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# HUMAN IMPACT ON SMALL-MAMMALS FROM LATEGLACIAL TO LATE HOLOCENE OF WESTERN MEDITERRANEAN REGION: NEW ENVIRONMENTAL AND CLIMATE APPROACH

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# ABSTRACT

In this PhD thesis, we have studied the small-mammal assemblages from the Lateglacial to the Late Holocene of Western Mediterranean region. We analyzed the palaeoenvironment through the Habitat Weighting method and the palaeoclimate with the Mutual Ecogeographic Range method, the Bioclimatic Model and the study of the Chorotypes. These analyses allow us to observe a general evolution from cool and arid climate conditions during Lateglacial to warm and humid climate conditions during the Holocene, similar to nowadays. Concretely, during the Lateglacial we observed cold and arid conditions related with the Heinrich Event 1 in the lower layers (15100-13180 cal BP) of El Mirador cave (Atapuerca, northern Iberian Peninsula). Moreover, the temperatures obtained from Balma del Gai (Moià, north-eastern Iberian Peninsula) at 13150-12813 cal BP are similar to current climatic data coinciding with the characteristics of Bølling-Allerød period. Also, cold conditions during the beginning of the Younger Dryas have been detected in Grottina dei Covoloni del Broion (Vicenza, north-eastern Italian Peninsula) with high percentages of Euro-Siberian species and in Balma del Gai at 12300-11800 cal BP the Habitat Weigthing method shows an arboreal cover recovery that is characteristic of the end of the Younger Dryas and the onset of the Holocene period. Furthermore, during the Holocene, we detected, after the cold event occurred at 8200 cal BP, a general climate and landscape recovery at 7401-7308 cal BP in Cova Bonica (Vallirana, north-eastern Iberian Peninsula) and in El Mirador at 7030-6870 cal BP. The semi-arid conditions related with the end of the African Humid period have been observed in El Mirador at 7400-7000 cal BP. Besides, a temperate and humid conditions have been documented in El Portalón (Atapuerca, northern Iberian Peninsula), Cova Bonica and Grottina dei Covoloni del Broion (around 5200-4700 cal BP) probably consequence of the expansion of the Mediterranean climate. Moreover, we observed environmental changes on the landscape associated to human impact, especially since the Late Holocene in El Mirador at 3700-3000 cal BP. The human impact has been observed by the presence of synanthropic species, which have adapted their ethology to conditions created or modified by human activities. This method allow us to observed that the anthropogenic transformations in El Mirador occurred in two phases, the first phase (7000-5900 cal BP) related with the livestock activities and the second phase (5900-3000 cal BP) related with agricultural practices. Moreover, in this site and El Portalón a seasonal human occupation have been observed. Finally, in Cova Bonica at 4835-4711 cal BP has been documented the first appearance of the Algerian mouse (*Mus spretus*) in the northeastern Iberian Peninsula during the Neolithic which could be related with a route of Neolithization.

# RIASSUNTO

Per questa tesi di dottorato, sono stati studiati gli insiemi di micromammiferi dal Tardoglaciale alla fine dell'Olocene delle regioni del Mediterraneo occidentale. Sono stati analizzati il paleomabiente attraverso il metodo dell'Habitat Weighting ed il paleoclima attraverso il metodo del Mutual Ecogeographic Range, il Bioclimatic Model e lo studio dei Chorotypes. Queste analisi permettono di osservare una generale evoluzione da condizioni climatiche fredde e aride durante il Tardiglaciale a condizioni umide e temperate durante l'Olocene, simili a quelle odierne. Nei fatti, è possibile osservare condizioni fredde e aride, in relazione all'Heinrich Event 1 nei livelli inferiori (15100-13180 cal BP) della Grotta del Mirador (Atapuerca, penisola iberica settentrionale). Inoltre, le temperature ottenute da Balma del Gai (Moià, penisola iberica settentrionale) a 13150-12813 cal BP sono similiai dati climatici odierni e coincidono con le caratteristiche del periodo Bølling-Allerød. In piú, condizioni fredde durante l'inizio del Younger Dryas sono state rilevate per la Grottina dei Covoloni del Broion (Vicenza, penisola italiana nordorientale), con un'alta percentuale di specie euro-siberiane e, per la Balma del Gai, nel livello datato 12300-11800, il metodo dell' Habitat Weighting mostra il ritorno della copertura arborea che é caratteristico della fine del Younger Dryas e dell'inizio dell'Olocene. Infine, durante l'Olocene, sono stati rilevati dopo l'evento freddo datato ad 8200 cal BP, un generale miglioramento del clima e dell'ambiente a Cova Bonica, a 7401-7308 cal BP (Vallirana, penisola iberica nordorientale) ed a El Mirador, a 7030-6870 cal BP. Le condizioni semi-aride corrispondenti alla fine dell'African Humid Period sono state osservate a El Mirador a 7400-7000 cal BP. Inoltre condizioni umide e temperate sono state documentate a El Portalón (Atapuerca, penisola iberica settentrionale), Cova Bonica e Grottina dei Covoloni del Broion (5200-4700 cal BP circa), probabile conseguenza dell'espansione del clima mediterraneo. Infine, si possono osservare cambiamenti ambientali nel paesaggio associati all'intervento antropico, specialmente a partire dal tardo Olocene a El Mirador a 3700-3000 cal BP. L'impatto umano é stato osservato grazie alla presenza di specie commensali che hanno adattato il loro comportamento alle condizioni create o modficate dalle attività umane. Questo metodo ha permesso di documentare che le trasformazioni antropiche a El Mirador si articolano in due fasi, la prima fase (7000-5900 cal BP) in relazione ad attività pastorali mentre la seconda relativa ad attività agricole. Inoltre, in questo sito e a El Portalón, é stato possibile osservare una frequentazione antropica stagionale. Infine, a Cova Bonica, a 4835-4711 cal BP, è stato documentata la prima comparsa del Topo del Mediterraneo occidentale (*Mus spretus*) nel Nord-Est della penisola iberica durante il Neolitico, che potrebbe essere in relazione con una via di Neolitizzazione.

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# FORMAL STRUCTURE

The formal structure of this PHD thesis is composed by main 5 Chapters and 2 Appendix:

**- CHAPTER 1: Introduction**

In this chapter, we explain the main objectives of this PHD thesis. Our first objetive is describe the importance of small mammals analysis for the palaeoevironmental and palaeoclimatic reconstructions in the Holocene, and the second is the study of the diversity and the relation of synanthropic species with the human impact.

**- CHAPTER 2: Manuscripts**

In this PHD thesis, we present three papers published in cientific journals with science citation index (SCI). The first manuscript has been published in *Comptes Rendus Palevol*. In this paper, we exposed the state of art of the main previously small mammals studies of the Holocene in the Iberian Peninsula. In the others two papers, we have explained the methodologies applied in this PHD thesis and the results obtained with the small mammals of El Mirador cave. The first have been published in *Palaeogeography, Palaeoclimatology, Palaeoecology*. In this paper, shows the palaeoenvironmental and palaeoclimatic reconstruction of El Mirador cave. While the other one, published in *The Holocene* , shows the diversity analisys and the study of synanthropic species in relation with the human impact on the landscape in this site.

**- CHAPTER 3: Other Studied Sites**

We explain the results obtained from the study of the non-published sites, such as El Portalón (Sierra de Atapuerca, Burgos, Iberian Peninsula), Cova Bonica (Vallirana, Barcelona, Iberian Peninsula), Balma del Gai (Moià, Barcelona, Iberian Peninsula) and Grottina dei Covoloni del Broion (Vicenza, Italian Peninsula). From every sites, the results obtained had been detailed with the small mammals analysis, a little discussion and the most important conclusions.

- **CHAPTER 4: General Discussion**

This chapter has been divided in two parts. In the first part, we have explained the most important palaeoenvironmental and palaeoclimatic characteristics and the diversity and the synanthropic species of the Iberian Peninsula. On the other hand, we have explained these items in the Italian Peninsula.

- **CHAPTER 5: General Conclusions**

The most important conclusions obtained with the small mammals analysis in this PHD thesis.

- **CHAPTER 6: Future perspectives**

The main topics that we would like to expand after this Ph.D. thesis

- **APPENDIX 1: Systematic Paleontology**

In this part, we have described from the systematic paleontology point of view, the most important morphologic characters of the every studied species in this PHD thesis.

- **APPENDIX 2: Manuscript**

Paper published in *Comptes Rendus Palevol,* 15, 958-967.

- **APPENDIX 3: Manuscript**

Paper published in *Palaeogeography, Palaeoclimatology, Palaeoecology* , 471, 78-81.

- **APPENDIX 4: Manuscript**

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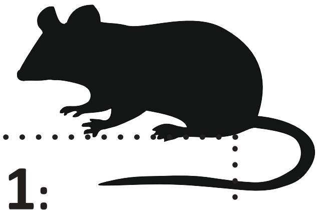

# CHAPTER 1:

# INTRODUCTION

# 1.INTRODUCTION

Two are the main objectives of this Ph.D. thesis: firstly, we have proposed to do the palaeoenvironmental and palaeoclimatic reconstruction since Lateglacial to Late Holocene by means of the small-mammals assemblages. Moreover ,we show the human influence on landscape and on the small-mammals diversity.

## 1.1. PALAEOENVIRONMENTAL AND PALAEOCLIMATIC RECONSTRUCTION

The main proxies normally used for the study of the palaeoenvironmental and palaeoclimatic inferences during the Holocene are pollen (Burjachs, 1988; Salas, 1992; Carrión et al., 1999; Jalut et al., 2000; Davis et al., 2003; Fernández et al., 2007; Ruíz-Zapata et al., 2010; Valero-Garcés et al., 2009; Pérez-Olbiol et al., 2010; López-Merino et al., 2012; Expósito and Burjachs, 2016), marine cores (Johnsen et al., 1972; Shakleton et al., 2000; Cacho et al., 2001; Kageyama et al., 2005) continental cores (Pons and Reille, 1988; Moreno et al., 2007; Bernárdez et al., 2008; Morellón et al., 2009; Sancho et al., 2011), charcoals (Badal et al., 2012; Kaal et al., 2011; López-Doriga et al., 2012; Euba et al., 2016) and sedimentology (Benito et al., 2010; Domínguez-Villar et al., 2012; Gómez-Paccard et al., 2013; Pérez-Lambán et al., 2014), among others. While, the analysis of the small mammals as palaeoenvironmental and palaeoclimatic proxy is less used in this chronological period.

In general, mammals, such as other animals, have the capability of adaptation to climate changes. The name of this physiologic character is "endothermia". This character consists on generating body heat from its own metabolism and with it maintains its temperature in very narrow ranges; avoiding drastic fluctuations in the corporal temperature in spite of there are important changes in the environmental temperature (Eliosa León and Silva Gómez, 2011). Inside of the mammals group, the small mammals, on account of their size, are more sensitive to small changes in the surrounding environment (López-García et al., 2013).

Recently, the small mammals have benn used as palaeoenvironmental and palaeoclimatic proxy (Cuenca-Bescós et al., 2010, 2011; López-García et al., 2010, 2011; Rofes et al., 2009; Bañuls-Cardona et al., 2012; 2014; García-Ibaibarriaga et al., 2015; Laplana et al., 2016; Bennàsar et al., 2016; Galán et al., 2016; Berto et al., 2016; Rey-Rodríguez et al., 2016). Previously, the maim finality of the small-mammals studies was the biochronology (Agustí et al., 1997, 2001; Cuenca-

Bescós et al., 1999, 2010, 2013, 2016; Nadachowski et al., 2011; Van der Meulen et al., 2011; Lozano-Fernández et al., 2013, 2015; Stotzel, 2014; Maul et al., 2014; López-García et al., 2015).

The accumulation of small mammals is produced by the activity of other animals, mainly birds of prey and small carnivores. The predation modifies the bones in a different way and intensity depending on ingestion and digestion of nocturnal raptors, diurnal birds of prey and mammalian carnivores (Denys 1985). Based on modern avian pellets and carnivore excrements, Andrews (1990) distinguished five categories of modification (little, moderate, intermediate, heavly and extreme) and established a methodology to identify the predator. Furthermore, in the case of chiropters, their accumulation in caves may be also involving a hibernation colony in which the most adult individuals died by natural death or a birth colony where the most individuals died are babies and infants (Sevilla, 1986).

Taking account these methodologies, the small mammals assemblages found in a site represents an important part or a total group of the species closed to the site.

As we have already mentioned, the use of small mammals as a proxy for palaeoenvironmental and palaeoclimatic reconstruction are not as abundant as in the case of other proxies such as palinology, anthracology or sedimentology. Moreover, this kind of studies are scarce during in the most recent chronologies. The study of the Holocene begins to be important at palaeoenvironmental level and small mammals studies in the recent years. This trend is beginning to change thanks to studies at European level (Stoetzel et al 2011; Ponomarov et al 2013; López-García et al 2014; Popova, 2015, Berto et al 2016), but mainly within the Iberian Peninsula (Laplana Conesa and Cuenca-Bescós, 1995; Guillém-Calatayud, 1999; Murelaga et al., 2007; Oms et al., 2009; Cuenca-Bescós et al., 2009; Bañuls-Cardona and López-García, 2009; López- García et al., 2011; Sesé, 2011; Cuenca-Bescós and García-Pimienta, 2012; Rofes et al., 2013; Bañuls-Cardona et al., 2013). For this reason with this PHD thesis, we exposed new data to a better knowledge of the climate and the landscape change during the Holocene and exposed its differences with the Lateglacial with one of the most complete sequences of the Iberian Peninsula, as is the case of El Mirador cave (Sierra de Atapuerca, Burgos, Iberian Peninsula).

## 1.2.THE SMALL MAMMALS DIVERSITY

The other important part of this work is the study of the diversity and the relation of synanthropic species with the human impact.

During the Holocene, the new economy based on agriculture and livestock farming contribute to modifying and homogenizing the landscape, influencing the ethology of small mammals and resulting in changes in biodiversity (Benton et al., 2003; Barnosky et al., 2011; Torres-Romero and Olalla-Tárraga, 2014. DeLong (1996) defined the Biodiversity as "a state or attribute of a site or area and specifically refers to the variety within and among living organisms, assemblages of living organisms, biotic communities, and biotic processes, whether naturally occurring or modified by humans".

Moreover, the biodiversity changes exposed above, during the Holocene the commensal or synanthropic species became more abundant. The commensal species which lives inside or close to human constructions, were introduced by humans groups (Palomo et al., 2009), but the pattern of expansion of these species through the Mediterranean basin suggests that they did not colonise the Iberian Peninsula until the first millennium BC (Cucchi et al., 2005).

In this work, we have studied the presence of the synanthropic species, i.e. indigenous species adapted to conditions created or modified by human activities, such as *Microtus (Terricola) duodecimcostatus*, *Microtus (Terricola) lusitanicus*, *Microtus arvalis*, *Microtus agrestis*, *Eliomys quercinus*, *Crocidura russula* (Mistrot, 2000; Pokines, 1998). Within our assemblage there are four synanthropic species: *Crocidura russula*, *Microtus arvalis*, *Microtus (Terricola) duodecimcostatus* and *Eliomys quercinus*.

# CHAPTER 2:

# MANUSCRIPTS

**Manuscript:** ***Comptes Rendus Palevol***

# 2.1-CLIMATIC AND ENVIRONMENTAL CONDITIONS FROM THE NEOLITHIC TO THE BRONZE AGE (7000-3000 BP) IN THE IBERIAN PENINSULA ASSESSED USING SMALL-MAMMAL ASSEMBLAGES.

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## Abstract

We have analyzed the palaeoenvironment and palaeoclimate of the beginning of the Holocene in the Iberian Peninsula on the basis of the small-mammal assemblages from three sites within the geography of the Iberian Peninsula: Mirador (Sierra de Atapuerca, Burgos), Colomera (Sant Esteve de la Sarga, Lleida) and Valdavara-1 (Becerreá, Lugo). These associations reveal that the palaeoenvironment was more humid than today in the sites under study, and the landscape was dominated by woodland and woodland margins in all the studied layers. Further, the climatic conditions were stable, but with winters colder than at present, above all in the Mediterranean area.

Finally, our data have been compared with other environmental and climatic proxies, showing that human activities exerted little impact on the palaeoenvironmental conditions that occurred from 7000 to 3000 BP in the Iberian Peninsula.

**Keywords:** Small mammals, Holocene, Palaeoenvironment, Palaeoclimate, Iberian Peninsula.

## Resumé

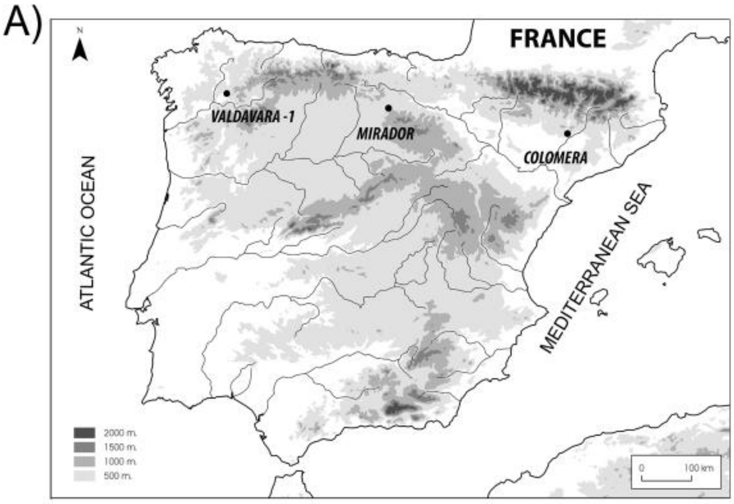
Nous avons analysé le paléoenvironnement et paléoclimats du début de l’Holocène dans la Péninsule Ibérique, sur la base des assemblages de petits mammifères provenant de trois sites de la Péninsule Ibérique: Mirador (Sierra de Atapuerca), Colomera (Sant Esteve de la Sarga, Lleida) et Valdavara-1 (Becerreá, Lugo). Ces associations révèlent que le paléoenvironnement était plus humide qu’aujourd’hui dans les sites étudiés, et le paysage dominé par des forêts et marges de forêts dans tous les niveaux étudiés. En outre, les conditions climatiques étaient plus ou moins stables, mais avec des hivers plus froids qu’à l’heure actuelle, surtout dans la région méditerranéenne.

Finalement, nos données ont été comparées avec d’autres données environnementales et climatiques, montrant que les activités humaines avaient peu d’influence sur les conditions paléoenvironnementales entre 7000 à 3000 BP dans la Péninsule Ibérique.

**Mots clés:** Micromammifères, Holocène, Paléoenvironnement, Paléoclimat, Péninsule Ibérique.

## 1. Introduction

The Holocene climate in the Iberian Peninsula is known mainly from different scientific studies (palaeobotany, sedimentology, mineralogy, isotopes, solar variability), which can obtain new palaeoenvironmental and palaeoclimatic data either from continental records alone (Carrión, 2002; López Sáez et al., 2005; Fletcher and Sánchez-Goñi, 2008; Jalut et al., 2009; Sancho et al., 2011; Carrión et al., 2010; García-Amorena et al., 2011; Luzón et al., 2011; Pérez-Obiol et al., 2011; Domínguez-Villar et al., 2012; Bastida et al., 2013; Gómez-Paccard et al., 2013; López-Merino et al., 2012; Jiménez-Moreno et al., 2013; Pérez-Lambán et al., 2014) or from continental records in conjunction with marine records (Cacho et al., 2001; Mayewski et al., 2004; Fletcher and Zielhofer, 2013). This period is characterized by major changes in the vegetation and rapid oscillations in the climate (Cacho et al., 2001; Mayewski et al., 2004; Domínguez-Villar et al., 2012; Jimenez-Moreno et al., 2013; Fletcher and Zielhofer, 2013).



B)

| LAYER | Laboratory number | Measured Radiocarbon age | 2σ calibrated result BP | Mean of 2σ calibrated result BP |
|---|---|---|---|---|
| MIR4 (top) | Beta-154894 | 3020±40 | 3350-3140 | 4026 |
| MIR4 (bass) | Beta-153366 | 3380±40 | 3720-3560 | |
| MIR9 | Beta-220912 | 5050±40 | 5920-5730 | 5825 |
| MIR18 | Beta-208132 | 6090±40 | 7180-7110 /7100-6880 | 7067 |
| MIR19 | Beta-182040 | 6130±50 | 7180-6870 | 6990 |
| MIR24 | Beta-220914 | 6080±40 | 7160-7120 /7030-6870 | 7880 |
| | Beta-197386 | 7030±40 | 7960-7800 | |
| EE1 | Beta-241704 | 3630±40 | 4080-3840 | 3980 |
| CE12 | Beta-248523 | 6020±50 | 6990-6740 | 6870 |
| CE13-14 | Beta-240551 | 6120±40 | 7170-6940 | 7060 |
| VUU | Beta-235727 | 4490±40 | 5340-4980 | 5130 |

**Figure 1.** A) Geographic location of the sites under study. B) Radiocarbon dates measured of the layers chosen from each site, the calibrated dates 2σ (p = 95%) and the mean of the calibrated dates.

However, the Holocene is understudied in the Iberian Peninsula, especially in terms of small-mammal studies, and for this reason we want to provide a broader reference framework for interpreting the Holocene in the region (Figure 1).

Recently, studies of small mammals in the Holocene have started to become more abundant. These studies have involved palaeoenvironmental and palaeoclimatic reconstructions (Cuenca-Bescós et al., 2009; Bañuls-Cardona and López-García, 2009; López- García et al., 2011; Bañuls-Cardona et al., 2013), which have been useful for characterizing the small changes that occurred at the beginning of the Holocene.

In this paper, our study of small mammals is focused chronologically on the early and middle Holocene. The aim is to characterize the environmental and climatic conditions of the period by the study of small mammals, and compare our results with other data in order to establish natural or human causes that influenced these results.

To this end, the small-mammal data chosen belong to archaeological sites situated in different climatic zones of the Iberian Peninsula. We have taken new small-mammal data from the Neolithic layers of Mirador cave and the data from the Bronze Age layer (MIR4) published in Bañuls-Cardona et al. (2013), as well as other small-mammal data published from Colomera cave (Sant Esteve de la Sarga, Lleida) (Bañuls-Cardona and López-García, 2009; López-García et al., 2010) and Valdavara-1 cave (Becer¬reá, Lugo) (Vaquero et al., 2009; López-García et al., 2011b). The faunal assemblages used here are included in the small-mammal studies of three middle Holocene sites (from the early Neolithic to the Bronze Age) that correspond to 11 different layers dated to between ca. 8 and 3 kyr BP: six layers from the early Neolithic (MIR24, MIR19, MIR18 and MIR17 of Mirador cave, CE12 and CE13-14 of Colomera cave), two layers from the middle-late Neolithic (MIR9 and MIR5 of Mirador cave) and finally three layers from the Bronze Age (MIR4 of Mirador, VUU of Valdavara-1 and EE1 of Colomera cave ).

## 2. Material and Methods

The new data of this paper are from Mirador cave (Sierra de Atapuerca, Burgos). For this paper, layers MIR5, MIR9, MIR17, MIR18, MIR19 and MIR24 have been analyzed. From these layers, 1154 remains (NR) have been identified, with a minimum number of individuals (MNI) of 706. Nine small-mammal taxa have been identified: *Sorex* gr. *coronatus-araneus*, *Crocidura russula*, *Myotis myotis-blythii*, *Miniopterus schreibersii*, *Microtus arvalis*, *Microtus agrestis*, *Microtus (Terricola) duodecimcostatus*, *Apodemus sylvaticus* and *Eliomys quercinus* (Table 1).

| Taxa | Mirador | | | | | | | | | | | | | | Colomera | | | | | | Valdavara-1 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | MIR4 | | MIR5 | | MIR9 | MIR17 | | | MIR18 | | MIR19 | | MIR24 | | EE1 | | CE12 | | CE13-14 | | VUU | |
| | NMI | NMI% | NMI | NMI% | NMI | NMI% | NMI | NMI% | NMI | NMI% | NMI | NMI% | NMI | NMI% | NMI | NMI% | NMI | NMI% | NMI | NMI% | NMI | NMI% |
| *Crocidura russula* | 19 | 19.8 | 6 | 6.7 | 17 | 32.1 | 16 | 12.5 | 21 | 11.4 | 6 | 5.1 | 8 | 6.0 | 1 | 2.3 | 3 | 4.3 | 2 | 2.4 | 2 | 3.4 |
| *Sorex coronatus-araneus* | 6 | 6.3 | 4 | 4.5 | 5 | 9.4 | 9 | 7.0 | 21 | 11.4 | 4 | 3.4 | 3 | 2.2 | | | | | | | | |
| *Sorex sp.* | | | | | | | | | | | | | | | | | | | | | 1 | 1.7 |
| *Erinaceus europaeus* | | | | | | | | | | | | | | | | | | | | | 1 | 1.7 |
| *Talpa occidentalis* | | | | | | | | | | | | | | | | | | | | | 4 | 6.8 |
| *Rhinolophus sp.* | | | | | | | | | | | | | | | | | | | | | 1 | 1.7 |
| *Myotis myotis* | | | | | 2 | 3.8 | | | 3 | 1.6 | | | 4 | 3.0 | | | | | | | | |
| *Myotis nattereri* | | | | | | | | | | | | | | | | | | | | | 1 | 1.7 |
| *Miniopterus schreibersii* | | | | | 2 | 3.8 | | | 1 | 0.5 | 1 | 0.9 | 2 | 1.5 | | | | | | | | |
| *Arvicola sapidus* | | | | | | | | | | | | | | | | | | | | | 2 | 3.4 |
| *Iberomys cabrerae* | | | | | | | | | | | | | | | 1 | 2.3 | 2 | 2.9 | 1 | 1.2 | 2 | 3.4 |
| *Clethrionomys glareolus* | | | | | | | | | | | | | | | | | | | | | 1 | 1.7 |
| *Micromys minutus* | | | | | | | | | | | | | | | | | | | | | 1 | 1.7 |
| *Chionomys nivalis* | | | | | | | | | | | | | | | 6 | 14.0 | 11 | 15.9 | 24 | 28.9 | 1 | 1.7 |
| *Microtus arvalis* | 21 | 21.9 | 20 | 22.5 | 3 | 5.7 | 18 | 14.1 | 16 | 8.6 | 9 | 7.7 | 22 | 16.4 | 5 | 11.6 | 4 | 5.8 | 4 | 4.8 | 1 | 1.7 |
| *Microtus agrestis* | 14 | 14.6 | 37 | 41.6 | 13 | 24.5 | 34 | 26.6 | 26 | 14.1 | 22 | 18.8 | 15 | 11.2 | 3 | 7.0 | 7 | 10.1 | 7 | 8.4 | 1 | 1.7 |
| *Microtus (Terricola) lusitanicus* | | | | | | | | | | | | | | | | | | | | | 17 | 28.8 |
| *Microtus (Terricola) duodecimcostatus* | 17 | 17.7 | 14 | 15.7 | 1 | 1.9 | 18 | 14.1 | 21 | 11.4 | 11 | 9.4 | 24 | 17.9 | 1 | 2.3 | 4 | 5.8 | 5 | 6.0 | | |
| *Apodemus sylvaticus* | 18 | 18.8 | 8 | 9.0 | 1 | 1.9 | 32 | 25.0 | 73 | 39.5 | 58 | 49.6 | 56 | 41.8 | 22 | 51.2 | 32 | 46.4 | 36 | 43.4 | 16 | 27.1 |
| *Glis glis* | | | | | | | | | | | | | | | | | | | | | 6 | 10.2 |
| *Eliomys quercinus* | 1 | 1.0 | | | 9 | 17.0 | 1 | 0.8 | 3 | 1.6 | 6 | 5.1 | | | 4 | 9.3 | 6 | 8.7 | 4 | 4.8 | 1 | 1.7 |
| Total | 96 | 100 | 89 | 100 | 53 | 100 | 128 | 100 | 185 | 100 | 117 | 100 | 134 | 100 | 43 | 100 | 69 | 100 | 83 | 100 | 59 | 100 |

**Table 1.** Minimum number of individuals (MNI) and percentage of minimum number of individuals (MNI%).

## 2.1. Palaeontological study

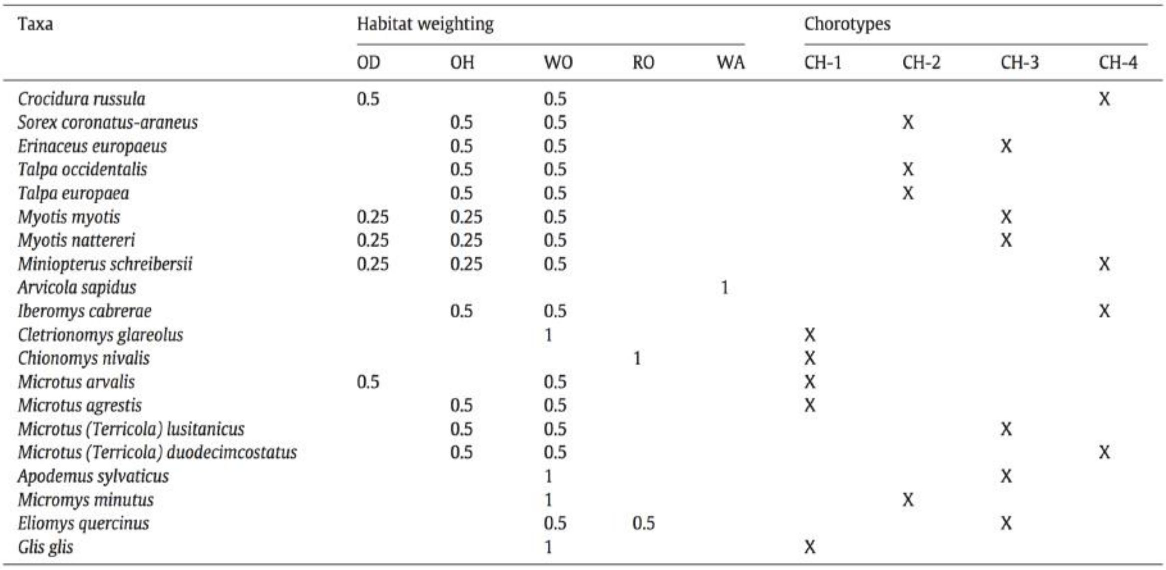
The small mammals belonging to levels MIR5, MIR9, MIR17, MIR18, MIR19 and MIR24 of Mirador cave (Sierra de Atapuerca, Burgos) have been identified by systematic palaeontology. For Soricidae, we used mandibles and isolated teeth (Reumer, 1984; Cuenca-Bescós et al., 2008; López-García, 2008); for chiropters, the mandibles, isolated teeth and humeri (Bruijn and Rumke, 1974; Menu and Popelard, 1987; Sevilla, 1988); for Arvicolinae, the first lower molars (van der Meulen, 1973; Cuenca-Bescós et al., 2008; López-García, 2008); while for *Apodemus sylvaticus* and *Eliomys quercinus* identification relied on isolated teeth (Pasquier, 1974; Damms, 1981; Cuenca-Bescós et al., 2008; López-García, 2008).

## 2.2. Palaeoenvironmental reconstruction

To produce the palaeoenvironmental reconstruction, we used the Habitat Weighting method (Andrews, 2006; modified by Blain et al., 2008; López-García et al., 2011). We took into account the geographical location of each species today, as all of them still exist in the Iberian Peninsula. We ascertained a percentage distribution for the habitat(s) preferentially occupied by each taxon, dividing the habitats into five categories defined according to a series of highly concrete environmental features: dry meadow, wet meadow, woodland, rocky areas and watercourse areas. “Dry meadow” consists of meadowland subject to seasonal climate change; “wet meadow” indicates evergreen meadowland with pastures and dense topsoil; “woodland” ranges from leafy forests to wood¬land margins, with moderate vegetation cover; “rocky areas” refer to rocky habitats without vegetation cover; and “watercourse areas” include streams, lakes and ponds (Table 2).

