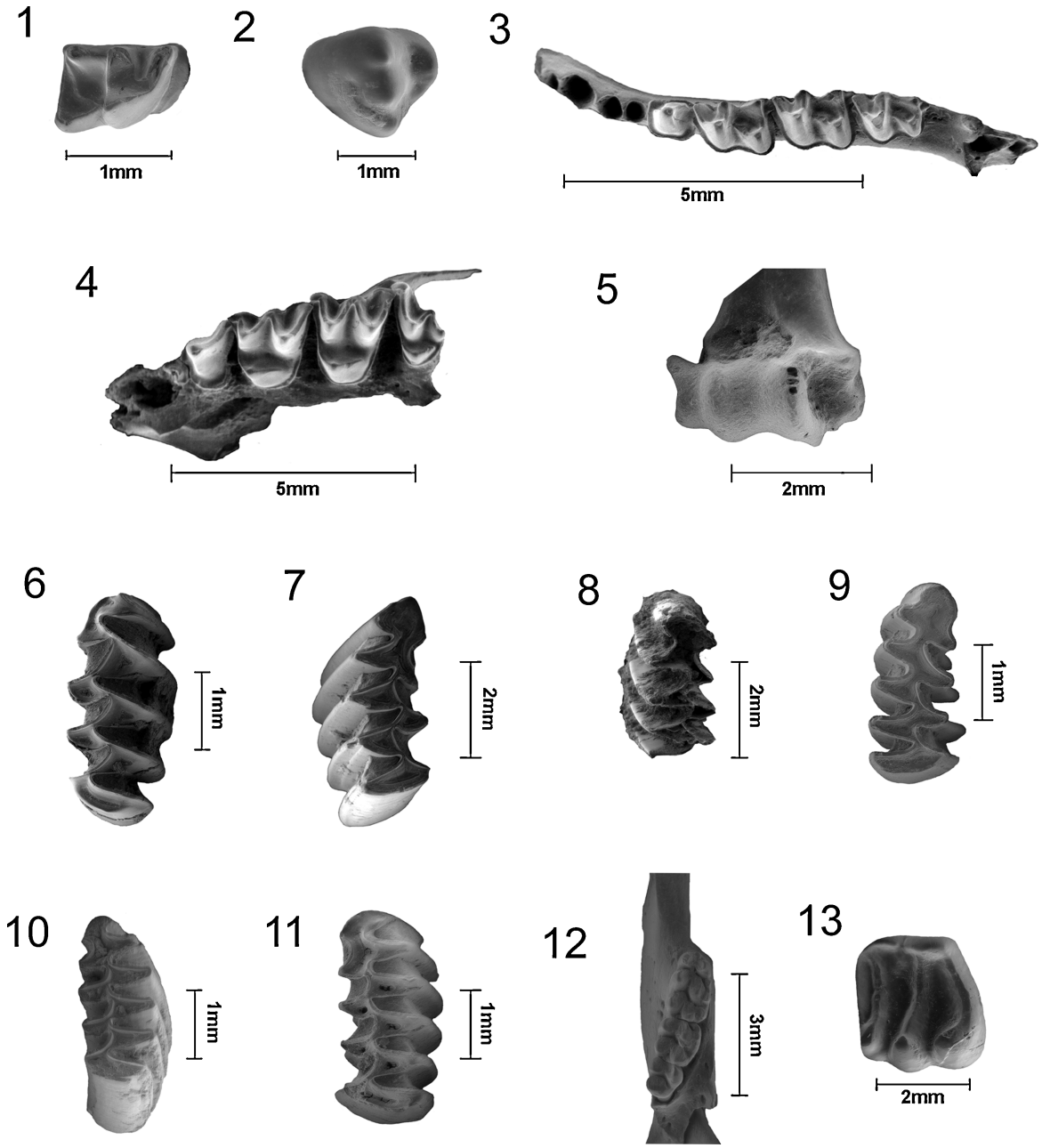

Fig. 3. Diagnostic elements of the mammal taxa from La Sala de las Chimeneas, in occlusal view: **1.** *Crocidura russula*, right m1. **2.** *Erinaceus europaeus*, right deciduous m3. **3.** *Myotis* sp., left mandible. **4.** *Myotis myotis-blythii*, left maxilla. **5.** *Myotis myotis-blythii*, distal epiphysis of right humerus. **6.** *Microtus* (*Iberomys*) *cabrerae*, left m1. **7.** *Arvicola sapidus*, left m1. **8.** *Arvicola terrestris*, left m1. **9.** *Microtus (Terricola) duodecimcostatus*, right m1. **10.** *Microtus arvalis*, left m1. **11.** *Microtus agrestis*, left m1. **12.** *Apodemus sylvaticus*, right mandible. **13.** *Eliomys quercinus*, right m1.

