Environmental and climatic context of Neanderthal occupation in southwestern Europe during MIS3 inferred from the small-vertebrate assemblages

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ABSTRACT

According to pollen analysis, Marine Isotope Stage 3 (MIS3, ca. 60–30 ka) is characterized in southern Europe by dynamic alternations of forest vs. semi-arid area expansion in accordance with the warming and cooling, respectively, of the sea-surface temperatures. It is in this context of rapid fluctuations that the Neanderthal occupation of the northeastern Iberian Peninsula took place. This paper sets forth a synthesis of the previously published environmental and climatic data obtained from the small vertebrates (herpetofauna and small mammals) of the Neanderthal localities of Cova del Gegant, Abric Romani, l'Arbreda cave, Canyars and Teixoneres. Using habitat weighting and mutual climatic range methods to reconstruct the environment, temperature and rainfall, the Middle Paleolithic occupations in northeastern Iberia are closely related to the presence of woodlands, irrespective of the climatic conditions. However, there are differences in the percentage of forest formations from the south to the northeast of Iberia. Southern Iberia (Gorham's cave) was much more forested than the northern parts (A. Romaní, l'Arbreda, Canyars, Teixoneres, C. Gegant). This observation coincides with the status of the southernmost Iberian Peninsula as a climatic refuge, where Neanderthals survived until ca. 28 ka BP.

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1. Introduction

Interest in Marine Isotope Stage 3 (MIS3) has been stimulated by the extreme variability of this period, as displayed by ice-core and marine records (e.g. Cacho et al., 1999; Sánchez-Goñi and d'Errico, 2005, among others), and the questions raised by archaeological research into the extinction of the Neanderthals and the transition from the Mousterian (Neanderthal) to Aurignacian (Anatomically Modern Human) cultures that occurred at the end of MIS3 (Vaquero, 2006; Zilhao, 2006; Finlayson et al., 2006, among others). The Late Pleistocene climatic history of the Iberian Peninsula has been well known since 1995, when the Iberian marine margin was cored as part of the IMAGES program (International Marine Global Change Study). The samples obtained show in detail the continuous development of the northern and southern ecosystems of the Iberian Peninsula and the climatic changes that have occurred in the northeastern Atlantic over the last 140,000 years (Cacho et al., 1999; Sánchez-Goñi and d'Errico, 2005). In general, according to pollen analysis, Marine Isotope Stage 3 (MIS3) (ca. 60–30 ka BP) is characterized by a dynamic that alternates between phases of forest development and the expansion of semi-arid areas in accordance with the warming and cooling, respectively, of the sea-surface temperatures (Fletcher and Sánchez-Goñi, 2008). Such multiple fluctuations provide the context for the Neanderthal occupations in Europe.

There are many European sites with Neanderthal remains (Delson and Harvati, 2006; Wenzel, 2007; Banks et al., 2008; Urbanowski et al., 2010; Benazzi et al., 2011; Dabrowski et al., 2013; Nowaczewska et al., 2013), and in recent years there has been an increase in findings of Neanderthal remains in the Iberian Peninsula (Díez et al., 2010; Lorenzo et al., 2012). These have shown that the Neanderthals survived in Iberia as late as ca. 30–28 ka BP

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in the context of a climatic refugium associated with woodland formations (Finlayson et al., 2006; Finlayson and Carrión, 2007; Jennings et al., 2011; López-García et al., 2012b). Against this background of rapid climatic fluctuations and Neanderthal occupations in Iberia, this paper presents a synthesis of the environmental and climatic data obtained by analyzing the small vertebrates (amphibians, squamates, and small mammals) at five archaeo-paleontological sites from MIS3 located in northeastern Iberia (Catalonia): Cova del Gegant, Abric Romaní, l'Arbreda cave, Canyars, and Teixoneres cave.

Catalonia currently has a Mediterranean climate, albeit with large temperature variations between the mild climate of the coastal zone (with mild winters and very hot summers), the Mediterranean continental climate (with cold winters and hot summers), and the pre-Pyrenean and Pyrenean mountain area (with minimums below zero, heavy snow in winter, rainfall over 1000 mm and less hot summers). Against this background, the data is placed in context with the climatic phases of the Late Pleistocene and with the Neanderthal occupations in the southern Iberian Peninsula (Gorham's cave).

2. Material and methods

The small-vertebrate fossil remains used for this study consist of disarticulated bone fragments collected by water-screening during the excavation campaigns at Cova del Gegant, Abric Romaní, l'Arbreda cave, Canyars and Teixoneres cave. All the sediment was water-screened using superimposed mesh screens, and bagged by levels. The levels used for this study are packages that contain human remains or evidence of human activity from MIS3. The fossils were processed, sorted and classified at the IPHES/URV (Tarragona, Spain) and previously published separately by Burjachs et al. (2012), López-García (2011), López-García and Cuenca-Bescós (2010), and López-García et al. (2008, 2009, 2012a, 2012b, 2013). The herpetofauna of l'Arbreda cave is not included because it is still in the process of being studied.

The assemblages from the studied levels include a total of 1986 fragments that correspond to a minimum number of 864 small vertebrates, representing at least 47 taxa (Table 1). The fragments were identified following the general criteria of systematic paleontology.

Table 1
Representation of the Number of Identified Specimens (NISP), the Minimum Number of Individuals (MNI) and the percentage of the MNI (%) for the small vertebrates from the studied sites. CG: Cova del Gegant; AR: Abric Romaní; ARB: l'Arbreda cave; TC: Canyars; Tx: Teixoneres cave.

