Palaeogeography, Palaeoclimatology, Palaeoecology 292 (2010) 453–464

Contents lists available at ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeo

Palaeoenvironmental and palaeoclimatic reconstruction of the Latest Pleistocene of El Portalón Site, Sierra de Atapuerca, northwestern Spain

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ARTICLE INFO

Article history:
Received 30 November 2009
Received in revised form 6 April 2010
Accepted 10 April 2010
Available online 18 April 2010

Keywords:
Small vertebrates
Assemblage evolution
Last Glacial Maximum
Late Pleistocene
Atapuerca
Spain

ABSTRACT

The site of El Portalón is the entrance to the Cueva Mayor karst system, located in the Sierra de Atapuerca (Burgos, Spain). This is an important Holocene archaeological site, which was excavated in the 1970s but from which little has been published. New excavations starting in 2000 have highlighted a deep stratigraphical sequence, with human occupations starting at the end of the Late Pleistocene. In this paper, we present for the first time, on the basis of the small-vertebrate assemblage, palaeoenvironmental and palaeoclimatic reconstructions of the Latest Pleistocene of the Sierra de Atapuerca, well known for its Early to Middle Pleistocene human-bearing localities. The small vertebrates of El Portalón comprise at least 25 species: 4 amphibians (*Alytes obstetricans*, *Bufo bufo*, *Bufo calamita* and *Rana temporaria*); 3 squamates (an indeterminate small-size lacertid, an indeterminate large colubrine and *Vipera* sp.); 6 insectivores (*Sorex* gr. *coronatus-araneus*, *Sorex minutus*, *Neomys fodiens*, *Neomys anomalus*, *Talpa europaea* and *Galemys pyrenaicus*); 2 bats (*Myotis myotis* and *Myotis* gr. *myotis-blythi*); 10 rodents (*Microtus arvalis*, *Microtus agrestis*, *Microtus oeconomus*, *Iberomys cabrerae*, *Chionomys nivalis*, *Terricola duodecimcostatus*, *Arvicola sapidus*, *Arvicola terrestris*, *Apodemus sylvaticus* and *Eliomys quercinus*). These taxa, many of which are ecothermal (sensitive to temperature) show variations in their taxonomic diversity throughout the sequence. Although, with the exception of *M. oeconomus*, they do not differ from the extant fauna of the Iberian Peninsula, they do so in the abundance of their taxonomic assemblage. When the small vertebrates are grouped and studied in terms of vertical trends through the sequence, it is possible to follow environmental and climatic changes. Results from the small-vertebrate associations indicate that the landscape had open habitats in the vicinity of the Atapuerca caves throughout the sequence, with wet locales in the surrounding area. Woodland and water stream meadows were more developed during "warm" periods (Is5, Is6/Is7 and Is3/Is4), whereas during "cold" periods (H3 and LGM) the environment was slightly more humid in response to winter precipitation and the opening of the landscape. These results are compared with pollen analysis and marine isotopic curves, giving a scenario for the palaeoclimatic and palaeoenvironmental changes that occurred during the Latest Pleistocene in the Sierra de Atapuerca.

1. Introduction

The Sierra de Atapuerca is a small hill, roughly 1080 m above sea level, located 15 km to the east of the city of Burgos. It represents a positive montane relief that emerges above the valleys of the Arlanzón, Vena and Pico. It is situated in the north of the Iberian Peninsula, on the northeastern edge of the Northern Meseta and the Duero Basin, and forms part of the Mesozoic fringe of the Iberian System. The Sierra de Atapuerca is separated from the southern edge of the Cantabrian Range by a tectonic corridor known as the *Estrecho de Burgos* ("Strait of

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doi:10.1016/j.palaeo.2010.04.006

Burgos") or *Corredor de La Bureba* ("Bureba Corridor"), which links the Tertiary depressions of the Duero and the Ebro. It displays a transition landscape between mountainous regions and plains, constituting a natural step towards the inland area of the Iberian Peninsula.

Geologically, the Sierra de Atapuerca is composed of Mesozoic rocks, primarily limestones and dolomites from the Upper Cretaceous (Turonian–Lower Santonian), and the syntectonic fringe of the Oligocene–Lower Miocene, which appear folded and fractured under the influence of an anticlinal structure exhibiting a NE-plunge and an Iberian chain direction. About 17 km^2 in extent, the relief of the Sierra de Atapuerca fits the evolution of a Neogene model, with a relatively gentle topography and a warm climate, dissected in part as a result of the imposition of the Quaternary fluvial network (Benito-Calvo & Pérez-González, 2007).

The karst of the Sierra de Atapuerca is characterized by the absolute predominance of endokarstic forms as opposed to exokarstic morphologies, developed in the limestones and dolomites of the Turonian–Lower Santonian of the western edge of the San Vicente Unit. These represent a Mediterranean karst with subhorizontal conduits constituting multilevel systems and formed by subterranean waters close to a former base level, above the level of the current river (the Arlanzón) (Ortega et al., 2005; Ortega, 2009). The set of cavities of San Vicente denotes an inherited, inactive series of more than 4 km of cavities that have been explored (the karstic system of Cueva Mayor-Cueva del Silo and Cueva Peluda, together with Cueva del Compresor) and about 30 fossilized conduits sectioned by a railway cutting (the Trinchera del Ferrocarril), which contain major archaeological and paleontological records from the Lower and Middle