Fig. 3. Eléments diagnostiques des taxa de Mammifères de La Sala de las Chimeneas, en vue occlusale. **1.** *Crocidura russula*, m1 droite. **2.** *Erinaceus europaeus*, m3 droite caduque. **3.** *Myotis* sp., mandibule gauche, **4.** *Myotis myotis-blythii*, maxillaire gauche. **5.** *Myotis myotis-blythii*, épiphyse distale d'humérus droit. **6.** *Microtus* (Iberomys) cabrerae, m1 gauche. **7**. *Arvicola sapidus*, m1 gauche. **8.** *Arvicola terrestris*, m1, gauche. **9.** *Microtus (Terricola) duodecimcostatus*, m1 droite. **10.** *Microtus arvalis*, m1 gauche. **11.** *Microtus agrestis*, m1 gauche. **12.** *Apodemus sylvaticus*, mandibule droite. **13.** *Eliomys quercinus*, m1 droite.

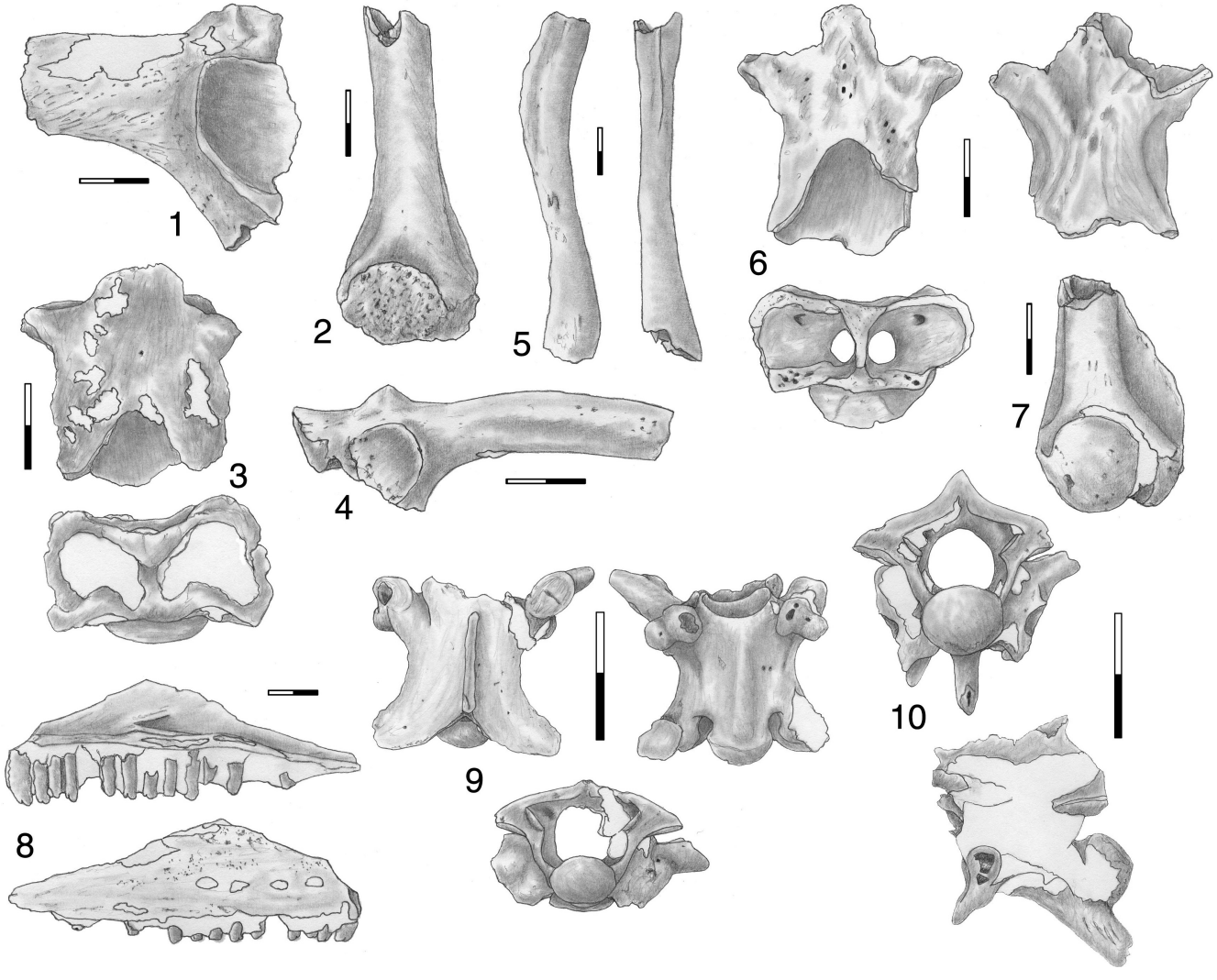

Fig. 4. Diagnostic elements of the herpetofaunal taxa from La Sala de las Chimeneas: **1**. *Bufo bufo*, left ilium, lateral view. **2.** *Bufo bufo*, right humerus, ventral view. **3.** *Bufo calmita*, sphenethmoid, dorsal and anterior views. **4.** *Bufo calamita*, right ilium, lateral view. **5.** *Bufo calamita*, femur, dorsal and medial views. **6.** *Pelophylax perezi*, sphenethmoid, dorsal, ventral and anterior views. **7.** *Pelophylax perezi*, right humerus, ventral view. **8.** *Timon lepidus*, right maxilla, lingual and labial views. **9.** *Coronella girondica*, dorsal vertebra, dorsal, ventral and posterior views. **10.** *Vipera latasti*, cervical vertebra, posterior and left lateral views. Scale 2 mm.

Fig. 4. Eléments diagnostiques des taxa de l'herpétofaune de La Sala de las Chimeneas: **1.** *Bufo bufo*, ilium gauche, vue latérale. **2.** *Bufo bufo*, humérus droit, vue ventrale. **3.** *Bufo calmita*, sphénethmoïde, vues dorsale et antérieure. **4.** *Bufo calamita*, ilium droit, vue latérale. **5.** *Bufo calamita*, fémur, vues dorsale et médiale. **6.** *Pelophylax perezi*, sphénethmoïde, dorsal, vues ventrale et antérieure. **7.** *Pelophylax perezi*, humérus droit, vue ventrale. **8.** *Timon lepidus*, maxilaire droit, vues linguale et labiale. **9.** *Coronella girondica*, vertèbre dorsale, vues ventrale et postérieure. **10.** *Vipera latasti*, vertèbre cervicale, vues postérieure et latérale gauche. Échelle: 2 mm.

Table 2
Relation of temperatures and precipitations obtained using the MCR (Mutual Climate Range) method for the micromammals from La Sala de las Chimeneas.