	CG-IV		AR-O		AR-N		AR-J		AR-E		AR-D		ARB-I		TC-1		TX-II	
	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI
Salamandra salamandra	0	0	0	0	0	0	0	0	0	0	0	0	–	–	0	0	41	21
Alytes obstetricans	0	0	0	0	0	0	0	0	0	0	0	0	–	–	0	0	46	16
Pelobates cf. *cultripes*	1	1	0	0	0	0	0	0	0	0	0	0	–	–	0	0	0	0
Pelodytes punctatus	0	0	0	0	0	0	0	0	0	0	0	0	–	–	24	4	18	9
Pelodytes sp.	1	1	0	0	0	0	0	0	0	0	0	0	–	–	0	0	0	0
Bufo bufo	0	0	0	0	0	0	1	1	1	1	16	8	–	–	0	0	8	4
Bufo cf. *bufo*	4	2	0	0	0	0	0	0	0	0	0	0	–	–	3	1	0	0
Bufo calamita	3	1	0	0	0	0	0	0	24	12	12	6	–	–	97	5	168	39
Rana temporaria	0	0	2	1	0	0	1	1	18	9	0	0	–	–	0	0	46	18
Anura indet.	2	1	0	0	0	0	0	0	0	0	0	0	–	–	0	0	9	0
cf. *Podarcis/Psammodromus*	6	3	0	0	0	0	0	0	0	0	0	0	–	–	0	0	0	0
Anguis fragilis	0	0	0	0	0	0	0	0	0	0	2	1	–	–	5	1	6	5
Lacertidae indet.	0	0	2	1	0	0	0	0	0	0	0	0	–	–	6	2	12	10
Coronella austriaca	0	0	0	0	0	0	0	0	0	0	0	0	–	–	0	0	8	6
Coronella cf. *austriaca*	0	0	0	0	0	0	0	0	0	0	0	0	–	–	6	1	0	0
Malpolon monspessulanus	0	0	0	0	0	0	0	0	0	0	0	0	–	–	0	0	2	1
Vipera aspis	0	0	0	0	0	0	0	0	0	0	2	1	–	–	0	0	34	10
Vipera sp.	2	1	0	0	0	0	0	0	0	0	0	0	–	–	8	1	0	0
Colubrinae indet.	2	1	0	0	0	0	0	0	0	0	0	0	–	–	0	0	0	0
Ophidia indet.	6	3	0	0	0	0	0	0	0	0	0	0	–	–	12	–	8	0
Erinaceus europaeus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Crocidura russula	0	0	10	5	4	2	0	0	0	0	0	0	0	0	0	0	9	7
Crocidura sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
Sorex minutus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2
Sorex gr. *coronatus-araneus*	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	4	2
Neomys fodiens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Talpa europaea	2	1	6	3	0	0	2	1	0	0	0	0	0	0	1	1	6	2
Rhinolophus ferrumequinum	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1
Rhinolophus euryale-mehelyi	5	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2
Myotis myotis	0	0	0	0	0	0	0	0	0	0	0	0	218	95	0	0	143	50
Myotis myotis-blythii	12	6	0	0	0	0	0	0	0	0	0	0	84	42	0	0	0	0
Myotis cf. *M. nattereri*	7	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nyctalus lasiopterus	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Miniopterus schreibersii	3	1	0	0	2	1	0	0	0	0	0	0	0	0	0	0	17	5
Pipistrellus pipistrellus	0	0	0	0	3	2	0	0	0	0	0	0	0	0	0	0	4	2
Chiroptera indet.	9	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1
Microtus arvalis	0	0	24	13	0	0	4	2	2	1	2	1	13	12	3	2	105	58
Microtus agrestis	0	0	10	5	0	0	0	0	4	2	0	0	18	16	2	1	62	37
M. arvalis-agrestis	0	0	0	0	0	0	0	0	0	0	0	0	2	2	0	0	28	17
Chionomys nivalis	0	0	0	0	0	0	0	0	0	0	0	0	8	7	0	0	14	8
M. (Iberomys) cabrerae	5	3	40	20	17	8	4	2	0	0	2	1	0	0	1	1	0	0
M. (Terricola) duodecimcostatus	1	1	22	11	1	1	0	0	8	4	4	2	5	4	2	1	14	9
M. (Terricola) gerbei	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0
Pliomys lenki	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	1
Arvicola sapidus	0	0	60	29	6	3	16	8	6	3	10	5	7	5	0	0	4	2

Table 1 (*continued*)

	CG-IV		AR-O		AR-N		AR-J		AR-E		AR-D		ARB-I		TC-1		TX-II	
	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI
Apodemus sylvaticus	0	0	40	20	6	3	2	1	10	5	8	4	20	12	9	3	56	19
Eliomys quercinus	21	10	1	1	0	0	0	0	1	1	1	1	10	7	2	1	16	8
Total	**95**	**46**	**219**	**111**	**39**	**20**	**30**	**16**	**76**	**39**	**59**	**30**	**385**	**202**	**182**	**26**	**901**	**374**

Specific identification of this material rests principally on the best diagnostic elements: humerus, ilium, scapula and sacrum for anurans; skull elements for lizards and trunk vertebrae for snakes; mandible, maxilla and isolated teeth for shrews; mandible and isolated teeth for bats; first lower molars for the Arvicolinae subfamily; and isolated teeth for the Murinae and Glirinae subfamilies. The fossils were grouped using the minimum number of individuals (MNI) method, with the sample (i.e. from each level) determined by counting a diagnostic element, taking into account, whenever possible, laterality and sex (for anurans).

The small-vertebrate accumulation in caves is the consequence of "rejection pellets" produced by a predator or predators. There are different types of predators according to Andrews (1990). As shown by the previously published data (López-García, 2011; López-García and Cuenca-Bescós, 2010; López-García et al., 2008, 2009, 2012a, 2012b, 2013), the high percentage of anatomical representation of the fragments identified, the low level of fragmentation of these remains, and the slight signs of digestion found in the microtine teeth show that the small-vertebrate association encountered in the sequences from the studied sites was produced by opportunistic predators (see Andrews, 1990). Consequently, the associations are representative of the ecosystem in the direct vicinity of the caves.

From another standpoint, occasional predation on bats by nocturnal birds of prey might account for the isolated teeth at the various caves that have been analyzed, though *in-situ* death might also account for these in some cases, since the species in question are known to frequent caves. The same may apply with certain amphibians (such as *Bufo calamita*) that usually use caves as a refuge for aestivation or wintering (Blain et al., 2008).

In order to reconstruct the environment at the studied sites, the method of habitat weightings (Evans et al., 1981; Andrews, 2006) was used, distributing each small-vertebrate taxon in the habitat(s) where it can be found at present in the Iberian Peninsula. The ecological signatures of particular taxa and taxonomic habitat indices used in the present analyses are listed in the previously published studies of the sites (López-García, 2011; López-García and Cuenca-Bescós, 2010; López-García et al., 2008, 2009, 2012a, 2012b, 2013), the habitats were divided into five types (according to Cuenca-Bescós et al., 2005, 2009; Blain et al., 2008). However, for this synthesis only the data pertaining to the relationship between woodland and open land habitats have been used in order to observe their direct relationship with the presence of Neanderthals. Open land is divided into two categories: meadows with seasonal change (open dry) and evergreen meadows with dense pastures and suitable topsoil (open moist); woodland is taken to comprise mature forest including woodland margins and forest patches (Table 2).