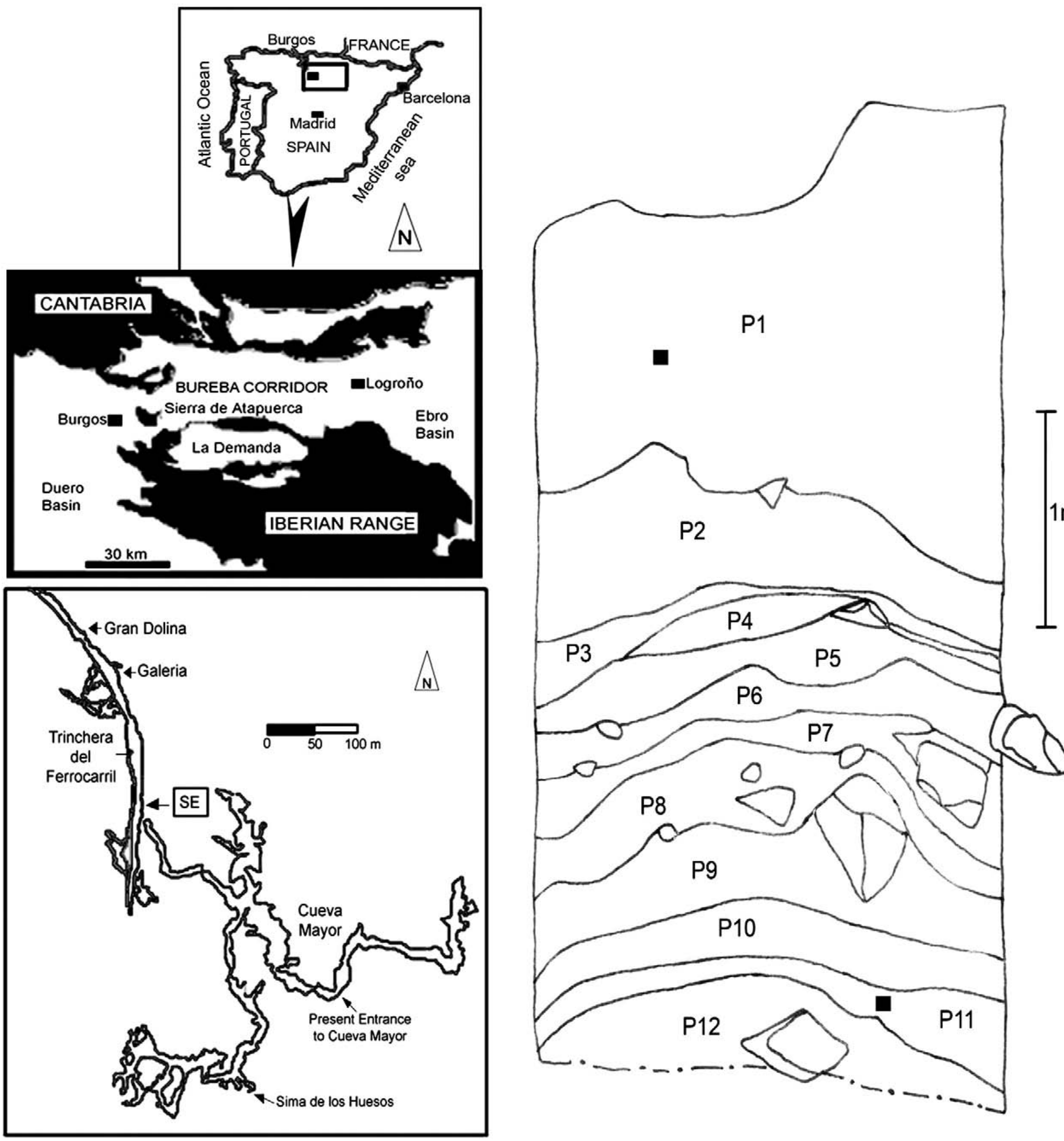

Fig. 1. Upper left: location of the Sierra de Atapuerca (Burgos, Spain). Lower left: location of the trinchera del Ferrocarril (railway trench) and Cueva Mayor karst systems of Atapuerca (modified form Martín Merino et al., 1981). Stratigraphic section of the late Pleistocene layers of El Portalón site until 2005. Black square indicates dated samples.

Pleistocene that are inscribed on the World Heritage List. These sites, such as Elefante, Dolina, Galería and Sima de los Huesos (Fig. 1), will become landmark references for the geomorphological events in their relation to the evolution of the regional landscape.

This area is well documented in the scientific literature on account of the important archaeological and palaeontological discoveries that have been made there, especially the findings of hominids from the Lower Pleistocene of Sima del Elefante and Gran Dolina (*Homo antecessor*) and the Middle Pleistocene of Sima de los Huesos (*Homo heidelbergensis*).

Sima del Elefante and Gran Dolina have provided the oldest hominid fossils from Europe (Carbonell et al., 1995; Bermúdez de Castro et al., 1997; Carbonell et al., 2008).

Sima de los Huesos has yielded the most comprehensive evolutionary and palaeobiological information on the Middle Pleistocene, on the basis of roughly 5000 remains (from some 30 individuals) of *Homo heidelbergensis* (Arsuaga et al., 1997; Martínez et al., 2004).

The first palaeontological interventions at the Trinchera sites were initiated by Villalta and Crusafont towards the end of the 1960s, but it was to be Torres in 1976, during his search for fossil bears of the Iberian Peninsula (Torres, 1987), who first discovered a human mandible at Sima de los Huesos. This finding prompted Professor Emiliano Aguirre to inaugurate the Atapuerca Research Project in 1977, a project that is currently being directed by Juan Luís Arsuaga, Jose María Bermúdez de Castro and Eudald Carbonell (Aguirre, 2001; Carbonell et al., 1995).

2. El Portalón site

The site of El Portalón represents the present-day entrance to Cueva Mayor, which has been used as a habitat on an intense and reiterated basis by the communities that have occupied the Arlanzón Basin at least since recent prehistory. The first work was carried out by G. Clark in 1972 (Clark, 1979), who brought to light an interesting sequence from the Bronze and Iron Ages and the existence of important ancient activities. The work of J. M. Apellániz of the University of Deusto was undertaken between 1973 and 1982, and although his results were never published he showed that there was intense occupation of the area during the Bronze Age (Apellániz & Domingo, 1987; Mínguez, 2005).

The Sierra de Atapuerca sites research team took up these studies again in 2000, noting the mining techniques employed in the former excavation described by Clark. This involved a shaft of roughly 2–2.5 m diameter and more than 10 m depth, which made it possible to study a broad stratigraphic sequence of two main sedimentary units (Fig. 1). The upper unit displays a Holocene chronology and is influenced by human activity (levels 1–9), a consequence of the considerable intensity of the human occupations in the enclave during the Neolithic and the Metal Age. The top of this unit includes the Bronze Age sequences discovered by the teams led by Clark and Apellániz (Ortega et al., 2008a,b).

The lower unit represents the Pleistocene sequence of the site of El Portalón. It is identified with level 10, a sedimentary unit 360 cm in thick and subdivided into 16 sublevels (P1–P16), subject of this study and characterized by natural processes of embedding of clasts within a clayey matrix, the absence of organic material, and an orange coloration. Particularly noteworthy is the presence of macromammal remains and an abundant set of microvertebrate remains, providing the unit with a significant palaeontological character, while it records the weak presence of human activity represented between sublevels P8 and P15, the deposits of which have provided small chips stemming from remains of carvings in flint and quartzite. In chronological terms, this lower sedimentary unit, or level 10, belongs to the final third of the Late Pleistocene. The top of the sequence (sublevel P1) has been dated at 16,890 +/− 80 BP (Beta-209452) by means of ^{14}C AMS, whereas sublevel P11 has been dated at 30,300 +/− 190 BP (Beta-212190).

It is interesting to note that level N9a has a distinct contact with the top of the unit below it. Level N9a is biological in origin and corresponds to deposits of bat guano or "murcielaguina"; it is sterile in archaeological, palaeontological and pollen remains and constitutes a sedimentary hiatus in the stratigraphic sequence of el Portalón de Cueva Mayor (Ortega et al., 2008a,b; Carretero et al., 2008).

Pollen studies carried out on level 10 show that the sequence is dominated by *Pinus*, Ericaceae and Asteraceae, with sporadic appearances of the taxa *Picea*, deciduous *Quercus* and *Corylus*, indicating the existence of woodlands that are cold and humid in character and are not very dense or are in the process of degradation, with non-arboreal pollen (NAP) representing more than 50% in almost all the sublevels, except sublevel P9, where arboreal pollen (AP) attains 50% of the total of pollen grains. The pollen is not distributed homogeneously in the sequence as a whole, and the pollen associations detected in sublevels P12–P1 permit us to distinguish two phases: a lower one (P12–P3) characterized by a progressive decline in diversity that culminates in a sterile phase (P3 and P5); and an upper one (P2 and P1), which exhibits a pattern similar to the lower phase (P12–P3) (Appendix A) (Ruiz Zapata et al., 2006; Ruiz Zapata et al., 2008).

3. Material and methods

3.1. Small-vertebrate sorting and paleontological study

The small-vertebrate fossil remains used for this study consist of disarticulated bone fragments collected by water-screening during the work on the walls of the El Portalón mining shaft. Sediments were recovered from a surface of approximately 1 m^2 along the shaft sequence and divided into 16 samples in accordance with the lithostratigraphy, from sublevel P16 at the bottom to sublevel P1 at the top. A total of 1584 kg of sediment was processed. All the sediment was water-screened using superimposed 10, 5 and 0.5 mm mesh screens, and bagged by layer. In subsequent years, the fossils were processed, sorted and classified at the Institut de Paleoecologia Humana y Evolucio Social of the University Rovira i Virgili (Tarragona, Spain). The small-mammal bony remains were analysed and quantified as part of a PhD thesis (López-García, 2008). The amphibian and squamate reptile bones were analysed subsequently by one of the present authors (H.-A.B.). This assemblage includes a total of 18,602 fragments that correspond to a minimum number of 1221 small mammals and 1024 amphibians and squamates, representing at least 25 taxa (Table 1; Figs. 2–3). The fragments were identified following the general criteria given by Reumer (1984), Rümke (1985) and Niethammer (1990) for insectivores, Brujin and Rumke (1974), Menu (1985) and Sevilla (1988) for bats, Van der Meulen (1973), Cuenca-Bescós et al. (1995), Pasquier (1974) and Damms (1981) for rodents, Bailon (1999), Sanchiz (1984), Esteban and Sanchiz (1985, 1991) and Blain (2005) for anurans, and Szyndlar (1984) and Blain (2005) for squamate reptiles.