Tableau 2
Relation entre température et précipitation, obtenue en utilisant la méthode MCR (échelle de climat mutuel) pour les micro-mammifères de La Sala de las Chimeneas.

	n	MEAN ± SD	MIN	MAX	Δ
MAT	62	12.4 ± 1.1 °C	9 °C	15 °C	−3.7 °C
MTC	62	6.6 ± 2.2 °C	2 °C	9 °C	−1.1 °C
MTW	62	18.8 ± 1.6 °C	15 °C	23 °C	−7.2 °C
MAP	62	1193 ± 461 mm	500 mm	2000 mm	+712 mm

MAT: mean annual temperature; MTC: mean temperature of the coldest month; MTW: mean temperature of the warmest month; MAP: mean annual precipitation; *n*: number of 10 × 10 km UTM squares forming the intersection obtained for micromammals; mean ± SD: mean and standard deviation of the values obtained; min: minimum of the values obtained; max: maximum of the values obtained; Δ: difference between the current mean for Cáceres weather station over 30 years and that obtained for the micromammals.

Colubrinae indet., cf *Natrix maura* and *Vipera latasti* (Fig. 4).

All the taxa in the association under study are currently represented in the area around Cáceres, with the exception of *Arvicola terrestris*, which is currently found in the North of the Iberian Peninsula (Palombo and Gisbert, 2005). This species implies an environment of humidity that existed at the end of the Late Pleistocene, but that does not currently occur in the area around Cáceres.

4.2. Palaeoclimatic reconstruction

The region in which the association of taxa under study is currently found occupies a geographical area comprising a total of sixty-two (62) 10 × 10 km UTM squares. All of these are located across the North of the Iberian Peninsula. More specifically, they are concentrated in Asturias, the South of the Basque Country and La Rioja, and are present less densely in the North of Galicia and the Northeast of Girona. On the basis of these findings, we ascertained that the MAT is 12.4 ± 1.1 °C; the MTW is 18.8 ± 1.6 °C; whereas the MTC is 6.6 ± 2.2 °C. As for the MAP, this amounts to 1193 ± 461 mm (Table 2).

4.3. Palaeoenvironmental reconstruction

With respect to the type of environment represented, the association under study includes above all species characteristic of open spaces, meadows or low-density woodland. There is a predominance of individuals associated with wet areas, 70% preferring such habitats as opposed to 30% of the individuals that are associated with drier environments.