In order to evaluate the paleoclimatic changes, the mutual climatic range method (MCR) (Blain et al., 2009) was used for small mammals. On the basis of the distribution of the extant Iberian fauna, the geographical region where all the species present in a given stratigraphical level currently coincide is identified by overlapping ranges. As the atlas used for this purpose is based on a 10×10 km Universal Transverse Mercator (UTM) network (Palomo and Gisbert, 2005), the climatic data were evaluated for each of these 10×10 km squares. Several climatic factors were estimated with the previously published data (López-García, 2011; López-García and Cuenca-Bescós, 2010; López-García et al., 2008, 2009, 2012a, 2012b, 2013), but for this synthesis the averages of the mean annual temperature (MAT), the mean temperature of the coldest month (MTC), the mean temperature of the warmest month (MTW) and the mean annual precipitation (MAP) are used to compare these data directly with the MIS3 ^{18}O-isotope curve (Table 3). The climatic data were obtained using various climatic maps of Spain (Font-Tullot, 1983, 2000) and data provided by the network of Spanish meteorological research stations over a period of 30 years. From this variably sized region, the climatic parameters can be estimated and compared with the weather stations at the different points in the Iberian Peninsula (current data from Font-Tullot, 2000).

Table 3
Average difference between the current mean weather station data over 30 years (data from Font-Tullot, 2000) and the data obtained for small vertebrates. MAT: mean annual temperature; MTW: mean temperature of warmest month; MTC: mean temperature of coldest month; MAP: mean annual precipitation.

	ΔMAT (in °C)	ΔMTC (in °C)	ΔMTW (in °C)	ΔMAP (in mm)
Teixoneres II	−7.7	−8.1	−6.1	349
Canyars	−5.2	−6.08	−4.5	98.6
L'Arbreda I	−6	−5.4	−4.8	118
Romaní D	−5.39	−5.84	−3.58	60
Romaní E	−5.7	−7.11	−5.5	148
Romaní J	−5.4	−5.75	−3.57	60
Romaní N	−4.5	−5.47	−2.28	76
Romaní O	−7.5	−6.5	−4.05	349
Gegant IV	−5.3	−5.3	−1.7	350

3. Studied sites and results

3.1. Cova del Gegant

The Cova del Gegant is a partially sea-flooded cave situated in the Massis del Garraf, at the Punta de les Coves (Caves' Point), some 40 km south of Barcelona (Fig. 1). The cave is part of a karst system in the Upper Jurassic to Lower Cretaceous marine limestones and dolomites of the Massis del Garraf, a low-relief mountain chain with maximum heights of less than 600 m, in the Catalan Coastal Range.

The first excavations were conducted in 1952 by an amateur team from the Agrupació Muntanyenca de Sitges (AMUNT), supervised by the paleontologist Santiago Casanova (Casanova, 2004—2005; Daura, 2008). Subsequently, work was carried out in
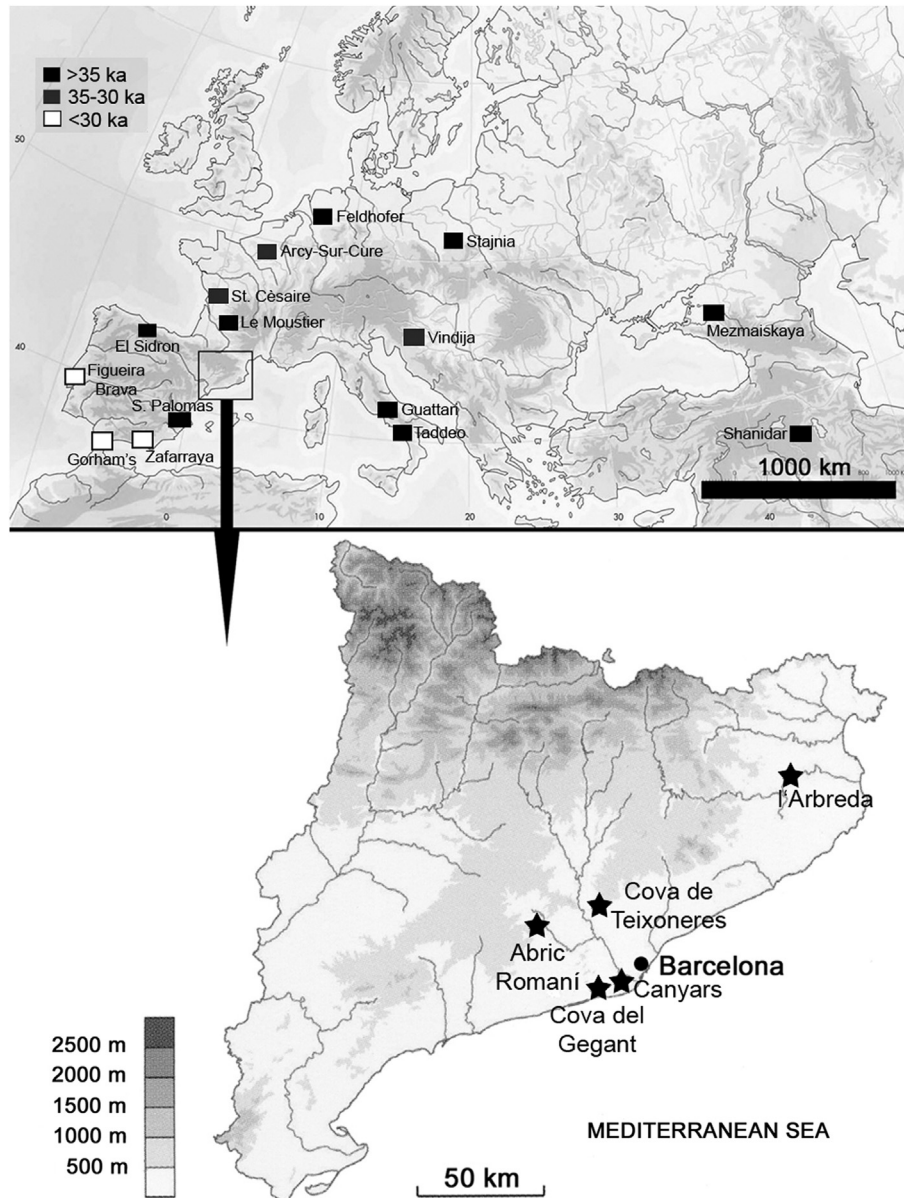
Table 2
Percentage representation of forest environments versus open dry and open humid meadows from the analyzed sites. The Romaní data represent the mean values of the studied levels. Data are taken from López-García and Cuenca-Bescós (2010) and López-García et al. (2011, 2012a, 2012b, 2013).