The specific attribution of this material rests principally on the best diagnostic elements: humerus and scapula for *Alytes obstetricans*; humerus, ilium, scapula and sacrum for bufonids; ilium for *Rana temporaria*; trunk vertebrae for snakes; mandibles, maxilla and isolated teeth for shrews; isolated teeth and humerus for the Talpidae family; isolated teeth for bats; first lower molars for the Arvicolinae subfamily; and isolated teeth for *Apodemus sylvaticus* and *Eliomys quercinus*.

Moreover, the fossils were grouped using the minimum-number-of-individuals (MNI) method, by means of which we determined the sample (i.e. from each sublevel) by counting the best diagnostic elements, taking into account, whenever possible, side and (for amphibians) sex.

3.2. Palaeoenvironmental reconstruction

Palaeoenvironmental curves ("woodland" and "water") were obtained from the percentage representation of the MNI by species for

Table 1
Representation of the minimum number of individuals (MNI) for microvertebrates from the cave of El Portalón, by sublevels (P1–P16).

	Amphibians				Squamates			Rodents						
	Alytes obtetricans	*Bubo bufo*	*Bufo calamita*	*Rana temporaria*	Lacertidae indet.	Colubrinae indet.	*Vipera* sp.	*Microtus agrestis*	*Microtus arvalis*	*M.agrestis-arvalis*	*Microtus oeconomus*	*Iberomys cabrerae*	*Chionomys nivalis*	*Terricola duodecimcostatus*
P1	1	0	2	2	1	0	0	22	19	17	3	2	11	0
P2	2	1	5	3	0	0	0	18	8	9	0	1	4	0
P3	5	1	12	2	0	0	0	4	1	1	2	0	1	0
P4	2	1	9	2	1	0	1	6	5	3	1	0	1	0
P5	1	0	1	1	0	0	0	4	5	4	0	0	5	0
P6	3	1	9	8	0	0	0	8	14	9	0	0	9	0
P7	22	1	32	24	1	0	1	23	17	39	1	1	8	1
P8	44	3	58	47	1	0	1	53	25	16	7	1	8	2
P9	25	0	14	153	1	0	0	59	79	19	9	2	2	0
P10	34	8	38	28	1	0	1	25	41	9	1	3	9	1
P11	29	3	82	55	1	0	0	29	39	4	4	4	3	1
P12	2	0	10	8	0	0	0	3	15	1	3	0	2	0
P13	1	0	5	5	0	0	0	19	36	3	3	4	1	0
P14	11	0	13	51	0	1	0	19	61	0	1	5	0	0
P15	14	0	49	65	0	0	0	89	116	0	1	3	6	0
P16	1	0	2	1	0	0	0	4	0	0	0	0	4	0
Total	197	19	341	455	7	1	4	385	481	134	36	26	74	5

each sublevel of El Portalón site. In order to reconstruct the "woodland" and "water" environments at El Portalón, we use the method of habitat weightings (see Evans et al., 1981; Andrews, 2006) distributing each small-vertebrate taxon in the habitat(s) they occur at present in the Iberian Peninsula. In accordance with Cuenca-Bescós et al. (2008, 2009), and Blain et al. (2008a), the following were taken as representative "woodland" species, associated with mature forest including woodland margins and forest patches with moderate ground cover: *Apodemus sylvaticus*, *Eliomys quercinus*, *Bufo bufo*, *Rana temporaria* and in a minor way *Vipera* sp.; the following as representative "water" species, along

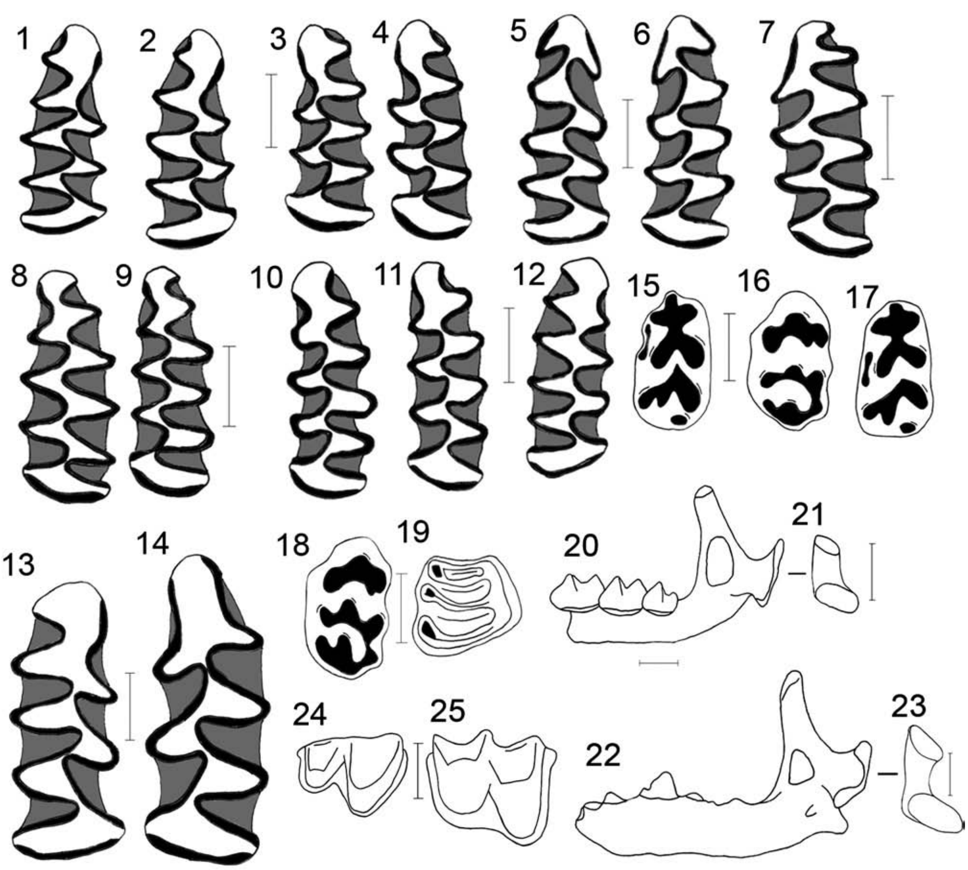

Fig. 2. Some small-mammal remains from El Portalón. 1–4. Two right and two left first lower molars (m1) of *Microtus oeconomus* (occlusal view) (sublevel P9); 5–6. One right and one left m1 of *Chionomys nivalis* (occlusal view) (sublevel P6); 7. Left m1 of *Iberomys cabrerae* (occlusal view) (sublevel P14); 8–9. Two left m1 of *Microtus agrestis* (occlusal view) (sublevel P9); 10–11. Two left m1 of *Microtus arvalis* (occlusal view) (sublevel P9); 12. Right m1 of *Terricola duodecimcostatus* (occlusal view) (sublevel P8); 13. Right m1 of *Arvicola sapidus* (occlusal view) (sublevel P15); 14. Left m1 of *Arvicola terrestris* (occlusal view) (sublevel P15); 15–18. Two left m1 and two right first upper molars (M1) of *Apodemus sylvaticus* (occlusal view) (sublevel P10); 19. Left m1 of *Eliomys quercinus* (occlusal view) (sublevel P10); 20. Right mandible of *Sorex* gr. *coronatus-araneus* (lingual view); 21. Articular condyle of *Sorex* gr. *coronatus-araneus* (posterior view) (sublevel P8); 22. Right mandible of *Neomys fodiens* (lingual view); 23. Articular condyle of *Neomys fodiens* (posterior view) (sublevel P9); 24–25. Third right lower molar (m3) and m1 of *Myotis* gr. *myotis-blythi* (occlusal view) (sublevel P15). Scale 1 mm.