## 2.3. Palaeoclimatic reconstruction

For the palaeoclimatic reconstruction, we used the Mutual Climate Range method (MCR) (Blain, 2005; Blain et al., 2010; López-García et al., 2010a). With this method, we defined the current distribution area of the faunal association, superimposing current distribution maps divided into 10 x 10 km UTM grids (Palomo and Gisbert, 2005). The resulting intersection indicates an area where the climatic characteristics are similar to those of our association. On the basis of this intersection we calculated the MAT (mean annual temperature), MTC (mean temperature of the coldest month) and the MTW (mean temperature of the warmest month), as well as the MAP (mean annual precipitation). These climatic characteristics are obtained using current data relating to temperature and precipitation, collected between 1982 and 2012 (Climate_Data.org). The data obtained were compared with the present-day climate of this region of the Iberian Peninsula, enabling us to note the changes in temperature and precipitation with respect to this point of the Holocene period.



| Taxa | Habitat weighting | | | | | Chorotypes | | | |
|---|---|---|---|---|---|---|---|---|---|
| | OD | OH | WO | RO | WA | CH-1 | CH-2 | CH-3 | CH-4 |
| *Crocidura russula* | 0.5 | | 0.5 | | | | | | X |
| *Sorex coronatus-araneus* | | 0.5 | 0.5 | | | | X | | |
| *Erinaceus europaeus* | | 0.5 | 0.5 | | | | | X | |
| *Talpa occidentalis* | | 0.5 | 0.5 | | | | X | | |
| *Talpa europaea* | | 0.5 | 0.5 | | | | X | | |
| *Myotis myotis* | 0.25 | 0.25 | 0.5 | | | | | X | |
| *Myotis nattereri* | 0.25 | 0.25 | 0.5 | | | | | X | |
| *Miniopterus schreibersii* | 0.25 | 0.25 | 0.5 | | | | | | X |
| *Arvicola sapidus* | | | | | 1 | | | | |
| *Iberomys cabrerae* | | 0.5 | 0.5 | | | | | | X |
| *Cletrionomys glareolus* | | | 1 | | | X | | | |
| *Chionomys nivalis* | | | | 1 | | X | | | |
| *Microtus arvalis* | 0.5 | | 0.5 | | | X | | | |
| *Microtus agrestis* | | 0.5 | 0.5 | | | X | | | |
| *Microtus (Terricola) lusitanicus* | | 0.5 | 0.5 | | | | | X | |
| *Microtus (Terricola) duodecimcostatus* | | 0.5 | 0.5 | | | | | | X |
| *Apodemus sylvaticus* | | | 1 | | | | | X | |
| *Micromys minutus* | | | 1 | | | | X | | |
| *Eliomys quercinus* | | | 0.5 | 0.5 | | | | X | |
| *Glis glis* | | | 1 | | | X | | | |

**Table 2.** Distribution of the taxa by habitat: the abbreviations are as follows: R: Rocky; WA: Water; OD: Open Dry; OH: Open Humid; WO: Woodland. Distribution of the taxa by chorotype: CH-1: Chorotype 1 (species with Euro-Siberian requirements); CH-2: Chorotype 2 (Euro-Siberian species that nonetheless tolerate Mediterranean conditions); CH-3: Chorotype 3 (species with strictly Mediterranean requirements); CH-4: Chorotype 4 (generalist species).

We have omitted certain taxa from the palaeoclimatic reconstruction. This applies to chiropters, because studies of chiropteran distribution are currently very scarce; in many cases their mobility makes it difficult to ascertain their present geographical distribution, which could thus falsify our data.

Moreover, we have used a classification of taxa according to chorotypes established by Sans-Fuentes and Ventura (2000), Real et al. (2003) and López-García et al. (2010b). A chorotype can be defined as a group of species whose distributions in space overlap more than expected at random. Chorotype 1 (CH-1) refers to species with Euro-Siberian requirements; this implies a mean summer temperature lower than 20 ºC, a mean annual temperature that should be between 10 ºC and 12 ºC, and a mean annual precipitation higher than 800 mm. Chorotype 2 (CH-2) refers to Euro-Siberian species that nonetheless tolerate Mediterranean conditions, with a mean annual precipitation greater than 600 mm. Chorotype 3 (CH-3) denotes generalist species, and finally Chorotype 4 (CH-4) denotes species with strictly Mediterranean requirements (Table 2).

## 3. Results and Discussion

The Holocene is a warm and wet period, with some episodes with increased aridity and global climatic pulsations. However, there are many regional differences. Little is known about Holocene climatic variability from the continental records of Europe, and there is a need to gather more information from terrestrial sources whose reach across Europe is well known (Leira and Santos, 2002, Bernárdez et al., 2008). In the Iberian Peninsula the detailed examination of high-frequency climatic variability in the present interglacial has focused mainly on ice cores and marine or continental records. Studies such as the Alboran sea (MD95-2043) core record off the Mediterranean coast have been carried out on marine deep-sea cores, using oxygen isotope curves (Cacho et al., 2001), while the record from core SMP02-3 from the Galician continental shelf off the NW Iberian Peninsula (Bernárdez et al., 2008) has also been used to understand the vegetation response to climate variability in the Holocene (Carrión, 2002; Fletcher et al., 2007; Morellón et al., 2009; Jimenez-Moreno et al., 2013; Fletcher et al., 2013) (Figure 2).

Our study focuses chronologically in particular on the early and middle Holocene, and in order to characterize this period climatically and environmentally on the basis of a small-mammal study, we have chosen sites with special geographic characteristics, because the Iberian Peninsula represents one of the largest and most diverse areas of Mediterranean-type climate in the Mediterranean region (Moreno et al., 2007).

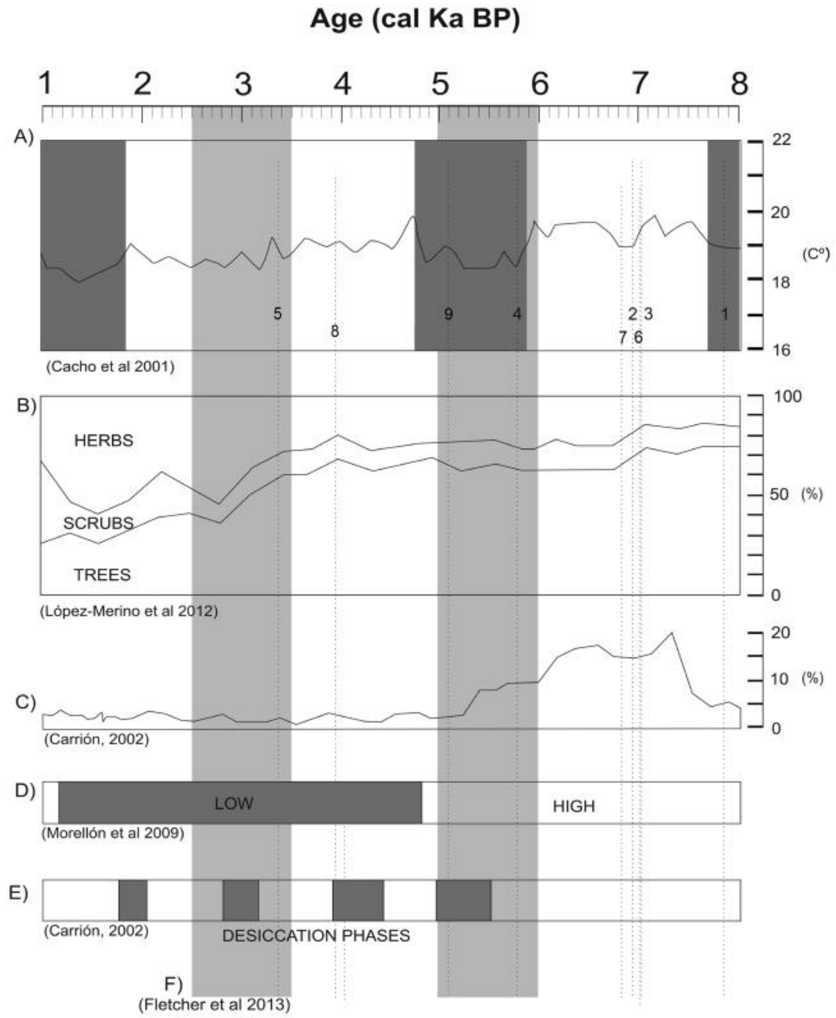


**Figure 2.** Relation between the dating of each of the layers under study and other palaeoenvironmental and palaeoclimatic studies: A) the Alboran sea (MD95-2043) isotope curve showing cooling events (Cacho et al., 2001), B) percentages of trees, shrubs and herbs in the northwest (López-Merino et al., 2012), C) percentages of deciduous trees in the southeast (Carrión, 2002), D) level of water in Lake Estanya, northeast (Morellón et al., 2009), E) level of water in Lake Siles, southeast (Carrión, 2002), F) cold periods (Fletcher et al., 2013). The abbreviations are as follows: 1: MIR24 (7880 kyr BP); 2: MIR19 (6990 kyr BP); 3:MIR18 (7067 kyr BP); 4: MIR9 (5825 kyr BP); 5: MIR4 (4026 kyr BP); 6: CE13-14 (7060 kyr BP); 7: CE12 (6870 kyr BP); 8: EE1(3980 kyr BP); 9:VUU (5130 kyr BP).

## a) Northern Spanish Meseta

El Mirador cave (Sierra de Atapuerca, Burgos) is located 1033 m above sea level on the northeastern edge of the northern Spanish Meseta, which currently has a continental Mediterranean climate or Cfb climate (according to the Köppen-Geiger system), with special characteristics: long, cold winters with moderate rainfall and short, warm summers (Kottek et al., 2006).

According to our taphonomic study of the small mammals from Mirador cave, the remains analyzed present slight signs of digestion. From these results, it can be surmised that the main animal responsible for the accumulation in the cave was a category 1 predator, a nocturnal bird of prey that displays an opportunistic trophic pattern and produces slight modifications of the bones it ingests (Andrews, 1990). The small mammals form an assemblage of great taxonomic variety, indicating that it was the work of an opportunistic hunter.

The results obtained from Mirador cave by the MCR method show that the same climatic characteristics prevailed throughout the Holocene period, because the species represented in the layers studied did not undergo great changes. The temperatures are seen to undergo minimal changes of less than one degree celsius throughout the sequence, and the same applies when we compare our data with current climate data. However, the precipitation is higher (between 200mm -252 mm) than at present. Moreover, the study of chorotypes shows some climatic changes. The percentages of Euro-Siberian species are significant in the middle-late Neolithic and Bronze Age layers, particularly in MIR5 (64.0 %), while in the early Neolithic (MIR24, MIR19, MIR18) generalist species (CH-3) are more abundant (Figure 4).

Within the sequence of El Mirador cave, however, various singular characteristics are seen to occur. During the early Neolithic (MIR24, MIR19, MIR18), climatic conditions are warmer than in the rest of the sequence, generalist species occupying 43-54% of the total sample due to the high presence of *Apodemus sylvaticus* in these layers (from 40% to 50%). This warm period breaks off in MIR17, with a sharp increase (20%) in Euro-Siberian species, in this case with a high proportion (26.6%) of *M. agrestis* (Figure 4). In the middle Neolithic (MIR9), we registered an increase of 10% in CH-4, Mediterranean species, especially manifest in the figure of 32.1% for *Crocidura russula* (Figure 4). These data suggest a slight thermal recovery with respect to MIR17. They could also be due to the incipient establishment of a Mediterranean climate that occurred in the Mirador area before 5000 BP (Jalut et al., 1997), but until all the layers have been analyzed it will not be possible to say for sure. This mild climate persisted until the Bronze Age (MIR4), when there was another very slight increase (5%) in Euro-Siberian species, with the typical conditions of a continental Mediterranean climate prevailing in the northern Meseta, i.e. long, cold winters with short, warm summers (Kottek et al., 2006). However, these mild conditions were interrupted in MIR5. In this layer another increase in the percentage of Euro-Siberian species (64.0 %) is observed, corresponding to the cold period registered at this time in the Alboran sea (MD95-2043) core record (Cacho et al., 2001; Fletcher et al., 2013) (Figure 2).

The Habitat Weighting study shows a gradual increase in open areas to the detriment of woodland areas (Figure 5); this is observed especially in MIR9 and MIR4, where the percentage of open dry areas reaches 20%. In MIR4 there is also a small decrease in rainfall of 52 mm with respect to MIR5. Fletcher and Zielhofer (2013) refer to an increase in dry conditions in the intervals lasting from 6−5 and 3.5-2.5 cal kyr BP, as also observed in the record (SMP02-3) from the Galician continental shelf (NW Iberian Peninsula) from 4.7 to 3.3 cal kyr BP (Bernárdez et al., 2008). However, this could be due to the major human impact on the environment, as indicated by archaeobotanical studies based on pollen, charcoal, seeds and phytoliths at the Mirador site (Rodríguez and Buxó, 2008; Cabanes et al., 2009). These studies have confirmed the presence of herbaceous plants related to the development of agriculture and livestock. On the other hand, García-Antón et al. (2011) have indicated that the human impact on the environment in this area of the northern Meseta was not intense in the first millennium B.C.

## b) Pyrenees area

Colomera cave (Sant Esteve de la Sarga, Lleida) is located at an altitude of 670 m above sea level, on the southern face of the Pyrenees in a continental Mediterranean zone or Cfb climate (Köppen-Geiger system). Such a location is generally characterized by very cold winters and warm summers, and, unlike the northern Meseta, by very low rainfall (Kottek et al., 2006).

The chorotype study shows a predominance of chorotype 3 or generalist species (48% - 60%) such as *Apodemus sylvaticus*, which exceeds 40% in all layers. But despite this there is a notable percentage of Euro-Siberian species throughout the sequence, mainly represented by *Chionomys nivalis*, which lives in strictly Euro-Siberian climatic zones, especially in CE13-14, with a substantial percentage of 28.9%. Nonetheless, Colomera also shows the greatest variety of Mediterranean species, with *C. russula*, *M. (T.) duodecimcostatus* and especially *Iberomys cabrerae*, which live in strictly Mediterranean climate zones and are not found in Euro-Siberian climates (Figure 4). These percentages indicate abrupt changes in temperatures, because we do not find species belonging to CH-2, i.e. Euro-Siberian species that nonetheless tolerate Mediterranean conditions. Together, these climatic characteristics are typical of a continental Mediterranean climate, generally characterized by very cold winters and warm summers (Kottek et al., 2006). These typical characteristics can be seen especially in layers CE12 and EE1, because within the sequence we see small changes in the percentages of chorotypes that indicate an improving climate from the early Neolithic (CE12), similar to during the Bronze Age (EE1). We also observe an increase of 10% in the percentage of thermo-Mediterranean taxa, which increases from 57.8% in CE12 to 68.1% in CE13-14.

The climatic characteristics deduced from the MCR study, when compared with current data, indicate that the temperatures during the Holocene were 2.4 ºC lower than at present and that the precipitation was higher than at present (557 mm). Temperatures are observed to be 1ºC lower for the MTC, while for the MTW they were less than 1ºC lower.

Our study of the habitat reveals a minor increase in open dry areas to the detriment of open humid areas, and the level of precipitation is shown to be the same in all the layers. The zooarchaeological data also attest a scarce presence of ovicaprids, which would indicate the presence of pastures, suggesting that herds might have been stabled inside the cavity (fumier). From archaeobotanical data agricultural practices are evidenced by the significant presence of cereals and legumes, but this presence is likewise scarce (Oms et al., 2008, 2009).

This low pressure on the environment is reflected in the predominance of woodland in all layers of Colomera cave, increasing towards more recent layers. This could be due to the type of cave occupation. The human communities that frequented Colomera cave were probably nomadic, since the narrow circumstances of the cave (in the middle of a gorge) do not seem appropriate for the establishment of a camp of shepherds or an agricultural holding around the cave (Oms et al., 2008, 2009). This was common in mountain areas at the time, where occupations have been found to occur later than in the plains (Tarroso et al., 2014).

## c) Northwest area

Valdavara-1 cave is located in the Iberian Massif at an altitude of 600 m above sea level (Becerreá, Lugo). This site represents a continental Mediterranean climate, with influences from an Atlantic climate or Csb climate (Köppen-Geiger system). The summers are dry, as in the previous case, but precipitation is more abundant and occurs mainly in winter, with the arrival of fronts from the Atlantic (influence of the temperate zone), and in the winter the temperatures are mild (Font Tullot, 2005).

The MCR analysis of the small-mammal assemblages in the Bronze Age (VUU) of Valdavara-1 cave indicates mild temperatures (Figure 3): i.e. the MTC is 5 ºC, the highest of the sites studied in this paper, and the MTW is 17.20ºC, the lowest of the sites studied in this paper (Table 3). These low temperatures in the warmer months (MTW) could be related to a cold climate period in the Iberian Peninsula, as observed in the temperature curve of the Alboran sea (MD95-2043) core record (Cacho et al., 2001; Fletcher and Zielhofer, 2013) (Figure 2). At the same time, the precipitation for this layer is very high (1690 mm), the highest in our study.

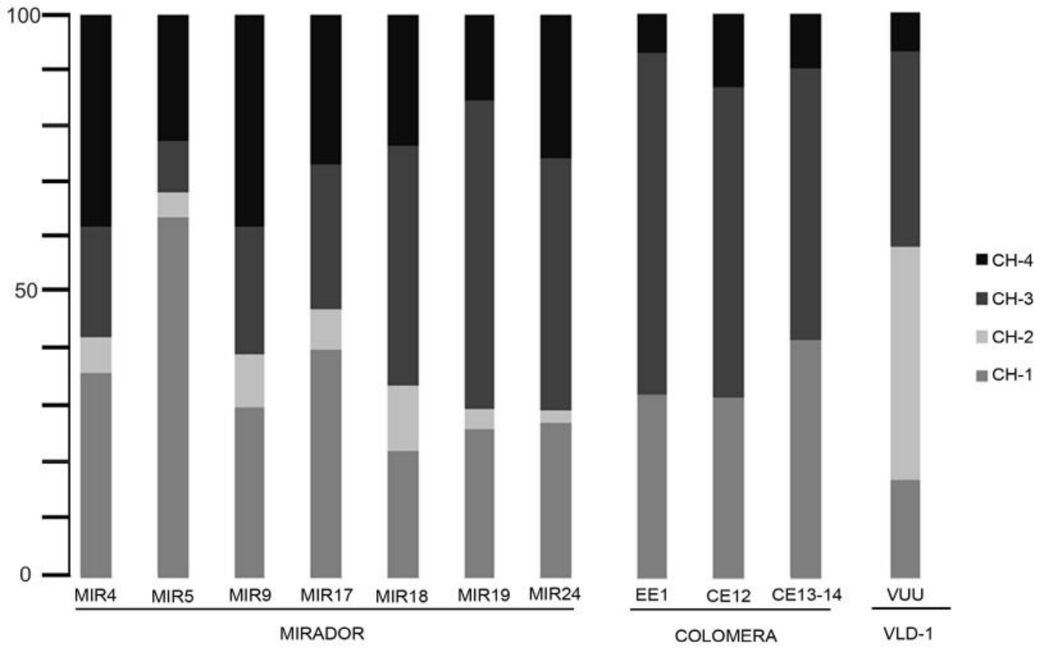
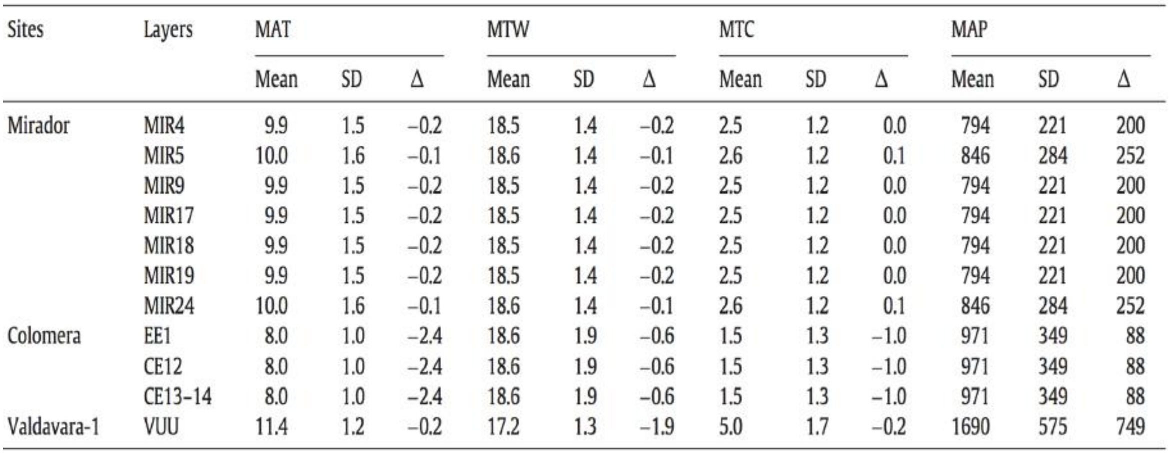


**Figure 3.** Percentage of chorotypes at each of the sites under study.

These features are also observed in the study of the chorotypes from Valdavara-1 cave (Becerreá, Lugo). Similar percentages of Mediterranean and Euro-Siberian species tolerant to Mediterranean conditions are seen, while the percentage of Euro-Siberian species *sensu stricto* is negligible (Figure 4).

Mild temperatures are thus indicated by the MCR and the chorotypes, and the temperatures are a little higher nowadays than in the Holocene, above all the MTW, with temperatures 1.9 ºC higher (Table 3). The same results are shown by the record (SMP02-3) from the Galician continental shelf (NW Iberian Peninsula). This record indicates a warm and dry period characterized by low nutrient levels and productivity, as also revealed by planktonic foraminifera (Bernárdez et al., 2008)



| Sites | Layers | MAT | | | MTW | | | MTC | | | MAP | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Mean | SD | Δ | Mean | SD | Δ | Mean | SD | Δ | Mean | SD | Δ |
| Mirador | MIR4 | 9.9 | 1.5 | −0.2 | 18.5 | 1.4 | −0.2 | 2.5 | 1.2 | 0.0 | 794 | 221 | 200 |
| | MIR5 | 10.0 | 1.6 | −0.1 | 18.6 | 1.4 | −0.1 | 2.6 | 1.2 | 0.1 | 846 | 284 | 252 |
| | MIR9 | 9.9 | 1.5 | −0.2 | 18.5 | 1.4 | −0.2 | 2.5 | 1.2 | 0.0 | 794 | 221 | 200 |
| | MIR17 | 9.9 | 1.5 | −0.2 | 18.5 | 1.4 | −0.2 | 2.5 | 1.2 | 0.0 | 794 | 221 | 200 |
| | MIR18 | 9.9 | 1.5 | −0.2 | 18.5 | 1.4 | −0.2 | 2.5 | 1.2 | 0.0 | 794 | 221 | 200 |
| | MIR19 | 9.9 | 1.5 | −0.2 | 18.5 | 1.4 | −0.2 | 2.5 | 1.2 | 0.0 | 794 | 221 | 200 |
| | MIR24 | 10.0 | 1.6 | −0.1 | 18.6 | 1.4 | −0.1 | 2.6 | 1.2 | 0.1 | 846 | 284 | 252 |
| Colomera | EE1 | 8.0 | 1.0 | −2.4 | 18.6 | 1.9 | −0.6 | 1.5 | 1.3 | −1.0 | 971 | 349 | 88 |
| | CE12 | 8.0 | 1.0 | −2.4 | 18.6 | 1.9 | −0.6 | 1.5 | 1.3 | −1.0 | 971 | 349 | 88 |
| | CE13–14 | 8.0 | 1.0 | −2.4 | 18.6 | 1.9 | −0.6 | 1.5 | 1.3 | −1.0 | 971 | 349 | 88 |
| Valdavara-1 | VUU | 11.4 | 1.2 | −0.2 | 17.2 | 1.3 | −1.9 | 5.0 | 1.7 | −0.2 | 1690 | 575 | 749 |

**Table 3.** Relation of temperature and precipitation, obtained by the MCR (Mutual Climate Range) analysis of the small mammals at each of the sites studied: MAT (mean annual temperature); MTW (mean temperature of the warmest month); MTC (mean temperature of the coldest month) and MAP (mean annual precipitation). SD (standard deviation): Max (maximum); Min (minimum); Δ (difference in relation to the current means at the meteorological stations).

The palaeoenvironmental reconstruction has revealed a high percentage of woodland (67.9 %) (Figure 4). Some authors have confirmed the persistence of pine forest in NW Iberia until the late Holocene (Morales-Molino et al., 2011). However, a considerable percentage of open areas (26%) can also be observed. These results coincide with other palaeobotanical analyses, which have confirmed that shrubland expansion was significant by around 5500 cal yr BP in the Iberian Peninsula in general (Carrión, 2002; Carrión et al., 2010b), but particularly in the NW, where the study by López-Merino et al. (2012) recorded an increase in shrubs to the detriment of trees (Figure 3).

In summary, it has been observed that in all the studied sites, despite the regional variations resulting from their different geographic locations, the climatic evolution followed the same pattern. From the early Neolithic to the Bronze Age, the temperature and rainfall were maintained stable at Colomera and Mirador caves. The study of the palaeoenvironment showed slight variation between the studied sequences which are not related to the palaeoclimatic data. For this reason we think that some landscape variations are related to the human impact, though this impact is slight. We recovered synanthropic species (taxa adapted to the conditions created or modified by human activities) such as *M. (Terricola) duodecimcostatus*, *M. (Terricola) lusitanicus*, *M. arvalis*, *M. agrestis*, *E. quercinus* and *C. russula* (Mistrot, 2000). However, we did not find commensal species (e.g., *Mus spretus*, as found in Bolumini cave, or *Mus musculus domesticus*) in any of the sites studied. Such species would have indicated a strong human impact. The pattern of expansion of these species through the Mediterranean basin suggests that they did not colonise the Iberian Peninsula until the first millennium BC (Cucchi et al., 2005).

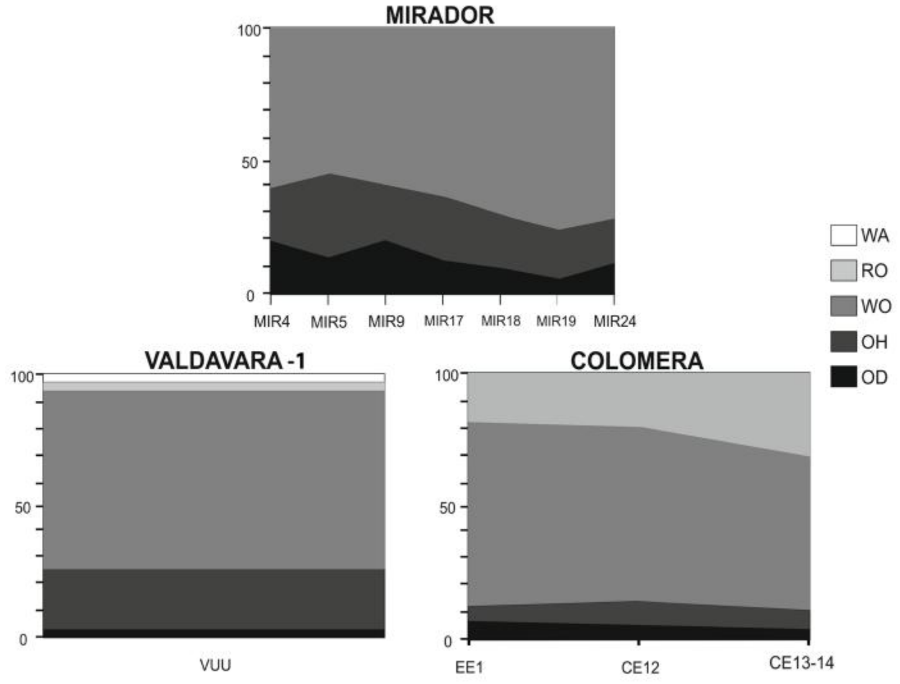


**Figure 4.** Percentage of the habitats represented at each site. The abbreviations are as follows: R: Rocky; WA: Water; OD: Open Dry; OH: Open Humid; WO: Woodland.

## 4. Conclusions

From the early Neolithic to the Bronze Age (ca. 7000-3000 BP) of the Iberian Peninsula, the evolution of the palaeoenvironment was conditioned not only by palaeoclimatic conditions, but was also linked to human activity.

In general, the climatic conditions in this period were more or less stable. The MCR analysis shows winters that were colder than nowadays, above all in the Mediterranean area (Colomera), while in the northern Meseta (Mirador) we observe lower temperatures in the warmer months, and in the northwest (Valdavara-1) the temperatures were similar to today. As regards precipitation during the Holocene, in the northwestern site of Valdavara-1 this was lower than at present, whereas in the other studied sites it was higher.

The chorotype study shows that the dominant species in most of the studied layers were generalist species, but despite this we have detected a small weather pulse that occurred at different times in each study area. These changes could be related to the establishment of the Mediterranean climate in each area from ca. 7000 BP.

The landscape is dominated by woodland, with a gradual increase in open dry meadows in the major part of the studied sites during the Bronze Age. In some cases this increase in open dry areas is linked to rising temperatures and declining rainfall, as is the case for Valdavara-1, while in Colomera and above all Mirador one notices a change in the landscape that follows a different dynamic, possibly caused by human activity. While the reduction in arboreal cover has been linked to the start of anthropogenic activity after 4500 cal BP, in Mirador cave and Valdavara-1 cave we see a decrease in woodland, but in Colomera cave there was an increase in woodland. Although some synanthropic species are represented in the studied sites, a strong human impact cannot be ascertained, because there is no evidence of the presence of commensal species.

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# 2.2-LATEGLACIAL TO LATE HOLOCENE PALAEOCLIMATIC AND PALAEOENVIRONMENTAL RECONSTRUCTION OF EL MIRADOR CAVE (SIERRA DE ATAPUERCA, BURGOS, SPAIN) USING THE SMALL-MAMMAL ASSEMBLAGES

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## Abstract

El Mirador is a cave in the Sierra de Atapuerca (northern Iberian Peninsula) that contains 27 archaeological layers from the Lateglacial to the Late Holocene. A total of 4436 small-mammal remains have been analysed from these layers, and 19 taxa have been identified (three insectivores, seven chiropters and nine rodents). The palaeoenvironmental reconstruction based on a small-mammal analysis suggests that the entire sequence is dominated by a woodland landscape. Our climatic analysis characterises the climate in terms of an evolution from a cool and arid period in the Pleistocene layers (16000 to 14000 cal yr BP), probably related to Heinrich Event 1, to humid conditions and temperatures similar to nowadays in the Holocene layers in general. In MIR23 and MIR22 (7300 to 6800 cal yr BP) we detect an increase in temperature to levels above current values and an important decrease in rainfall. These climatic characteristics could be related to the end of the African Humid Period. Moreover, a short, slightly cooler event is registered in MIR11 (ca. 6300 to 5900 cal yr BP), coinciding with a change in the economic pattern in El Mirador. The results obtained on the basis of small-mammal studies are compared with multiproxy terrestrial data (pollen, charcoal, phytoliths, geochemistry, large mammals) and the Greenland ice-core record, as well as various other core records closer to the coasts of the Iberian Peninsula (MD95-2042, MD99-2331, MD95-2043 and SMP02-3). These comparisons show the agreement of the palaeoenvironmental and palaeoclimatic results with all the previous multiproxy and core-record data.