Among the humid spaces, 40% of the species were found to be associated with open woodland. Noteworthy among these was the abundant representation of *Apodemus sylvaticus*, as well as of other taxa with a marked preference for this habitat, as is the case with *Bufo bufo*. At the same time, 21% of the species were found to be associated mainly with open, wet meadows, as is the case with *Microtus agrestis*, *Microtus (Iberomys) cabrera* and *Erinaceus europaeus*. Further, there is a lower percentage of species (9%) whose habitat is associated with the presence of water, such as *Pelophylax perezi*, *Natrix maura* and *Arvicola sapidus*.

On the other hand, there are also species associated with a drier habitat (18%), among which we find *Microtus arvalis* and *Crocidura russula*, as well as *Bufo calamita*, most of which occupy this type of habitat. Finally, mention should be made of species that can also occupy rocky areas (11%), such as *Bufo calamita*, *Timon lepidus*, *Coronella girondica*, *Vipera latasti* and *Eliomys quercinus*.

5. Discussion

The results of the pollen studies based on marine cores collected off Greenland indicate that over the last 140,000 years, climate variability has been exceedingly complex (Sánchez-Goñi and d'Errico, 2005). These authors point out that cores collected off the coast of the Iberian Peninsula have shown that such variability extends to this territory as well. Around 22 to 19,000 BP, a period known as the Last Glacial Maximum (LGM), the presence of ice was recorded at very southerly latitudes (Fletcher and Sánchez-Goñi, 2008). However, palynological and microvertebrate studies have shown that the climate was not so adverse on the Iberian Peninsula (Cuenca-Bescós et al., 2008, 2009; López-García and Cuenca-Bescós, 2010; López-García et al., 2010, 2011a). Pollen studies based on marine core MD95-2042, located off the southwest coast of Portugal (Sánchez-Goñi and d'Errico, 2005), the closest to Maltravieso Cave, have revealed that the climate conditions during this most recent glacial age were not as harsh on the southwest coast of the Iberian Peninsula as had previously been thought, since the major ice masses are now known to have melted on coming into contact with the Portuguese coast (Sánchez-Goñi and d'Errico, 2005).

Our data have shown a clear fall in MTW (−7.2 °C) in relation to the present ($MTW_{Cáceres}$ = 26 °C; recent data from Font Tullot, 2000), whereas MTC does not show a major difference (−1.1 °C) in comparison to the present ($MTC_{Cáceres}$ = 7.7 °C; recent data from Font Tullot, 2000). This results in a decrease in MAT of −3.7 °C in relation to the present ($MAT_{Cáceres}$ = 16.1 °C; recent data from Font Tullot, 2000). As for precipitation, a substantial increase can be observed (+712 mm) in relation to the present ($MAP_{Cáceres}$ = 481 mm; recent data from Font Tullot, 2000) (Table 2). All these figures indicate colder temperatures and higher precipitation than at present, climatic conditions within which *Microtus* (*Iberomys*) *cabrerae* would fit perfectly. Even though this species was excluded from the intersection, its environmental needs include mild temperatures and a high water table (Palombo and Gisbert, 2005).

Moreover, analysis of the micromammals at La Sala de las Chimeneas (Maltravieso Cave) has provided us with