				Insectivores						Bats		
Arvicola terrestris	*Arvicola sapidus*	*Apodemus sylvaticus*	*Eliomys quercinus*	*S.coronatus-araneus*	*Sorex minutus*	*Neomys fodiens*	*Neomys anomalus*	*Talpa europaea*	*Galemys pyrenaicus*	*Myotis myotis*	*M.myotis-blythi*	Total
0	0	0	1	0	0	0	2	0	0	0	0	83
0	1	1	0	0	0	0	0	0	0	0	0	53
0	0	0	1	0	0	0	0	0	0	0	0	30
0	0	0	1	1	0	0	0	0	0	1	0	35
0	0	0	0	0	0	0	0	0	0	0	0	21
0	0	1	0	0	0	0	0	0	0	0	0	62
0	0	0	0	1	0	0	0	0	0	0	0	172
0	1	1	1	2	1	1	0	1	0	1	0	275
1	0	0	1	1	0	2	0	0	0	0	0	368
3	2	5	2	2	2	0	0	3	0	0	1	219
0	1	5	0	3	0	0	0	0	0	0	0	263
0	0	0	0	1	0	0	0	0	0	0	0	45
0	0	0	1	0	2	0	0	0	0	0	0	80
1	0	2	0	0	0	0	0	1	2	0	0	168
3	3	1	0	2	0	1	0	1	0	2	2	358
0	0	0	0	0	0	0	0	0	0	0	0	12
8	8	16	8	13	5	4	2	6	2	4	3	2244

streams, lakes and ponds: *Arvicola sapidus*, *Neomys fodiens* and *Galemys pyrenaicus*.

The “heat” curve was obtained from the percentage representation of the MNI by species that prefer warm conditions for each sublevel of El Portalón site. Taking into account the small-vertebrate species with currently Mediterranean climatic preferences (Palombo & Gisbert, 2005), this includes the taxa associated with wet-winter and dry-summer conditions, like *Iberomys cabrerae* and *Terricola duodecimcostatus*.

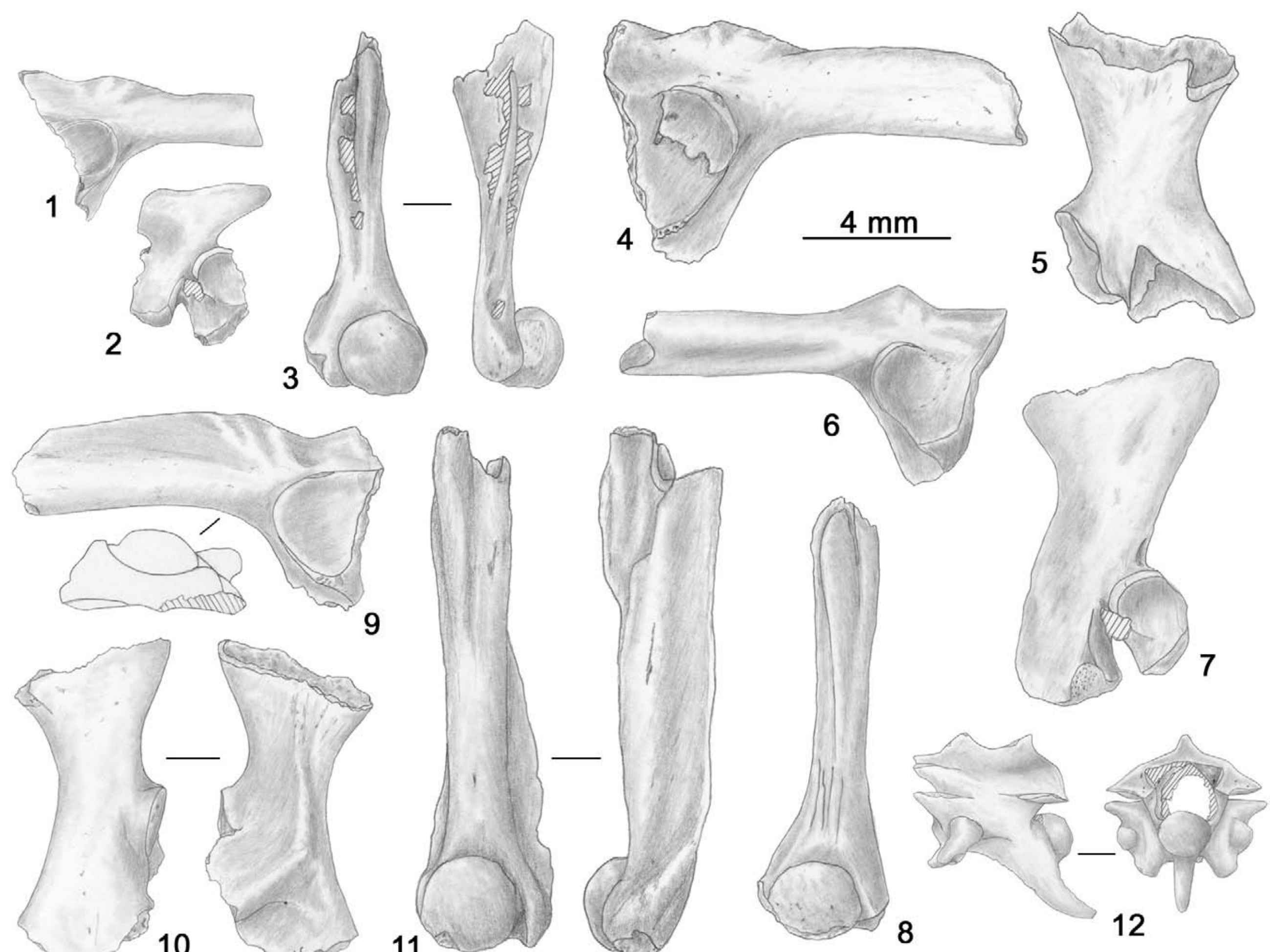

Fig. 3. Some amphibian and squamate reptile remains from El Portalón (sublevel P7). 1–3: *Alytes obstetricans*. 1. Right ilium, lateral view; 2. Left scapula, dorsal view; 3. Left humerus, ventral and medial views. 4 and 5: *Bufo bufo*. 4. Right ilium, lateral view; 5. Right scapula, dorsal view. 6–8: *Bufo calamita*. 6. Left ilium, lateral view; 7. Left scapula, lateral view; 8. Right humerus of female, ventral view. 9–11: *Rana temporaria*. 9. Left ilium, lateral and posterior views; 10. Left scapula, dorsal and ventral views; 11. Right humerus of male, ventral and medial views. 12: *Vipera* sp., anterior trunk vertebra, left lateral and posterior views.

3.3. Palaeoclimatic reconstruction

Climatically, the Iberian Peninsula may be considered as a minicontinent due to its large latitudinal range (between the parallels 36° and 44°N), its geographical position between Atlantic (temperate-cold) and African–Mediterranean (temperate-warm or subtropical) influences, and its complex orography. The Iberian Peninsula is one of the most mountainous areas of Europe, and these mountains play a major role in the characterization of its climatic diversity. Thus, climatic conditions may change abruptly over a few hundred kilometers, from the mildness of the seashore to the harshness of coastal mountain summits resulting in a great variety of climates. As a result, diverse small-vertebrate assemblages with opposing climatic requirements may coexist over a short distance and time allowing correlation of taxonomic change in a fossil locality with a climate change.