	Gegant	Romani	Arbreda	Canyars	Teixoneres	Gorham's
Woodland	79	67	73	49	67	87
Open dry	10	10	4	37	18	3
Open humid	11	23	23	14	15	10
Total	**100**	**100**	**100**	**100**	**100**	**100**

Fig. 1. Location of the studied sites (Cova del Gegant, Abric Romani, l'Arbreda cave, Canyars and Teixoneres cave) and approximate location of the some of the most important sites in Europe (above) with Neanderthal remains or evidence (modified from Delson and Harvati, 2006; Díez et al., 2010).

various parts of the cave in 1974 and 1975 were prompted by the Secció d'Ecologia del Quaternari of the Institut Jaume Almera (Barcelona). Some studies came from this period (Viñas and Villalta, 1975), and in 1985 and 1989 the members of the Centre de Recerques Paleo-Eco-Social (Girona) carried out an archaeological rescue operation (Martínez et al., 1985). The archaeological remains recovered from these previously works consist of lithic tools of the Mousterian techno-complex (Mir, 1975; Martínez et al., 1985) and faunal remains (Viñas and Villalta, 1975; Alcalde, 1986) that are strongly associated. According to their interpretations, the cave may have been used as a den by large carnivores (Martínez et al., 1985), though the presence of Mousterian stone tools (Mir, 1975; Viñas and Villalta, 1975; Daura et al., 2005) suggests that the cave could also have been used by Neanderthals.

The description by Daura et al. (2005) of a Neanderthal mandible found in 1954 by Casanova (2004–2005) in Gallery 1 (GL1) and preserved in the collections of Sitges Town Council (Arxiu Històric Municipal de Sitges) has aroused recently new interest in the locality. The Neanderthal fossil remains are represented by three fragments of a mandible which preserves most of the mandibular corpus. Though no teeth are preserved, the mandible displays some archaic anatomical characteristics absent in modern humans (Daura et al., 2005). The exact stratigraphic provenance of the mandible is unknown, because the lithostratigraphy was not established until more recent excavations. However, uranium-series dating performed on the fossil has given an age of 52.3 ± 2.3 ka (Daura et al., 2010).

The small-vertebrate remains from earlier excavation have been published by López-García (2011) and López-García et al. (2008), and the remains from recent excavations have been published by López-García et al. (2012a). The level belonging to MIS3 that is of interest for this article is level IV, dated by uranium series to 60 ± 3.8 ka (Daura et al., 2010). The small vertebrates recovered in this level comprise 95 identified remains and 46 individuals,

corresponding to a total of 19 taxa (Table 1; Fig. 2). The predator responsible for this accumulation was probably an avian predator (Category 1 *sensu* Andrews, 1990) possibly a barn owl (*Tyto alba*), also represented in the Pleistocene assemblage at the Cova del Gegant (Sánchez, 2005) and known to be an opportunistic predator (López-García et al., 2012b). The results obtained using the habitat weightings method indicate a landscape dominated by open Mediterranean forest (51%) as opposed to open areas, which represent 19% (Table 2). On the other hand, the results obtained by the mutual climatic range method show that mean annual temperatures were lower than at present (MAT$_{Gegant (IV)}$ = −5.3 °C; at present MAT = 15.3 °C at the meteorological station of Barcelona airport, located nearly 30 km to the north of the cave, data from Font-Tullot (2000) (Table 3). Moreover, the mean annual

precipitation was higher than at present (MAP$_{Gegant (IV)}$ = +350 mm; at present MAP = 659 mm, data from Font-Tullot (2000) (Table 3).

3.2. Abric Romaní

The Abric Romaní is a classical reference site with Neanderthal industries in a rock shelter. The site is near the town of Capellades, some 45 km to the northwest of Barcelona, and it lies about 310 m above the present sea level. Its location, between the contact of the basin of the River Anoia and the Catalan pre-littoral mountain range, constitutes a good enclave on the route between the Mediterranean littoral and the inland basin of the River Ebro (Fig. 1). The shelter is carved in Quaternary travertine, and the Mousterian
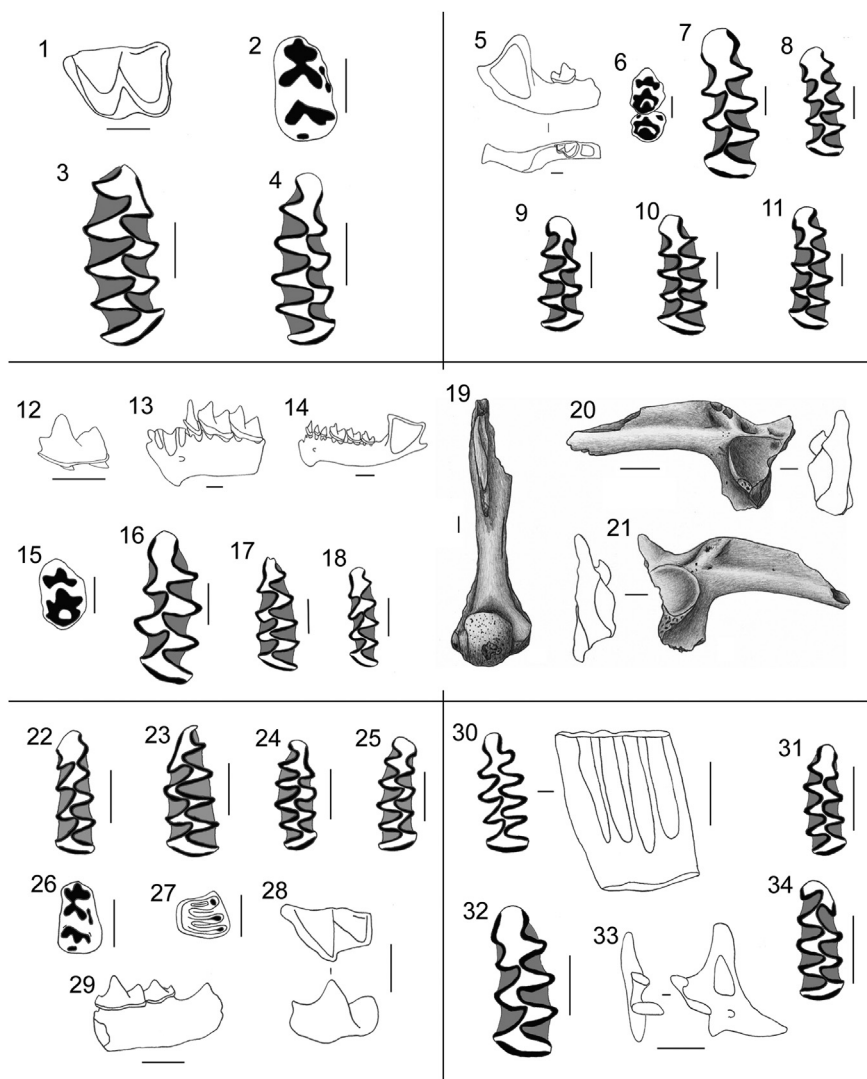