**Keywords:** Small mammals, Lateglacial, Middle Holocene, Heinrich Event 1, African Humid Period, Iberian Peninsula.

## 1.Introduction

During the last glacial period a sensitive response by Mediterranean vegetation to rapid climate variability has been detected in studies of the Alborán Sea core MD95-2043, with rapid woodland development during interstadials and the spread of semi-desert vegetation during Dansgaard-Oeschger events and Heinrich Events (Sánchez-Goñi et al., 2002; Kageyama et al., 2005; Fletcher and Sánchez-Goñi, 2008). By contrast, the Holocene was in general a warm and wet period, with episodes of increased aridity and global climatic pulsations, but with many regional differences, whose reach across Europe is well known (Bond et al., 2001; Davis et al., 2003; Kalis et al., 2003; Mayewsky et al., 2004; Jalut et al., 2009; Mercuri et al., 2011; Aranbarri et al., 2014). Although the Holocene has been defined as a relatively stable period in comparison to the Pleistocene, diverse climate and environmental changes have been widely recognized (Morellón et al., 2009). From 11000 to 9000 cal yr BP, in the Northern Hemisphere dry and cool conditions persisted, while the beginning of the mid-Holocene (9000-5000 cal yr BP) was characterised by warm and moister conditions in the northern mid-to-high latitudes (Wanner et al., 2008; Morellón et al., 2009; Aranbarri et al., 2014). Within this period, a short-lived cold event was recorded, the event of 8200 cal yr BP (Mercuri et al., 2011). This was followed by a transition phase (ca.7000-5500 yr BP) known as the Holocene Climate Optimum, characterised by a period of climate stability, but this stability was interrupted by the end of the African period, characterised by an abrupt decrease in precipitation and an increase in temperatures (de Menocal et al., 2000). Finally there was a phase (ca. 5500 yr BP) of drier conditions with major environmental changes (Carrión et al., 2010; Jiménez-Moreno and Anderson, 2012; Aranbarri et al., 2014; Morales-Molino and García-Antón, 2014). These changes were linked to climate variability but also to human activities, a consequence of the incorporation of new agricultural and livestock techniques that conditioned the subsequent evolution of the potentialities of the landscape ecosystems (López Sáez et al., 2005; Carrión et al., 2007; Tarroso et al., 2014; Revelles et al., 2015).

In this paper we use the study of small mammals to undertake a palaeoclimatic and palaeoenvironmental reconstruction. This proxy is not generally used for Holocene sequences, since until recently small mammals have mainly been important for their contribution to biochronology. Fortunately, these preferences have recently been changing, and palaeoenvironmental and palaeoclimatic reconstructions have been carried out from small-mammal studies of the Holocene (Laplana Conesa and Cuenca-Bescós, 1995; Murelaga et al., 2007; Oms et al., 2009; Cuenca-Bescós et al., 2009; Bañuls-Cardona and López-García, 2009; López- García et al., 2011; Cuenca-Bescós and García-Pimienta, 2012; Rofes et al., 2013; Bañuls-Cardona et al., 2013). These studies have provided interesting palaeoclimatic and palaeoenvironmental information on the Iberian Peninsula. On account of their size, small mammals are more sensitive in detecting small changes in the surrounding environment (López-García et al., 2013).

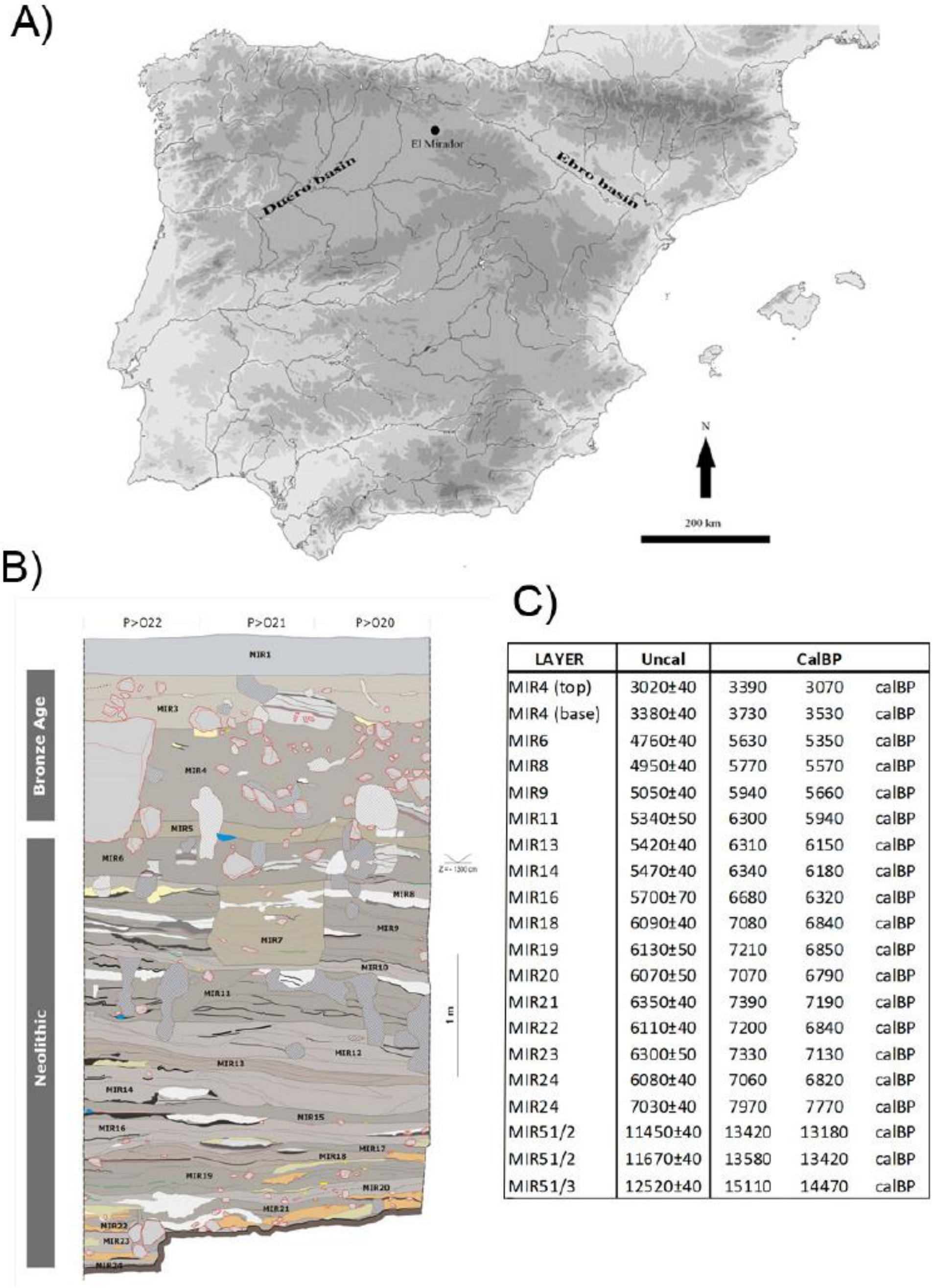
Our study analyses climatic pulsations and their relation to environmental changes in the Iberian Peninsula on the basis of the small-mammal assemblages of El Mirador cave. These range from the Lateglacial to the Late Holocene (15000 to 3000 cal yr BP). In El Mirador cave, a complete sequence from the Lateglacial to the Early Bronze Age has been documented. This is of great significance for characterising the Pleistocene-Holocene transition in northern Iberia.

In addition, the results obtained are supported with other palaeoenvironmental data acquired from El Mirador cave, such as pollen (Expósito and Burjachs, 2016), anthracology (Euba et al., 2015), carpology (Rodríguez et al., 2016), phytoliths (Cabanes et al., 2009) and large-mammal remains (Martín et al., 2014; 2015). Further, marine core studies using oxygen isotope curves in the Alboran Sea (MD95-2043) (Cacho et al., 2001) and core SMP02-3 from the Galician continental shelf (Bernárdez et al., 2008) have also been used to understand the response of vegetation to the climate variability of the Lateglacial and Late Holocene.

## 2.El Mirador cave

El Mirador cave is situated in the south of the Sierra de Atapuerca (Ibeas de Juarros, Burgos, Spain). The site is located at an altitude of 1033 m a. s. l., and its geographical coordinates are 42° 20' 58" N, 03° 30' 33" E (Fig. 1). In 1999 drilling work was started on an area of 6m² in the central part of the cave, on the basis of which the stratigraphic sequence was established. This is composed of a total of 27 layers that display high lateral and vertical variability due to the sedimentary characteristics of the cave and the post-depositional processes that took place there, such as the collapse of blocks and anthropic spatial organization, as well as bioturbation (Fig. 1). For this reason, it was decided that the naming and excavation should be in assemblages, distinguishing between the characteristic facies in the anthropized units (Vergés et al., 2002). There are a total of

17 radiocarbon dates for the sequence of El Mirador cave, which range from the Lateglacial to the Bronze Age (Vergés et al., 2002, 2016; Angelucci et al., 2009) (Fig. 2).



| LAYER | Uncal | CalBP | | |
|---|---|---|---|---|
| MIR4 (top) | 3020±40 | 3390 | 3070 | calBP |
| MIR4 (base) | 3380±40 | 3730 | 3530 | calBP |
| MIR6 | 4760±40 | 5630 | 5350 | calBP |
| MIR8 | 4950±40 | 5770 | 5570 | calBP |
| MIR9 | 5050±40 | 5940 | 5660 | calBP |
| MIR11 | 5340±50 | 6300 | 5940 | calBP |
| MIR13 | 5420±40 | 6310 | 6150 | calBP |
| MIR14 | 5470±40 | 6340 | 6180 | calBP |
| MIR16 | 5700±70 | 6680 | 6320 | calBP |
| MIR18 | 6090±40 | 7080 | 6840 | calBP |
| MIR19 | 6130±50 | 7210 | 6850 | calBP |
| MIR20 | 6070±50 | 7070 | 6790 | calBP |
| MIR21 | 6350±40 | 7390 | 7190 | calBP |
| MIR22 | 6110±40 | 7200 | 6840 | calBP |
| MIR23 | 6300±50 | 7330 | 7130 | calBP |
| MIR24 | 6080±40 | 7060 | 6820 | calBP |
| MIR24 | 7030±40 | 7970 | 7770 | calBP |
| MIR51/2 | 11450±40 | 13420 | 13180 | calBP |
| MIR51/2 | 11670±40 | 13580 | 13420 | calBP |
| MIR51/3 | 12520±40 | 15110 | 14470 | calBP |

**Figure 1**. A. Geographical location of El Mirador cave. B. Stratigraphy of El Mirador cave (Angelucci et al., 2009). C. Radiocarbon datings of studied layers. Uncal: Mean of the radiocarbon dates. CalBP: 2σ range of the calibrated dates in cal yr BP.

The Pleistocene deposit is composed of 14 m of metric and decimetric limestone blocks with no sedimentary matrix in between. It is the result of the collapsed roof (MIR51/4 and MIR51/1) and contains two intercalated levels: MIR51/3, a shallow, archaeologically sterile level composed of wind-borne sediment, and MIR51/2, with the same sedimentary characteristics but with evidence of human activity: remains of a hearth, and lithic and faunal materials (Vergés et al., 2016). The 6-m-thick Holocene sedimentary layers rest directly on top of MIR51. Four meters are attributed to Neolithic occupations (levels MIR24 to MIR6) (Vergés et al., 2008), while the remaining two meters are from the Middle Bronze Age (MIR4 and MIR3A) (Vergés et al., 2002). These Holocene levels were essentially formed as a result of the use of the cave as a livestock pen. The activities related to animal husbandry left sedimentary layers of dung, which was piled together and burned at regular intervals in order to reduce its volume and to eliminate parasites (Angelucci et al., 2009). These burned layers alternate with partially burnt and unburned layers of manure and nodules of ash from burned dung. An artefact record related to domestic occupations is often present in these levels. This kind of deposit is known as "fumier" (Vergés et al., 2016).

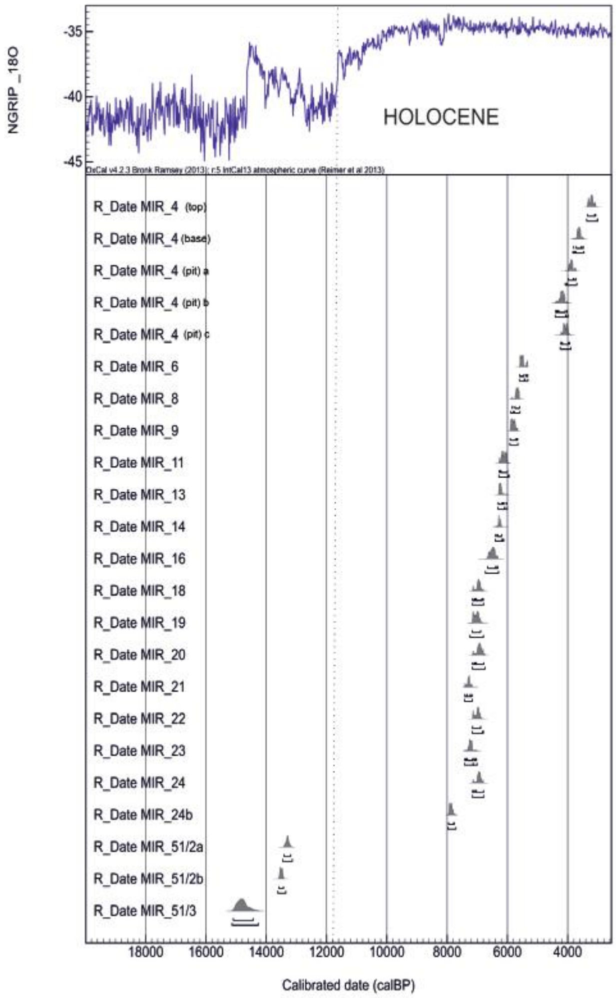


**Figure 2**. Radiocarbon age of El Mirador cave calibrated by Oxcal v4.2.3 (Bronk Ramsey et al., 2013) placed in relation to the IntCal13 atmospheric curve (Reimer et al., 2013).

Archaeological remains are abundant in this site, and many scientific papers on them have been published. These include analyses of ceramic and lithic artefacts (Vergés et al., 2002, 2008, 2016), archaeobotanical studies (Allué and Euba, 2008; Rodríguez and Buxó, 2008; Cabanes et al., 2009; Euba et al., 2015; Expósito and Burjachs, 2016; Rodríguez et al., 2016), studies of human remains (Cáceres et al., 2007; Ceperuelo et al., 2015; Lozano et al., 2015) and of large mammals (Martín et al., 2009, 2014a, 2014b, 2016), and also preliminary studies of small-mammal remains (López-García, 2008; Bañuls-Cardona et al., 2013).

## 3.Material and methods

The small mammals analysed for this manuscript belong to seventeen layers (MIR51, MIR50, MIR49, MIR24, MIR23, MIR22, MIR21, MIR19, MIR18, MIR17, MIR16, MIR11, MIR10, MIR9, MIR6, MIR5 and MIR4).

## 3.1. Palaeontological study

In order to obtain the small-vertebrate remains, a system of water screening was used with sieves of decreasing mesh size (1 cm, 0.5cm and 0.05 cm). Once the microfossils were separated from the now dry sediment, we proceeded to identify each species. This was based on both cranial and post-cranial diagnostic elements from the small-vertebrate skeletons.

The small mammals were identified using the methods of systematic palaeontology. For the identification of chiropters, mandibles and isolated teeth were used (Reumer, 1984; Cuenca-Bescós et al., 2008; López-García, 2008); for insectivores, mandibles, isolated teeth and humeri were used (Bruijn and Rumke, 1974; Menu and Popelard, 1987; Sevilla, 1988); for Arvicolinae, the first lower molars (van der Meulen, 1973; Cuenca-Bescós et al., 2008; López-García, 2008); while for *Apodemus sylvaticus* and *Eliomys quercinus* identification was based on isolated teeth (Pasquier, 1974; Damms, 1981; Cuenca-Bescós et al., 2008; López-García, 2008).

## 3.2. Habitat weighting method

We used the habitat weighting method (Evans et al., 1981; Andrews, 2006; modified by Blain et al., 2008, López-García et al., 2011) for the palaeoenvironmental reconstruction. This method involves ascertaining a percentage distribution for the habitat or habitats preferentially occupied by each taxon at present. We divided the habitats into four categories, defined according to a series of highly concrete environmental features: dry meadow, wet meadow, woodland and rocky areas: “dry meadow” consists of meadowland subject to seasonal climate change; “wet meadow” indicates evergreen meadowland with pastures and dense topsoil; “woodland” ranges from leafy forests to woodland margins, with moderate vegetation cover; and “rocky areas” refer to rocky habitats without vegetation cover (Table 2).

## 3.3. Bioclimatical approach

### 3.3.1. Mutual Ecogeographic Range method (MER)

In order to reconstruct the features of the climate, we used the Mutual Ecogeographic Range method (MER) (Blain, 2005; Blain et al., 2010; Blain et al., 2016). We removed *Microtus oeconomus* and the chiropters from the sample remains. *Microtus oeconomus* is not currently found in the Iberian Peninsula (Pokines, 1998). In spite of this, its environmental requirements are taken into account in the general interpretation of the work. The omission of the chiropters is due to the fact that in many cases their mobility makes it difficult to ascertain their present geographical distribution, which could thus result in a distortion of the data.

The method involves defining the current distribution area of the faunal association, superimposing current distribu¬tion maps divided into 10 x 10 km UTM grids (Palombo and Gisbert, 2005). The resulting intersection indicates an area where the climatic characteristics are similar to those of our association. On the basis of this intersection we calculated the MAT (mean annual temperature), MTC (mean temperature of the coldest month), MTW (mean temperature of the warmest month), and MAP (mean annual precipitation). These climatic characteristics are obtained using current maps of temperature and precipitation (Climate-Data.org). The data obtained were compared with the present-day climate of this region of the Iberian Peninsula, enabling us to note the changes in temperature and precipitation in relation to the various points of the Pleistocene and the Holocene (Table 3).

### 3.3.2. Continentality index: Gorczynski (1920)

Continentality is one of the basic characteristics of climate. It reflects how much a particular area is influenced by the ocean or by large expanses of land. It is a result of the impact of climatic elements such as temperature, precipitation, solar radiation and cloudiness (Mikolášková, 2009). Gorczynski (1920) suggested estimating the continentality of a region on the basis of the amplitude of the annual temperature oscillation and the latitude of the place (Mineti, 1989). The values of the lowest-ranking units are classified as hyperoceanic with the index of continentality (Ic) lower than 11, as oceanic with Ic between 11 and 21, and as continental with Ic higher than 21 (Rivas et al., 2011).

$$Ic = 1.7 * (Mi-mi)/\sin(Lat+10)-14$$

Mi: mean temperature of the warmest month

mi: mean temperature of the coldest month

Lat: latitude where the site is located

### 3.3.3. Rainfall index: Lang (1915)

Aridity refers to when there is insufficient water in the soil and the atmosphere, and it occurs when precipitation is lower than evaporation. It thus depends on the relationship between precipitation and temperature, which largely determines the evaporation of water. Lang relates the precipitation (mm) to the temperature (° C) to determine whether or not there is a shortage of water in a place (Capel Molina, 1963). In this classification a climate is defined as arid with L values lower than 40, as humid with L between 40 and 160, and as perhumid with L values higher than 160 (Lang, 1915; Quan et al., 2013).

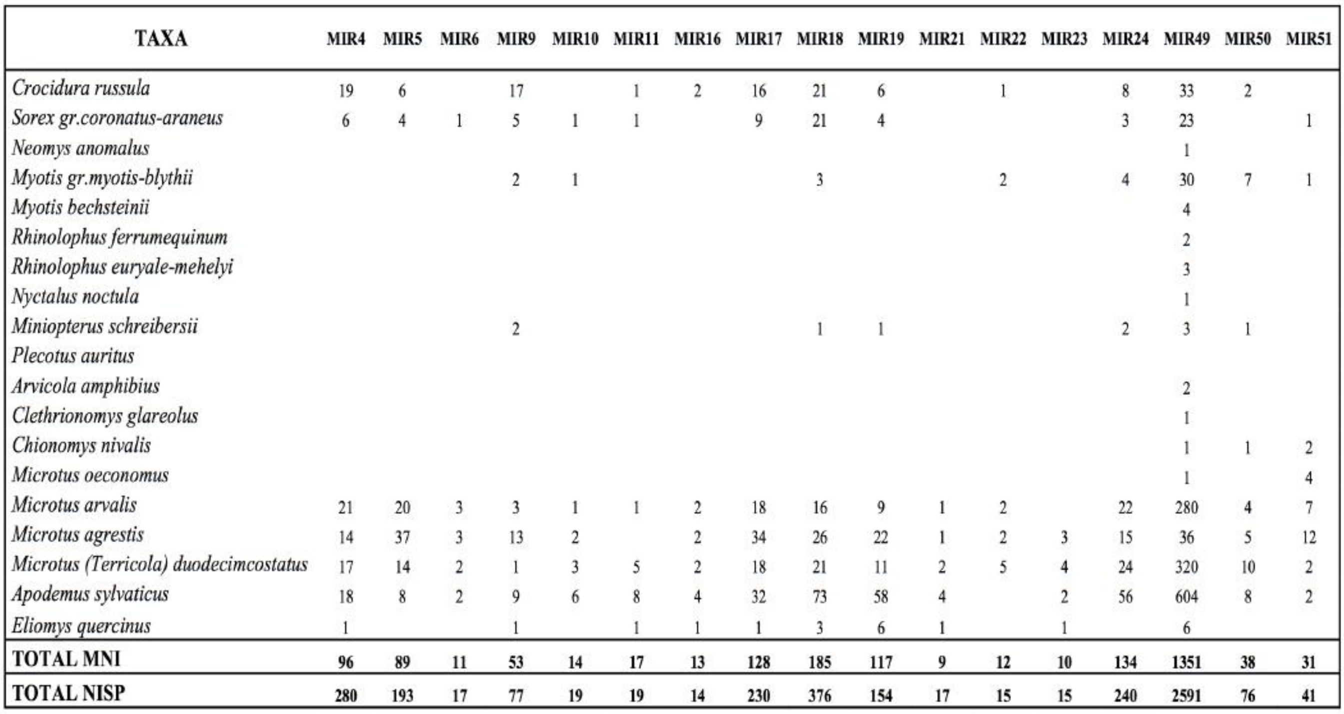
$$L=P/T$$

P: mean annual precipitation

T: mean annual temperature

## 4.Results

From these seventeen layers (MIR51, MIR50, MIR49, MIR24, MIR23, MIR22, MIR21, MIR19, MIR18, MIR17, MIR16, MIR11, MIR10, MIR9, MIR6, MIR5 and MIR4), 4374 remains (NISP) have been analysed, with a minimum number of individuals (MNI) of 2283 (Table 1). Nineteen small-mammal taxa have been identified: *Sorex* gr. *coronatus-araneus*, *Neomys anomalus*, *Crocidura russula*, *Myotis myotis-blythii*, *Myotis bechsteinii*, *Miniopterus schreibersii*, *Rhinolophus ferrumequinum*, *Rhinolophus euryale-mehelyi*, *Nyctalus noctula*, *Plecotus austriacus*, *Arvicola amphibius*, *Clethrionomys glareolus*, *Chionomys nivalis*, *Microtus oeconomus*, *Microtus arvalis*, *Microtus agrestis*, *Microtus (Terricola) duodecimcostatus*, *Apodemus sylvaticus* and *Eliomys quercinus* (Fig. 3).



| TAXA | MIR4 | MIR5 | MIR6 | MIR9 | MIR10 | MIR11 | MIR16 | MIR17 | MIR18 | MIR19 | MIR21 | MIR22 | MIR23 | MIR24 | MIR49 | MIR50 | MIR51 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Crocidura russula* | 19 | 6 | | 17 | | 1 | 2 | 16 | 21 | 6 | | 1 | | 8 | 33 | 2 | |
| *Sorex gr.coronatus-araneus* | 6 | 4 | 1 | 5 | 1 | 1 | | 9 | 21 | 4 | | | | 3 | 23 | | 1 |
| *Neomys anomalus* | | | | | | | | | | | | | | | 1 | | |
| *Myotis gr.myotis-blythii* | | | | 2 | 1 | | | | 3 | | | 2 | | 4 | 30 | 7 | 1 |
| *Myotis bechsteinii* | | | | | | | | | | | | | | | 4 | | |
| *Rhinolophus ferrumequinum* | | | | | | | | | | | | | | | 2 | | |
| *Rhinolophus euryale-mehelyi* | | | | | | | | | | | | | | | 3 | | |
| *Nyctalus noctula* | | | | | | | | | | | | | | | 1 | | |
| *Miniopterus schreibersii* | | | | 2 | | | | | 1 | 1 | | | | 2 | 3 | 1 | |
| *Plecotus auritus* | | | | | | | | | | | | | | | | | |
| *Arvicola amphibius* | | | | | | | | | | | | | | | 2 | | |
| *Clethrionomys glareolus* | | | | | | | | | | | | | | | 1 | | |
| *Chionomys nivalis* | | | | | | | | | | | | | | | 1 | 1 | 2 |
| *Microtus oeconomus* | | | | | | | | | | | | | | | 1 | | 4 |
| *Microtus arvalis* | 21 | 20 | 3 | 3 | 1 | 1 | 2 | 18 | 16 | 9 | 1 | 2 | | 22 | 280 | 4 | 7 |
| *Microtus agrestis* | 14 | 37 | 3 | 13 | 2 | | 2 | 34 | 26 | 22 | 1 | 2 | 3 | 15 | 36 | 5 | 12 |
| *Microtus (Terricola) duodecimcostatus* | 17 | 14 | 2 | 1 | 3 | 5 | 2 | 18 | 21 | 11 | 2 | 5 | 4 | 24 | 320 | 10 | 2 |
| *Apodemus sylvaticus* | 18 | 8 | 2 | 9 | 6 | 8 | 4 | 32 | 73 | 58 | 4 | | 2 | 56 | 604 | 8 | 2 |
| *Eliomys quercinus* | 1 | | | 1 | | 1 | 1 | 1 | 3 | 6 | 1 | | 1 | | 6 | | |
| **TOTAL MNI** | **96** | **89** | **11** | **53** | **14** | **17** | **13** | **128** | **185** | **117** | **9** | **12** | **10** | **134** | **1351** | **38** | **31** |
| **TOTAL NISP** | **280** | **193** | **17** | **77** | **19** | **19** | **14** | **230** | **376** | **154** | **17** | **15** | **15** | **240** | **2591** | **76** | **41** |

**Table 1.** Distribution of the small-mammal remains of El Mirador cave by layers. Minimum number of individuals (MNI) and number of identified specimens (NISP).

The remains analysed present slight signs of digestion. From these results, it can be surmised that the main animal responsible for the accumulation in the cave was a category 1 predator, a nocturnal bird of prey that displays an opportunistic trophic pattern and produces slight modifications of the bones it ingests (Andrews, 1990). The small mammals form an assemblage of great taxonomic variety, indicating that it was the work of an opportunistic hunter.

### 4.1. Lateglacial: MIR51(15100-13180 cal yr BP), MIR50 and MIR49

#### 4.1.1. Palaeontological study

From the small-mammal assemblages of MIR51, MIR50 and MIR49, 2708 remains (NISP) have been analysed, with a minimum number of individuals (MNI) of 1420 (Table 1). Nineteen small-mammal taxa have been identified: *Crocidura russula*, *Sorex* gr. *coronatus-araneus*, *Neomys anomalus*, *Myotis myotis-blythii*, *Myotis bechsteinii*, *Miniopterus schreibersii*, *Rhinolophus ferrumequinum*, *Rhinolophus euryale-mehelyi*, *Nyctalus noctula*, *Plecotus austriacus*, *Arvicola amphibius*, *Clethrionomys glareolus*, *Chionomys nivalis*, *Microtus oeconomus*, *Microtus arvalis*, *Microtus agrestis*, *Microtus (Terricola) duodecimcostatus*, *Apodemus sylvaticus* and *Eliomys quercinus* (Fig. 3).

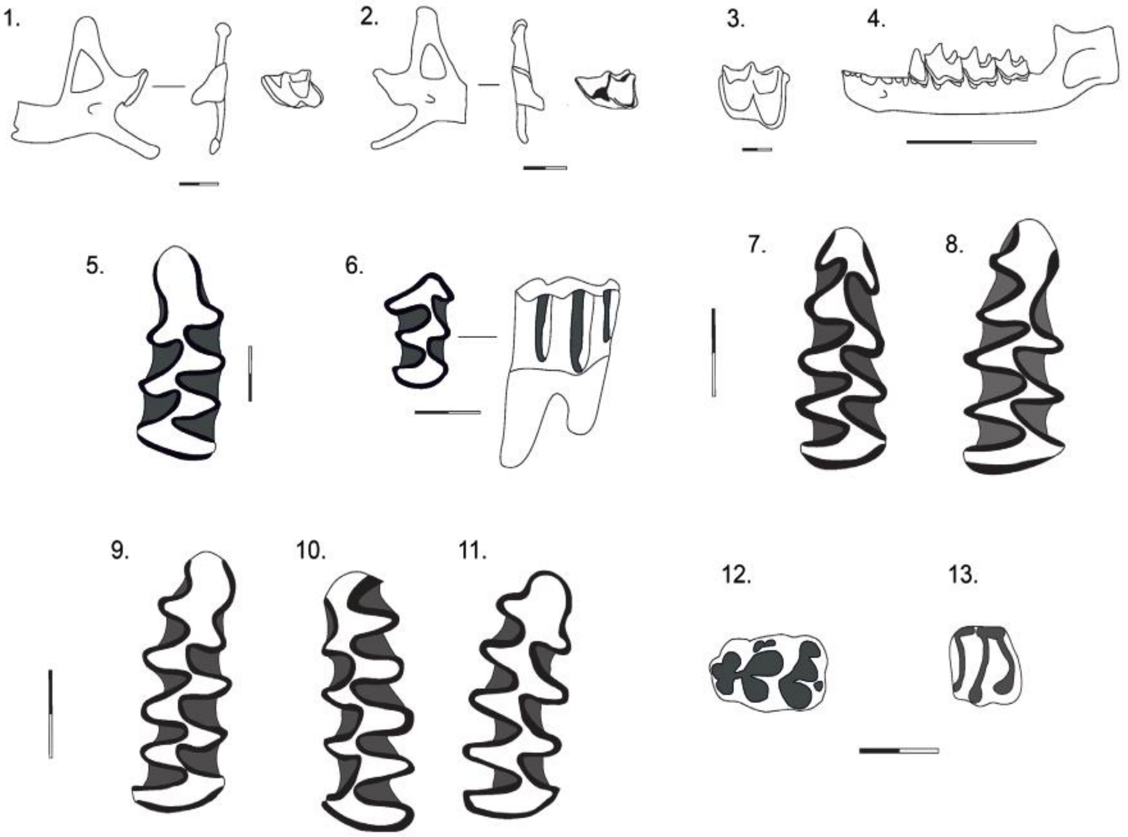


**Figure 3**. Small-mammal fossil remains from layer MIR4 of El Mirador cave. From left to right: 1. *Crocidura russula*, right mandible (lingual and posterior view) and right m2 (occlusal view); 2. *Sorex* gr. *coronatus-araneus*, left mandible (lingual and posterior view) and left m1 (occlusal view); 3. *Myotis* gr. *myotis-blythii*, first right molar (occlusal view); 4. *Miniopterus schreibersii*, right mandible (labial view); 5. *Arvicola amphibius*, first right molar (occlusal view); 6. *Clethrionomys glareolus*, first right molar (occlusal view and labial view); 7. *Chionomys nivalis*, first right molar (occlusal view); 8. *Microtus oeconomus*, first right molar (occlusal view); 9. *Microtus agrestis*, left m1 (occlusal view); 10. *Microtus arvalis*, right m1 (occlusal view); 11. *Microtus (Terricola) duodecimcostatus*, right m1 (occlusal view); 12. *Apodemus sylvaticus*, right m1 (occlusal view); 13. *Eliomys quercinus*, left m2 (occlusal view). Scale bars = 1 mm.