In order to evaluate the palaeoclimatic changes along the El Portalón sequence, we evaluated the current distribution of all taxa occurring in each level permitting us to calculate potential palaeoclimatic conditions (mutual climatic range method = MCR). On the basis of the distribution of the extant Iberian fauna we simply identify the geographical region where all the species present in a stratigraphical level currently live. As explained in López-García et al. (2008) and Agustí et al. (2009), there are some fossil or extant taxa that do not currently intersect with other species in the Iberian Peninsula (in our case *Microtus oeconomus* shows a northernmost distribution today). Nevertheless if they do not participate to the intersection, climatic requirements of their extant representatives may be compared with climatic values obtained from the overall association. Because our sources for the distribution of the small-vertebrate taxa (Palombo & Gisbert, 2005; Pleguezuelos et al., 2004) are based on a 10×10 km UTM network, climatic data are resolved to 10×10 km squares. Careful attention was paid to ensure that the real current distribution of each species corresponds to the potential ecological/climatic distribution and has not been strongly affected by other limiting or perturbing parameters such as urban development, the human impact on the landscape, predation, competition with other species, etc. Several climatic factors are estimated: the mean temperature of the coldest (MTC) and warmest (MTW) month, and the mean precipitation of winter (December, January and February = DJF) and summer (June, July and August = JJA), 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 we can estimate the climatic parameters and compare them with the weather station in Burgos (current data from Font Tullot, 2000). The Burgos area is currently situated at the boundary between two bioclimatic regions: the Mediterranean realm in its major southern part and the Euro-Siberian realm in its northernmost part. Nevertheless, from a climatic point of view, the small variations in altitude over most of the Burgos territory (700–1000 m) mean that within the Mediterranean part, only the supra-Mediterranean bioclimatic level is represented (Rivas-Martínez, 1986). Burgos has a MTC (January) of 2.6 °C with absolute minima reaching −22 °C (weather station of Burgos air base, 881 m above sea level), making it one of the coldest cities in the Iberian Peninsula (Font Tullot, 2000). The MTW (July) is 18.4 °C with absolute maxima reaching 38 °C (in July and August). The mean winter precipitation (DJF) is 136 mm and the mean summer precipitation (JJA) is 71 mm (Font Tullot, 2000).

4. Taphonomic remarks

Although a complete taphonomic study has not been performed in the El Portalón sublevels, some preliminary remarks can be made. The pattern of skeletal element frequencies indicates a good representation of small-mammal skeleton elements. These show little breakage, and little or no gastric digestion. When present, digestion is light. These characteristics indicate that the fossils were probably accumulated by an avian predator of the category 1 (*sensu* Andrews, 1990) such as the barn owl or the Eurasian eagle owl (Fernández-Jalvo, 1995; Weissbrod et al., 2005). On the other hand, with the exception of *Microtus oeconomus* and *Iberomys cabrerae*, all the small-mammal taxa represented in the late Pleistocene layers of El Portalón site are currently found in the Sierra de Atapuerca. Nowadays there are 41 small-mammal species in this part of the Burgos Province, including insectivores, bats and rodents (Palombo & Gisbert, 2005; Blanco 1998a,b; Velasco et al., 2005). Excluding bats because of the fragility of their bones and the species linked with anthropization (like *Rattus* and *Mus*) El Portalón small-mammal assemblage corresponds to 80% of the current small-mammal fauna in the Sierra de Atapuerca.

Although we are not able to specify the predator responsible for the accumulation, there are no indications of alteration to suggest that the El Portalón assemblage is not representative of the ecosystem in the immediate vicinity of the cave at the time when the remains were deposited.

From another standpoint, occasional predation on bats by nocturnal birds of prey might account for the isolated teeth at El Portalón site, though *in-situ* death might also account for these, since the species in question is known to frequent caves.

As far as amphibians and squamate reptiles are concerned, the NISP/MNI ratio is rather high and similar for each taxon, suggesting good preservation of the remains and possibly also that these remains were the result of both the action of nocturnal birds of prey and the accumulation of dead animals in the course of hibernation or estivation in the cave. Moreover, at least in the Iberian Peninsula, predators that occasionally catch amphibians and/or squamates are considered opportunistic, so fossil accumulations are qualitatively and quantitatively representative of the immediate environment surrounding the cave.

5. Small-vertebrate assemblages of El Portalón site

There are no taxonomical differences in the small vertebrates between the base and the top of the El Portalón sequence. The assemblage remains qualitatively quite unchanged throughout the cold and temperate phases of the Latest Pleistocene. Among the species occurring in El Portalón some are well represented throughout the sequence whereas others only appear in small numbers.

5.1. Small mammals

The small-mammal distribution in the cave of El Portalón is characterized by the presence throughout the whole sequence of *Microtus arvalis*, *Microtus agrestis*, *Microtus oeconomus* and *Chionomys nivalis*. The thermophilous taxa such as *Iberomys cabrerae* and *Terricola duodecimcostatus* and the species associated with water streams such as *Arvicola sapidus*, *Neomys fodiens* and *Galemys pyrenaicus* seem to have a distribution linked with the warm temperate interstadial periods (Fig. 4). The lower, central and top parts of the sequence that contain sublevels P15–P14, P11 to P7 and P2–P1 show the highest small-mammal diversity (Fig. 4). From a quantitative point of view, the common vole (*Microtus arvalis*) and the field vole (*Microtus agrestis*) are very abundant in all the El Portalón sequence, often accounting for more than 50% of the total in each sample. Among the fossil material analysed here, *M. arvalis* corresponds to 865 remains (i.e. 42.5%) and 481 individuals (i.e. 39.5%), and *M. agrestis* corresponds to 683 remains (i.e. 33.5%) and 385 individuals (i.e. 31.5%). This great abundance is relatively common in Late Pleistocene cave localities (Pokines, 1998; Sesé, 1994, 2005; Cuenca-Bescós et al., 2008, 2009, 2010a; López-García, 2008), and today as well both species are very abundant in the north of Spain, including the province of Burgos. The abundance of *M. arvalis* and *M. agrestis* is currently reported to be higher in open lands, for they are common in relatively humid regions of Spain (Palombo & Gisbert, 2005; Velasco et al., 2005).