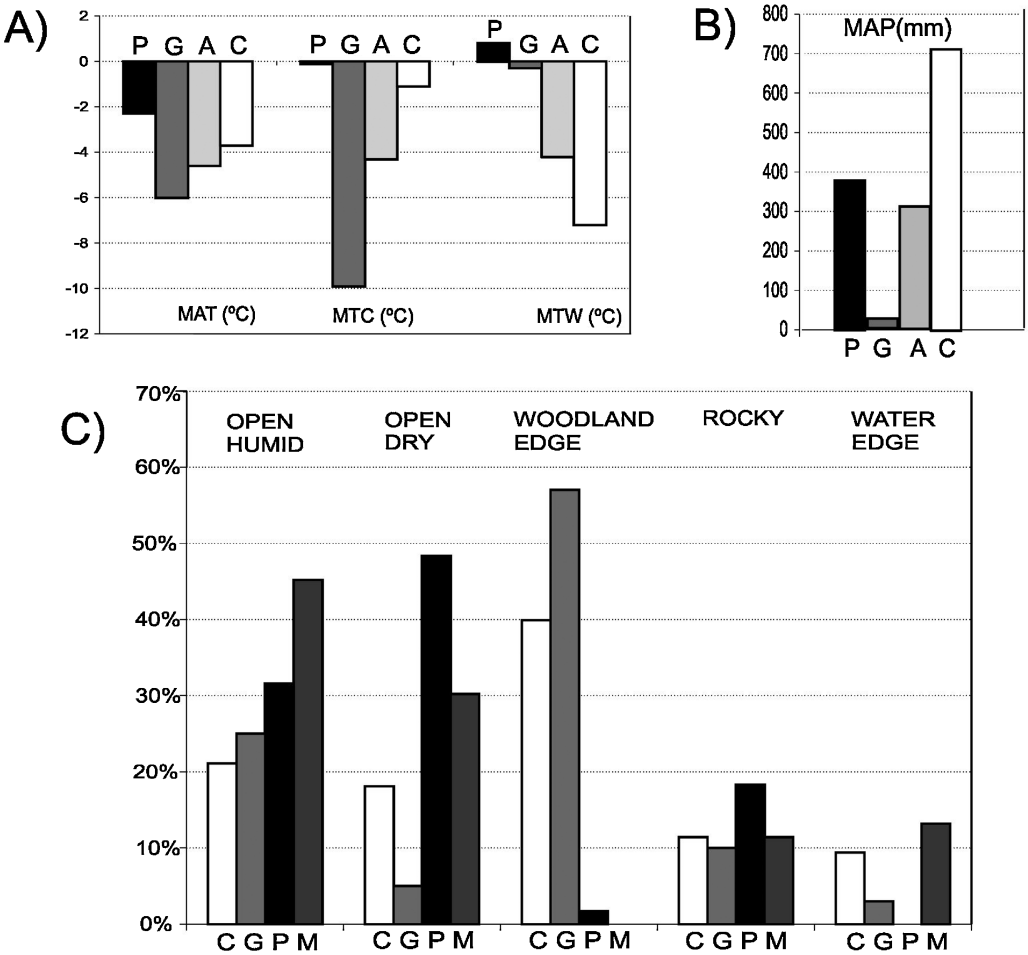

Fig. 5. A. Represents the difference in MAT (mean annual temperature), MTC (mean temperature of the coldest month) and MTW (mean temperature of the warmest month) between the present and the figures obtained on the basis of the micromammals from El Portalón (López-García et al., 2010), Gorham's Cave (López-García et al., 2011b), L'Arbreda (López-García and Cuenca-Bescós, 2010) and La Sala de las Chimeneas. **B.** Represents the difference in MAP (mean annual precipitation) between the present and the figures obtained on the basis of the micromammals from El Portalón (López-García et al., 2010), Gorham's Cave (López-García et al., 2011b), L'Arbreda (López-García and Cuenca-Bescós, 2010) and La Sala de las Chimeneas. **C.** Distribution by habitat of the taxa from La Sala de las Chimeneas, Gorham's Cave (López-García et al., 2011b), El Portalón (López-García et al., 2010) and El Mirón (Cuenca-Bescós et al., 2008, 2009). The abbreviations are as follows: A: L'Arbreda; C: Chimeneas; G: Gorham's Cave; M: El Mirón; P: El Portalón.

Fig. 5. A. Représente les différences de MAT (température moyenne annuelle), MTC (température moyenne du mois le plus froid) et MTW (température moyenne du mois le plus chaud) entre le Présent et les figurations obtenues sur la base des micro-mammifères de d'El Portalón (López-García et al., 2010), la grotte de Gorham (López-García et al., 2011b), L'Arbreda (López-García and Cuenca-Bescós, 2010) et La Sala de las Chimeneas. B. Représente les différences de MAP (précipitations moyennes annuelles) entre le Présent et les figurations obtenues sur la base des micro-mammifères d'El Portalón (López-García et al., 2010), la grotte Gorham (López-García et al., 2011b), L'Arbreda (López-García and Cuenca-Bescós, 2010) et La Sala de las Chimeneas. C. Répartition par habitat des taxa de La Sala de las Chimeneas, de la grotte Gorham (López-García et al., 2011b), El Portalón (López-García et al., 2010) et El Mirón (Cuenca-Bescós et al., 2008, 2009). Les abréviations sont les suivantes: A: L'Arbreda; C: Chimeneas; G: grotte Gorham,; M: El Mirón; P: El Portalón.

important data allowing a comparison to be drawn with micromammals from other sites with similar chronologies, with a view to establishing some common features of the period in question. These sites are El Mirón Cave (Ramales de Victoria, Cantabria) (Cuenca-Bescós et al., 2008, 2009), L'Arbreda Cave (Serinyá, Girona) (López-García and Cuenca-Bescós, 2010), El Portalón (Sierra de Atapuerca, Burgos) (López-García et al., 2010) and Gorham's Cave (Gibraltar) (López-García et al., 2011b). All these sites indicate generally lower temperatures than at present (Fig. 5) with an environment dominated by open, humid spaces, as at La Sala de las Chimeneas (Table 1). Further, at L'Arbreda Cave (López-García and Cuenca-Bescós, 2010), Gorham's Cave (López-García et al., 2011b) and La Sala de las Chimeneas, the presence of thermophilous taxa such as *Microtus* (*Iberomys*) *cabrerae* and *Microtus* (*Terricola*) *duodecimcostatus* has been observed. These would not have been present in harsh climate conditions.