### 4.1.2. Palaeoenvironmental analysis

In MIR51 (15100-13180 cal yr BP) the most highly represented taxon is *M. agrestis*. This is probably related to the high percentage of open environments (50%). In MIR50, *Microtus (Terricola) duodecimcostatus* is the most highly represented taxon, and in this layer we have registered a minor increase in woodland with respect to MIR51. Finally, in MIR49 the trend of *Apodemus sylvaticus* predominating over the rest of the species, with a mainly woodland landscape, begins.

#### 4.1.3. Palaeoclimatical approach

The results of the continentality index indicate climatic conditions characteristic of an oceanic climate in MIR51 (15100-13180 cal yr BP) and MIR50, but characteristic of a hyperoceanic climate in MIR49. As regards the mean annual temperatures (MAT), in MIR51 we have registered the lowest temperatures in the sequence, 7.9 ºC, related with the cool event, while in MIR49 we have registered 10.2 ºC.

The results obtained from the rainfall index show wet and temperate climatic conditions, but the MER method reveals a difference of 200mm between the MAP of MIR51-50 (1013-1067 mm) and MIR49 (1200 mm).

### 4.2. Middle Holocene (7060-5350 cal yr BP)

#### 4.2.1. Palaeontological study

From the small-mammal assemblages of MIR24, MIR23, MIR22, MIR21, MIR19, MIR18, MIR17, MIR16, MIR11, MIR10, MIR9, MIR6, and MIR5, 1386 remains (NISP) have been analysed, with a minimum number of individuals (MNI) of 792 (Table 1). Nine small-mammal taxa have been identified: *Crocidura russula*, *Sorex* gr. *coronatus-araneus*, *Myotis myotis-blythii*, *Miniopterus schreibersii*, *Microtus arvalis*, *Microtus agrestis*, *Microtus (Terricola) duodecimcostatus*, *Apodemus sylvaticus* and *Eliomys quercinus* (Fig. 3).

#### 4.2.2. Palaeoenvironmental analysis

The most highly represented taxon is *Apodemus sylvaticus*. The presence of this species is directly related with the predominant representation of woodland in the Middle Holocene sequence. Woodland percentages range from 54% to 74% of the entire landscape around the cave. This is the general trend, but we have detected variations at specific times that should be noted. One of them took place at 7300-7100 cal yr BP (MIR23). In this layer, we have documented a decrease in woodland from 71% (MIR24) to 60% (MIR23), associated with the predominance of *Microtus (Terricola) duodecimcostatus* to the detriment of *Apodemus sylvaticus*. Starting from 6800 cal yr BP, there is another decrease in the percentage of arboreal cover around El Mirador. This decrease is from 70% in MIR18 to 62% in MIR17, and in this case it is associated with the increase in the presence of *Microtus agrestis*. Finally, we have observed from 6000 cal yr BP (MIR9) a decrease in woodland of 13% with respect to MIR10, and this trend continues until the end of the Middle Holocene in El Mirador cave. Moreover this trend is accompanied by the complete replacement of *A. sylvaticus* as the predominant species.

### 4.2.3. Palaeoclimatic approach

The continentality index in the Middle Holocene indicates climatic conditions characteristic of an oceanic climate. We have detected only two exceptions, with the climatic characteristics showing a hyperoceanic climate at 5900 cal yr BP (MIR10) and at 5600-5300 cal yr BP (MIR6). However, the MER analysis has revealed thermal oscillations that we consider important. During the Middle Holocene of El Mirador, we have observed that the mean annual temperature averages 10ºC, but this trend is interrupted at two points. From 7000 to 6800 cal yr BP (MIR23-MIR22), we have recorded an increase of 1ºC with respect to MIR24, while in MIR11 (6300-5900 cal yr BP) the general trend of 10 ºC drops to 9.6ºC. This is not a sharp decrease, but it is the lowest temperature recorded in the Holocene sequence of El Mirador. Moreover, after this decrease the general trend (10ºC) is recovered through to the end of the Middle Holocene.

As regards the results obtained from the rainfall index for the Middle Holocene, these indicate pluviometric values characteristic of a warm and temperate climate, with the exception of MIR22 (7200-6800 cal yr BP), where the pluviometric values indicate a semi-arid climate.

By means of the MER climatic analysis, we have observed that the MAP (mean annual precipitation) generally ranges from 790 to 870 mm, with slight variations throughout the Middle Holocene. Nevertheless, we have documented a short arid period lasting from 7300 to 6800 cal yr BP (MIR23-MIR21). During this short period, the precipitation was 100 mm lower in MIR23 and MIR21, while in MIR22 it decreased by 200 mm with respect to MIR24. Another important decrease is recorded in MIR16 (6600-6300 cal yr BP), from 794 mm in MIR17 to 715 mm in MIR16.

## 4.3. Late Holocene (4330-3070 cal yr BP)

### 4.3.1. Palaeontological study

From the small-mammal assemblage of MIR4, 280 remains (NISP) have been analysed, with a minimum number of individuals (MNI) of 71 (Table 1). Seven small-mammal taxa have been identified: *Crocidura russula*, *Sorex* gr. *coronatus-araneus*, *Microtus arvalis*, *Microtus agrestis*, *Microtus (Terricola) duodecimcostatus*, *Apodemus sylvaticus* and *Eliomys quercinus* (Fig. 3).

### 4.3.2. Palaeoenvironmental analysis

In this layer the predominant landscape is woodland (59%), following the trend of the Middle Holocene.

### 4.3.3. Palaeoclimatic approach

The climatic values for MIR4 are similar to those obtained for the Middle Holocene layers. The continentality index indicates climatic conditions characteristic of an oceanic climate, with a mean annual temperature of 9.9 ºC, i.e. almost the same as the Middle Holocene layers. The rainfall index reveals pluviometric values for this layer that are characteristic of a warm and temperate climate, with a mean annual precipitation of 794 mm.

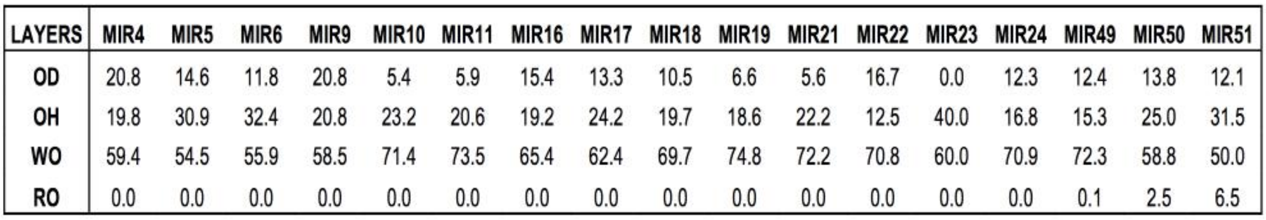
## 5.Discussion

In the Iberian Peninsula, major changes in the vegetation and rapid oscillations in the climate have been identified between the Lateglacial and the Late Holocene (Mayewski et al., 2004; Kageyama et al., 2005; Pérez-Sanz et al., 2013). This is shown by studies such as the ice-core record from Greenland (Johnsen et al., 1972, 1992), marine core records closer to the coasts of the Iberian Peninsula such as marine core MD95-2042 off the southwestern coast of Portugal (Shackleton et al., 2000), MD99-2331 off the coast of Galicia (Naught et al., 2007; Bernárdez et al., 2008), and MD95-2043 from the Alboran Sea (Kageyama et al., 2005), as well as continental cores from Padul (Sierra Nevada) (Pons and Reille, 1988) and core SMP02-3 retrieved from the Galician shelf (NW Iberian Peninsula) (Bernárdez et al., 2008). Furthermore, these changes in vegetation have also been seen from the pollen sequences of the Iberian Peninsula from the Lateglacial to the Early Holocene (Fletcher and Sánchez-Goñi, 2008; Carrión et al., 2010; Jiménez-Moreno et al., 2012; Aranbarri et al., 2014).

### 5.1. Lateglacial (15100-13180 cal yr BP)

The palaeoclimatic data obtained from the small-mammal assemblage show that in layer MIR51 the MAT is 7.9 ºC, 2.2 ºC lower than currently in Burgos (Climate-Data.org). This may well be related with a cool period from the end of the Lateglacial. The MD95-2042 record (southwestern Spain) has detected phases comprising a significant cooling of ocean surface waters caused by the influx of icebergs as far as Iberian shores (Shackleton et al., 2000). These phases have been called Heinrich Events (Fig. 2) (Sánchez-Goñi and d'Errico, 2005). Taking into account the absolute dating for this layer to between 15100 and 13180 cal yr BP, this cool period could correspond to Heinrich

Event 1 (H1), dated to between 16000 and 14000 cal yr BP (Fletcher and Sánchez-Goñi, 2008). Expansions of semi-desert vegetation also characterised the Lateglacial (Kageyama et al., 2005; Fletcher and Sánchez-Goñi, 2008), although we do not observe arid conditions from MIR51 to MIR49. A high MAP is registered with the small-mammal assemblage, between 400-600 mm higher than nowadays (Table 2). In fact, the Lang rainfall index characterises these pluviometric data as humid, and not as pertaining to a semi-arid Mediterranean climate as is currently characteristic of Burgos (Table 3). These records show that during the Lateglacial the Iberian Peninsula was characterised by conditions that were slightly more humid than the rest of Europe (Kageyama et al., 2005; Peyron et al., 1998; Fletcher and Sánchez-Goñi, 2008).



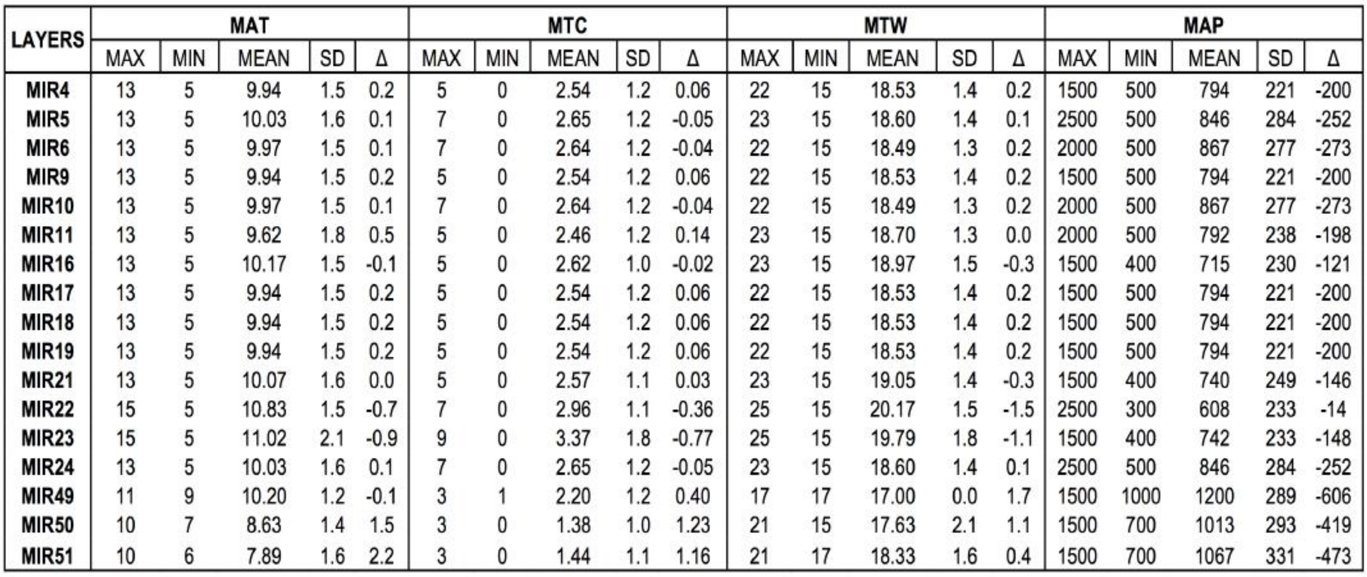
| LAYERS | MIR4 | MIR5 | MIR6 | MIR9 | MIR10 | MIR11 | MIR16 | MIR17 | MIR18 | MIR19 | MIR21 | MIR22 | MIR23 | MIR24 | MIR49 | MIR50 | MIR51 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| OD | 20.8 | 14.6 | 11.8 | 20.8 | 5.4 | 5.9 | 15.4 | 13.3 | 10.5 | 6.6 | 5.6 | 16.7 | 0.0 | 12.3 | 12.4 | 13.8 | 12.1 |
| OH | 19.8 | 30.9 | 32.4 | 20.8 | 23.2 | 20.6 | 19.2 | 24.2 | 19.7 | 18.6 | 22.2 | 12.5 | 40.0 | 16.8 | 15.3 | 25.0 | 31.5 |
| WO | 59.4 | 54.5 | 55.9 | 58.5 | 71.4 | 73.5 | 65.4 | 62.4 | 69.7 | 74.8 | 72.2 | 70.8 | 60.0 | 70.9 | 72.3 | 58.8 | 50.0 |
| RO | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.1 | 2.5 | 6.5 |

**Table 2.** Distribution of the minimum number of individuals (MNI) of small mammals from the different layers of El Mirador cave sequence according to their habitat preferences. We divided the habitats into four cat¬egories: OD, dry meadow; OH, wet meadow; WO, woodland; RO, rocky areas.

During H1 there was a major reduction in arboreal pollen (Fletcher and Sánchez-Goñi, 2008). From the small-mammal assemblage we observe an increase in woodland, rising from MIR51 (50%) to MIR50 (59%) and particularly MIR49 (72%) (Fig. 2).

## 5.2. Holocene

In general, small-mammal accumulations were produced when the cave was inhabited, but during the Holocene El Mirador cave was a site with human occupation throughout its sequence. Zooarchaeological studies indicate that in some levels of El Mirador cave foetal remains from the final days of the third gestational trimester have been identified, and in all levels foetal remains from the final weeks of gestation have been recovered. These data testify to the very likely use of the cave as a breeding and birthing space for ovicaprines, at least during the end of winter and early spring (Martín et al., 2015). The palaeoclimatic and palaeoenvironmental results for the Holocene sequence of El Mirador cave thus represent summer and autumn conditions.



| LAYERS | MAT | | | | | MTC | | | | | MTW | | | | | MAP | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | MAX | MIN | MEAN | SD | Δ | MAX | MIN | MEAN | SD | Δ | MAX | MIN | MEAN | SD | Δ | MAX | MIN | MEAN | SD | Δ |
| **MIR4** | 13 | 5 | 9.94 | 1.5 | 0.2 | 5 | 0 | 2.54 | 1.2 | 0.06 | 22 | 15 | 18.53 | 1.4 | 0.2 | 1500 | 500 | 794 | 221 | -200 |
| **MIR5** | 13 | 5 | 10.03 | 1.6 | 0.1 | 7 | 0 | 2.65 | 1.2 | -0.05 | 23 | 15 | 18.60 | 1.4 | 0.1 | 2500 | 500 | 846 | 284 | -252 |
| **MIR6** | 13 | 5 | 9.97 | 1.5 | 0.1 | 7 | 0 | 2.64 | 1.2 | -0.04 | 22 | 15 | 18.49 | 1.3 | 0.2 | 2000 | 500 | 867 | 277 | -273 |
| **MIR9** | 13 | 5 | 9.94 | 1.5 | 0.2 | 5 | 0 | 2.54 | 1.2 | 0.06 | 22 | 15 | 18.53 | 1.4 | 0.2 | 1500 | 500 | 794 | 221 | -200 |
| **MIR10** | 13 | 5 | 9.97 | 1.5 | 0.1 | 7 | 0 | 2.64 | 1.2 | -0.04 | 22 | 15 | 18.49 | 1.3 | 0.2 | 2000 | 500 | 867 | 277 | -273 |
| **MIR11** | 13 | 5 | 9.62 | 1.8 | 0.5 | 5 | 0 | 2.46 | 1.2 | 0.14 | 23 | 15 | 18.70 | 1.3 | 0.0 | 2000 | 500 | 792 | 238 | -198 |
| **MIR16** | 13 | 5 | 10.17 | 1.5 | -0.1 | 5 | 0 | 2.62 | 1.0 | -0.02 | 23 | 15 | 18.97 | 1.5 | -0.3 | 1500 | 400 | 715 | 230 | -121 |
| **MIR17** | 13 | 5 | 9.94 | 1.5 | 0.2 | 5 | 0 | 2.54 | 1.2 | 0.06 | 22 | 15 | 18.53 | 1.4 | 0.2 | 1500 | 500 | 794 | 221 | -200 |
| **MIR18** | 13 | 5 | 9.94 | 1.5 | 0.2 | 5 | 0 | 2.54 | 1.2 | 0.06 | 22 | 15 | 18.53 | 1.4 | 0.2 | 1500 | 500 | 794 | 221 | -200 |
| **MIR19** | 13 | 5 | 9.94 | 1.5 | 0.2 | 5 | 0 | 2.54 | 1.2 | 0.06 | 22 | 15 | 18.53 | 1.4 | 0.2 | 1500 | 500 | 794 | 221 | -200 |
| **MIR21** | 13 | 5 | 10.07 | 1.6 | 0.0 | 5 | 0 | 2.57 | 1.1 | 0.03 | 23 | 15 | 19.05 | 1.4 | -0.3 | 1500 | 400 | 740 | 249 | -146 |
| **MIR22** | 15 | 5 | 10.83 | 1.5 | -0.7 | 7 | 0 | 2.96 | 1.1 | -0.36 | 25 | 15 | 20.17 | 1.5 | -1.5 | 2500 | 300 | 608 | 233 | -14 |
| **MIR23** | 15 | 5 | 11.02 | 2.1 | -0.9 | 9 | 0 | 3.37 | 1.8 | -0.77 | 25 | 15 | 19.79 | 1.8 | -1.1 | 1500 | 400 | 742 | 233 | -148 |
| **MIR24** | 13 | 5 | 10.03 | 1.6 | 0.1 | 7 | 0 | 2.65 | 1.2 | -0.05 | 23 | 15 | 18.60 | 1.4 | 0.1 | 2500 | 500 | 846 | 284 | -252 |
| **MIR49** | 11 | 9 | 10.20 | 1.2 | -0.1 | 3 | 1 | 2.20 | 1.2 | 0.40 | 17 | 17 | 17.00 | 0.0 | 1.7 | 1500 | 1000 | 1200 | 289 | -606 |
| **MIR50** | 10 | 7 | 8.63 | 1.4 | 1.5 | 3 | 0 | 1.38 | 1.0 | 1.23 | 21 | 15 | 17.63 | 2.1 | 1.1 | 1500 | 700 | 1013 | 293 | -419 |
| **MIR51** | 10 | 6 | 7.89 | 1.6 | 2.2 | 3 | 0 | 1.44 | 1.1 | 1.16 | 21 | 17 | 18.33 | 1.6 | 0.4 | 1500 | 700 | 1067 | 331 | -473 |

**Table 3.** Relation of temperatures and precipitation obtained using the MER (Mutual Ecogeographic Range) method. MAT: mean annual temperature; MTC: mean temperature of the coldest month; MTW: mean temperature of the warmest month; MAP: mean annual precipitation; n: number of 10×10km UTM squares forming the intersection obtained for micromammals; mean±SD: mean and standard deviation of the values obtained; min: minimum of the values obtained; max: maximum of the values obtained: Δ difference between the current mean for Burgos weather station over 30 years and that obtained for the small mammals.

### 5.2.1. Middle Holocene

At 8200 yr BP a cold event took place, characterised by cooler temperatures (Mayewski et al., 2004) and by drier conditions (López-Sáez et al., 2008; González-Sampériz et al., 2009; Gómez-Paccard et al., 2013). This event is most clearly recorded as a marked shift in oxygen isotope records from the Greenland Ice Sheet, and for this reason it has been used to signal the beginning of the Middle Holocene (Walker et al., 2012).

#### 5.2.1.1.PHASE I: 8000-6000 cal yr BP

After this cold climatic event, however, the cores of the North Atlantic Ocean indicate warm temperatures from ca. 8000 to 5000 yr BP (Steig, 2009). At 7030-6870 cal yr BP (MIR24), we find mild and humid conditions. According to the Lang rainfall index, the climate of this layer was semi-humid; the MER method reveals the MAT to be 0.1 ºC lower than nowadays, while the MAP is 252 mm higher than at present in the Burgos area. Even the pollen record of Padul in southeastern Spain shows signs of the onset of warm and humid conditions at ca. 8000 yr BP (Pons and Reille, 1988). We also observe in this layer a clear predominance of woodland (70. 9%)(Fig. 4) due to the high level of precipitation (865mm) within the Holocene sequence of El Mirador (Table 2). This is not a local case. Palaeobotanical studies (Fernández et al., 2007; Jiménez-Moreno and Anderson, 2012) have shown that in this period there were wetter conditions and a substantial increase in the percentage of arboreal pollen in the western Mediterranean (Jiménez-Moreno et al., 2013), in the Ebro Valley (González-Sampériz et al., 2009; Gómez-Paccard et al., 2013), and in the south of the Iberian Peninsula (Fernández et al., 2007).

The highest temperatures in the El Mirador sequence (Table 3) are recorded from 7400 to 7000 cal yr BP (MIR23-22). In these layers the MAT exceeds the current level by 1ºC (Table 3). However, the MAP of these layers is the lowest in the entire sequence. The MAP in MIR23 is 148mm higher than at present, while in the case of MIR22 the MAP is 608 mm, only 14 mm higher than nowadays (Table 2). According to the Lang index, MIR22 presents a semi-arid level of precipitation similar to present-day data (Table 3). Nevertheless, these lower levels of precipitation had no immediate effect on the palaeoenvironmental conditions of these layers: the percentage of arboreal cover in MIR22 is 71%, and in MIR23 it is 60% (Table 2). In terms of vegetation cover, dry conditions have been recorded in northern Iberia in general (Muñoz Sobrino et al., 2004; Santos et al., 2000).

These conditions could be related to the end of the African Humid Period (ca. 9000 - 6000 cal yr BP). In fact, humid conditions had started as early as ca. 14.5 cal ka BP following the fully glacial hyperarid conditions during the latest Pleistocene. This event has been attributed to a strengthening of the African monsoon due to gradual orbital increases in summer season insolation. However, the onset and termination of this humid period were very abrupt (deMenocal et al., 2000).

As regards the percentage representation of the small mammals, in most of the El Mirador cave sequence the most representative species is *A. sylvaticus*, a generalist species, whereas in MIR23 the most highly represented taxon (40%) is *M.(T). duodecimcostatus*, a thermo-Mediterranean taxon (Table 1).

After the African Humid Period the climatic conditions were more similar to present-day conditions in the Iberian Peninsula (Fig. 2) (Ruíz-Zapata et al., 2010). In fact, the MER method reveals that the MAT from 7390-7190 cal yr BP (MIR21) is equal to current data, although the MAP is 146 mm higher than now (Table 2). However, from ca. 7000 to 5000 yr BP, a decrease in temperature and an increase in precipitation are recorded in several regions of Europe (Leira, 2005; Kalis et al.,

2003) and North Africa (Mercuri et al., 2011). These conditions are observed from 7200-6600 cal yr BP in MIR19, MIR18 and MIR17. Palaeoclimatic analysis shows an increase in precipitation in comparison to MIR21, for the MAP is 54 mm higher, and the temperatures are lower: a decrease of 0.5ºC is recorded in the mean of the coldest months (MTC) (Table 2).

After this slight cooling, from 6600-6300 cal yr BP (MIR16) the temperatures returned to levels similar to nowadays, with the MAT 0.1 º C higher than today (Table 2), and a significant decrease of 79 mm in rainfall is observed with respect to MIR17. Despite the climate changes revealed by MER, the landscape is virtually unchanged in relation to MIR17 (Table 2), and the Lang rainfall index lies within the parameters of a semi-humid interval, like MIR17 (Table 3).

At 6000 yr BP there was a steep decline in Northern Hemisphere solar insolation that brought global cooling with alpine glacier advances (Davis et al., 2003). The result was a short, slightly cooler and humid period (Bond et al., 1997; Kalis et al., 2003; Mayewski et al., 2004; Pérez-Sanz et al., 2013). These slightly cooler conditions have been identified in El Mirador at 6300-5940 cal yr BP (MIR11). With the MER we see the MAT (9.6ºC) at its lowest in the Holocene sequence of El Mirador cave, 0.5 ºC lower than at present, mainly due to the low MTC (2.4ºC) (Table 2). Moreover, these results could be associated with a change in herding strategies at this point in El Mirador. The importance of goats and sheep decreases while the presence of equids, whose origin is likely to be wild, becomes more significant in this layer (Martín et al., 2016a). This change in livestock management may in part have been influenced by the low temperatures shown by the small-mammal study. Furthermore, this period was characterized by a wet event, with a general trend towards more humid conditions (Carrión, 2002; Tarroso et al., 2014). The climatic data obtained from the small mammals of El Mirador suggest that the MAP in MIR11 (792mm) underwent an increase in relation to the pluviometric data for MIR16 (715mm).

#### 5.2.1.2.PHASE II: 6000-5000 cal yr BP

As well as several short cooling events detected throughout Europe within relatively stable climatic conditions (Mayewski et al., 2004), dry events have also been detected during the Holocene (Fig. 2) (Jalut et al., 2000; Carrión et al., 2010). Such a stage of marked aridity has been identified in Europe (Mercuri et al., 2011), and in the Iberian Peninsula such an event occurred towards ca. 5800-5600 yr BP (Domínguez-Villar et al., 2012; Tarroso et al., 2014). More concretely, in the Iberian Meseta it occurred at around 5740 cal yr BP (Pérez-Olbiol et al., 2010). In El Mirador we detect one of these dry events in 5940-5660 cal yr BP (MIR9). This level shows a decrease in MAP from 867 mm in MIR10 to 794 mm in MIR9 (Table 2).

The palaeoenvironmental analysis shows a clear change in the landscape with respect to the lower layers. A major decrease in woodland formations is observed from 71% in MIR10 to 58% in MIR9 (Fig. 4). The pollen remains indicate a significant increase in crops around the cave (Expósito et al., submitted). The agricultural intensification caused a deterioration in landscape throughout the Iberian Peninsula (Fletcher and Sánchez-Goñi, 2008; Pérez-Sanz et al., 2013).

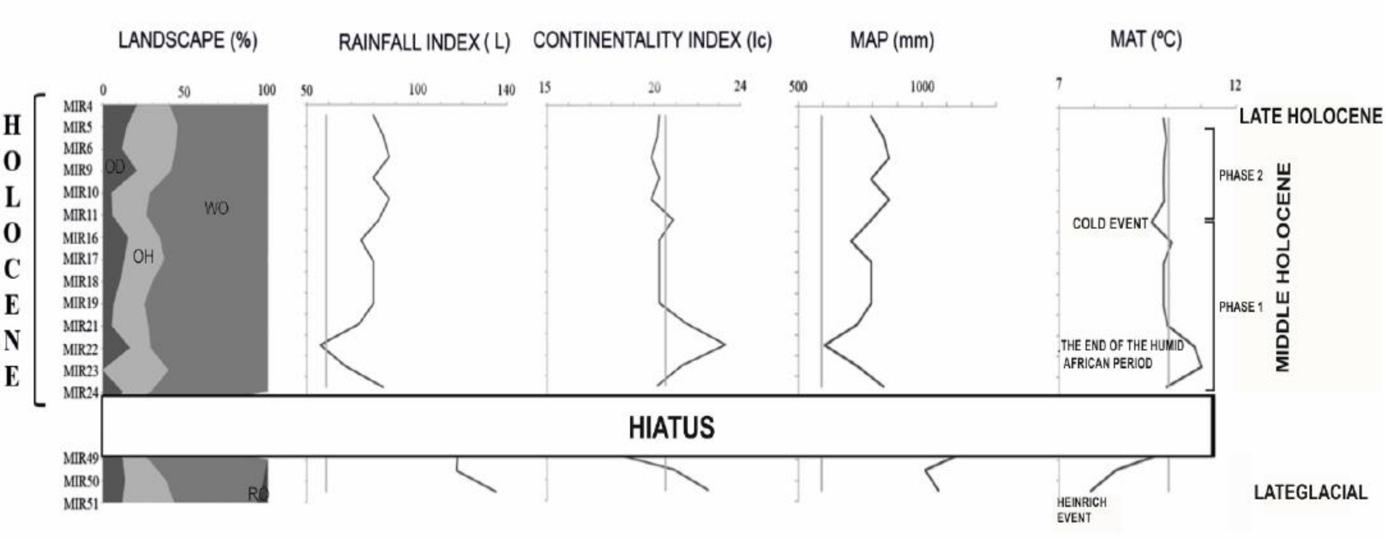


**Figure 4.** Climatic and environmental comparisons between various proxies used throughout the El Mirador cave sequence. From left to right: Habitat interpretation for the El Mirador cave based on the habitat weighting method. Reconstruction of the rainfall index (Lang). Reconstruction of the continentality index (Gorczynski). Mean annual precipitation (MAP) and mean annual temperature (MAT) of the El Mirador cave sequence. Grey bar in rainfall index, continentality index, MAP and MAT represents the current values.

Moreover, some studies have described this event as preceding the development of a dry Mediterranean climate, corresponding to the expansion of sclerophyllous woodlands (Carrión et al., 2010; Pérez-Sanz et al., 2013; Tarroso et al., 2014). In MIR9 the best-represented small mammal taxon is a thermo-Mediterranean species, *C. russula* (32%) (Table 1). This suggests a slight thermal recovery with respect to MIR10. It could also be due to the incipient establishment of a Mediterranean climate that occurred in the area around El Mirador before ca. 5000 yr BP (Pérez-Olbiol et al., 2010). As regards the temperatures, by contrast, no change is observed from MIR10, and this trend is to persist until the Bronze Age.

After the dry event of MIR9 (5940-5660 cal yr BP), an increase in humidity and woodland expansion has been observed in the Iberian Peninsula (Fig. 4) (Carrión et al., 2010), although there are regional areas where forest cover is reduced and shrub vegetation expands (López-Merino et al., 2012). From 5630-5350 cal yr BP (MIR6 and MIR5), we observe a substantial increase in precipitation (73 mm more than in MIR9) (Table 2), although there is no gain in forest cover. On the contrary, we observe a major increase in open wet meadows (10 % with respect to MIR9), which in both layers results in the highest percentages in El Mirador cave (Fig. 4).

The palaeoenvironmental and palaeoclimatic conditions of these layers (5630-5350 cal yr BP) of El Mirador cave suggest that there was probably another factor that contributed to the decline in woodland (Fig. 4). In central Europe, adaptation to the forest ecosystem was abandoned during the Early Neolithic in favour of an agricultural system (Kalis et al., 2003). Some authors claim that the landscape in the Iberian Peninsula after ca. 5000 yr BP is likely to have been influenced by non-natural ecosystem changes due to the spread of human activities, first in the lowlands and expanding to mountainous environments (Carrión et al., 2010a; Tarroso et al., 2014). Other authors believe that the first evidence of a human impact on the landscape of the Iberian Peninsula was produced during this time period (Badal et al., 1994; Carrión, 2002; Fletcher and Sánchez-Goñi, 2008; Martínez-Cortizas et al., 2009; López-Merino et al., 2012; Tarroso et al., 2014; Pérez-Díaz et al., 2014; Aranbarri et al., 2015; Revelles et al., 2015; Lillios et al., 2016).