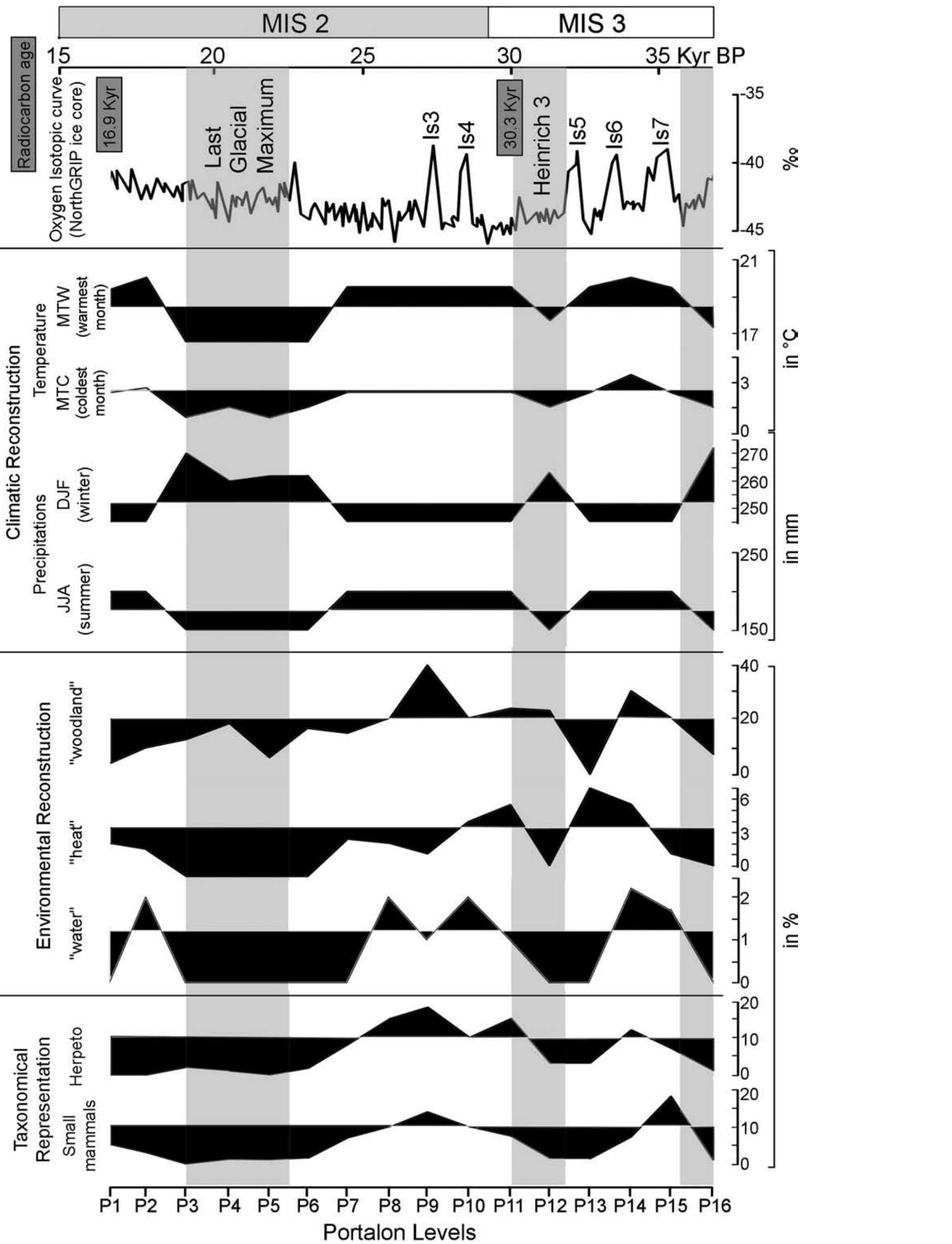

Fig. 4. The proposed correlation of the El Portalón sequence with the Late Pleistocene oxygen-isotope units. From right to left: $\delta^{18}O$ curve obtained from the NorthGRIP ice core, calibrated; temperature of the warmest month (MTW); temperature of the coldest month (MTC); winter precipitation (DJF); summer precipitation (JJA); representation of microvertebrate taxa associated with woodland environments ("woodland"); representation of thermophilous microvertebrate taxa ("heat"); representation of micromammal taxa associated with aquatic environments ("water"); evolution of the taxonomic representation of amphibians and reptiles (Herpeto) and small mammals respectively. The separation line of the curves represents the average values obtained for each sublevel of El Portalón.

5.2. Amphibians and squamate reptiles

In comparison with the Early–Middle Pleistocene localities of Atapuerca (Blain, 2005; Blain et al., 2008a,b, 2009; Cuenca-Bescós et al., 2010b), the El Portalón assemblage is characterized by a large number of remains that display a much lower diversity than the earlier associations.

Within the amphibian and squamate reptile assemblage, *Rana temporaria* (44.4%) and *Bufo calamita* (33.3%) are most abundant. Although varying in their numbers, the amphibians and squamate reptiles do not show important qualitative variation at any point in the El Portalón sequence. In the whole sequence, *Alytes obstetricans*, *Bufo calamita*, *Rana temporaria* and to a lesser extent *Bufo bufo*, small lacertids and *Vipera* sp. are well represented. An indeterminate large colubrine snake is only present in sublevel P14, a relatively temperate period.

5.3. Quantitative evolution

The change in the representation of taxa in the El Portalón sequence (Fig. 4) follows a similar pattern both for amphibians and squamate reptiles and for small mammals. There are two peaks of increase in the representation of the taxa from these groups in sublevels P14–P15 and P8–P9, coinciding with a rise in the representation of thermophilous taxa, a rise in the representation of taxa associated with forest environments, a rise in the representation of taxa associated with aquatic environments, and an increase in the MTW, the MTC and the JJA precipitation. By contrast, there is lower representation of the taxa in sublevels P12–P13 and P7–P3, coinciding with a decrease in the representation of thermophilous taxa, a decrease in the representation of taxa associated with forest environments, the absence of a representation of taxa associated with aquatic environments, and a fall in the MTW, the MTC and the JJA precipitation.

6. Palaeoclimatic and palaeoenvironmental reconstruction

6.1. Climatic reconstruction

The mean temperature of the warmest month (MTW) in the sublevels of El Portalón (P16–P1) varies between −2.5 °C and 2.5 °C with respect to the current mean (MTW_{Burgos} = 18.5 °C; recent data Font Tullot, 2000). In sublevels P16, P12 and P6–P3 the MTW is between 2 °C and 1.2 °C lower than at present, reaching its lowest levels in sublevels P6–P3 (MTW_{P6-P3} = 16.5 °C). In sublevels P15–P13, P11–P7 and P2–P1 the MTW is between +0.8 °C and +1.2 °C higher than at present, reaching its highest levels in sublevels P14 (MTW_{P14} = 20 °C) and P2 (MTW_{P2} = 20.2 °C) (Table 2; Fig. 4). The mean temperature of the coldest month (MTC) in the sublevels of El Portalón (P16–P1) varies between −1 °C and 3.5 °C with respect to the current mean (MTC_{Burgos} = 2.6 °C; recent data Font Tullot, 2000). In sublevels P16, P12–P13 and P6–P3 the MTC is between 1.1 °C and 0.6 °C lower than at present, reaching its lowest levels in sublevels P6–P3 (MTC_{P6-P3} = 1.5 °C). In sublevels P14 and P2 the MTC is between +0.2 °C and +0.7 °C higher than at present, reaching its highest level in sublevel P14 (MTC = 3.3 °C). In the other levels (P1, P7–P11, P13 and P15), the MTC is similar to the current one in Burgos (Table 2; Fig. 4).

All these values are concordant with the present ecology of *M. oeconomus* whose current distribution in northern Europe corresponds to mean annual temperatures lower than 10 °C with MTW lower than 17 °C and MTC lower than 5 °C.

The percentage representation for thermophilous taxa throughout the sequence of the Late Pleistocene of El Portalón is not very high (Table 3; Fig. 4). Even so, an increase in the representation of these taxa can be made out in sublevels P15–P14, coinciding with the increase in the taxa associated with woodland in P15, and the increase in the MTW, the MTC and the JJA precipitation. By contrast, a decrease in the representation of the thermophilous taxa can be observed in sublevel P12, coinciding with the fall in the representation of the taxa associated with woodland in sublevels P12–P13, the decrease in the AP in sublevel P12 and the fall in the MTW, the MTC and the JJA in the same sublevel. Moreover, a decrease in the representation of these taxa can be ascertained in sublevels P7–P3, coinciding with the progressive decline in the representation of microvertebrate taxa associated with forest environments and connected with the decrease in the MTW, the MTC and the JJA precipitation.

Both the mean winter precipitation (DJF: i.e. 240–275 mm) and the mean summer precipitation (JJA: i.e. 150–250 mm) are higher in the sublevels of El Portalón than currently observed in these two seasons in Burgos (DJF = 136 mm; JJA = 71 mm; recent data Font Tullot, 1983, 2000). As can be observed in Fig. 4, the figures for JJA follow the tendency of the MTW and the MTC, whereas the figures for DJF show an opposite tendency. We thus observe that winter precipitation (DJF) increases in cold periods, whereas in mild periods this precipitation decreases. The inverse is the case for JJA precipitation, which falls in cold periods and reaches its highest levels in more temperate periods.

6.2. Environmental reconstruction

The relationship between microvertebrate taxa associated with woodland environments and with open environments shows various points of increase in the representation of the woodland taxa in sublevels P14 and P9 (Table 3; Fig. 4), coinciding moreover with the increase in the MTW, the MTC and the JJA precipitation for both levels. By contrast, there is a pronounced reduction in the representation of the taxa associated with forest environments in sublevels P12–P13, coinciding with the beginning of the decrease in the MTW, the MTC and the JJA in these sublevels. Furthermore, starting from sublevel P7 there is a progressive decline in the representation of the taxa

Table 2
Relation of temperature and precipitation for the sublevels of the cave of El Portalón. MTW (mean temperature of the warmest month); MTC (mean temperature of the coldest month); DJF (mean precipitation for winter); JJA (mean precipitation for summer). Mean (mean of the values obtained); Max (maximum of the values obtained); Min (minimum of the values obtained); SD (standard deviation of the values obtained).