As regards the palaeoenvironment, on the other hand, we have ascertained the presence of a majority of taxa characteristic of open, humid spaces, environmental features that coincide with those of the LGM, in which slightly wetter conditions are recorded, permitting the development of bushy vegetation (Fletcher and Sánchez-

Goñi, 2008). However, we also observe the presence of 29% of the taxa whose habitat is drier, such as *Bufo calamita*, *Coronella girondica*, *Timon lepidus* and *Eliomys quercinus*.

Chronologically, La Sala de las Chimeneas (17,840 ± 90 BP and 17,930 ± 100 BP) falls within MIS 2 in the LGM (Last Glacial Maximum), characterized by climate conditions that were cold and wet in the Mediterranean region (Fletcher and Sánchez-Goñi, 2008). The results of the micromammal intersection indicate that the association under study would currently be located in the North of the Iberian Peninsula; in other words, it would correspond to a climate with a greater Atlantic influence, with only slight differences in temperature between summer and winter and with abundant precipitation, differing from the present-day continentalized Mediterranean climate of Cáceres (Extremadura, Spain), which is characterized by extreme temperatures and scarce precipitation.

6. Conclusions

The data presented in this paper represent a palaeoenvironmental and palaeoclimatic study that is new for the Southwest of the Iberian Peninsula. The sample analysed consists of a total of 343 remains, from which 150 individuals have been identified, belonging to 21 taxa: *Crocidura russula*, *Erinaceus europaeus*, *Myotis* sp., *Myotis myotis-blythii*, *Microtus (Iberomys) cabrerae*, *Arvicola sapidus*, *Arvicola terrestris*, *Microtus (Terricola) duodecimcostatus*, *Microtus arvalis, Microtus agrestis*, *Apodemus sylvaticus*, *Eliomys quercinus*, *Bufo bufo*, *Bufo calamita*, *Pelophylax perezi*, *Timon lepidus*, Lacertidae indet., *Coronella girondica*, Colubrinae indet., cf. *Natrix maura* and *Vipera latasti*. Most of these were brought to the site by a category 1 predator, probably a nocturnal bird of prey, in view of the scant digestion of the remains. However, in the case of the chiropterans, it has been established that the accumulation was a product of natural death, given the high level of wear shown by the teeth; it may well have been a hibernation colony. As for the palaeoenvironment, humid spaces have been seen to predominate, in particular woodland areas and wet meadowland, with the presence also of dry meadows and areas without vegetation cover. While the mean temperatures are slightly colder than at present, the warmest temperatures are seen to be considerably lower, unlike the coldest temperatures, as also shown by the presence of taxa such as *Microtus* (*Iberomys*) *cabrerae* and *Microtus* (*Terricola*) *duodecimcostatus*. There is a substantial rise in precipitation in relation to the present, more typical of the current climate in the north of the Iberian Peninsula than of Cáceres. The environment and the climate of La Sala de las Chimeneas are in keeping with the final cold spells of the LGM.

Acknowledgments

We should like to thank the team *Primeros Pobladores de Extremadura*, for providing us with the material studied. Thanks go to Juan Ignacio Morales for his comments and clarifications. This paper has been supported by projects PO BOS 2003-8938, DGI CGL 2006 13532-C03-01-02, 2002-02-4.1-U-048, CGL2009-07896/BTE, SGR2009-324. J.M.L-G has a postdoctoral grant from the Juan de la Cierva subprogram (JCI-2009-04026), financed by the Spanish Ministry of Science and Innovation.

References

Agustí, J., Blain, H.A., Cuenca-Bescós, G., Bailon, S., 2009. Climate forcing of first hominid dispersal in Western Europe. Journal of Human Evolution 57, 815–821.

Andrews, P., 1990. Owls, Caves and Fossils. Oxford University Press, London, 231 p.

Andrews, P., 2006. Taphonomic effects of faunal impoverishment and faunal mixing. Palaeogeography, Palaeoclimatology, Palaeoecology 241, 572–589.

Bailon, S., 1999. Différenciation ostéologique des Anoures (Amphibia, Anura) de France. In: Desse, J., Desse-Berset, N. (Eds.), Fiches d'ostéologie animale pour l'archéologie, Série C: varia. Centre de Recherches Archéologiques, CNRS, Valbonne, pp. 1–38.

Blain, H.A., 2005. Contribution de la paléoherpétofaune (Amphibia and Squamata) à la connaissance de l'évolution du climat et du paysage du Pliocène supérieur au Pléistocène moyen d'Espagne. Museum National d'Histoire Naturelle, Paris, Tesis Doctoral: 402 p.