### 5.2.2. Late Holocene

This was characterised by an increase in temperature but with slight fluctuations, and by irregular rainfall with summers undergoing mild droughts and very rainy winters (Fig. 3) (Mariscal, 1993)

Palaeoclimatic studies have claimed that the period from ca. 4300-3400 yr BP was an arid, cool phase in MIR4 (Fig. 4) (Jalut et al., 2000; Carrión, 2002; Mayewsky et al., 2004; Martín-Puertas et al., 2008). Other authors have pointed to a slight cooling and increased dryness manifested by an increase in xerophytic and cold taxa at the expense of Mediterranean species (Murelaga et al., 2009; Ruíz-Zapata et al., 2010; Domínguez-Villar et al., 2012; Pérez-Sanz et al., 2013). In the case of MIR4, a high percentage of *M. arvalis*, a Eurosiberian taxon (Table 1), is recorded. The MER method indicates a minor decrease in temperatures and in precipitation with respect to MIR5 (Table 2). The results obtained by the MER method for MIR 4 concur with those obtained from palaeobotanical studies in the same layer (Vergès et al., 2002; Cabanes et al., 2009) and from other pollen studies within the Iberian Peninsula (López Sáez et al., 2005), which indicate a mixed environment and an expansion of pine forests. However, the habitat weighting method in MIR4 shows an increase in open dry to the detriment of open humid ecosystems (Table 2).

This increase in open dry environments could be related with the MER results that indicate a small decrease in precipitation, or it could be linked to the human impact on the landscape. In the Bronze Age, cereal-growing and livestock-keeping are widely documented in all deposits of human groups (Aranbarri et al., 2015; Revelles et al., 2015). On the other hand, García-Antón et al. (2011) have suggested that the human impact on the environment in this area of the northern Meseta was not intense in the first millennium B.C. However, the human impact on the environment is indicated by archaeobotanical studies based on pollen, charcoal, seeds and phytoliths at El Mirador site (Rodríguez and Buxó, 2008; Cabanes et al., 2009). These studies have confirmed the presence of herbaceous plants related to the development of agriculture and livestock.

All these data thus indicate that this part of the Bronze Age is characterised by temperatures that are similar to, or slightly lower than, present-day ones, and levels of mean annual precipitation that are slightly higher than present-day ones, suggesting the start of the climatic conditions typical of the Mediterranean climate (Terral and Mengüal, 1999).

## 6.Conclusions

The palaeoclimatic data obtained by means of the small-mammal assemblage of the Lateglacial in general show humid and cool climate conditions. Within this context, it should be noted that layer MIR51 represents a cool period that may well be related with Heinrich Event 1. The palaeoenvironmental analysis indicates the greatest reductions in woodland in the lowest layers of the sequence and an increase in MIR49 with respect to MIR51and MIR50.

In the Holocene layers of El Mirador cave, we observe seasonal anthropic occupation. The palaeoclimatic and palaeoenvironmental data obtained from the study of small mammals represent typical climatic conditions registered in summer and autumn.

During the Middle Holocene we detect important climatic events. From 7000 to 6800 (MIR 23 and MIR22), we register climatic characteristics that could be related to the end of the African Humid Period, namely an increase in temperatures and a progressive reduction in arboreal cover as a result of a decrease in precipitation. The temperatures exceeded current levels by 1ºC, especially in MIR23, where the most highly represented taxon is a thermo-Mediterranean species, *M. (T.) duodecimcostatus*. After this period, the climatic conditions became more similar or equal to present-day conditions, while the precipitation decreased but always remained above current levels. When this warm period finished, the temperatures from MIR19 to MIR17 underwent a slight decline and there was a slight increase in precipitation. This was associated with a minor increase in open landscape to the detriment of woodland. After this slight cooling, at 6600-6300 cal yr BP (MIR16) the temperatures recorded again become higher than nowadays, and a significant increase in aridification is observed.

In MIR11 (6300-5940 cal yr BP) a short, slightly cooler event is recorded. The temperature in this period is the lowest in the Holocene sequence of El Mirador cave, 0.5 ºC lower than nowadays.

On the other hand, there is a significant increase in precipitation in MIR10 (867mm). Moreover, in this layer a period of thermal stability begins, which could be related with the incipient establishment of a Mediterranean climate, corresponding to the expansion of Mediterranean species such as *C. russula* (32%) in MIR9.

From MIR9 to MIR 4 we note a significant palaeoenvironmental change. In MIR6 (5630-5350 cal yr BP) and MIR5 there is an increase in precipitation, but the reduction in woodland continues, with a major increase in open humid landscapes. This indicates that there was probably another factor that contributed to the decline in woodland, such as an agricultural system that exploited the environment. This trend was to persist until the Bronze Age.

In the late Holocene, the application of the MER method to the small-mammal assemblage of level MIR4 (4330-3070 cal yr BP) of El Mirador cave reveals a rather cool, arid phase with a high percentage of *M. arvalis*, a Eurosiberian taxon. Moreover, the palaeoenvironmental analysis indicates an increase in open dry landscapes to the detriment of open humid landscapes. This increase could be associated with the MER results, which indicate a minor decrease in precipitation, or it could be related with the human impact on the landscape, as in MIR5 and MIR6.

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# 2.3-HUMAN IMPACT OF SMALL MAMMALS DIVERSITY DURING THE MIDDLE-LATE HOLOCENE IN IBERIA: THE CASE OF EL MIRADOR CAVE (SIERRA DE ATAPUERCA, BURGOS, SPAIN).

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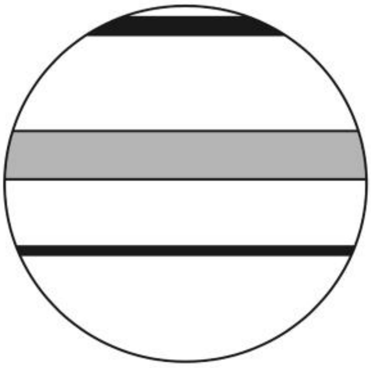


## Abstract

The human impact during the Holocene on the environment has usually been characterized from palaeobotanical records but distinguish anthropogenic impact from natural events in landscape evolution has been subject of much debate during recent years. The aim of this paper is the analysis of small-mammals diversity and synanthropic species because their small size they are more sensitive to any change in their environment occurs. This study has allowed us to characterize the palaeoclimatic and paleoenvironmental changes and record small changes either by human influence or not. Our object of study is El Mirador cave that has a sequence with well-documented human occupation since 7200 to 3000 cal BP. This study has allowed us to differentiate two phases. In one phase, we can see small changes in diversity related to the climatic oscillations since ca. 7200 to 6800 cal BP, while in second phase, since ca. 6800 to 3000 cal BP, the diversity and synanthropic species changes are related with human economic strategies. Moreover, we can distinguish which kind of economic activities (agricultural and farming) have influenced in these changes, because some small mammals species are influenced, positively or negatively, by environmental changes derivatives of agriculture and livestock. And all of this information has been contrasted against other archaeological proxies such as the large mammals and palaeobotanic assemblages from El Mirador cave.

Further, this integrative analysis allowed to identify the existence of altered environments from ca. 6000 cal BP generalized throughout the Iberian Peninsula from ca. 6000 cal BP. Moreover confirm the theory of low human occupation intensity in the northern Meseta and in high mountainous areas during the early Neolithic.

**Keywords:** Anthropogenic impact, small-mammals, Diversity, Neolithic, Bronze Age.

## 1.Introduction

The climate during the Holocene was warm and wet with some arid episodes, but with many regional differences of which we know their reach across Europe (Bond et al., 2001; Davis et al., 2003; Kalis et al., 2003; Mayewsky et al., 2004; Jalut et al., 2009; Mercuri et al., 2011; Aranbarri et al., 2014). All of these climatic characteristics contributed to modifying the landscape, but so did the human use of the territory for economic purposes (Heinz et al., 2004; Ruíz-Zapata et al., 2010; Morales-Molino et al., 2011; Tarroso et al., 2014; Pérez-Díaz et al., 2014). In fact, human disturbances have been considered the major agent of vegetation change in the Iberian Peninsula for at least the last 7500 years (Pérez-Obiol et al., 2011).

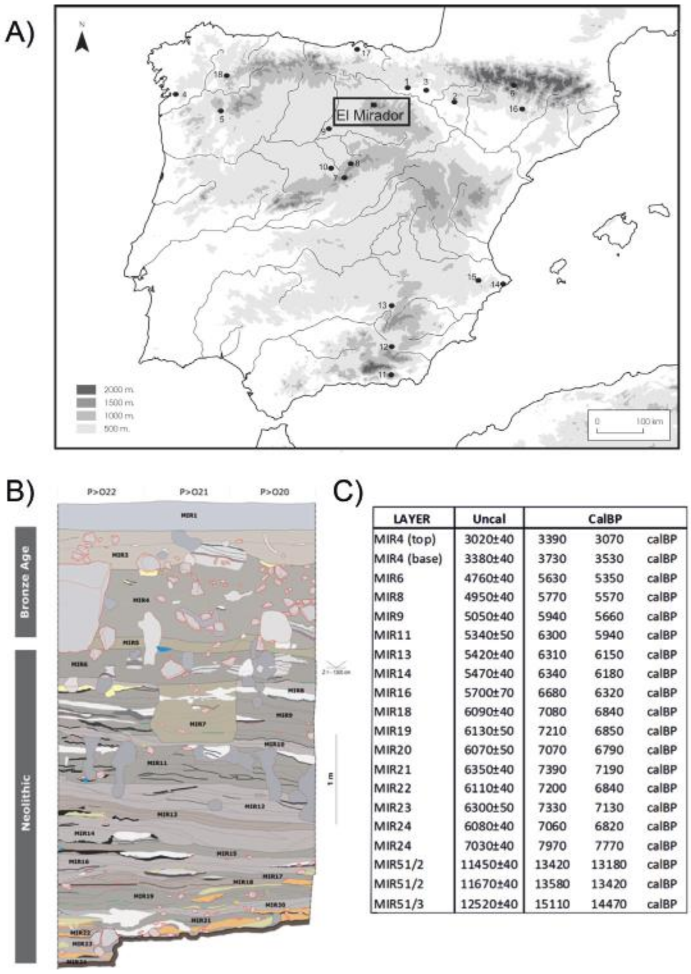
El Mirador is situated in the northwest of the Iberian Peninsula where the climate is typically Mediterranean, whereas in the northern areas, variability is primarily in tune with central European climatic oscillations (Rivas-Martínez et al., 2011). In this area the palaeoecological studies have registered the influence of anthropogenic activity on natural vegetation for ca. 6000 years (Iriarte, 2009; Tarroso et al., 2014). This influence has continuously increased over several millennia of human occupation of these environments, with the resulting fire and grazing pressure (Santos et al., 2000; Morales-Molino et al., 2011; López-Merino et al., 2012).

In the present study, we have included the small mammals samples and the environmental (Habitat Weighting) and climatic (Mutual Ecogeographic Range) conditions exposed in Bañuls-Cardona et al. , 2017), in order to analyze the relationship between natural (environmental and climatic) and anthropic influences on changes in small mammals diversity. The activities associated with an economy based on agriculture and livestock farming are known to contribute to modifying and homogenizing the landscape, influencing the ethology of small mammals and resulting in changes in biodiversity (Benton et al., 2003; Barnosky et al., 2011; Torres-Romero and Olalla-Tárraga, 2014).

In El Mirador cave (northern Meseta of Iberia), various archaeobotanical and archaeological proxies have been analysed to try to ascertain the difference between the anthropic and the natural origin of the landscape changes that took place during the Holocene (Cabanes et al., 2009; Euba et al., 2015; Expósito and Burjachs, 2016; Rodríguez et al., 2016; Martín et al., 2014; 2016a; 2016b).

## 2.Site

El Mirador cave is situated in the south of the Sierra de Atapuerca (Ibeas de Juarros, Burgos, Spain). The site is located at an altitude of 1033 m a. s. l. (Fig. 1). It was in 1999 that work was started on it, with the excavation of an area of 6m² in the central part of the cave, on the basis of which the stratigraphic sequence was established. This is composed of a total of 26 layers displaying high lateral and vertical variability due to the sedimentary characteristics of the cave and the post-depositional processes that took place there, such as the collapse of blocks and anthropic spatial organization, as well as bioturbation (Fig. 1). For this reason, it was decided that the naming and excavation of the site should be in assemblages, distinguishing between the characteristic facies of the anthropized units, mainly consisting of burned and unburned dung (Vergés et al., 2002, 2008). Most of these layers have been dated. There are a total of 17 radiocarbon dates for the sequence of El Mirador cave, which range from the Latest Pleistocene to the Bronze Age (Vergés et al., 2002, 2016; Angelucci et al., 2009) (Fig. 1).



| LAYER | Uncal | CalBP | | |
|---|---|---|---|---|
| MIR4 (top) | 3020±40 | 3390 | 3070 | calBP |
| MIR4 (base) | 3380±40 | 3730 | 3530 | calBP |
| MIR6 | 4760±40 | 5630 | 5350 | calBP |
| MIR8 | 4950±40 | 5770 | 5570 | calBP |
| MIR9 | 5050±40 | 5940 | 5660 | calBP |
| MIR11 | 5340±50 | 6300 | 5940 | calBP |
| MIR13 | 5420±40 | 6310 | 6150 | calBP |
| MIR14 | 5470±40 | 6340 | 6180 | calBP |
| MIR16 | 5700±70 | 6680 | 6320 | calBP |
| MIR18 | 6090±40 | 7080 | 6840 | calBP |
| MIR19 | 6130±50 | 7210 | 6850 | calBP |
| MIR20 | 6070±50 | 7070 | 6790 | calBP |
| MIR21 | 6350±40 | 7390 | 7190 | calBP |
| MIR22 | 6110±40 | 7200 | 6840 | calBP |
| MIR23 | 6300±50 | 7330 | 7130 | calBP |
| MIR24 | 6080±40 | 7060 | 6820 | calBP |
| MIR24 | 7030±40 | 7970 | 7770 | calBP |
| MIR51/2 | 11450±40 | 13420 | 13180 | calBP |
| MIR51/2 | 11670±40 | 13580 | 13420 | calBP |
| MIR51/3 | 12520±40 | 15110 | 14470 | calBP |

**Figure 1.** A. Geographical location of El Mirador cave and the sites mentioned in the discussion. 1. Peña Larga; 2. Padre Areso; 3. Puy Águila I; 4. Coto da Fenteria; 5. Arcucelos; 6. Basa de la Mora; 7. Tolla Collado de El Berrueco; 8. Rascafría; 9. Espinosa de Cerrato; 10. El Carrizal; 11. Sierra de Gádor; 12. Sierra de Baza; 13. Siles lake; 14. Cova de les Cendres; 15. Cova de l'Or; 16. Cova Colomera; 17. El Mirón; 18. Valdavara. B. Stratigraphy of El Mirador cave (Angelucci et al., 2009). C. Radiocarbon datings of studied layers. Uncal: Mean of the radiocarbon dates. CalBP: 2σ range of the calibrated dates in cal BP.

The Pleistocene deposit is composed of 14 m of metric and decimetric limestone blocks with no sedimentary matrix in between. It is the result of the collapsed roof (MIR51/4 and MIR51/1) and contains two intercalated layers: MIR51/3, a shallow, archaeologically sterile layer composed of wind-borne sediment, and MIR51/2, with the same sedimentary characteristics but with evidence of human activity: remains of a hearth, and lithic and faunal materials (Vergés et al., 2016). The 6-m-thick Holocene sedimentary layers rest directly on top of MIR51. Four meters are attributed to Neolithic occupations (layers MIR24 to MIR6) occurring between the last third of the 6th millennium and the first half of the 4th millennium cal BC (Vergés et al., 2008), while the remaining two meters are from the Middle Bronze Age (MIR4 and MIR3A), between the 2nd and 4th quarters of the 2nd millennium cal BC (Vergés et al., 2002). These Holocene layers were essentially formed as a result of the use of the cave as a livestock pen. The activities related to animal husbandry left sedimentary layers of dung, which was piled together and burned at regular intervals in order to reduce its volume and to eliminate parasites (Angelucci et al., 2009). These burned layers alternate with partially burnt and unburned layers of dung and nodules of ash from burned dung. An artefact record related to domestic occupations is often present in these layers. This kind of deposit is known as a *fumier* (Brochier, 1988, Vergés et al., 2016).

Archaeological remains are abundant in this site, and many specific studies are available in the literature. These include analyses of ceramic and lithic artefacts (Vergés et al., 2002, 2008, 2016), archaeobotanical studies (Cabanes et al., 2009; Euba et al., 2015; Expósito and Burjachs, 2016; Rodríguez et al., 2016), studies of human remains (Cáceres et al., 2007; Ceperuelo et al., 2015; Lozano et al., 2015) and of large mammals (Martín et al., 2009, 2014, 2016a, 2016b), and also preliminary studies of small-mammal remains (López-García, 2008; Bañuls-Cardona et al., 2013).

## 3-Material and Methods

### 3.1.Small mammals

The small mammals analysed in this study belong to 14 Holocene layers (MIR24, MIR23, MIR22, MIR21, MIR19, MIR18, MIR17, MIR16, MIR11, MIR10, MIR9, MIR6, MIR5 and MIR4). These small mammals were identified using the methods of systematic palaeontology from Bañuls-Cardona et al., 2017). We used mandibles and isolated teeth to identify insectivores (Reumer, 1984; Cuenca-Bescós et al., 2008; López-García, 2008); for chiropters, mandibles, isolated teeth and humeri (Bruijn and Rumke, 1974; Menu and Popelard, 1987; Sevilla, 1988); for Arvicolinae, the first lower molars (van der Meulen, 1973; Cuenca-Bescós et al., 2008; López-García, 2008); while the identification of *Apodemus sylvaticus* and *Eliomys quercinus* was based on isolated teeth (Pasquier, 1974; Damms, 1981; Cuenca-Bescós et al., 2008; López-García, 2008).

In this manuscript we describe the sample of small mammals that is the subject of this study, we start from the premise that all ecosystems are described in terms of the number of individuals of each species represented (Margalef, 1974). The first method that we apply in this basic analysis of biodiversity is Chao-1 (Colwell and Coddington, 1994). This method consists of a simple estimator of the richness in an assemblage.

$$S_{Chao1} = S_{obs} + \frac{F_1^2}{2F_2}$$

$S_{obs}$ = number of species in the sample

$F_1$= number of observed species represented by a single individual

$F_2$ = number of observed species represented by two individuals

Measurement of species diversity is based on the Simpson index, which emphasizes dominance as opposed to richness in assessing the development and evolution of an ecosystem (Magurran, 2004).

$$D = \sum\left(\frac{n_{i[n_i-1]}}{N[N-1]}\right)$$

$n_i$ = number of individuals in the i species

N = total number of individuals

We further analyse the percentage of synanthropic species, i.e. species that are adapted to conditions created or modified by human activities (Mistrot, 2000). The synanthropization of indigenous small mammals was considered to be a recent phenomenon in European mammals. However, the recent studies show that is readily observable during the late Neolithic in southeastern Europe, and perhaps before (Cucchi et al., 2011).Within our assemblage there are four: *Crocidura russula*, *Microtus arvalis*, *Microtus (Terricola) duodecimcostatus* and *Eliomys quercinus* (Table 2). *C. russula* favours human-inhabited areas because its winter survival depends on heat and nutritive resources generated by human activities (Tarjuelo et al., 2010). *M. arvalis* prefers landscapes with high percentage of arable land and low habitat diversity (Burel et al., 2004; Fisher et al., 2011). *M.(T) duodecimcostatus* select open environments, often in human-inhabited areas. It is common in growing areas and pastures and fallow land, as long as there is sufficient grass cover and easy excavability (Campos Marcos et al., 2003). Finally *E. quercinus* can live in many terrestrial and arboreal habitats and also be found close to rural homes, on roofs or on stone walls between cultures, is a semi-commensal species (Pokines, 1998).

### 3.2.Chorotypes

This palaeoclimatic reconstruction is completed by classifying the taxa in accordance with the chorotypes established by Sans-Fuentes and Ventura (2000), Real et al. (2003) and López-García et al. (2010b). A chorotype can be defined as a group of species whose distributions in space overlap more than expected at random. Chorotype 1 (CH-1) refers to species with Euro-Siberian requirements; this implies a mean summer temperature lower than 20 ºC, a mean annual temperature that should be be¬tween 10 ºC and 12 ºC, and a mean annual precipitation higher than 800 mm. Chorotype 2 (CH-2) refers to Euro-Siberian species that nonetheless tolerate Mediterranean conditions, with a mean annual precipitation greater than 600 mm. Chorotype 3 (CH-3) denotes generalist species, and finally Chorotype 4 (CH-4) denotes species with strictly Mediterranean requirements (Table 3).

## 4.Results

### 4.1.Small mammals

We have identified 1666 remains (NISP), with a minimum number of individuals (MNI) of 888 pertaining to nine small-mammal taxa: two insectivore, two chiropter and five rodent species (Table 1).

The preliminary taphonomic study of the small mammals present slight signs of digestion on the remains. These slight alterations were examined and it can be surmised that the main animal responsible for the accumulation in the cave was a category 1 predator, a nocturnal bird of prey such as the Barn Owl (*Tyto alba*) or the Long-eared Owl (*Asio otus*), both species are present in semi-open forests, with the nearby presence of large clear areas that displays an opportunistic trophic pattern and produces slight modifications of the bones it ingests (Andrews, 1990). The small mammals form an assemblage of great taxonomic variety, indicating that it was the work of an opportunistic hunter.

| TAXA | MIR4 | MIR5 | MIR6 | MIR9 | MIR10 | MIR11 | MIR16 | MIR17 | MIR18 | MIR19 | MIR21 | MIR22 | MIR23 | MIR24 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Crocidura russula* | 19 | 6 | 0 | 17 | 0 | 1 | 2 | 16 | 21 | 6 | 0 | 1 | 0 | 8 |
| *Sorex coronatus-araneus* | 6 | 4 | 1 | 5 | 1 | 1 | 0 | 9 | 21 | 4 | 0 | 0 | 0 | 3 |
| *Myotis myotis-blythii* | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 4 |
| *Miniopterus schreibersii* | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 2 | 0 | 2 |
| *Microtus arvalis* | 21 | 20 | 3 | 3 | 1 | 1 | 2 | 18 | 16 | 9 | 1 | 2 | 0 | 22 |
| *Microtus agrestis* | 14 | 37 | 3 | 13 | 2 | 0 | 2 | 34 | 26 | 22 | 1 | 0 | 3 | 15 |
| *Microtus (Terricola) duodecimcostatus* | 17 | 14 | 2 | 1 | 3 | 5 | 2 | 18 | 21 | 11 | 2 | 2 | 4 | 24 |
| *Apodemus sylvaticus* | 18 | 8 | 2 | 9 | 6 | 8 | 4 | 32 | 73 | 58 | 4 | 5 | 2 | 56 |
| *Eliomys quercinus* | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 3 | 6 | 1 | 0 | 1 | 0 |
| **Total MNI** | 96 | 89 | 11 | 53 | 14 | 17 | 13 | 128 | 185 | 117 | 9 | 12 | 10 | 134 |
| **Total NISP** | 280 | 193 | 17 | 77 | 19 | 19 | 14 | 230 | 376 | 154 | 17 | 15 | 15 | 240 |

**Table 1.** Distribution of the small-mammal remains of El Mirador cave by layers. Minimum number of individuals (MNI) and number of identified specimens (NISP).

Systematic palaeontology allowed nine different species to be identified: *Crocidura russula*, *Sorex* gr. *coronatus-araneus*, *Myotis myotis-blythii*, *Miniopterus schreibersii*, *Microtus arvalis*, *Microtus agrestis*, *Microtus (Terricola) duodecimcostatus*, *Apodemus sylvaticus* and *Eliomys quercinus* (Fig. 2). The most abundant species in the sequence of El Mirador is *Apodemus sylvaticus* (Table 3) (Bañuls-Cardona et al., under review).

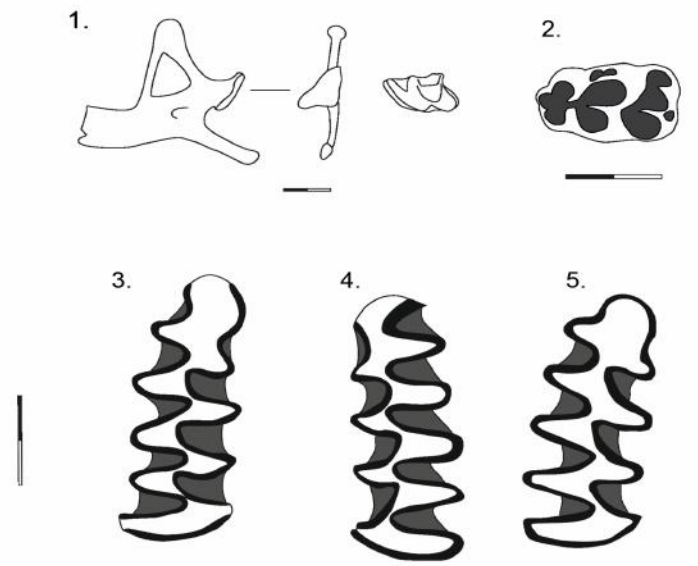


**Figure 2.** Most representative species of El Mirador cave. From left to right: 1. *Crocidura russula*, right mandible (lingual and posterior view) and right m2 (occlusal view); 2. *Apodemus sylvaticus*, right m1 (occlusal view); 3. *Microtus arvalis*, right m1 (occlusal view); 4. *Microtus agrestis*, left m1 (occlusal view); 5. *Microtus (Terricola) duodecimcostatus*, right m1 (occlusal view). Scale bars = 1 mm.

The Chao-1 analysis of diversity indicates that the highest number of species is in MIR18 and MIR9, with nine species each, whereas the lowest number of species is registered in MIR23, with four species. The Simpson index indicates that the greatest diversity is in MIR11 (0.68, MIR19 (0.70) and MIR23 (0.70), whereas the lowest diversity is recorded in MIR4 (0.82) and MIR17 (0.81). Moreover, the lowest percentage of synanthropic species is detected in MIR19 (27.4%) and MIR10 (28.6 %), while the highest percentage is registered in MIR4 (60.4 %) and MIR16 (53.8 %) (Table 2).

| LAYERS | MIR4 | MIR5 | MIR6 | MIR9 | MIR10 | MIR11 | MIR16 | MIR17 | MIR18 | MIR19 | MIR21 | MIR22 | MIR23 | MIR24 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Chao-1** | 7 | 6 | 5 | 9 | 6 | 6 | 6 | 7 | 9 | 8 | 5 | 5 | 4 | 8 |
| **Simpson_1-D** | 0.82 | 0.74 | 0.78 | 0.79 | 0.73 | 0.68 | 0.80 | 0.81 | 0.78 | 0.70 | 0.72 | 0.74 | 0.70 | 0.75 |
| **Synanthropic** | 60.42 | 44.94 | 45.45 | 41.51 | 28.57 | 47.06 | 53.85 | 41.41 | 32.97 | 27.35 | 44.44 | 41.67 | 50.00 | 40.30 |

**Table 2.** Richness and diversity index and percentage representation of synanthropic species (*Crocidura russula*, *Microtus arvalis*, *Microtus (Terricola) duodecimcostatus* and *Eliomys quercinus*) obtained from small-mammal remains of El Mirador cave by layers.

## 4.2.Climate

From the base to the top, the climatic analysis of the Holocene sequence yields the following results. MIR24 displays mild, humid conditions. By the MER method, we observe that the MAT is 0.1 ºC lower than nowadays, while the MAP is 252 mm higher than nowadays in the Burgos area (Table 4). The chorotype analysis indicates that 45% of species are generalist (CH-3) (Table 3).

| LAYERS | Habitat Weighting | | Chorotypes | | | |
|---|---|---|---|---|---|---|
| | OPEN | WOODLAND | CH1 | CH2 | CH3 | CH4 |
| **MIR4** | 40.6 | 59.4 | 36.5 | 6.3 | 19.8 | 37.5 |
| **MIR5** | 45.5 | 54.5 | 64.0 | 4.5 | 9.0 | 22.5 |
| **MIR6** | 44.2 | 55.9 | 54.5 | 9.1 | 18.2 | 18.2 |
| **MIR9** | 41.6 | 58.5 | 30.2 | 9.4 | 22.6 | 37.7 |
| **MIR10** | 28.6 | 71.4 | 21.4 | 7.1 | 50.0 | 21.4 |
| **MIR11** | 26.5 | 73.5 | 5.9 | 5.9 | 52.9 | 35.3 |
| **MIR16** | 34.6 | 65.4 | 30.8 | 0.0 | 38.5 | 30.8 |
| **MIR17** | 37.5 | 62.4 | 40.6 | 7.0 | 25.8 | 26.6 |
| **MIR18** | 30.2 | 69.7 | 22.7 | 11.4 | 42.7 | 23.2 |
| **MIR19** | 25.2 | 74.8 | 26.5 | 3.4 | 54.7 | 15.4 |
| **MIR21** | 27.8 | 72.2 | 22.2 | 0.0 | 55.6 | 22.2 |
| **MIR22** | 29.2 | 70.8 | 16.7 | 0.0 | 58.3 | 25.0 |
| **MIR23** | 40 | 60.0 | 30.0 | 0.0 | 30.0 | 40.0 |
| **MIR24** | 29.1 | 70.9 | 27.6 | 2.2 | 44.8 | 25.4 |

**Table 3.** Percentage of open and woodland areas and chorotypes represented in the studied layers of El Mirador cave.

The temperatures recorded in MIR23-22 are the highest in the entire sequence. In these layers the MAT exceeds the current level by 1º C (Table 4). The principal chorotype in MIR23 is chorotype 4, i.e. Mediterranean species (40%), and in MIR22 it is chorotype 3 (58%) (Table 3). By contrast, the MAP of these layers is the lowest in the entire sequence. The MAP in MIR23 is 148 mm higher than nowadays, while in the case of MIR22 the MAP is 608 mm, only 14 mm higher than nowadays (Table 4). In these layers the end of the African Humid Period can be identified (Bañuls-Cardona et al., 2017).

| LAYERS | MAT | | | | | MTC | | | | | MTW | | | | | MAP | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | MAX | MIN | MEAN | SD | Δ | MAX | MIN | MEAN | SD | Δ | MAX | MIN | MEAN | SD | Δ | MAX | MIN | MEAN | SD | Δ |
| MIR4 | 13 | 5 | 9.94 | 1.52 | 0.16 | 5 | 0 | 2.54 | 1.17 | 0.06 | 22 | 15 | 18.53 | 1.41 | 0.18 | 1500 | 500 | 794 | 221 | -200 |
| MIR5 | 13 | 5 | 10.03 | 1.57 | 0.07 | 7 | 0 | 2.65 | 1.25 | -0.05 | 23 | 15 | 18.60 | 1.44 | 0.10 | 2500 | 500 | 846 | 284 | -252 |
| MIR6 | 13 | 5 | 9.97 | 1.55 | 0.13 | 7 | 0 | 2.64 | 1.20 | -0.04 | 22 | 15 | 18.49 | 1.36 | 0.21 | 2000 | 500 | 867 | 277 | -273 |
| MIR9 | 13 | 5 | 9.94 | 1.52 | 0.16 | 5 | 0 | 2.54 | 1.17 | 0.06 | 22 | 15 | 18.53 | 1.41 | 0.18 | 1500 | 500 | 794 | 221 | -200 |
| MIR10 | 13 | 5 | 9.97 | 1.55 | 0.13 | 7 | 0 | 2.64 | 1.20 | -0.04 | 22 | 15 | 18.49 | 1.36 | 0.21 | 2000 | 500 | 867 | 277 | -273 |
| MIR11 | 13 | 5 | 9.62 | 1.81 | 0.48 | 5 | 0 | 2.46 | 1.24 | 0.14 | 23 | 15 | 18.70 | 1.33 | 0.00 | 2000 | 500 | 792 | 238 | -198 |
| MIR16 | 13 | 5 | 10.17 | 1.47 | -0.07 | 5 | 0 | 2.62 | 1.01 | -0.02 | 23 | 15 | 18.97 | 1.51 | -0.27 | 1500 | 400 | 715 | 230 | -121 |
| MIR17 | 13 | 5 | 9.94 | 1.52 | 0.16 | 5 | 0 | 2.54 | 1.17 | 0.06 | 22 | 15 | 18.53 | 1.41 | 0.18 | 1500 | 500 | 794 | 221 | -200 |
| MIR18 | 13 | 5 | 9.94 | 1.52 | 0.16 | 5 | 0 | 2.54 | 1.17 | 0.06 | 22 | 15 | 18.53 | 1.41 | 0.18 | 1500 | 500 | 794 | 221 | -200 |
| MIR19 | 13 | 5 | 9.94 | 1.52 | 0.16 | 5 | 0 | 2.54 | 1.17 | 0.06 | 22 | 15 | 18.53 | 1.41 | 0.18 | 1500 | 500 | 794 | 221 | -200 |
| MIR21 | 13 | 5 | 10.07 | 1.56 | 0.03 | 5 | 0 | 2.57 | 1.12 | 0.03 | 23 | 15 | 19.05 | 1.44 | -0.35 | 1500 | 400 | 740 | 249 | -146 |
| MIR22 | 15 | 5 | 10.83 | 1.53 | -0.73 | 7 | 0 | 2.96 | 1.14 | -0.36 | 25 | 15 | 20.17 | 1.51 | -1.47 | 2500 | 300 | 608 | 233 | -14 |
| MIR23 | 15 | 5 | 11.02 | 2.07 | -0.92 | 9 | 0 | 3.37 | 1.77 | -0.77 | 25 | 15 | 19.79 | 1.83 | -1.09 | 1500 | 400 | 742 | 233 | -148 |
| MIR24 | 13 | 5 | 10.03 | 1.57 | 0.07 | 7 | 0 | 2.65 | 1.25 | -0.05 | 23 | 15 | 18.60 | 1.44 | 0.10 | 2500 | 500 | 846 | 284 | -252 |

**Table 4.** Relation of temperatures and precipitation obtained using the MER (Mutual Ecogeographic Range) method. MAT: mean annual temperature; MTC: mean temperature of the coldest month; MTW: mean temperature of the warmest month; MAP: mean annual precipitation; n: number of 10×10km UTM squares forming the intersection obtained for micromammals; mean±SD: mean and standard deviation of the values obtained; min: minimum of the values obtained; max: maximum of the values obtained: Δ difference between the current mean for Burgos weather station over 30 years and that obtained for the small mammals.