Fig. 2. Some small-vertebrate remains recovered from the studied sites. **Cova del Gegant**: 1. Left m1 of *Rhinolophus ferrumequinum* (occlusal view); 2. Right m1 of *Apodemus sylvaticus* (occlusal view); 3. Right m1 of *Microtus (Iberomys) cabrerae* (occlusal view); 4. Right m1 of *Microtus arvalis* (occlusal view). **L'Arbreda cave**: 5. Right mandible of *M. myotis* (buccal and occlusal views); 6. Left M1 and M2 of *Apodemus sylvaticus* (occlusal view); 7. Left m1 of *Arvicola sapidus* (occlusal view); 8. Left m1 of *Microtus (Terricola) duodecimcostatus* (occlusal view); 9. Right m1 of *Chionomys nivalis* (occlusal view); 10. Left m1 of *Microtus agrestis* (occlusal view); 11. Left m1 of *Microtus arvalis* (occlusal view). **Abric Romani**: 12. Left m2 of *Crocidura russula* (buccal view); 13. Left mandible of *Nyctalus lasiopterus* (buccal view); 14. Left mandible of *Pipistrellus pipistrellus* (buccal view); 15. Right M1 of *Apodemus sylvaticus* (occlusal view); 16. Left m1 of *Arvicola sapidus* (occlusal view); 17. Left m1 of *Microtus (Iberomys) cabrerae* (occlusal view); 18. Left m1 of *Microtus (Terricola) duodecimcostatus* (occlusal view); 19. Right humerus of female of *Bufo bufo* (ventral view); 20. Left ilium of *Rana temporaria* (lateral and posterior views); 21. Right ilium of *Rana temporaria* (lateral and posterior views). **Canyars**: 22. Left m1 of *Microtus (Terricola) duodecimcostatus* (occlusal view); 23. Left m1 of *Microtus (Iberomys) cabrerae* (occlusal view); 24. Right m1 of *Microtus agrestis* (occlusal view); 25. Right m1 of *Microtus arvalis* (occlusal view); 26. Right m1 of *Apodemus sylvaticus* (occlusal view); 27. Right m1 of *Eliomys quercinus* (occlusal view); 28. m3 of *Talpa europaea* (occlusal and labial views); 29. Left mandible of *Crocidura* sp. (m2−m3) (labial view). **Teixoneres cave**: 30. Left m1 of *Pliomys lenki* (occlusal and labial views); 31. Right m1 of *Microtus (Terricola) duodecimcostatus* (occlusal view); 32. Left m1 of *Arvicola sapidus* (occlusal view); 33. Left mandible of *Neomys fodiens* (posterior and lingual views); 34. Right M1 of *Chionomys nivalis* (occlusal view). All scales = 2 mm.

lithics preserved in the succession of layers provide evidence that Neanderthals occupied the site at different times within what is known as Marine Isotopic Stage 3 (MIS 3), about 70–40 ka (Carbonell, 2002). The excavations at the site have been conducted in three different periods, the first of which extended from 1909 to 1929, the second from 1956 to 1961, while the currently on-going excavations, to which this paper refers, started in 1983 (Carbonell et al., 1996). Sampling for pollen analysis at different levels of the succession shows changes in the structure and composition of the vegetation over time, leading to the differentiation of five distinct paleoclimatic phases (Burjachs and Julià, 1994; Allué et al., 2012; Burjachs et al., 2012).

The small-vertebrate remains from the Abric Romaní come from level O to level D, where they are discontinuously represented. The age of these levels, dated by uranium-series, ranges between 58 and 44 ka (Bishoff et al., 1988). The microvertebrate data from the Abric Romaní have been previously published by Allué et al. (2012), Burjachs et al. (2012), López-García (2008, 2011), López-García and Morales-Hidalgo (2007), López-García and Cuenca-Bescós (2010) and López-García et al. (2009). The small vertebrates recovered from these levels comprise 404 identified remains and 216 individuals, corresponding to 21 taxa (Table 1; Fig. 2). From a taphonomical point of view, most of the analyzed elements show no signs of digestion. Light digestion is observed in femur and humerus bones. Moderate digestion is only represented in an isolated lower first molar (m1) of *Microtus arvalis*. According to Andrews (1990), this degree of alteration falls within category 1 modification. Category 1 may indicate several bird predators, but only two of these are possibly responsible for the Abric Romaní small-vertebrate accumulations: *Asio otus* (long-eared owl) and *T. alba* (barn owl). Both species are present in semi-open forests, with the nearby presence of large clear areas, at altitudes below 1300–1500 m a.s.l. (Allué et al., 2012; Burjachs et al., 2012). The results obtained by the habitat weightings method show for all levels a landscape dominated by forest formations (55%), although open meadows are well represented at around 21% (Table 2). The results obtained using the mutual climatic range method show that all levels had mean annual temperatures lower than at present (MAT$_{Romani (O-D)}$ = −7.5 to −4.5 °C; at present MAT = 15.3 °C at the meteorological station of Barcelona airport, data from Font-Tullot (2000) (Table 3). Furthermore, the mean annual precipitation was higher than at present in all the levels analyzed (MAP$_{Romani (O-D)}$ = +60 to +349 mm; at present MAP = 659 mm, data from Font-Tullot (2000) (Table 3).