	MTW				MTC				DJF				JJA			
	Mean	Max	Min	SD	Mean	Max	Min	SD	Mean	Max	Min	SD	Mean	Max	Min	SD
P1	19.3	20.5	18.5	1.0	2.5	3.0	2.0	0.5	244	244	244	0	197	197	197	0
P2	20.2	20.5	20.0	0.3	2.7	3.0	2.5	0.3	244	244	244	0	197	197	197	0
P3	16.4	21.0	14.0	1.2	1.5	10.0	−2.0	2.3	270	408	95	86	153	230	93	51
P4	16.5	20.5	14.0	1.1	1.9	10.0	−2.0	2.9	260	408	95	77	153	230	93	55
P5	16.5	20.0	14.0	1.2	1.5	9.0	−2.0	2.2	263	408	95	76	154	230	93	53
P6	16.5	20.5	14.0	1.2	1.9	10.0	−2.0	2.8	263	408	95	76	154	230	93	53
P7	19.6	20.5	18.5	1.0	2.5	3.0	2.0	0.5	244	244	244	0	197	197	197	0
P8	19.6	20.5	18.5	1.0	2.5	3.0	2.0	0.5	244	244	244	0	197	197	197	0
P9	19.6	20.5	18.5	1.0	2.5	3.0	2.0	0.5	244	244	244	0	197	197	197	0
P10	19.6	20.5	18.5	1.0	2.5	3.0	2.0	0.5	244	244	244	0	197	197	197	0
P11	19.6	20.5	18.5	1.0	2.5	3.0	2.0	0.5	244	244	244	0	197	197	197	0
P12	17.6	21.0	14.0	1.5	2.1	10.0	−2.0	2.7	263	408	95	83	156	230	93	53
P13	19.6	20.5	18.5	1.0	2.5	3.0	2.0	0.5	244	244	244	0	197	197	197	0
P14	20.0	20.5	19.5	0.4	3.3	4.5	2.5	0.8	244	244	244	0	197	197	197	0
P15	19.6	20.5	18.5	1.0	2.5	3.0	2.0	0.5	244	244	244	0	197	197	197	0
P16	17.3	21.0	14.0	1.5	2.0	9.0	−2.0	2.7	273	408	95	86	156	230	93	52

Table 3
Representation of percentages obtained by means of MNI for the sublevels of El Portalón. "Woodland": percentage representation of microvertebrate taxa associated with woodland environments. "Heat": percentage representation of thermophilous microvertebrate taxa. "Water": percentage representation of micromammal taxa associated with aquatic environments. Herpeto: percentage representation of amphibians and reptiles. Small mammals: percentage representation of micromammals.

	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10	P11	P12	P13	P14	P15	P16
"Woodland"	3.6	9.4	13.3	17.1	4.8	16.1	15.1	19.6	48.1	20.5	24.0	23.2	1.4	31.5	19.6	8.3
"Heat"	2.4	1.9	0.0	0.0	0.0	0.0	1.2	1.1	0.5	1.8	1.9	0.0	5.0	3.6	0.8	0.0
"Water"	0.0	2.0	0.0	0.0	0.0	0.0	0.0	1.7	1.1	1.8	1.1	0.0	0.0	2.2	1.7	0.0
Herpeto	0.6	1.1	2.0	1.6	0.3	2.1	7.9	15.0	18.8	10.7	16.6	3.0	3.0	12.5	7.4	0.4
Small mammals	6.3	3.4	0.8	1.5	1.4	3.3	7.4	9.9	14.3	8.9	7.6	1.5	1.5	7.5	18.8	0.6

associated with woodland environments as one advances through the stratigraphic sequence.

7. Discussion

By means of the variation in the temperature of the atmosphere of Greenland in the course of the last 40 kyr, as reflected in the $\delta^{18}O$ curve obtained from the NorthGRIP ice core and duly calibrated with roughly 28 ^{14}C-dates (Shackleton et al., 2004; Bard et al., 2004), in conjunction with the dates obtained using ^{14}C AMS for sublevels P1 (16,980 ± 80 BP) and P11 (30,300 ± 190 BP) of El Portalón, we have correlated our data for temperature, precipitation, arboreal taxa, thermophilous taxa, aquatic taxa and the change in the representation of microvertebrate taxa with different interstadials and cold events that occurred at the Marine Isotopic Stage transition MIS3–MIS2. Many studies have been carried out on correlations of these periods, with a view to characterizing their effects at the continental level. Most of these have been made using samples from marine pollen sequences (Sánchez-Goñi & d'Errico, 2005; Fletcher & Sánchez-Goñi, 2008; Sánchez-Goñi et al., 2000; Kageyama et al., 2005) and in a few cases continental sequences (such as Lago Grande di Monticchio and Padul) (Allen et al., 1999; Nimmergut, et al., 1999; Pons & Reiller, 1988; Peyron et al., 1998; Sánchez-Goñi et al., 2000). These pollen analyses provide a reasonably detailed record of the fluctuations in the vegetation during MIS3–MIS2 in accordance with the various climatic changes that occurred during these isotopic stages. The evolution of the microvertebrate taxa of the Upper Pleistocene sequence of El Portalón does not provide such detailed fluctuations as those produced by marine or lacustrine pollen. However, they constitute a first attempt at correlation between the various cold events and temperate interstadials on the basis of a non-pollen continental record, allowing us to identify various of these periods within our sequence: an interestadial, Is5, Is6 or Is7 in sublevels P14–P15 (ca. 35 ka), H3 in sublevels P13–P12 (ca. 30 ka), Is3 or Is4 in sublevels P10–P8 (ca. 27 ka), and Last Glacial Maximum in sublevels P6–P3 (ca. 19–22 ka).

7.1. Marine Isotope Stage 3 (48.1 to 26.8 ka BP)

In general, according to pollen analysis, MIS3 is characterized by a dynamic that alternates between phases of forest development and expansion of semi-arid areas in accordance with the warming and cooling, respectively, of the marine surface temperatures (Fletcher & Sánchez-Goñi, 2008). Our study of the microvertebrates of the sublevels of the Upper Pleistocene of El Portalón has allowed us to identify three phases of climatic fluctuation within Marine Isotope Stage 3: Is5, Is6 or Is7; H3; and Is3 or Is4.

7.1.1. Interstadials 5, 6, 7

According to pollen studies, Interstadials Is 8–5 are characterized by the frequent appearance of thermo-Mediterranean taxa (Fletcher & Sánchez-Goñi, 2008). The degree of resolution obtained by studying microvertebrates does not permit us to specify the interstadial in question, but the correlation between our data and the $\delta^{18}O$ curve would place sublevels P14–P15 of El Portalón site in Interstadials 5, 6 or 7 (Is5, Is6 or Is7). As suggested by pollen analysis (Fletcher & Sánchez-Goñi, 2008), the study of microvertebrates characterizes this interstadial period by an increase in the temperatures of the warmest month (MTW) and the coldest month (MTC), and a decrease in winter precipitation (DJF) in conjunction with an increase in summer precipitation (JJA). It is also characterized by a rise in the representation of taxa associated with woodland environments (*Apodemus sylvaticus*, *Eliomys quercinus*, *Bufo bufo*, *Rana temporaria* and *Vipera* sp.), an increase in the representation of thermophilous microvertebrate taxa (*Iberomys cabrerae*, *Terricola duodecimcostatus* and Colubrinae indet.), a rise in the representation of aquatic taxa (*Arvicola sapidus*, *Neomys fodiens* and *Galemys pyrenaicus*) and an increase in the representation of species of amphibians and reptiles and small mammals (Fig. 4; Appendix A).