Blain, H.A., 2009. Contribution de la paléoherpétofaune (Amphibia and Squamata) à la connaissance de l'évolution du climat et du paysage du Pliocène supérieur au Pléistocène moyen d'Espagne. Treballs del Museu de Geologica de Barcelona 16, 39–170.

Blain, H.A., Bailon, S., Agustí, J., 2007. Anurans and squamate reptiles from the latest Early Pleistocene of Almenara-Casablanca-3 (Castellón East of Spain). Systematic, climatic and environmental considerations. Geodiversitas 29 (2), 269–295.

Blain, H.-A., Bailon, S., Cuenca-Bescós, G., 2008. The Early-Middle Pleistocene palaeoenvironmental change based on the squamate reptile and amphibian proxy at the Gran Dolina site, Atapuerca, Spain. Palaeogeography, Palaeoclimatology, Palaeoecology 261, 177–192.

Blain, H.-A., Bailon, S., Cuenca-Bescós, G., Arsuaga, J.L., Bermúdez de Castro, J.M., Carbonell, E., 2009. Long-term climate record inferred from Early-Middle Pleistocene amphibian and squamate reptile assemblages at the Gran Dolina Cave, Atapuerca, Spain. Journal of Human Evolution 56 (1), 55–75.

Blain, H.-A., Bailon, S., Cuenca-Bescós, G., Bennàsar, M., Rofes, J., López-García, J.M., Huguet, R., Arsuaga, J.L., Bermúdez de Castro, J.M., Carbonell, E., 2010. Climate and environment of the earliest West European hominins inferred from amphibian and squamate reptile assemblages: Sima del Elefante Lower Red Unit, Atapuerca, Spain. Quaternary Science Reviews 29, 3034–3044.

Bruijn, H., Rumke, K., 1974. On a peculiar mammalian association from the Miocene of Oschiri (Sardinia) I and II. Koniklijke Nederlandse Akademie 77 (1), 46–79.

Canals, A., Rodríguez-Hidalgo, A., Peña, L., Mancha, E., García-Díez, M., Bañuls, S.; Euba, I., López-García, J.L., Barrero, N., Bermejo, L., García, F.J., Mejías, D., Modesto, M., Morcillo, A., Aranda, V., Carbonell, E., 2010. Nuevas aportaciones al Paleolítico superior del suroeste peninsular: "La cueva de Maltravieso, más allá del santuario extremeño de las manos". In: Mangado, X. (Ed.), Jornadas internacionales sobre el Paleolítico superior peninsular. Novedades del S.XXI. Homenaje al profesor Javier Fortea. SERP-Seminaris d'estudis i recerques prehistòriques-UB, pp. 199–219.

Cuenca-Bescós, G., Strauss, L.G., González Morales, M.R., García Pimienta, J.C., 2008. Paleoclima y paisaje del final del cuaternario en Cantabria: los pequeños mamíferos de la cueva del Mirón (Ramales de la Victoria). Revista Española de Paleontología 23 (1), 91–126.

Cuenca-Bescós, G., Straus, L.G., González Morales, M.R., García Pimienta, J.C., 2009. The reconstruction of past environments through small mammals: from the Mousterian to the Bronze Age in El Mirón Cave (Cantabria, Spain). Journal of Archaeological Science 36 (4), 947–955.

Damms, R., 1981. The dental pattern of the dormice *Dryomys*, *Myomimus*, *Microdyromys* and *Peridryomys*. Micropaleontological Bulletins 3, 1–115.

Evans, E.M.N., Van Couvering, J.A.H., Andrews, P., 1981. Palaeoecology of Miocene sites in Western Kenya. Journal of Human Evolution 10, 99–116.

Fletcher, W.J., Sánchez Goñi, M.F., 2008. Orbital and sub-orbital-scale climate impacts on vegetation of the western Mediterranean basin over the last 48.000 yr. Quaternary Research 70, 451–464.

Font Tullot, I., 2000. Climatología de España y Portugal. Universidad de Salamanca, Salamanca, 422 p.

Gutiérrez Elorza, M., 1994. Introducción a la Geomorfología española. In: (ed.): Geomorfología de España, Editorial Rueda. pp. 1–22.

López-García, J.M., Cuenca-Bescós, G., 2010. Évolution climatique dans le Pléistocène supérieur en Catalogne (Nord- Est de l'Espagne) d'après l'étude des micromammifères. Quaternaire 21, 249–258.