The MER method reveals that the MAT in MIR21 is equal to current levels, but the MAP is 146 mm higher than nowadays. In MIR19, MIR18 and MIR17 the palaeoclimatic analysis shows an increase in precipitation, with the MAP 54 mm higher with respect to MIR21; the temperatures were lower, and we have registered a decrease of 0.5 ºC in the mean temperature of the coldest months (MTC). The most highly represented chorotype from MIR21 to MIR18 is chorotype 3, whereas in MIR17 species with Euro-Siberian requirements (CH-1) are most abundant. After this slight cooling, in MIR16 temperatures are again similar to nowadays; the MAT is 0.1 ºC higher than today, and a significant decrease in rainfall of 79 mm is observed with respect to MIR17.

In MIR11 slightly cooler conditions are detected (from ca. 6300-5940 cal. BP). The MER shows the MAT (9.6ºC) to be the lowest in the Holocene sequence of El Mirador cave, 0.5 ºC lower than nowadays, mainly due to the low MTC (2.4 ºC). The climatic data obtained on the basis of the small mammals suggest an increase in MAP in MIR11 (792 mm) with respect to the pluviometric data for MIR16 (715 mm). The chorotype data indicate generalist species to be most abundant in this layer (53%). In MIR10 a significant increase in the rainfall (75 mm) and temperatures (0.4ºC) is observed with respect to MIR11, while the principal chorotype is chorotype 3, i.e. generalist species (CH-3). In MIR9 we detect a dry event. This shows a decrease in MAP from 867 mm in MIR10 to 794 mm in MIR9. As regards temperatures, however, we do not observe major changes. The chorotype data indicate that species with Mediterranean requirements (CH-4) are most abundant (38%).

After this dry event, in MIR6 and MIR5 we observe a significant increase in rainfall (73 mm more than in MIR9). The temperature remains similar to MIR9, but chorotype 1 is most abundant (55% and 64% in MIR6 and MIR5 respectively).

Finally, in MIR4 we do not observe changes in temperature with respect to MIR6 and MIR5, but the MAP recorded is 52 mm higher, while chorotype 4 is the most important (Bañuls-Cardona et al., under review).

### 4.3.Environment

Woodland is the most representative kind of habitat in El Mirador, but with some changes along the sequence. The highest percentages of woodland are registered in MIR19 (75%) and MIR11 (74%), while the lowest percentages are registered in MIR5 (54%) and MIR6 (56%). The other habitat that is well represented is the “Open Humid” habitat, indicating evergreen meadowland with pastures and dense topsoil. It is in MIR23 and MIR6 that the highest percentages of open humid habitat are identified (40% and 32.4% respectively), whereas MIR24 and MIR22 are the layers with the lowest values (16.8% and 12.5% respectively). The “Open Dry” habitat is the least represented habitat in El Mirador, and in MIR23 it is not registered at all. The maximum value for this type of habitat is recorded in MIR9 and MIR4 (20.8%), while the minimum values are registered in MIR11 (5.9%) and MIR10 (5.4%) (Bañuls-Cardona et al., under review).

## 5.Discussion

In the Iberian Peninsula, palaeobotanical studies document the first human landscape modifications around 6000 cal BP. However, some palaeoenvironmental changes that were probably not the result of the human impact are also recorded; these could have been in response to the arid climate event that occurred at 8200 cal. BP. The clear intensification of farming activities in the landscape started to appear later (Martínez-Cortizas et al., 2009; Iriarte, 2009). We used a range of multiproxy analyses (pollen, charcoal, sedimentology, geochemistry and chironomids) from different parts of the Iberian Peninsula in order to characterise the main features of the landscape evolution during the Holocene (Badal et al., 1994, 2012; Carrión, 2002; Carrión et al., 2004; Martínez-Cortizas et al., 2009; Iriarte, 2009; Pérez-Sanz et al., 2013).

In the north of Iberia the first human impact has been registered around 4000-3000 cal. BP. According to this chronology, the lowest values of forest coverage were in Peña Larga (Cripán, Álava) and Padre Areso (Bigüézal, Navarra). A special case was Puy Aguila I (Bárdenas Reales, Navarra), where the human influence was produced when the site was inhabited (Iriarte, 2009). Among the earliest evidence of significant landscape transformation by humans in northwestern Iberia was the Coto da Fenteira (Redondela, Pontevedra). In this site, two layers have been found (dated to 4690 and 3735 cal. BP) evidencing episodes of forest fire use, a technique that caused serious soil erosion. However, this erosion increases around 3000 cal. BP, with a significant decline in arboreal pollen, as occurs at Arcucelos (Orense) from 3040 cal. BP (Martínez-Cortizas et al., 2009). A multiproxy analysis (pollen, sedimentology, geochemistry, chironomids and charcoal) from the high-mountain glacier-lake of Basa de la Mora (Huesca) in northeastern Iberia reveals probably the first evidence of forest management, indicating negligible anthropogenic pressure until ca 1150 cal. BP (Pérez-Sanz et al., 2013).

Pollen analysis of sites situated on the northern Meseta has revealed an intense human impact on the environment, but only in very recent times (which ones). In the Tolla Collado de El Berrueco (Sierra de Guadarrama, Madrid), dated to 1830 cal. BP, very intense human action was detected by a regression of *Pinus* forest and an increase in anthropophilic species of pollen (Ruíz-Zapata et al., 2009a). In Rascafría (Valle del Lozoya, Madrid), increased soil erosion is detected from 920 ± 50 BP, due to increased grazing throughout the year (Ruiz-Zapata et al., 2009b). Human activity also appears in the Espinosa de Cerrato sequence (Palencia), where a change in the ratio between *Pinus* and *Quercus* pollens from 1400 cal. BP has been detected, and in El Carrizal lake (Cuéllar, Segovia) the presence of weed and *Cerealia* taxa from 2650 cal. BP is a sign of human activity (García-Antón et al., 2011).

In the southeastern part of the Iberian Peninsula, the intensity and timing of the human impact on vegetation varies from one part to another. In the Sierra de Gádor (Almeria), after 3940 cal. BP a frequent alternation in the dominance of *Pinus* and evergreen *Quercus* at the expense of deciduous *Quercus* is observed. This change is preceded by an increase in microcharcoal particles at 4200 cal. BP, suggesting an increase in fire use. In the Sierra de Baza (Granada) the replacement of mesophytic by more xeric Mediterranean vegetation around 3800 cal. BP is preceded by greater fire activity at 4100 cal. BP. However, deforestation expanded over the next two millennia, with anthropogenic disturbance (agriculture, mining and pastoralism) reaching its maximum after 2560 cal. BP (Carrión et al., 2010). In Siles lake (Jaén) high grazing pressure is registered from 2400 cal. BP; this may well have promoted local increases in the proportion of grasses, because extensive pastures are natural above the tree line (Carrión, 2002).

The debate about anthropogenic vs. climatic determinism has been particularly intense with regard to the Mediterranean area (Carrión et al., 2004). During the earliest Neolithic, Mediterranean woodland was dominated by Quercus while the presence of secondary plant formations was insignificant in Cova de l'Or (Beniarrés, Alicante) and Cova de les Cendres (Teulada-Moraira, Alicante). However, around 5000 cal BP, a reduction in Quercus is observed in favour of more open formations, and the sedimentology reveals one of the wettest periods in the Neolithic, so these changes may be related to the economic activities of human groups. As has been documented for most of the Iberian Peninsula, this reduction increases at Cova de les Cendres from the Bronze Age on, due to the intensification of farming activities (Badal et al., 1994, 2012).

On the other hand, the climatic and the human impact on small-mammal diversity are indiscriminately mentioned as causes of rapid oscillations in the environment during the Holocene, yet efforts to disentangle the specific causes of this process are complicated (Jalut et al., 2009; Mercuri et al., 2011; Jimenez-Moreno et al., 2012). At the beginning of the Holocene, the most frequently cited explanations for patterns of elevational diversity relate to gradients in single factors, such as rainfall, temperature, productivity, competition, resource abundance, habitat complexity, or habitat diversity, but current theory recognizes climatic factors as a principal influence on trends in diversity (Lomolino, 2001; McCain, 2004). In the mid-Neolithic and Bronze Age, by contrast, the richness and diversity of species have been associated with the human impact (Carrión et al., 2010; López-García et al., 2013).

Due to their size, small mammals are more sensitive to minor variations in climate and environment than larger ones, and these changes affect their ethology (López-García et al., 2013). It is for these reasons that we use small mammals in the present study. Some small-mammal species have a capacity for adaptation to these new conditions, enabling them to modify their climatic and environmental requirements (McKinney, 1997). This ability allows them to maintain populations in their area of current distribution despite changing environmental conditions, as well as to colonize other areas (Bellard et al., 2012; Arribas et al., 2012), as in the case of synanthropic species, which have adapted to conditions created or modified by human activities (Mistrot, 2000).

### 5.1.Climate influence

The small-mammal studies of levels MIR24 to MIR19 of El Mirador establish that changes in the environment and in the degree of diversity were related with climatic conditions. The palaeoclimatic analysis shows the temperatures to have hovered around 10 ºC (Table 4). Species belonging to chorotype 3 (species with generalist climatic requirements) are the most abundant (Table 3), and *A. sylvaticus* is the most representative species in these layers. However, MIR23 is an exception to this. In this layer we have identified the end of the African Humid Period, with higher temperatures than nowadays (Table 4) (Bañuls-Cardona et al., under review). Chorotype 4 is the most representative chorotype, and the most abundant species is *M. (T) duodecimcostatus*, a species with Mediterranean climatic requirements (Table 3).

According to some authors, moreover, the decline in diversity may have been a direct effect of the general transition from a cooler to a warmer climate and the corresponding habitat change (Blois et al., 2010). In contrast, in MIR23 the rise in diversity was related to an increase in temperature (1º C) and an increase in open environment (11%) (Figure 3). The simultaneous availability of water and high temperatures, is the best explanation for the variation in species richness (Real et al., 2003). In MIR19 the same Simpson index is recorded (0.70), associated with a minor decrease in temperature (0.3ºC) and a decrease in open environment, which is at its lowest level in the sequence of El Mirador (25%).

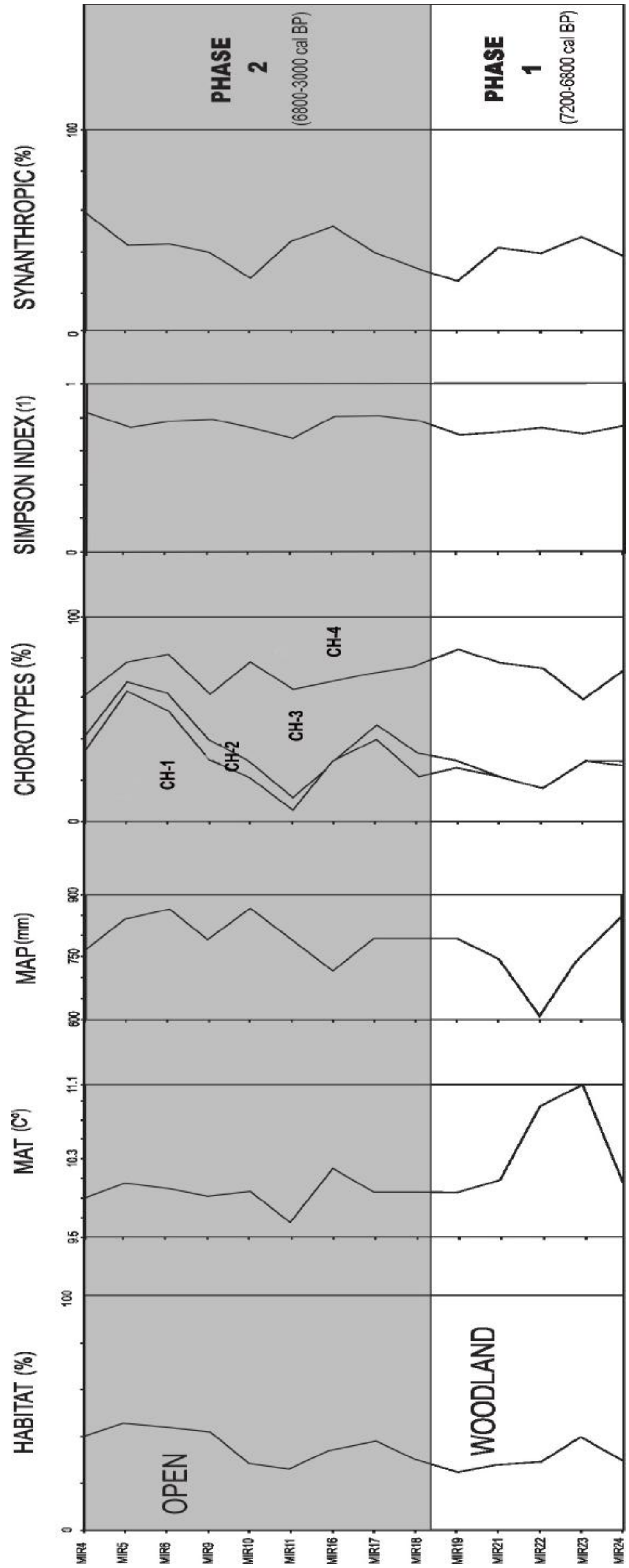


**Figure 3**. Comparisons between various proxies used throughout El Mirador cave sequence. From left to right: Habitat interpretation for El Mirador cave based on the Habitat Weighting method. Mean annual precipitation (MAP) and mean annual temperature (MAT) of the El Mirador cave sequence. Representation of the chorotypes: CH-1 (chorotype 1), CH-2 (chorotype 2), CH-3 (chorotype 3), CH-4 (chorotype 4). Diversity study with Simpson index. Finally representation of synanthropic species (*Crocidura russula*, *Microtus arvalis*, *Microtus (Terricola) duodecimcostatus* and *Eliomys quercinus*) for each layer. Phase 1. Climatic influence (changes associated with climatic influence); Phase 2. Human impact (changes associated with human impact).

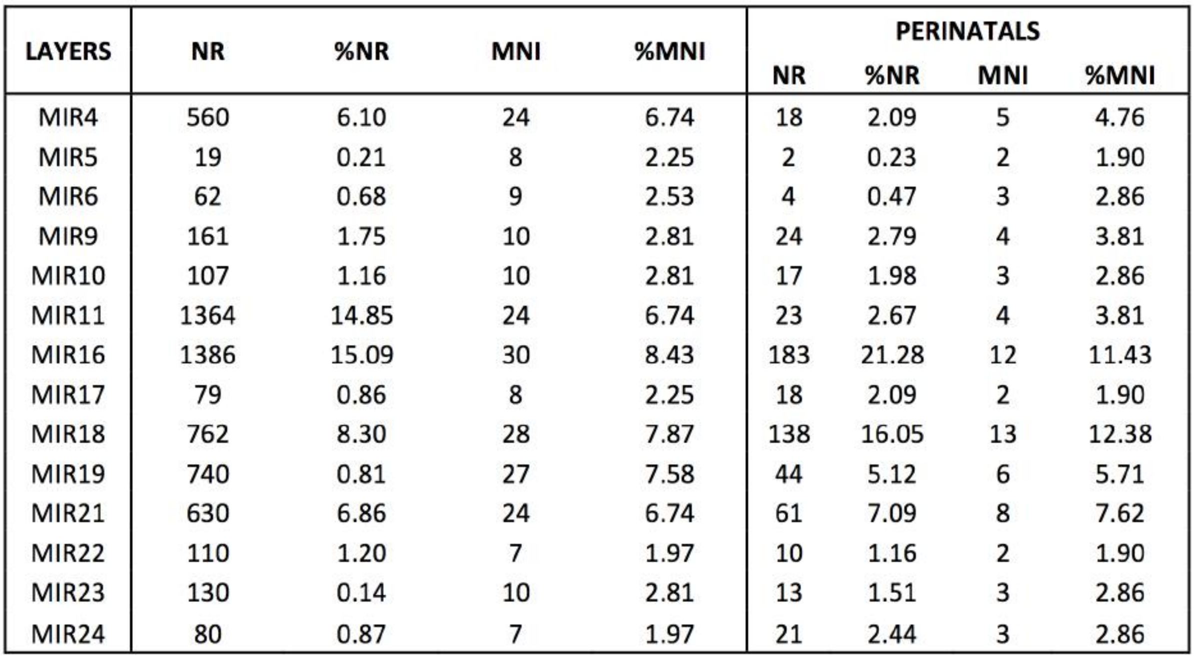
## 5.2.Human impact

From as early as ca. 6000 cal. BP, some archaeobotanical studies have detected the first evidence of a human impact on the landscape in the Iberian Peninsula (Badal et al., 1994; Fletcher and Sánchez-Goñi, 2008; Zazo et al., 2008; Martínez-Cortizas et al., 2009; Iriarte, 2009). However, this trend increases after ca. 5000 cal. BP, with a drastic reduction in the forest in Europe in general (Leira and Santos, 2002; Kalis et al., 2003; Heinz et al., 2004; López-Merino et al., 2012; Carrión et al., 2010a; Hernández-Beloqui et al., 2014 ; Tarroso et al., 2014).

Farming practices have been documented in El Mirador cave by studies based on pollen, charcoal, seeds and phytoliths (Cabanes et al., 2009; Euba et al., 2015; Expósito and Burjachs, 2016; Rodríguez et al., 2016). These studies have confirmed the forest degradation, which is most likely due to intensified human activity. For example, pollen analyses clearly show higher values of anthropogenic signatures related to human activities, especially during the Bronze Age period (MIR4) (Expósito et al., submitted). Zooarchaeological studies confirm the development of herding practices throughout the sequence. These were based on goat and sheep breeding. Moreover, the *fumier* sequence and an abundance of ovicaprine fetal and neonatal remains suggest the use of the cave for livestock penning and, especially, as a breeding cave (Angelucci et al., 2009; Martín et al., 2016b; Vergès et al., 2016).

### MIR18 - MIR16 (7000-6300 cal BP)

The small-mammal studies of El Mirador cave provide the first, minor evidence of a human impact on diversity in MIR18 (ca. 7000-6800 cal. BP). From MIR19 to MIR17 the MER analysis indicates the same temperatures and the same level of precipitation, but we have registered a progressive increase in an open environment type (Figure 3). Nevertheless, we observe a higher level of richness (nine species) and a significant decrease in diversity in MIR18 (Table 2), probably related to the increased volume of herds and / or the higher intensity of the occupation of the cave due to its use as a sheepfold (a large number of remains, large number of perinatal individuals) (Table 5) (Martín et al., 2016b).



| LAYERS | NR | %NR | MNI | %MNI | PERINATALS | | | |
|---|---|---|---|---|---|---|---|---|
| | | | | | NR | %NR | MNI | %MNI |
| MIR4 | 560 | 6.10 | 24 | 6.74 | 18 | 2.09 | 5 | 4.76 |
| MIR5 | 19 | 0.21 | 8 | 2.25 | 2 | 0.23 | 2 | 1.90 |
| MIR6 | 62 | 0.68 | 9 | 2.53 | 4 | 0.47 | 3 | 2.86 |
| MIR9 | 161 | 1.75 | 10 | 2.81 | 24 | 2.79 | 4 | 3.81 |
| MIR10 | 107 | 1.16 | 10 | 2.81 | 17 | 1.98 | 3 | 2.86 |
| MIR11 | 1364 | 14.85 | 24 | 6.74 | 23 | 2.67 | 4 | 3.81 |
| MIR16 | 1386 | 15.09 | 30 | 8.43 | 183 | 21.28 | 12 | 11.43 |
| MIR17 | 79 | 0.86 | 8 | 2.25 | 18 | 2.09 | 2 | 1.90 |
| MIR18 | 762 | 8.30 | 28 | 7.87 | 138 | 16.05 | 13 | 12.38 |
| MIR19 | 740 | 0.81 | 27 | 7.58 | 44 | 5.12 | 6 | 5.71 |
| MIR21 | 630 | 6.86 | 24 | 6.74 | 61 | 7.09 | 8 | 7.62 |
| MIR22 | 110 | 1.20 | 7 | 1.97 | 10 | 1.16 | 2 | 1.90 |
| MIR23 | 130 | 0.14 | 10 | 2.81 | 13 | 1.51 | 3 | 2.86 |
| MIR24 | 80 | 0.87 | 7 | 1.97 | 21 | 2.44 | 3 | 2.86 |

**Table 5**. General composition of the faunal assemblage in the studied layers of El Mirador cave and ovicaprine perinatal data, considering NR (number of remains) and MNI (minimum number of individuals). Percentages were calculated taking into account the sum of NR and MNI for all El Mirador layers.

On the other hand, in MIR17, although no climatic variations are observed with respect to MIR19 (Table 4), we see a change in the predominant chorotype (Table 3). In MIR17, *M. agrestis*, a Euro-Siberian species (with 26 % of the total of the assemblage), was more abundant than *A. sylvaticus*, a generalist species that was predominant from MIR24 to MIR18 (Table 1). The increase in the open environment (from 30% in MIR18 to 38% in MIR17) (Fig. 3) and the abundance of *Microtus agrestis* and microtines in general (54%) could indicate an increase in cultivated lands to the detriment of herding practices, as indicated by the low percentage of large mammals (MNI 2.25 %) (Table 5) (Martín, 2015). However, it remained a minor increase at this point, because agricultural intensification would have favoured the dominance of other species such as *Microtus arvalis* or *Crocidura russula* (Burel et al., 2004).

In MIR16 (ca. 6600-6300 cal. BP) an increased number of synanthropic small mammals is registered (53.8%) (Table 2), as well as the highest percentage of large-mammal remains (8.43% of MNI), especially perinatal remains (11.43% MNI) (Table 5) (Martín et al., 2016b). These data could indicate a more intense occupation of the cave in this period. The intense occupation had effects on the diversity and richness of small mammals (Cam et al., 2000). In this layer the diversity continued to be low (0.80) (Table 2). The data from El Mirón cave (Cantabria) reveal a higher diversity than in El Mirador for the same period (López-García et al., 2013). In El Mirón, *Miniopterus schreibersii* has been found, indicating that the cave was probably not occupied, because in general these bats do not cohabit with humans (Cuenca-Bescós et al., 2008).

Moreover, the MER indicates a small increase in temperature (0.3ºC) with respect to the previous layers (MIR19-MIR17), and the most abundant species is once again *A. sylvaticus*. This increase in temperature (Table 4) produces a reduction in the species that eat herbaceous plants throughout the year, such as species belonging to the genus *Microtus*. By contrast, omnivorous species such as *Apodemus sylvaticus* and *Eliomys quercinus* remain practically constant (Soriguer et al., 2003).

### MIR11-MIR10 (6.200-6.000 cal BP)

In MIR11 the MER method allows a minor cold event to be identified (Bañuls-Cardona et al., under review), and these climatic conditions would be expected to be associated with a lower percentage of diversity (Fig. 3). However, we register the greatest level of diversity (0.68) (Table 2), and there is also an increase in thermo-Mediterranean species such as *Crocidura russula* and *Microtus (Terricola) duodecimcostatus*, especially the latter, which increased 14% with respect to MIR16, in which the climatic conditions were milder. These results could be related with a change in herding strategies at this point in El Mirador. The importance of goats and sheeps decreases while the presence of equids, whose origin is likely to be wild, is more important in this layer (Martín et al., 2016a). This change in livestock management may in part be influenced by the low temperatures shown by the small-mammal study (Bañuls-Cardona et al., 2017). Furthermore, archaeobotanical studies of El Mirador indicate that there are no cereals in this layer (Rodríguez et al., 2016). All of these factors could have caused the increased presence of *Microtus (Terricola) duodecimcostatus*. This species requires areas free from rapid and frequent changes in order to build the underground galleries that provide it with refuge and food storage, which explains its scarcity in fields (Tarjuelo et al., 2010).

In contrast to MIR11, the changes seen in MIR10 could be associated with a lower intensity of herding activities, as indicated by the large-mammals remains (2.8 % MNI). The index of synanthropic species is lower and the diversity decreases 18.5 % with respect to MIR 11 (Table 2). Moreover, the presence of synanthropic species such as *Microtus (Terricola) duodecimcostatus* has decreased, and *Crocidura russula* has disappeared, in spite of the thermal recovery (from 9.6 to 10 ºC) (Fig. 3).

### MIR9 - MIR4 (5.900-3.000 cal BP)

From MIR9 to MIR4 the small-mammal analysis reveals an increase in open environments. In this period the MER results indicate a minor decrease in precipitation (Table 4), but this cannot justify the strong reduction in forest cover. This reduction is more likely to be related with the human impact on the landscape, as multidisciplinary studies have shown this amplified aridity to be due to the significant human impact and resulting soil disturbance (Frigola et al., 2007; Domínguez-Villar et al., 2012; Pérez-Lambán et al., 2014).

Moreover, the palaeoclimatic analysis of the small mammals of El Mirador shows that the temperature remains stable from MIR9 to MIR4, though the chorotype analysis indicates important changes. Thermo-Mediterranean species are more abundant in MIR9 and MIR4, whereas in MIR6 and MIR5 species with Euro-Siberian requirements are more important (Table 3). On the other hand, the amount of large-mammals is lower, as in MIR10, and there is a decrease in the intensity of the occupation as a sheepfold "sensu stricto", with a reduced herd or a limited number of shepherds (Martín, 2015). At the same time, however, the pollen remains indicate a significant increase in crops around the cave (Expósito et al., 2017). The agricultural intensification causes a deterioration in habitat quality and a reduction in availability, leading to a homogenization of the landscape. This phenomenon affects diversity, favouring the dominance of a few species, in particular more generalist species as opposed to others whose needs are more stringent (Dunning et al., 1992; Benton et al., 2003).

The Simpson diversity index in MIR9 undergoes a decline with respect to MIR10, while we see an increase in the percentage of synanthropic species (13%), and these tendencies persist through to MIR4 (Table 2). In general, the most abundant species in the entire sequence had been *Apodemus sylvaticus* but from MIR9 this trend changes. In MIR9, the most abundant species is *Crocidura russula*, a generalist species in terms of habitat and food requirements (Table 1). Such a species would benefit from a reduction in landscape heterogeneity that reduces the presence of other species such as *Apodemus sylvaticus* (Blanco, 1998; Tarjuelo et al., 2010). In MIR6-MIR5, the most abundant species is *Microtus agrestis*, whose presence has been shown to increase when grazing levels decrease (Wheeler, 2008). A comparison of the small-mammal diversity of MIR6 with that of a layer from El Mirón with the same chronology (layer 8.1) shows them to be equal (0.78) (López-García et al., 2013). This would indicate that, as observed in the palaeobotanical analysis, landscape anthropization was quite widespread throughout the Iberian Peninsula around 6000-5000 cal BP (Morales-Molino et al., 2011; López-Merino et al., 2012). In the case of MIR5, small-mammal diversity can be compared with that of three different sites: Colomera cave (Lleida), El Mirón cave (Cantabria) and Valdavara-1 cave (Lugo). The diversity in El Mirón cave (Cantabria) and Valdavara-1 cave (Lugo) can be seen to be higher and in Colomera cave (Lleida) lower than in El Mirador. This analysis confirms the theory of low human occupation intensity in the northern Meseta (Ruíz-Zapata et al., 2009a; García-Antón et al., 2011) and in high mountainous areas, as proposed by various authors (Carrión et al., 2010a; Ruíz-Zapata et al., 2011; Tarroso et al., 2014). Finally, during the Bronze Age cereal-growing and livestock farming are widely documented throughtout Europe (López-Sáez et al., 2001; Pérez-Díaz et al., 2014; Broothaerts et al., 2014). In MIR4 of El Mirador, bovid remains with pathologies related to traction force have been detected (Martín, 2015), and the palaeobotanical records and small-mammal analysis indicate that cultivated fields were gaining ground over forest (Allué and Euba, 2008; Expósito et al., 2017; Bañuls-Cardona et al., 2017). As we have seen in MIR9, this intense agricultural system favours the dominance of the most generalist species, compared to other species with more stringent requirements (Dunning et al., 1992; Arribas et al., 2012). In MIR4, we see the greatest values in diversity in El Mirador (0.82) and also the highest index of synanthropic species (60.4%). The most representative species was *Microtus arvalis*, a synanthropic species that occurred in landscapes with a high percentage of arable land. Also, this species can cause significant economic losses during population outbreaks (Jacob and Tkadlec, 2010; Luque-Larena et al., 2013) .