3.3. L'Arbreda cave

L'Arbreda cave is located in the area to the south of the caves of Reclau (Serinyà) between the western margin of Pla d'Usall and the Serinyadell River (Fig. 1). Pla d'Usall forms part of the lacustrine basin of Banyoles-Besalú bounded by Eocene and Neogene reliefs and filled with Plio-Pleistocene material. This cave is a shelter formed by a travertine cascade with a degree of karstification and contains sedimentary deposits from the beginning of the Upper Pleistocene to the Early Holocene. The Mousterian level (I), which is of interest here, has been dated by ^{14}C to between 41.4 ± 1.6 and 39.4 ± 1.4 ka (Bischoff et al., 1989). According to pollen studies, the changes in the composition and structure of plants allow seven pollen zones to be distinguished; level I corresponds to zone I, characterized by two alternating periods, one humid and temperate and another dry and cold period (Burjachs and Renault-Miskowski, 1992). The herpetofaunal remains are still under study, but the small mammals have been published by López-García (2011) and López-García and Cuenca-Bescós (2010). The material recovered from level I of l'Arbreda cave comprises 385 identified

remains and 202 individuals, corresponding to a total of 10 taxa (Table 1; Fig. 2). The predator responsible for the accumulation of non-flying small mammals was probably an avian predator (Category 1 *sensu* Andrews, 1990) (López-García and Cuenca-Bescós, 2010; López-García, 2011). On the other hand, the over-representation of the bat species *Myotis myotis* (70% of the total sample) suggests that this sample was attributed by a thanatocenosis from a colony of *M. myotis* (López-García, 2011). The habitat weightings method applied to the micromammal assemblage of l'Arbreda cave shows a landscape dominated by forest formations (68%), with a small percentage (25%) of open-meadow landscape (Table 2). The mutual climatic range method shows mean annual temperatures for level I lower than at present (MAT$_{Arbreda (I)}$ = −6 °C; at present MAT = 15.1 °C at the meteorological station of Girona, data from Font-Tullot (2000) (Table 3). On the other hand, the mean annual precipitation was higher than at present (MAP$_{Arbreda (I)}$ = +118 mm; at present MAP = 802 mm, data from Font-Tullot (2000).

3.4. Canyars

Canyars is a fluvial deposit located in the town of Gavà, some 20 km to the west of Barcelona, in the Vall de la Sentiu valley, one of the creeks originating at the foot of the Garraf Massif and flowing into the beaches of the Mediterranean seaboard (Fig. 1). The site was discovered in 2005 (Daura et al., 2013) by an amateur archaeologist (C. Valls) and completely excavated by the Grup de Recerca del Quaternari from June to November 2007.

Canyars is located in what is now an abandoned gravel-pit, which was active until the 1960s. Pleistocene fossils from the same area were already known. The first discovery from Vall de la Sentiu was an Upper Pleistocene paleontological collection from a location that is not known precisely (Villalta, 1953); another corresponds to isolated proboscidean remains (cf. *Mammuthus*) from a different gravel-pit 700 m from Canyars (Daura and Sanz, 2009). Other paleontological remains from 10 adjacent valleys have been recovered in the course of archaeological survey excavations; Riera de Sant Llorenç has provided large-mammal remains, mainly *Mammuthus*, *Coelodonta* and *Equus* (Daura et al., 2013).

Canyars is located at the confluence of two creeks, Riera dels Canyars and Riera de Can Llong. The former is the main stream, and its distal part probably consisted of a floodplain crossed by channels, nowadays modified by farming activity (Daura et al., 2013). A total of nine lithological units have been described, consisting of a poorly sorted and coarse-grained complex of gradational and incised fluvial deposits.

The paleontological remains come from the only archaeological unit (MLU), consisting of mud-supported gravel filling a well-defined paleochannel (LDU). Several charcoal samples were collected for radiocarbon dating, yielding a ^{14}C date of ∼34.6 ^{14}C (∼39.6 cal.) ka BP (overall mean age estimate from four radiocarbon dates by Daura et al. (2013). The small-vertebrate association from Canyars comprises 182 identified remains and 26 individuals, corresponding to a total of 16 taxa (Table 1; Fig. 2), which have been previously published by López-García et al. (2013). The taphonomic study of the microvertebrate fossils involved an analysis of the fragmentation and the digestion marks on the remains, and the results were compared with those obtained by studying modern pellets from well-known predators. Alterations caused by digestion were found in most of the small mammals and in 32% of the amphibians and reptiles (*Pelodytes punctatus*, *Bufo calamita* and *Anguis fragilis*). The high percentage of small-mammal incisors, molars and postcranial elements showing digestion marks and the degree of alteration point to the presence of a category 3 predator, which includes several avian predators (Andrews, 1990),

such as *Falco tinnunculus*. The general levels of representation and breakage lend weight to this hypothesis. This suggests that in both cases the accumulation is associated with predation (López-García et al., 2013). The habitat weightings method applied to the small-vertebrate assemblage shows an evenly balanced representation between an open-meadow (51%) and a woodland environment (49%) (Table 2). The mutual climatic range method shows lower mean annual temperatures than today (MAT$_{Canyars}$ = −5.2 °C; at present MAT = 15.3 °C at the meteorological station of Barcelona airport, data from Font-Tullot, 2000) (Table 3). The mean annual precipitation was higher than nowadays (MAP$_{Canyars}$ = +98.6 mm; at present MAP = 659 mm, data from Font-Tullot (2000) (Table 3).