López-García, J.M., Blain, H.A., Cuenca-Bescós, G., Ruiz-Zapata, M.F., Dorado-Valiño, M., Gil-García, M.J., Valdeolmillos, A., Ortega, A.I., Carretero, J.M., Arsuaga, J.L., Bermúdez de Castro, J.M., Carbonell, E., 2010. Palaeoenvironmental and palaeoclimatic reconstruction of the Latest Pleistocene of El Portalón Site, Sierra de Atapuerca, northwestern Spain. Palaeogeography, Palaeoclimatology, Palaeoecology 292, 453–464.

López-García, J.M., Blain, H.-A., Cuenca- Bescós, G., Alonso, C., Alonso, S., Vaquero, M., 2011a. Small vertebrates (Amphibia Squamata, Mammalia) from the Late Pleistocene-Holocene of the Valdavara-1 cave (Galicia, northwestern Spain). Geobios 44, 253–269.

López-García, J.M., Cuenca-Bescós, G., Finlayson, C., Brown, K., Giles Pacheco, F., 2011b. Palaeoenvironmental and palaeoclimatic proxies 1 of the Gorham's cave small mammal sequence, Gibraltar, southern Iberia. Quaternary International 243, 137–142.

Mancha, E., 2007. La cueva de Maltravieso (Cáceres, España): Geología sedimentaria de los depósitos de entrada de cueva. Área de Prehistoria/IPHES, Universitat de Tarragona. Tarragona DEA inédita: 111 p.

Menu, H., Popelard, J.B., 1987. Utilisation des caracteres dentaires pour la détermination des Vespertilionines de l'Ouest européen. Le Rhinolophe. Bulletin de la coordination ouest pour l'étude et la protection des chauves-souris. Musée d'Histoire Naturelle 4, 2–88.

Meulen van der, A.J., 1973. Middle Pleistocene small mammals from the Monte Peglia (Orvieto, Italy) with special reference to the phylogeny of *Microtus* (Arvicolidae Rodentia). Quaternaria 16, 1–144.

Palombo, J.L., Gisbert, J., 2005. Atlas de los Mamíferos Terrestres de España. Madrid, Dirección General para la Biodiversidad-SECEM-SECEMU, 564 p.

Pasquier, L., 1974. Dynamique évolutive d'un sous-genre de Muridae Apodemus (Sylvaemus). Etude biométrique des caractères dentaires de populations fossiles et actuelles d'Europe occidentale. Université de Montpellier, Montpellier, pp. 184.

Reumer, J.W.F., 1984. Ruscinian and early Pleistocene Soricidae (Insectívora Mammalia) from Tegelen (The Netherlands) and Hungary. Scripta Geologica 73, 1–173.

Ripoll Perelló, E., Ripoll López, S., Collado Giraldo, H., 1999. Maltravieso: El Santuario extremeño de las manos. Museo de Cáceres, Cáceres 56 (2), 21–33.

Rodríguez, A., Muñoz, L. y Canals, A., 2009. Una aproximación zooarqueológica al yacimiento de la cueva de Maltravieso. In: P. J. Sanabria (Ed) Actas del Congreso El Mensaje de Maltravieso 50 años después (1956-2006), 2006, Cáceres. Publicaciones del Museo de Cáceres. pp. 153–163.

Rodríguez-Hidalgo, A.J., 2008. Zooarqueología de los yacimientos kársticas del Complejo Cacereño. (Cueva de Santa Ana y Cueva de Maltravieso). Área de Prehistoria, Universitat Rovira i Virgili. Tarragona DEA, 349 p.

Rodríguez-Hidalgo, A.J., Canals, A., Saladié, P., García, A.B., García-Diez, M., 2010. Upper Paleolithic ornaments marine shells from Sala de las Chimeneas, Maltravieso cave Cáceres (Spain). Munibe (supplement) 31, 246–259.

Rodríguez-Hidalgo, A.J., Saladié, P., Canals, A., 2011. Following the white rabbit: A case of small game procurement site in the Upper Palaeolithic (Sala de las Chimeneas, Maltravieso Cave, Spain). International Journal of Osteoarchaeology, doi:10.1002/oa.1238.

Sánchez-Goñi, M.F., d'Errico, F., 2005. La historia de la vegetación y el clima del último ciclo climático (OIS5-OIS1, 140.000-10.000 años BP) en la Península Ibérica y su posible impacto sobre los grupos paleolíticos. Monografías del Museo de Altamira 20, 115–129.

Sevilla, P., 1986. Identificación de los principales quirópteros ibéricos a partir de sus dientes aislados. Valor sistemático de los caracteres morfológicos y métricos dentarios. Doñana Acta Vertebrata 13, 111–130.

Sevilla, P., 1988. Estudio Paleontológico de los Quirópteros del Cuaternario Español. Paleontología y Evolució 22, 113–233.

Szyndlar, Z., 1984. Fossil snakes from Poland. Acta Zoologica Cracoviensia 28, 1–156.