## 6.Conclusions

The small-mammal study of El Mirador has proved to be a useful tool to identifying the changes in diversity related to human activities during the middle-late Holocene of the northwest of the Iberian Peninsula. El Mirador is particularly valuable in this context because it has a sequence with a well-documented human occupation from 7200 to 3000 cal. BP. Two phases are identified by our studies of diversity and synanthropic species. In the first phase (7200-7000 cal. BP) small changes in diversity related with climatic oscillations have been established; while in the second phase

(7000-3000 cal. BP) changes in diversity associated with the human impact have been detected. Moreover, from 5900 to 3700 the dominance of microtines and the evidence from other remains studied (large mammals, seeds, charcoal, pollen, phytoliths) indicate changes probably caused by intensive agricultural practices. In general, the most significant decline in biological richness in El Mirador cave was caused in the layers with the greatest human pressure derived from both agriculture and livestock. Further comparison with other proxies has allowed us to corroborate generalized human pressure on the landscape throughout the Iberian Peninsula from 6000 cal. BP on. Moreover, it has confirmed the theory of low human occupation intensity in the northern Meseta and in high mountainous areas.

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# CHAPTER 3:
# OTHER STUDIED SITES

# 3. OTHER STUDIED SITES

In this PhD thesis, the study of El Mirador cave (Sierra de Atapuerca, northern Iberian Peninsula) have been published in science scientific journals, but other sites have been studied for this work and they have not been published because we have not had time. For this reason, we exposed here the obtained results of this unpublished sites.

These sites are four this chapter include the following sites: El Portalón (Sierra de Atapuerca, northern Iberian Peninsula), Cova Bonica (Vallirana, north-eastern Iberian Peninsula), Balma del Gai (Moià, north-eastern Iberian Peninsula) and finally Grottina dei Covoloni del Broion (Vicenza, north-eastern Italian Peninsula) (Fig.3.1). This sites comprised a chronology range between latest Pleistocene to late Holocene (ca. 15000-3000 BP).

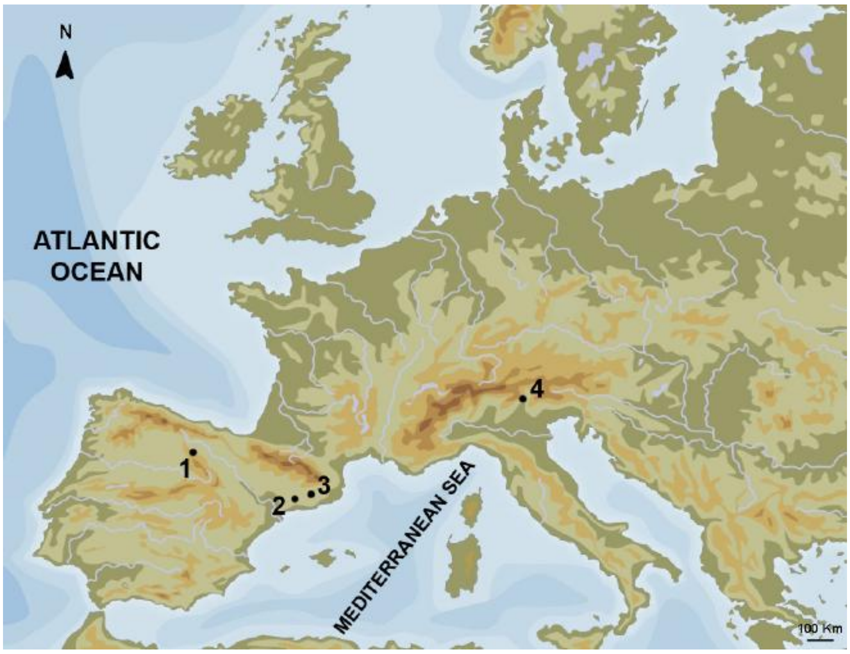


**Figure. 3.1.** Location of the studied sites: 1, El Portalón ; 2, Cova Bonica; 3, Balma del Gai; 4, Grottina dei Covoloni del Broion.

## 3.1. SITE DESCRIPTION: EL PORTALÓN

El Portalón site is a cave located in the Northern Plateau of the Sierra de Atapuerca (Burgos, Spain) (Fig.3.1.1). Within the Sierra de Atapuerca, there is a karst system reaching 3700 m in length, known as the Cueva Mayor (Ortega Martínez, 2009).

**Figure. 3.1.1**. Location of El Portalón site in the Iberian Peninsula.

This site is known since the 19th century (Clark et al., 1979). In 2000 the current research team of Sierra de Atapuerca iniciated an excavation in El Portalón with a multidisciplinary team. This team discovered a prolonged human occupation in the cave from the Paleolithic to historic times.

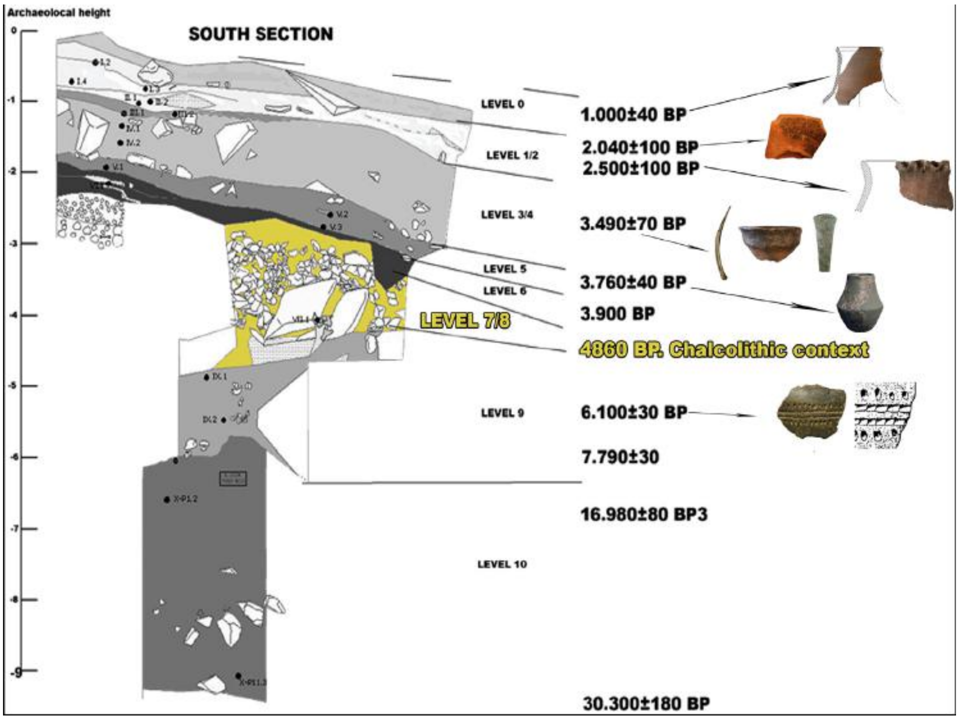


**Figure. 3.1.2.** Section site of El Portalón site and the radiocarbon dates with the “index fossil” (Carretero et al., 2008).

The stratigraphic sequence exceeds 10 m depth and is divided in 11 stratigraphic units grouped into two sedimentary units: Upper Pleistocene (level 11, and level 10 transitional Pleistocene/ Holocene) and Holocene. Neolithic/Mesolithic are represented in the layer 9 , the Chalcolithic in layers 6 and 7/8, Middle and Early Bronze Age correspond to levels 3/4 and 5 finally there are evidences of occupation from the Roman Age to the Iron Age I at layers 0, 1 and 2 respectively (Carretero et al., 2008; Pérez-Romero et al., 2015) (Fig.3.1.2).

In this case we work with the Chalcolithic stratigraphic units. These units are further divided into two phases. The older phase corresponds to a funerary context during the Early Chalcolithic or Precampaniform, with an anthropic tumular structure including human remains (Castilla et al., 2014) and evidences of funerary activities. The younger phase corresponds to the use of the site for herding and habitat during the Final Chalcolithic or Campaniform (Pérez-Romero et al., 2015) (Fig. 3.1.3).

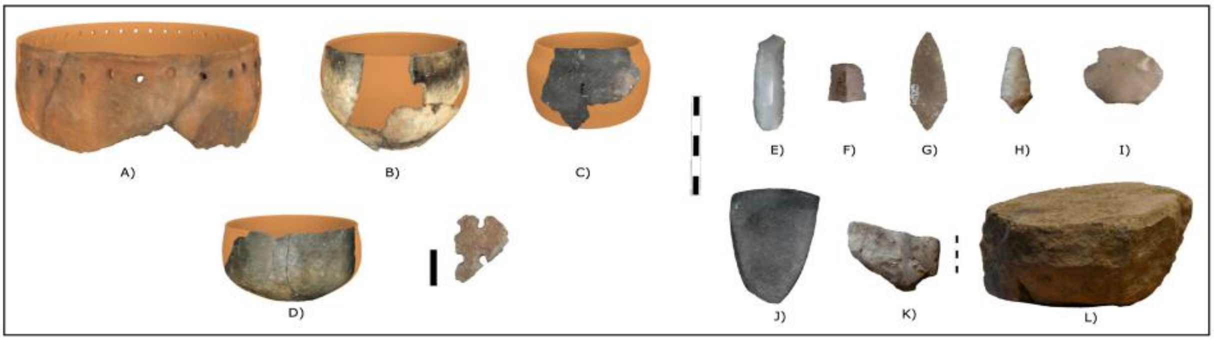


**Figure 3.1.3.** Archeological remains of Chalcolithic layers, pottery (a-d) and stone tools (e-l).(modified from Pérez-Romero et al., 2015)

Concretely, we have studied the UE79 and UE85. The UE79 is part of the burial phase (stratigraphic units 63 to 84) which comprises a tumular stacking of decimetric limestone clasts of approximately 8 m in diameter and 2 m high in the center. The characteristics of the funerary context suggest that it is the result of repetitive burial activity following a similar funerary pattern over time. Each event appears to have partially disturbed by a previous funerary context, with possible collapse of a large part of the roof of the cavity during this period. Furthermore, the latter habitation and stable use of the cave seems to have contributed to the disturbance of some of the funerary structures. Fortunately, an unaltered burial context with the presence of a complete sub-adult individual was discovered, allowing us to understand the complete funerary context (Castilla et al., 2014, Pérez-Romero et al., 2015) (Fig.3.4). There are a large amount of archaeological artifacts related to the burials: pottery fragments (56%), large mammals (40.17%), lithic industry (3.3%) and bone industry (0.2%), which provide significant data for a formal classification. From this grave goods the decorated pottery presents decorative motifs typical of the Early Chalcolithic (Pre-bell beaker) and the embossed tablets, given their nature as an "index fossil" (Pérez-Romero et al., 2015).

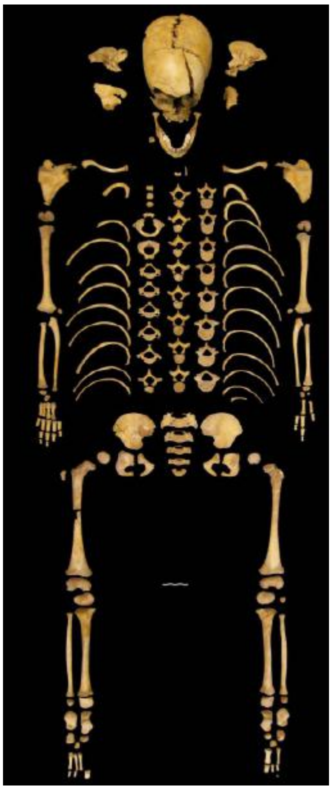


**Figure.3.1.4**. A complete sub-adult individual of UE79 (Castilla et al., 2014).

Following the funerary units, a sequence of prepared floors and "fumier" units alternate in the site stratigraphy. The UE85 has been interpreted as "Prepared floors". These "prepared floors" have less than 10 cm thick, made up of clayey silts of an intense orange-brown color with the incorporation of small limestone fragments. It was interpreted as anthropic preparation surfaces using endokarst clay (Pérez-Romero et al., 2015). On these floors, anthropic structures, such as hearths, postholes and fragmented archaeological remains have been recorded. The archaeological remains found (pottery, large mammals, lithic industry and bone industry) provide significant data for a formal classification as Late Chalcolithic (Pérez-Romero et al., 2015, Alday et al., 2011).

### 3.1.1. RESULTS

The small mammals analysed belongs to two stratigrafic units (UE79 and UE85). From these stratigrafic units, 805 remains (NISP) have been identified, with a minimum number of individuals (MNI) of 463. From these two Chalcolithic units twelve small-mammal species have been identified: *Crocidura russula*, *Sorex coronatus*, *Neomys anomalus*, *Talpa europaea*, *Myotis myotis-blythii*, *Miniopterus schreibersii*, *Arvicola sapidus*, *Microtus agrestis*, *Microtus arvalis*, *Microtus (Terricola) pyrenaicus*, *Apodemus sylvaticus* and *Eliomys quercinus* (Table.3.1.1) (APPENDIX 1).

| **TAXA** | **UE 85** | | | **UE 79** | | |
|---|---|---|---|---|---|---|
| | **NISP** | **MNI** | **MNI%** | **NISP** | **MNI** | **MNI%** |
| *Crocidura russula* | 134 | 80 | 20.67 | 28 | 16 | 21.05 |
| *Sorex coronatus* | 139 | 81 | 20.93 | 19 | 11 | 14.47 |
| *Neomys anomalus* | 1 | 1 | 0.26 | 2 | 1 | 1.32 |
| *Talpa europaea* | 3 | 1 | 0.26 | 1 | 1 | 1.32 |
| *Myotis myotis-blythii* | 18 | 11 | 2.84 | 3 | 2 | 2.63 |
| *Miniopterus schreibersii* | 8 | 6 | 1.55 | 1 | 1 | 1.32 |
| *Arvicola sapidus* | 3 | 2 | 0.52 | 1 | 1 | 1.32 |
| *Microtus arvalis* | 51 | 26 | 6.72 | 11 | 8 | 10.53 |
| *Microtus agrestis* | 22 | 13 | 3.36 | 13 | 10 | 13.16 |
| *Microtus (Terricola) pyrenaicus* | 27 | 14 | 3.62 | 5 | 3 | 3.95 |
| *Apodemus sylvaticus* | 266 | 142 | 36.69 | 31 | 21 | 27.63 |
| *Eliomys quercinus* | 17 | 10 | 2.58 | 1 | 1 | 1.32 |
| **TOTAL** | **689** | **387** | **100** | **116** | **76** | **100** |

**Table.3.1.1**. Distribution of the small-mammal remains of El Portalón by UE85 and UE79. Number of identified specimens (NISP), Minimum number of individuals (MNI) and the percentage of minimum number of individuals (MNI%).

### UE 79

At this unit we registered 116 remains (NISP) and 76 minimum number of individuals (MNI). Using the systematic palaeontology method (APPENDIX 1) we have identified 12 species: *Crocidura russula*, *Sorex coronatus*, *Neomys anomalus*, *Talpa europaea*, *Myotis myotis-blythii*, *Miniopterus schreibersii*, *Arvicola sapidus*, *Microtus agrestis*, *Microtus arvalis*, *Microtus (Terricola) pyrenaicus*, *Apodemus sylvaticus* and *Eliomys quercinus*. These species are the same in UE85 but the percentages are different. *Apodemus sylvaticus* is the most represented species in both layers (Table.3.1.1).

The percentage of woodland is high (62.50 %) , accompained by "Open Humid meadow" (18.09%) which indicates evergreen meadowland with pastures and dense topsoil, "Open Dry meadow" (17.11%) which consists of meadowland subject to seasonal climate change and "Water" (2.30%) namely watercourse areas that include streams, lakes and ponds (Fig.3.1.5).

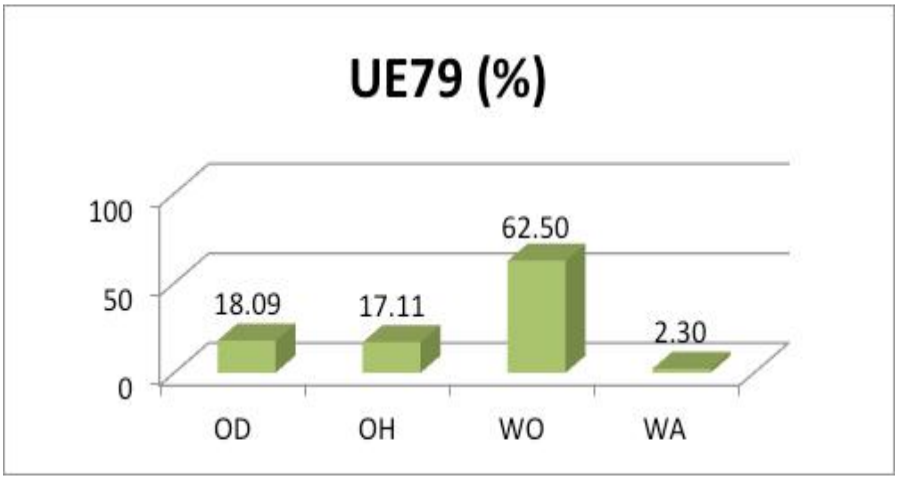


**Figure 3.1.5**. Distribution of small mammals according to their habitat preferences. We divided the habitats into four categories: OD (Open Dry meadow), OH (Open Humid meadow), WO (Woodland) and WA (Water).

The MER (Mutual Ecogeographic Range) (according to Blain et al., 2016) analysis has been used for the palaeoclimatic reconstruction, and these results have been compared with the current climatic data of Ibeas de Juarros (climate-data.org). The mean annual temperature (MAT) is 9.0 ºC, 1.1 ºC lower than nowadays (10.1ºC), the mean temperature of the warmest month (MTW) is 18.3 ºC, 0.4 ºC lower than nowadays (18.7ºC) and finally the mean temperature of the coldest month (MTC) is 3.0 ºC, 0.4 ºC lower than nowadays (2.6ºC). The Continentality index of *Gorczynski,* indicates that these climatic conditions are in the limit of Oceanic climate (Ic = 19). On the other hand, the MAP (mean annual precipitation) is 1067 mm, 473 mm higher than nowadays (594 mm) (Table.3.1.2). The Rainfall Index of *Lang*, indicates a temperate-humid event (L=119).

**UE85-79**

| | MEAN | MAX | MIN | SD | |
|---|---|---|---|---|---|
| MAT (°C) | 9.0 | 11 | 7 | 2.0 | -1.1 |
| MTC (°C) | 3.0 | 5 | 1 | 2.0 | -0.4 |
| MTW (°C) | 18.3 | 21 | 17 | 2.3 | -0.4 |
| MAP (mm) | 1067 | 1500 | 700 | 404.1 | 473 |

**Table.3.1.2.** Relation of temperatures and precipitation obtained using the MER (Mutual Ecogeographic Range) method of UE79 and UE85. MAT: mean annual temperature; MTC: mean temperature of the coldest month; MTW: mean temperature of the warmest month; MAP: mean annual precipitation; 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; Δ: difference between the current mean for Ibeas de Juarros (climate-data.org) and the data obtained with the small mammals.

The chorotypes analysis indicate that the most represented species were the generalist species (CH-3) (31.58%), but this percentage is 10% lower than UE85 and the Euro-Siberian species (CH-1) (27.63%) were more abundant. Moreover the Mediterranean species (CH-4) represents 25% and the CH-2 only represents 15.79 % of the assemblage (Fig.3.1.6).

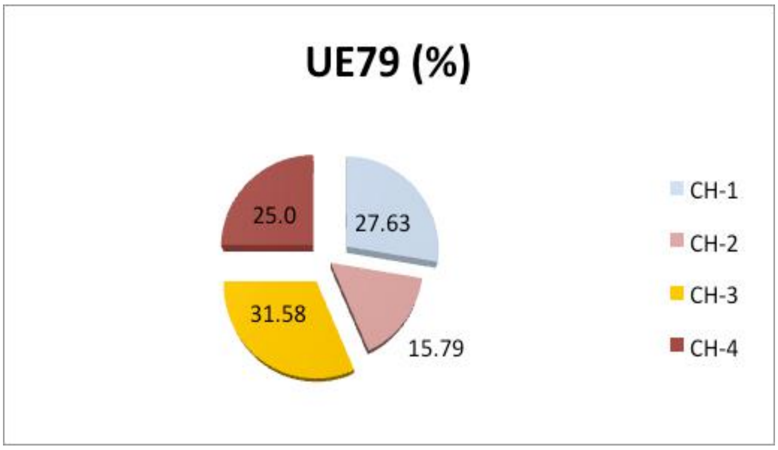


**Figure.3.1.6**. Representation of the chorotypes: CH-1 (chorotype 1, Euro-Siberian species), CH-2 (chorotype 2, Euro-Siberian species that nonetheless tolerate Mediterranean conditions), CH-3 (chorotype 3, Generalist species) and CH-4 (chorotype 4, Thermo-mediterranean species).

Finally the Simpson index indicates a very high diversity (0.82), and the synanthropic index represents a percentage slightly higher than UE85 (35.53 %).

### UE85

In this unit we are analyzed 689 remains (NISP) with 387 minimum number of individuals (MNI). From this assemblage we have identified 12 species: *Crocidura russula*, *Sorex coronatus*, *Neomys anomalus*, *Talpa europaea*, *Myotis myotis-blythii*, *Miniopterus schreibersii*, *Arvicola sapidus*, *Microtus agrestis*, *Microtus arvalis*, *Microtus (Terricola) pyrenaicus*, *Apodemus sylvaticus* and *Eliomys quercinus*. And the most represented taxa is *Apodemus sylvaticus* (36.69%) (Table.3.1.1).

Using the habitat weighting method we have analyzed the palaeoenvironment. We have distinguished four types of landscape: Open Humid meadow, Open Dry meadow, Woodland and Water. The percentage of woodland is very high (67.96 %), accompanied by "Open Humid meadow" (16.54%) which indicates evergreen meadowland with pastures and dense topsoil, "Open Dry meador" (14.79 %) which consists of meadowland subject to seasonal climate change and "Water" (0.71%) namely watercourse areas that include streams, lakes and ponds (Fig.3.1.7).

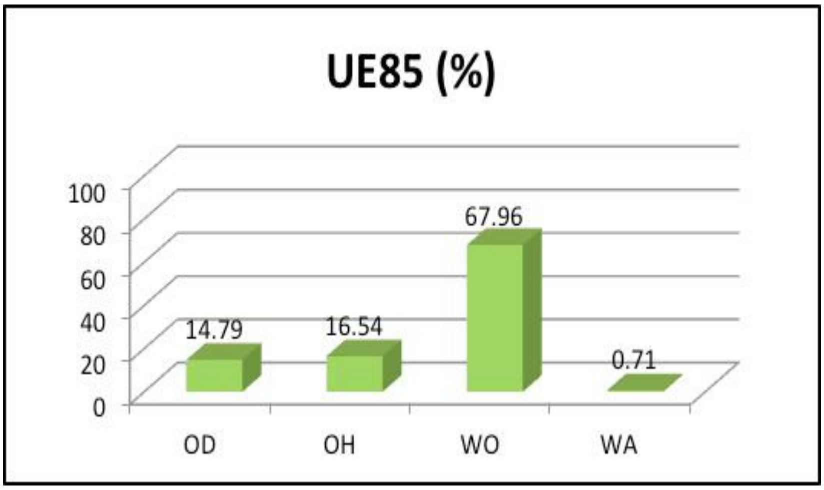


**Figure. 3.1.7.** Distribution of small mammals according to their habitat preferences. We divided the habitats into four categories: OD (Open Dry meadow), OH (Open Humid meadow), WO (Woodland) and WA (Water).

As noted above both units have the same species represented, for this reason the results obtained with the MER is the same. With the chorotypes analysis, the most represented species (42.12%) were the generalist species (CH-3), the Mediterranean species (CH-4) represent the 23%, the CH-2 namely Euro-Siberian species that nonetheless tolerate Mediterranean conditions represents 21.19%, and the Euro-Siberian species (CH-1) only represents 13.7 % of the assemblage (Fig.3.1.8).

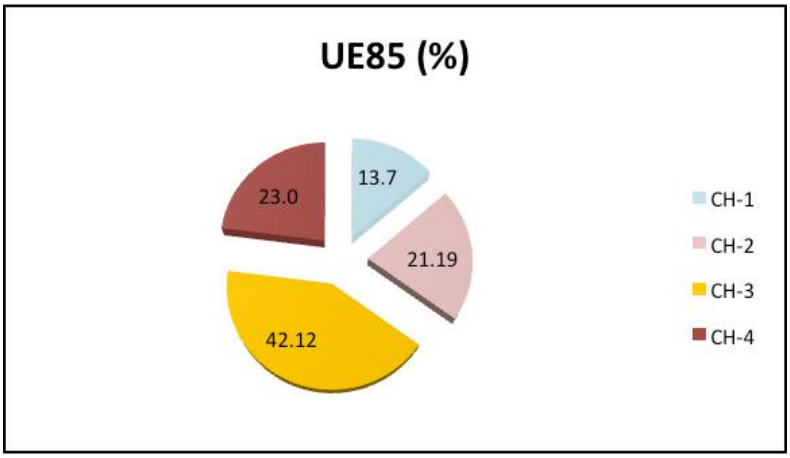


**Figure.3.1.8**. Percentage of chorotypes. Representation of the chorotypes: CH-1 (chorotype 1, Euro-Siberian species), CH-2 (chorotype 2, Euro-Siberian species that nonetheless tolerate Mediterranean conditions), CH-3 (chorotype 3, Generalist species), CH-4 (chorotype 4, Thermo-mediterranean species).

Moreover the diversity study from the Simpson index indicates a high diversity (0.77), and the synanthropic index represents a low human pressure in the cavity (29.97 %).

### 3.1.2. DISCUSSION: El Portalón

The two studied units (UE79 and UE85) of El Portalón cave pertaining to the Chalcolithic period, evidenced by archaeological remains (pottery, large mammals, lithic industry and bone industry) and a dating in UE79 (5200-4800 cal BP) (Fig.3.1.2) (Pérez-Romero et al., 2015).

In these units, we have registered that the mean annual temperature (MAT) is 9 ºC, in both studied units (Table.3.1.2). The comparison of the palaeoclimatic conditions with the current climatic data of Ibeas de Juarros, shows that the temperatures during the Chalcolithic period were similar than nowadays, there is a difference of 1.1ºC. Moreover, in the case of the mean annual temperature of the coldest month, is important to highlight, that was 0.4 ºC higher than nowadays. On the other hand, when we have studied the level of the rainfall, we have noted an important difference. In the Chalcolithic period the precipitation was 473 mm higher than nowadays (Table.3.1.2). From the Rainfall Index of *Lang*, this data indicates a temperate-humid event (L=119). Despite these results, the analysis of the Continentality index of *Gorczynski*, indicates that these climatic conditions are characteristics of Oceanic climate (Ic=19) as is currently happening in the area (Kottek et al., 2006). This temperate-humid climatic conditions registered in these layers of El Portalón have been observed in other studies such as the pollen analysis obtained in the Western Pyrenees (Pérez-Díaz et al., 2015) or the oxygen and carbon isotopic record of eastern Mediterranean (Bar-Mathews and Ayalon, 2011).

**UE79 (Late Holocene)**

The chorotypes analysis shows small differences in these units. In both units the generalist species are very abundant (CH- 3) but the percentages are different. The chorotypes analysis indicates that the percentage of generalist species in this unit is 31.58%, while the percentage of Euro-Siberian species is 27.63% (Fig.3.1.6) probably related to the decrease of the temperatures that have been described by the pollen study of the Iberian Peninsula (Tarroso et al., 2014).

The palaeoenvironmental data shows a predominance of the woodland formations (62.5%). While the open environments represent 37.5 % of the landscape (Fig.3.1.5). At this moment (5200-4800 cal BP), there are also some studies that argue this expansion of the open spaces by human pressure on the landscape due to intensification in the fire regime, as suggested by the increase in charcoal concentration (López-Merino et al., 2012), and the farming economy is consolidated (Pérez-Díaz et al., 2015). Despite this human impact, by means of the Simpson index in this unit has been registered a very high diversity (0.82) and a low synnathropic index (35.58%), these data indicates a low human pressure at this moment in El Portalón, related to the repetitive burial activity at this layer.

**UE85 (Late Holocene)**

The palaeoclimatic data, as we noted previously, are the same that in the UE79, i.e, a climate with temperate-humid conditions, however little differences have been observed with the chorotypes data. The generalist species (CH-3) are the most represented in UE85 (42.12%), but in this unit, we observed a decrease in the Euro-Siberian species from UE 85 (13.7%) to UE79 (27.63%) and an increase of the (CH-2) or Euro-Siberian species that tolerate Mediterranean conditions from 21.19% in UE85 to 15.79% in UE79 (Fig.3.1.6 and Fig.3.1.8). These data indicate an improvement of the climate at UE85 that could be related with the expansion of the Mediterranean climate before 5000 cal BP (Jalut et al., 2000).

The palaeoenvironmental characteristics were little different between UE85 and UE79 although the climatic conditions in these units were equals, while the percentage of woodland decrease 5.5% from UE85 to UE79 (Fig.3.1.5 and Fig.3.1.7). The same dynamic have been described in the north of Iberian Peninsula from pollen analysis that indicates a woodland expansion from 5000 cal BP (Santos et al., 2000, Muñoz Sobrino et al., 2007).

The Simpson index indicates a high diversity (0.77), and the synanthropic index represents a low value (29.97 %). Moreover, this unit has been interpreted by sedimentological studies as anthropic preparation surfaces "Prepared floor". These have less than 10 cm thick, made up of clayey silts of an intense orange-brown color with the incorporation of small limestone fragments (Pérez-Romero et al., 2015). Thus, we could say that during the formation of the UE85, the human presence is low.

### 3.1.3. CONCLUSIONS

The same palaeoclimatic conditions have been registered in both units (UE 79 and UE85). The comparison of the palaeoclimatic conditions with the current climatic data of Ibeas de Juarros, shows that the temperatures during the Chalcolithic period were similar than nowadays. The Rainfall Index indicates a temperate-humid conditions, the precipitation was 473 mm higher than nowadays. The Continentality index of *Gorczynski* indicates that these climatic conditions are characteristics of an Oceanic climate.

During the Early Chalcolithic (UE79) the chorotypes analysis indicates that the percentage of generalist species is the most important, but the percentage of Euro-Siberian species is also important. The palaeoenvironmental data shows an important percentage representation of the species related to open environments, probably related with human pressure on the landscape. Despite the human impact is low, probably eventual presence for the burial as indicates the very high diversity and the low percentage of synanthropic species reported.

On the other hand, during the Late Chalcolithic (UE 85), we have detected probably, the expansion of the Mediterranean climate. We observed a decrease in the Euro-Siberian species from UE 85 (13.7%) to UE79 (27.63%) and an increase of the (CH-2) or Euro-Siberian species that tolerate Mediterranean conditions from 21.19% in UE85 to 15.79% in UE79. The palaeoenvironmental characteristics registered in UE85 indicate a woodland expansion since values of UE79. These data and the high diversity with the low values of synanthropic species indicate a low human pressure.

## 3.2. SITE DESCRIPTION: Cova Bonica

Cova Bonica is a cave located in the NE of the Iberian Peninsula, ~30 km south of Barcelona (41°22’10.29”N, 1°53’38.64”E) 402 m a.s.l., in the Vallirana locality (Fig.3.2.1). It is open to the Jurassic-Cretaceous dolomites of the massif Garraf-Ordal. It is a karstic cavity to have originated from the confluence of different diaclases that have accentuated the fall of a large number of blocks from the roof of the cavity.