3.5. Teixoneres cave

Teixoneres cave is one of the caves belonging to the karst system called the Toll caves. Located near the village of Moià (Barcelona, Spain) at 900 m a.s.l. (Fig. 1), it forms a course of galleries more than 2 km long that contains several archaeological deposits from different chronologies. Some, such as the one known as the South Gallery, have been partially excavated since the 1950s and 1970s, bringing to light an important Holocene sequence and Late Pleistocene paleontological record (Rosell et al., 2010). This complex was formed by the drainage system of Mal torrent, which modeled the Neogene limestone (Collsuspina Formation) and configures the endokarst landscape observed nowadays. Teixoneres cave is thus an ancient fossilized outlet of the Toll cave system. Teixoneres is filled with a 6 m-thick sediment package containing at least 15 archaeo-paleontological levels. We have considered the first part of the sequence (levels I to IV), belonging to the Late Pleistocene. Levels I and IV correspond to warm and wet periods, during which water and carbonate precipitation sealed the stratigraphy forming two continuous stalagmitic beds. Uranium-series dating has confidently situated the level IV stalagmite within MIS5c, with an average date of 100.3 ± 6.1 ka (Tissoux et al., 2006). The data are uncertain for the level I stalagmite, which probably corresponds to MIS2. Method correction, to take account of the uranium contamination of the sample, places level I in the Late Glacial between ca 16—14 ka (Tissoux et al., 2006). Extensive work carried out in the outer part of the cave, which today is an open-air site due to the progressive collapse of the cornice, allowed the excavation of levels II, IIb, III and IIIb in the areas where the most intense human activity was expected (Rosell et al., 2010). The level that concerns us for this study, which belongs to MIS3, is level II, with a relative chronology between 50 and 30 ka (López-García et al., 2012b). The small-vertebrate association from this level comprises 901 identified remains and 374 individuals and corresponds to 33 taxa (Table 1; Fig. 2), which have been previously published by López-García et al. (2012b). The pattern of skeletal element frequencies indicates a good representation of small-vertebrate skeleton elements. These show little breakage, and the light-to-moderate digestion seen in the microtine teeth, with rounding of the triangles, indicates that the bones were probably accumulated by an avian predator of category 1 (*sensu* Andrews, 1990), such as the barn owl (*T. alba*) (López-García et al., 2012b). The habitat weightings method applied to the small-vertebrate assemblage shows the clear dominance of a forest environment (72%) against a low percentage (28%) of open meadows (Table 2). The mutual climatic range method shows lower mean annual temperatures than today (MAT$_{Teixoneres (II)}$ = −7.7 °C; at present MAT = 15.3 °C at the meteorological station of Barcelona airport, data from Font-Tullot (2000) (Table 3). Also, the mean annual precipitation was higher than nowadays (MAP$_{Teixoneres (II)}$ = +349 mm; at present MAP = 659 mm, data from Font-Tullot (2000) (Table 3).

4. Discussion

4.1. Paleoenvironmental and paleoclimatic approach

The environmental and climatic evolution during Marine Isotope Stage 3 (MIS3) in the northeastern Iberian Peninsula can be determined on the basis of study of the five archaeo-paleontological sites: Cova del Gegant, Abric Romaní, l'Arbreda cave, Canyars and Teixoneres. The chronological framework represented by these localities corresponds closely to MIS3 (60—30 ka) (Bischoff et al., 1988, 1989; Daura et al., 2010; López-García et al., 2012b; Daura et al., 2013). MIS3 is particularly well represented in Iberia. It is characterized by a dynamic that alternates phases of forest development and the expansion of semi-arid areas in accordance with the warming and cooling, respectively, of the sea-surface temperatures (Fletcher and Sánchez-Goñi, 2008). In general, the data obtained by the habitat weightings method show that independently of the climatic fluctuations the landscape during MIS3 was dominated by open-forest formations, as shown by the relative abundance of species such as *M. myotis* and *Apodemus sylvaticus* (Table 1) at the studied sites. On the other hand, the data obtained by the mutual climatic range method show that the mean annual temperatures (MAT) for the whole MIS3 were colder than at present by between 7.7 C° and 2.8 C°, and the mean annual precipitation (MAP) was higher by between 75 mm and 350 mm. It is not easy to link our results with the different Heinrich events and interstadials that occurred during MIS3, because the different authors who have studied the climate changes in the Iberian Peninsula (e.g. Sánchez-Goñi and d'Errico, 2005; Tzedakis et al., 2007; Fletcher and Sánchez-Goñi, 2008, and others) do not agree upon the exact chronology of these events. The only point upon which these authors do agree is that Heinrich events are connected with lower summer temperatures and an increase in precipitation, resulting in colder summers and wetter winters. Despite this, we have made an attempt to correlate the MAT, the MTW, the MTC, and MAP obtained by studying microvertebrates with global climate changes. Thus, level O of the Abric Romaní would correspond to a cold period between interstadials 14 (IS 14) and 17 (IS 17) (Fig. 3). This is indicated by the low values in MAT (−5.3 °C) and MTW (−5.3 °C) and by the presence in this level of taxa with mid-European requirements that currently live at higher latitudes of the Pyrenees and pre-Pyrenees, such as *Rana temporaria*, *Sorex* gr. *coronatus − araneus*, *Talpa europaea*, *M. arvalis* and *Microtus agrestis* (Sans-Fuentes and Ventura, 2000; López-García et al., 2010). Level E of the Abric Romaní can be correlated with Heinrich Event 5 (H5) (Fig. 3). The low values in MTW (−7.1 °C) and the abundance of species with mid-European requirements such as *R. temporaria*, *M. arvalis* and *M. agrestis* (Sans-Fuentes and Ventura, 2000; López-García et al., 2010) testify to this relationship between level E and H5. A similar case occurs with the Canyars level, which could be correlated with Henrich Event 4 (H4) (Fig. 3). The low MTW (−6.08 °C) and the presence of species with mid-European requirements such as *A. fragilis*, *T. europaea*, *M. arvalis* and *M. agrestis* allow us to correlate Canyars with H4. Finally, level II of Teixoneres, which shows the lowest values in MAT (−7.7 °C), MTW (−8.1 °C) and MTC (−6.1 °C), could be related with Heinrich Event 4 or 3 (H4 or H3) (Fig. 3). As occurs in Abric Romaní level O, level E and in Canyars, these data are evidenced in Teixoneres level II by the presence of taxa with mid-European requirements that today live at higher latitudes, such as *R. temporaria*, *Sorex* gr. *coronatus − araneus*, *T. europaea*, *Chionomys nivalis*, *M. arvalis* and *M. agrestis* (Sans-Fuentes and Ventura, 2000; López-García et al., 2010).
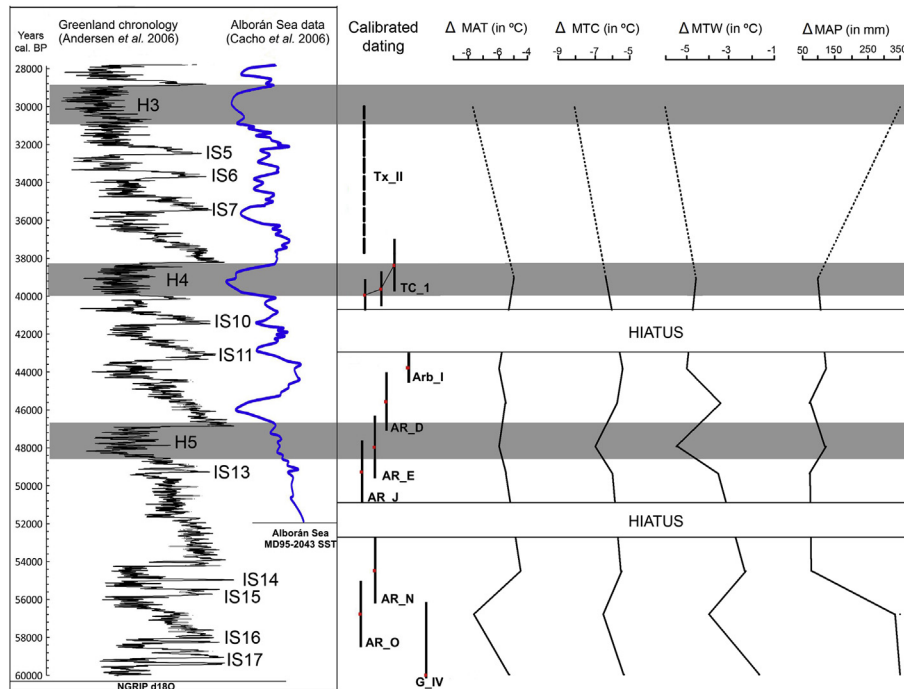
Fig. 3. Approximate correlation between the average (Δ) mean annual temperature (MAT), mean temperature of coldest month (MTC), mean temperature of warmest month (MTW) and mean annual precipitation (MAP) obtained by means of the small-vertebrate assemblages of the studied sites with the oxygen isotope curve of MIS3 and the Alboran sea-surface temperatures. H: Heinrich events: IS: Interstadials; G: Gegant level IV; AR: Abric Romaní; Arb: l'Arbreda cave: TC: Canyars; Tx: Teixoneres.