7.1.2. Heinrich Event 3

A decrease in the values of $\delta^{18}O$, peaks in magnetic susceptibility, an increase in the proportions of the foraminifer *Neogloboquadrina pachyderma*, as well as the appearance of IRD (Iceberg Rafted Detritus), are what define the last six Heinrich Events (H6 to H1) (Cayre et al., 1999). Like the two previous ones (H5 and H4), Heinrich Event 3 (H3) is characterized by a pattern divided into three phases: 1) the first features a reduction in the marine surface temperature, as indicated by a rise in the percentages of *N. pachyderma*. This phase is associated with the first arrival of IRD during Heinrich Event 3, and is contemporaneous with relatively high percentages of Euro-Siberian trees such as deciduous *Quercus* and Ericaceae, as well as with the end of a temperate and humid terrestrial phase; 2) the middle phase is characterized by the maximum input of IRD, the maximum of *N. pachyderma* and the optimal development of steppe vegetation, thus reflecting synchronous terrestrial and oceanic cooling; 3) the ceiling of Heinrich Event 3 (H3) is characterized by a fall in the values of IRD, magnetic susceptibility and $\delta^{18}O$, as well as a decline in the percentages of the cold species *N. pachyderma*. These characteristics are further associated with an increase in the proportions of Euro-Siberian trees and Ericaceae, reflecting a new temperate and humid period at average terrestrial latitudes and North Atlantic ocean latitudes (Sánchez-Goñi et al., 2000). The correlations between the data obtained by the study of microvertebrates and the $\delta^{18}O$ curve would situate sublevels P13–P12 of the cave of El Portalón in one of the humid and relatively cold phases of Heinrich Event 3 (H3). According to the analysis of microvertebrates, this event would be characterized by a slight decrease in the temperatures of the warmest month (MTW) and the coldest month (MTC), and an increase in winter precipitation (DJF) together with a decrease in summer precipitation (JJA). It would also feature a decline in the representation of taxa associated with woodland environments (*Apodemus sylvaticus*, *Eliomys quercinus*, *Bufo bufo*, *Rana temporaria* and *Vipera* sp.), a decrease in the representation of thermophilous microvertebrate taxa (*Iberomys cabrerae*, *Terricola duodecimcostatus* and Colubrinae indet.), the absence of any representation of aquatic taxa (*Arvicola sapidus*, *Neomys fodiens* and *Galemys pyrenaicus*) and a fall in the representation of species of amphibians and reptiles and small mammals (Fig. 4; Appendix A).

7.1.3. Interstadials 4 and 3

Pollen analyses show that Interstadials 4 and 3 (Is 4 and 3) are characterized by limited development of oak and holm-oak woodlands (Fletcher & Sánchez-Goñi, 2008). Correlations between our data and the δ^{18}O curve situate sublevels P10–P8 of the cave of El Portalón in Is4 or Is3. This period is characterized in El Portalón by: 1) maximum peaks of arboreal pollen (AP), represented basically by three taxa of trees or shrubs: *Pinus*, deciduous *Quercus* and *Alnus* (Appendix A); 2) maximum peaks of microvertebrate taxa associated with woodland (*Apodemus sylvaticus*, *Eliomys quercinus*, *Bufo bufo*, *Rana temporaria* and *Vipera* sp.); 3) a high percentage representation of thermophilous taxa; 4) high percentage representations of aquatic taxa (P10 and P8); 5) maxima in the abundance of species of amphibians and reptiles and small mammals. In turn, the climatic conditions as regards precipitation and temperature resemble the interstadial period previously noted (Is5, Is6 or Is7). There is thus an increase in summer temperatures (MTW) and winter temperatures (MTC), and an increase in summer precipitation (JJA) in conjunction with a decrease in winter precipitation (DJF).

7.2. Marine Isotope Stage 2 (26.8 to 14.9 ka BP)

In general, during Marine Isotope Stage 2 the pollen spectra suggest an open landscape dominated by semi-arid vegetation (Fletcher & Sánchez-Goñi, 2008). Our study of the microvertebrates of the Late Pleistocene sublevels of El Portalón has enabled us to identify a climatic fluctuation within this isotopic stage: LGM.

7.2.1. Last Glacial Maximum (19–22 ka BP)

Pollen studies show the LGM to be characterized by somewhat humid conditions in the Mediterranean region, which allow the development of arboreal vegetation, a factor that further distinguishes it from Heinrich Events 2 (earlier) and H1 (later), during which there is a notable predominance of semi-arid vegetation (Fletcher & Sánchez–Goñi, 2008; Kageyama et al., 2005; Peyron et al., 1998). Correlations between the data obtained by the study of microvertebrates and the δ^{18}O curve situate sublevels P6–P3 of the cave of El Portalón in a humid and cold phase concordant with the Last Glacial Maximum (LGM). This period is characterized by a pronounced decrease in the summer temperatures (MTW) and a more moderate decrease in the winter temperatures (MTC), together with a substantial increase in winter precipitation (DJF) and a decrease in summer precipitation (JJA). It is also characterized by a progressive reduction in taxa associated with woodland environments (Fig. 4; Appendix A), the complete absence of thermophilous taxa and taxa associated with aquatic environments, and a drastic decrease in the representation both of amphibian and reptile taxa and small-mammal taxa with respect to the underlying sublevels (Fig. 4).

8. Conclusions

The sequence of El Portalón site is one of the most complete stratigraphic series of the latest Pleistocene (ca. 35 to 16 kyr BP) in the Iberian Peninsula. The small-vertebrate bone remains from El Portalón have been analysed and quantified. There are a total of 18,602 fragments, which correspond to a minimum of 1221 small-mammal specimens and 1024 amphibian and squamate specimens, representing at least 25 taxa, including toads and frogs, lacertids, snakes, insectivores, bats and rodents. The small-vertebrate fossil remains were grouped by the minimum-number-of-individuals (MNI) method, bearing in mind that taphonomic factors might have influenced the assemblages and abundances of the species. In the latest Pleistocene sequence of El Portalón, the animal responsible for the assemblage was probably a nocturnal bird of prey. The small vertebrates of El Portalón site do not show taxonomical differences between the base and the top of the sequence, and their assemblages remain qualitatively fairly unchanged throughout the latest Pleistocene, although some are well represented throughout the sequence whereas others only appear sporadically. According to the small-vertebrate assemblage, the palaeoenvironment seems to have been relatively open and varyingly humid throughout the El Portalón sequence. The more humid periods occur during the cold periods (sublevel P16, sublevels P13–P12 and sublevels P6–P3) in response to higher winter precipitation, lower summer and winter temperatures and the opening of the landscape. During the “warm” periods (sublevels P14–P15 and sublevels P10–P8), by contrast, woodland and water stream meadows are well developed in response to higher summer precipitation and higher summer and winter temperatures. This is in accordance with the pollen record, which displays the maximum values of arboreal pollen in sublevel P8. Finally, this study corroborates that the temperatures and precipitation during the Latest Pleistocene concur with the quantitative variation in small vertebrates throughout the sequence.

Acknowledgments

We want to thank all the members of the El Portalón excavation team. We are also grateful to Prof. Peter Kershaw, Prof. Lawrence J. Flynn and the two anonymous reviewers for their suggestions and comments that strongly improved the manuscript. The sorting and curation of the material was supported by the Junta de Castilla y León, MEC projects BOS 2003-08938-C03-09, BOS 2003-8938, DGI CGL2006-13532-C03-02, INAEM, Fundación Atapuerca, Fundación Duques de Soria, Grupos Consolidados 2007 del Gobierno de Aragón, and the University of Zaragoza. Furthermore, this paper is a part of the projects CGL2009-07896/BTE and SGR2009-324. J.M.L.-G. and A.V have been supported by a postdoctoral grant from Juan de la Cierva Subprogram (JCI-2009-04026 and JCI-2007-56450), with the financial sponsorship of the Spanish Ministry of Science and Innovation.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.palaeo.2010.04.006.

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