4.2. The Iberian Peninsula and the Neanderthal context

The Neanderthals lived in the western Palearctic between about 200 and 30 ka (Stewart, 2007). Judging by the large number of fossil discoveries, the Neanderthal range extended significantly eastwards well into the central Palearctic, probably reaching the Altai Mountains and into the Transbaikal in southern Siberia (Davis and Ranov, 1999). In recent years there has been an increase in findings of Middle Paleolithic sites and evidence of Neanderthal remains in the Iberian Peninsula, showing that they survived here until ca. 30–28 ka in the context of a climatic refugium in the southernmost part of this area (Finlayson et al., 2006; Finlayson and Carrión, 2007; Jennings et al., 2011; López-García et al., 2012b). Taking into account the environmental data obtained by means of the small-vertebrate assemblages from the sites studied above (Cova del Gegant, Abric Romaní, l'Arbreda cave, Canyars and Teixoneres cave), it seems clear that the Neanderthals were well adapted to the different climatic and environmental conditions of MIS3 in north-eastern Iberia. Moreover, as occurred during the Early to Middle Pleistocene with other representatives of the genus *Homo* in southwestern Europe (Kahlke et al., 2011; Leroy et al., 2011), the data obtained for the above-mentioned sites (Fig. 4) show that the dispersal and survival of the Neanderthals in the northeastern Iberian Peninsula seem to be closely associated with the existence of woodland formations, as previously suggested by Finlayson and Carrión (2007). Although there are differences in the percentage of forest formations between Canyars (49%) and the other studied sites (Fig. 4), Roche et al. (2004) and Sepulchre et al. (2007) suggest that this may have to do with the fact that H4 is one of the most abrupt of the cooling episodes detected in the North Atlantic Ocean and adjacent continents, resulting in a high percentage representation of open dry meadows in the area around Canyars (Fig. 4). On the other hand, comparing our data with Gorham's cave (López-García et al., 2011), where the evidence of the last Neanderthals

in Europe is found (Finlayson et al., 2006), this site is more much forested (87%) (Fig. 4) than the northeastern parts of Iberia (Cova del Gegant, A. Romaní, l'Arbreda, Canyars and Teixoneres cave), where the woodland ranges between 49 and 79% (Fig. 4). These data are in accordance with the status of the southernmost Iberian Peninsula as a climatic refugium, where the Neanderthals survived until ca. 28 ka BP (Finlayson et al., 2006; Finlayson and Carrión, 2007; Jennings et al., 2011, among others). Furthermore, the southwestern fringes of the Palearctic were probably richer in forested habitats which required some rainfall, and the Neanderthals probably preferred this kind of habitat to open landscape (Stewart, 2007).
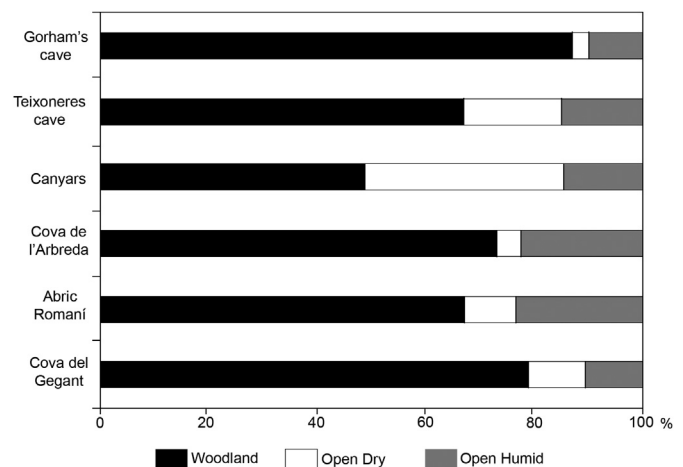

Fig. 4. Environmental comparison between Cova del Gegant, Abric Romaní, l'Arbreda cave, Canyars, Teixoneres cave and Gorham's cave. Data are taken from López-García and Cuenca-Bescós (2010) and López-García et al. (2011, 2012a, 2012b, 2013).

5. Conclusions

The analysis of the small-vertebrate (amphibian, squamate and small-mammal) remains from five MIS3 sites (Cova del Gegant, Abric Romaní, l'Arbreda cave, Canyars and Teixoneres cave) located in the northeastern Iberian Peninsula allows us to draw the following conclusions:

1) The environments during MIS3 mainly correspond to an open forest landscape.
2) The climate during MIS3 was colder and wetter than today in northeastern Iberia, and the fluctuations detected suggest that the Neanderthals who lived around the Iberian Peninsula during this period were well adapted to the territory they inhabited.
3) In the northeastern Iberian Peninsula, the Middle Paleolithic occupations are closely related to the presence of woodland formations.

Acknowledgments

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