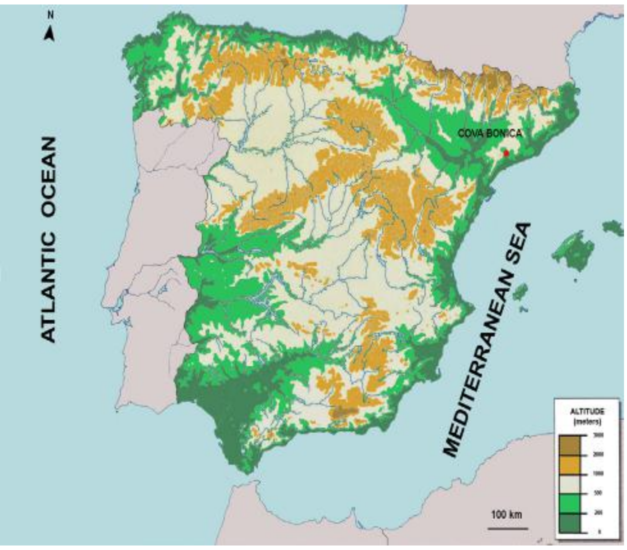


**Figure. 3.2.1.** Location of Cova Bonica site in the Iberian Peninsula.

The cave plant is about 30 m long, 20 m of maximum width and a height of about 15 m. Moreover, it presents two lateral rooms on the north side and a collapsed hole in the bottom sediments, heading south west. The original morphology of the cave was modified by mining for sparry calcite and the cave sediments were partially destroyed by earthmoving and subsequent mushroom farming.

Cova Bonica appears named in many studies of recent prehistory of Catalonia, but always with reference to materials without stratigraphic context. The first archaeological excavation was conducted in 1936 under the direction of Serra-Ràfols (Baldellou, 1974). Part of the archaeological material from these first excavations are currently deposited in the MAC (Archaeology Museum of Catalonia), which were studied by Baldellou (1974), the only existing scientific work on this important Garraf cavity. Some years later, in the Ph.D thesis of Maria Angels Petit (1986) there were revisited some of the materials of the site.

After the excavation of the thirties, we know that the cave was used for the cultivation of mushrooms. Around the sixties, members of the CEV (Centre Excursionista de Vallirana) conducted an archaeological excavations. Between 1978 and 1984 were made in the cavity clandestine excavations. In 2008 the current excavation team iniciated the first intervention.

This team is part of *Grup de Recerca del Quaternari* (GRQ) linked to the University of Barcelona. In this first intervention, geophysical survey was performed to evaluate the sedimentary potential of the cavity (Daura and Sanz, 2008). The following years this team carried out the first archaeological excavation by surveys (Daura and Sanz, 2009).

In this last stage of excavations by the GRQ they have distinguished three areas of excavation: a principal chamber (SP) and two small chambers on the right side of SP, one next to the entrance (SP1) and the second in the internal area (SP2) (Fig.3.2.2). In each of these parts of the cavity they have been several surveys to determine the functionality of the cavity. In these surveys have located many layers of mixed historic and prehistoric materials. We are going to focus our study on the survey in the Principal Chamber (SP), where they found two in situ archaeological levels (Fig.3.2.2).

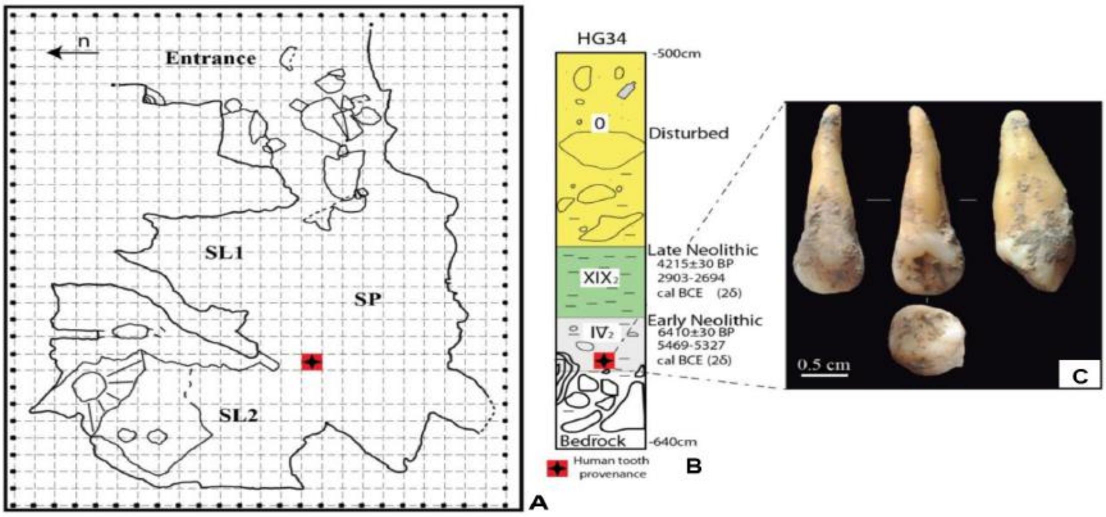


**Figure 3.2.2**. Archaeological context of Cova Bonica. A) Site plan , B) Stratigraphy column with radiocarbon dates C) Human tooth (upper canine) (Olalde et al., 2015)

The stratigraphic sequence is represented in the HG34 cross-section (Fig.3.2.2) and consists of mud sediments supporting varying amounts of speleothem, bedrock limestone clasts and archaeological remains.

The Layer IV is overlying the bedrock and corresponds to the first Holocene deposition in this area; it consists of clay and silt sediment supporting limestone and speleothem clasts. In this layer, they have been recovered numerous fragments of cardial pottery, lithic artifacts of rock crystal and jasper, a bone awl made from an ovicaprine metapodial, body ornaments, faunal and human remains, and abundant charcoal (Fig.3.2.3a). The chronology of this layer is 7308-7401 cal BP (Fig.3.2.2), directy radiocarbon dating the upper human canine.

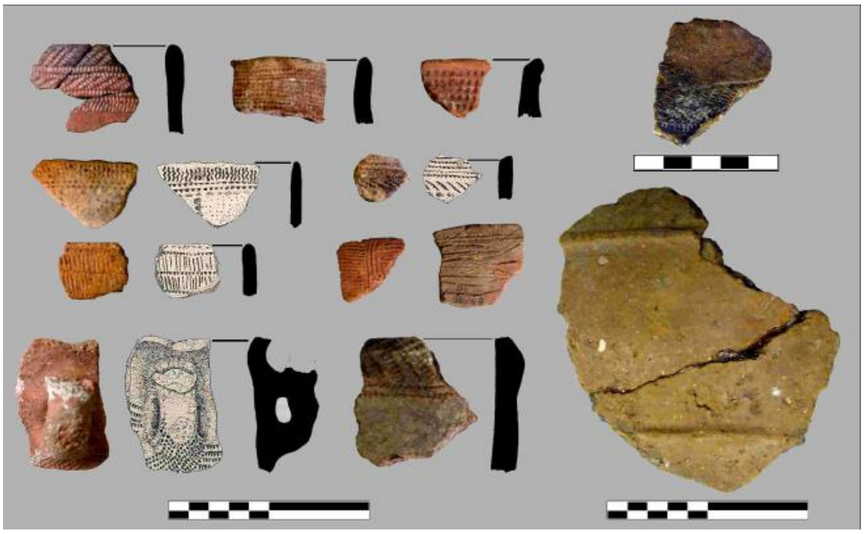


**Figure 3.2.3a**. Archaeological material: Pottery from layer IV (Baldellou, 1974; Sanz et al., 2011)

On the other hand, the Layer XIX (overlies this Early Neolithic unit) consists of dark plastic mud sediments supporting limestone clasts. This layer contains abundant charcoal, scant pottery and faunal remains (Fig. 3.2.3b). In this case they have dated a femur of *Ovis aries* and the result has been an obtained age of 4711-4835 cal  BP (Fig.3.2.2).

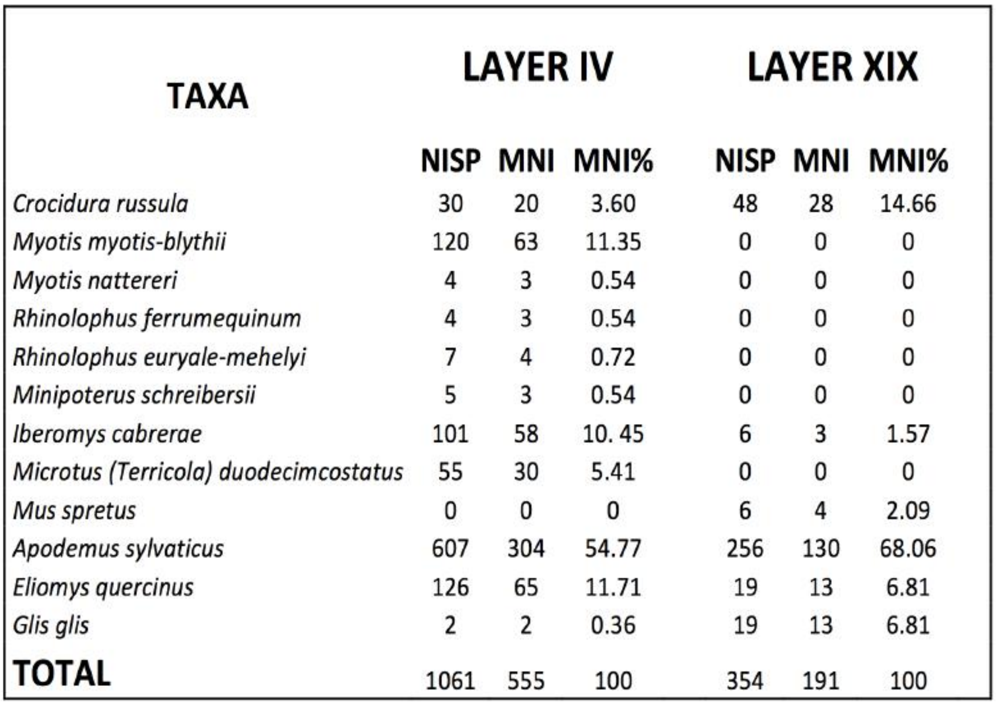
**Figure 3.2.3b**. Archaeological material: Pottery from layer XIX (Baldellou, 1974; Sanz et al., 2011)

Finally, the uppermost unit of the stratigraphic sequence (layer 0) is formed of mixed sediments reworked by mining and mushroom farming and contains prehistoric, Iberian-Roman, and Medieval-Modern ceramics as well as scattered Cardial remains.

The scientific studies of Cova Bonica are still scarce, since the project is still starting. But it should be noted the DNA study has been carried out on human remains from layer IV (Olalde et al., 2015).

### 3.2.1. RESULTS

The analysed small mammals of Cova Bonica, belongs to layer IV and layer XIX. From these layers, 1415 remains (NISP) have been identified, with a minimum number of individuals (MNI) of 754. Twelve small-mammal taxa have been identified (APPENDIX 1): *Crocidura russula*, *Myotis myotis-blythii*, *Myotis nattereri*, *Rhinolophus ferrumequinum*, *Rhinolophus euryale-mehelyi*, *Miniopterus schreibersii*, *Iberomys cabrerae*, *Microtus (Terricola) duodecimcostatus*, *Mus spretus*, *Apodemus sylvaticus*, *Eliomys quercinus* and *Glis glis* (Table.3.2.1).



| TAXA | LAYER IV | | | LAYER XIX | | |
|---|---|---|---|---|---|---|
| | NISP | MNI | MNI% | NISP | MNI | MNI% |
| *Crocidura russula* | 30 | 20 | 3.60 | 48 | 28 | 14.66 |
| *Myotis myotis-blythii* | 120 | 63 | 11.35 | 0 | 0 | 0 |
| *Myotis nattereri* | 4 | 3 | 0.54 | 0 | 0 | 0 |
| *Rhinolophus ferrumequinum* | 4 | 3 | 0.54 | 0 | 0 | 0 |
| *Rhinolophus euryale-mehelyi* | 7 | 4 | 0.72 | 0 | 0 | 0 |
| *Minipoterus schreibersii* | 5 | 3 | 0.54 | 0 | 0 | 0 |
| *Iberomys cabrerae* | 101 | 58 | 10. 45 | 6 | 3 | 1.57 |
| *Microtus (Terricola) duodecimcostatus* | 55 | 30 | 5.41 | 0 | 0 | 0 |
| *Mus spretus* | 0 | 0 | 0 | 6 | 4 | 2.09 |
| *Apodemus sylvaticus* | 607 | 304 | 54.77 | 256 | 130 | 68.06 |
| *Eliomys quercinus* | 126 | 65 | 11.71 | 19 | 13 | 6.81 |
| *Glis glis* | 2 | 2 | 0.36 | 19 | 13 | 6.81 |
| **TOTAL** | 1061 | 555 | 100 | 354 | 191 | 100 |

**Table 3.2.1**. Distribution of the small-mammal remains of Cova Bonica by layer IV and XIX. Number of identified specimens (NISP), Minimum number of individuals (MNI) and the percentage of minimum number of individuals (MNI%).

### Layer IV (Early Neolithic)

In this layer have been studied 1061 remains (NISP) and have been identified a minimum number of individuals (MNI) of 555, belong to eleven small-mammal species (APPENDIX 1): *Crocidura russula*, *Myotis myotis-blythii*, *Myotis nattereri*, *Rhinolophus ferrumequinum*, *Rhinolophus euryale-mehelyi*, *Miniopterus schreibersii*, *Iberomys cabrerae*, *Microtus (Terricola) duodecimcostatus*, *Apodemus sylvaticus*, *Eliomys quercinus* and *Glis glis* (Table.3.2.1). Into this assemblage we have analysed the diversity and the percentage of synanthropic species. The Simpson index indicates a low diversity (0.66) and the synanthropic index shows a low percentage (22.72%).

The habitat weighting method allows us to distinguish three types of landscape: Open Humid meadow, Open Dry meadow and Woodland. However the predominance of the woodland is important (74.86 %). Besides, we have registered "Open Humid meadow" (17.21%) which indicates evergreen meadowland with pastures and dense topsoil and "Open Dry meadow" (7.93 %) which consists of meadowland subject to seasonal climate change (Fig.3.2.4).

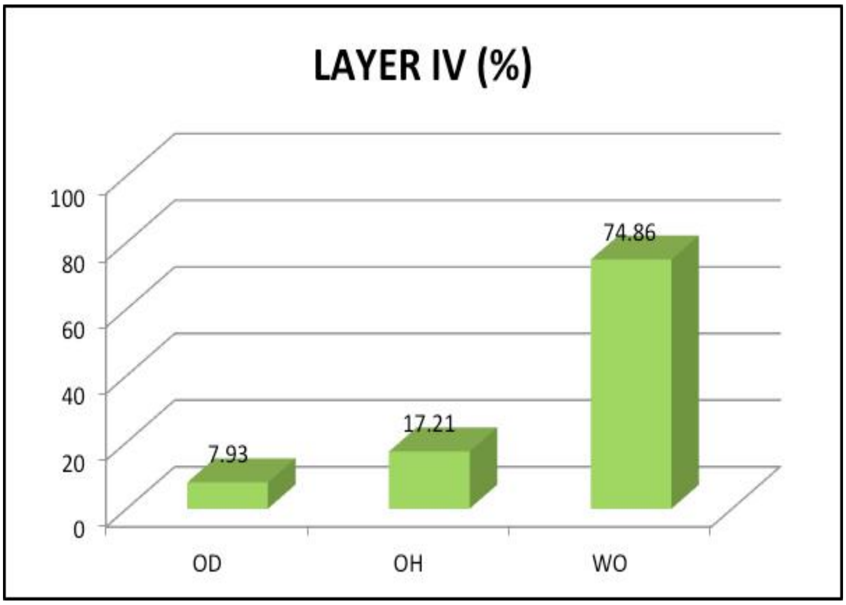


**Figure 3.2.4.** Distribution of small mammals from layer IV of Cova Bonica according to their habitat preferences. We divided the habitats into four categories: OD (Open Dry meadow), OH (Open Humid meadow) and WO (Woodland).

The MER indicates that the temperature was lower than current climatic data of Vallirana (Climate-data.org). The mean annual temperature (MAT) is 11.4 ºC, 4.2 ºC lower than nowadays

(15.6ºC), the mean temperature of the warmest month (MTW) is 19.6 ºC, 3.9 ºC lower than nowadays (23.5ºC) and finally the mean temperature of the coldest month (MTC) is 3.8 ºC, 4.9 ºC lower than nowadays (8.7ºC) (Table.3.2.2)

| | LAYER IV | | | | |
|---|---|---|---|---|---|
| | MEAN | MAX | MIN | SD | |
| MAT (° C ) | 11.4 | 15 | 5 | 2.9 | -4.2 |
| MTC (° C ) | 3.7 | 8 | 0 | 2.2 | -4.9 |
| MTW(° C ) | 19.6 | 23 | 15 | 1.9 | -3.8 |
| MAP (mm) | 907 | 2000 | 700 | 317 | 279 |

**Table.3.2.2.** Relation of temperatures and precipitation obtained using the MER (Mutual Ecogeographic Range) method of layer IV. MAT: mean annual temperature; MTC: mean temperature of the coldest month; MTW: mean temperature of the warmest month; MAP: mean annual precipitation; 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; Δ: difference between the current mean for Vallirana (climate-data.org) and that obtained for the small mammals.

The Continentality index of *Gorczynski*, indicates that these climatic conditions are in the limit of Oceanic and Continental climate (Ic = 21). On the other hand, the MAP (mean annual pre-cipitation) is 907 mm, 279 mm higher than nowadays (628 mm). The Rainfall Index of *Lang*, indicates a semi-humid event (L=79). The chorotypes analysis shows that the most representative species (79.64%) were the generalist species (CH-3), the Mediterranean species (CH-4) represents the 20 % and the Euro-Siberian species (CH-1) only represents 0.36 % of the assemblage (Fig.3.2.5).

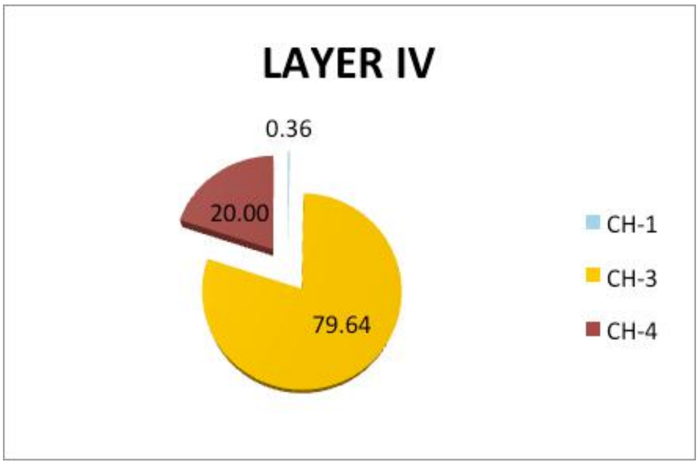


**Figure 3.2.5.** Chorotypes percentage of layer IV. Representation of the chorotypes: CH-1 (chorotype 1, Euro-Siberian species), CH-3 (chorotype 3, Generalist species), CH-4 (chorotype 4, Thermo-mediterranean species).

## Layer XIX (Late Neolithic)

In this layer have been studied 354 remains (NISP) and have been identified a minimum number of individuals (MNI) of 191, belong to six small-mammal taxa (APPENDIX 1): *Crocidura russula*, *Iberomys cabrerae*, *Microtus (Terricola) duodecimcostatus*, *Mus spretus*, *Apodemus sylvaticus*, *Eliomys quercinus* and *Glis glis* (Table. 3.2.1). The Simpson index indicates a low diversity (0.51), and the most represented taxa is *Apodemus sylvaticus* (68.06%). Moreover, the index of synanthropic species is low (23.56%).

In order to reconstruct the environment, the method of habitat weightings shows that "Woodland" represents almost all of the sample (87.43%) , namely ranges from leafy forests to wood¬land margins, with moderate vegetation cover, but we also find species that indicate that there, albeit under-represented, two types of landscape more. "Open Humid meadow" (8.38 %) which indicates evergreen meadowland with pastures and dense topsoil and "Open Dry meadow" (4.19 %) which consists of meadowland subject to seasonal climate change (Fig.3.2.6).

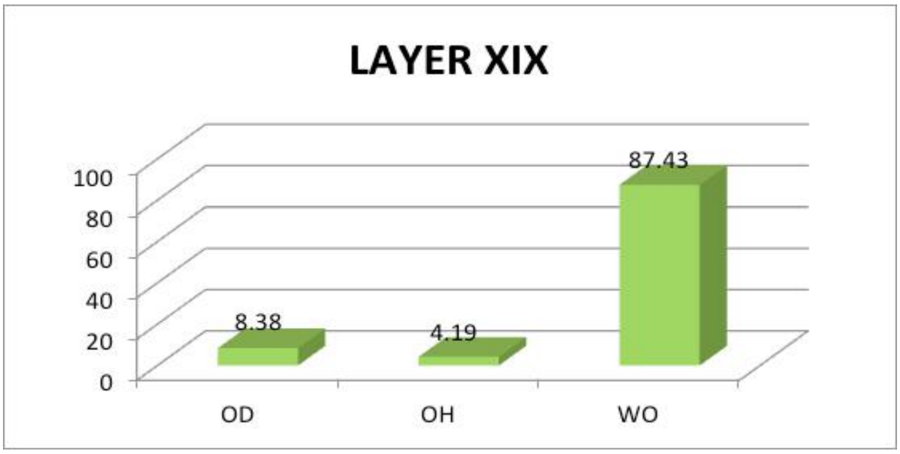


**Figure 3.2.6.** Distribution of small mammals from layer XIX of Cova Bonica according to their habitat preferences. We divided the habitats into four categories: OD (Open dry meadow), OH (Open Humid meadow) and WO (Woodland).

The results of the MER (Mutual Ecogeographic Range) analysis by means of the small-mammal intersections provides a mean annual temperature (MAT) of 11.9 ºC, 3.7 ºC lower than nowadays (15.6 ºC), a mean temperature of the warmest month (MTW) of 19.7 ºC, 3.8 ºC lower than nowadays (23.5 ºC) and finally a mean temperature of the coldest month (MTC) of 4.3 ºC, 4.4 ºC lower than nowadays (8.7 ºC). On the other hand, the MAP (mean annual precipitation) is 843 mm, 215 mm higher than nowadays (628 mm) (Table.3.2.3).

| | LAYER XIX | | | | |
|---|---|---|---|---|---|
| | MEAN | MAX | MIN | SD | |
| MAT (°C) | 11.9 | 15 | 7 | 2.5 | -3.7 |
| MTC (°C) | 4.3 | 8 | 1 | 1.7 | -4.4 |
| MTW (°C) | 19.7 | 23 | 16 | 2.0 | -3.7 |
| MAP (mm) | 843 | 1000 | 700 | 153 | 215 |

**Table.3.2.3**. Relation of temperatures and precipitation obtained using the MER (Mutual Ecogeographic Range) method of layer XIX. MAT: mean annual temperature; MTC: mean temperature of the coldest month; MTW: mean temperature of the warmest month; MAP: mean annual precipitation; 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; Δ: difference between the current mean for Vallirana (climate-data.org) and that obtained for the small mammals.

When we compare the precipitation and the temperatures with the Rainfall Index of *Lang*, it indicates semi-humid conditions (L=71). Whereas, the Continentality index of *Gorczynski*, indicates Oceanic climate (Ic=20) and nowadays this climate is the characteristic in Vallirana. The chorotypes analysis shows that the generalist species (CH-3) were the most represented species (74.87%), and the Mediterranean species (CH-4) represent the 18.32 %, while the Euro-Siberian species (CH-1) represents 6.81 % of the assemblage (Fig.3.2.7).

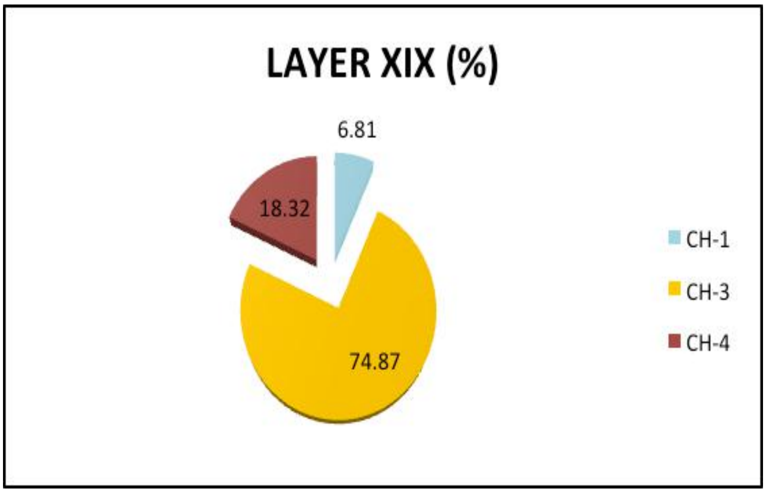


**Figure 3.2.7**. Chorotypes percentage of layer XIX. Representation of the chorotypes: CH-1 (chorotype 1, Euro-Siberian species), CH-3 (chorotype 3, Generalist species), CH-4 (chorotype 4, Thermo-mediterranean species).

### 3.2.2. DISCUSSION: Cova Bonica

#### Layer IV (Middle Holocene)

Around 8200 yr BP, occurred a cold event (Mercuri et al., 2011), characterised by cooler temperatures in polar regions (Mayewski et al., 2004) and drier conditions in mid to low latitudes (González-Sampériz et al., 2009; Gómez-Paccard et al., 2013). After this cold climatic event, the cores of the North Atlantic Ocean indicate warm temperatures from ca. 8000 to 5000 yr BP (Steig et al., 2009). In the Iberian Peninsula, warm and wet climatic conditions also were documented at that period (Tarroso et al., 2014).

In the layer IV (7401-7308 cal BP) of Cova Bonica, the temperatures obtained with the MER (Mutual Ecogeographic Range) shows mild climatic conditions. The MAT of this layer is 11.4 ºC, 4.2 ºC lower than nowadays and the MTC is 3.8 ºC, almost 5 ºC below current data in Vallirana meteorological station (Table. 3.2.3). Leira (2005) point, in 7300 cal BP, a time of transition from the cold conditions of the previous event to a warm and humid climate. This event could indicate that temperatures were still mild-warm at this time, because we have found *Iberomys cabrerae* (Table.3.2.1), whose requirements are strictly Mediterranean. We have also calculated the Continentality index. This index is a result of the impact of climatic elements such as temperature, precipitation, solar radiation and cloudiness (Mikolášková, 2009). The Continentality index obtained in this case (Ic=21) indicates a value which is between a climate with oceanic influence (Ic=11-21) and one with continental influence (Ic=21-66), and moreover, the chorotypes analysis shows a predominance of generalist species (74.64 %) (Fig.3.2.5), others indicators that occurs in climatic transition moment.

Besides, the MAP obtained with MER analysis are 907 mm, 279 mm higher than current data in Vallirana meteorological station (Table.3.2.2) and the results of the Rainfall index show semi-humid (L=79) conditions. Since 11000-7000 yr BP, have been detected a humid phase with pollen analysis in Sierra Nevada (south Iberian Peninsula) (Pérez-Olbiol et al., 2010) and in western Mediterranean of Iberian Peninisula (Jiménez-Moreno et al., 2012).

On the other hand, environmental data obtained from Habitat Weighting suggest a high predominance of Woodland formations (74.64 %) (Fig.3.2.4). The recovery of temperatures after the cold event, observed in other areas of the Iberian Peninsula shows a great development of forest masses (Muñóz-Rodrigo et al., 2005, Carrión et al., 2010 and Pérez-Sanz et al., 2013). This elevated value of "Woodland" is mainly due to the high percentage of *Apodemus sylvaticus* (54.77%) (Table.3.2.1).

Some data in this layer indicate that the human presence in this moment in Cova Bonica is sporadic, in this layer have been found burials with human remains (Olalde et al., 2015). The small-mammal assemblage shows a high diversity in this layer (0.66), and a low percentage of synanthropic species (20.72%), i.e. species that are adapted to conditions created or modified by human activities (Mistrot, 2000). Besides, five species of chiropters have been identified of which species should be noted the high representation of *Myotis myotis-blythii* (63 MNI) (Table.3.2.1), the presence of this taxa is indicative of a probably bat colony and bats do not cohabit with humans (Cuenca-Bescós et al., 2008). These data support a sporadic presence human at the precise moment of the burials.

**Layer XIX (Late Holocene)**

The MER analysis of this layer (4835 - 4711 cal BP) shows mild temperatures when we compared with current data and low precipitation when we compared with the value of layer IV of this same site. Especially the MAT 3.7 ºC are lower than nowadays and the MAP is 64 mm is lower than layer IV (Table.3.2.3), and also the presence of *Iberomys cabrerae* (Table.3.2.1), indicates that the temperatures are not very low, because their climatic requirements are strictly Mediterranean. Therefore, we may be at a time of transition between the "Holocene Climate Optimum" characterised by stable climate and higher precipitation and the aridification phase described from 5.5 000 kal BP to present in the North of Iberian Peninsula (Pérez-Olbiol et al ., 2010; Pérez-Sanz et al., 2013).

After the expansion of the woodland with "Holocene Climate Optimum" (Pérez-Sanz et al., 2013), from 5000-4800 BP the Iberian Peninsula landscape suffers big changes produced mainly by anthropic pressure on the environment, as the arboreal pollen reduction and the intensification in the anthropic fire regime (Santos et al .,2000; López-Merino et al., 2012), but the pressure starts in the lower areas and later in mountainous areas (Carrión et al., 2010a, Tarroso et al., 2014). However, the obtained results from Habitat Weighting indicate that at this time around the cavity, the woodland covers practically the entire landscape (87.43%) (Fig.3.2.6).

Moreover, the index of diversity is low (0.55) and the index of synanthropic species is low

(23.56%) too (Table.3.6), these data indicate a lower human presence in the cavity. This could be due to the drop in the temperatures in Cova Bonica, that moves humans to lower areas and this abandonment could cause forest recovery, as happened in other areas of the Iberian Peninsula, as in nothwestern (López and López, 1993). Another aspect to consider is the presence of *Mus spretus* in this layer. *Mus spretus* is a synanthropic species; his arrival in Europe is related with the agricultural expansion (Palomo et al., 2009) and prefers the agricultural land to live. However, in this layer the percentage of this species is lower (2.09 %) and the percentage of *Apodemus sylvaticus*, that prefer untilled soils (Tarjuelo et al., 2010; Noguerales, 2013), is very high (68.06%). These data could also show that the human pressure at the landscape is low.

In this layer of Cova Bonica, which is part of the Late Holocene (4711-4835 cal BP), we have the first appearance of *Mus spretus* in the northern Iberian at Neolithic period. In the Iberian Peninsula, the first mentions of *Mus spretus* are in the Iberian Levant from the Neolithic layers Bolumini cave (Beniarbeig, Alicante)(6950-5350 cal BP) and Cendres cave (Teulada, Alicante) (5593-5386 cal BP) (Guillem-Calatayud, 1999). Afterwards in the Bronze Age appears widespread in more sites, such as Cova 120 (Girona) (3190 cal BP) (Alcalde, 1986), Rafal Rubí (Menorca) (3450-3350 cal BP), La Encantada (Ciudad Real) ( 3530-3490 cal BP) and Cuesta del Negro (Granada) (3350 cal BP) (Morales Muñiz et al 1995).

### 3.2.3. CONCLUSIONS

At the Early Neolithic (7401-7308 cal BP) of Cova Bonica the palaeoclimatic conditions obtained shows weather conditions similary than nowadays, where found *Iberomys cabrerae*, whose requirements are strictly Mediterranean. Concretely, the MER method indicated mild-warm temperatures and detected a humid phase, characteristics of a climate between with oceanic influence and with continental influence.

The recovery of temperatures after the cold event of 8.2 cal BP and the humid conditions favoured a great development of woodland. This elevated value in “Woodland” fomrations is mainly due to a high percentage of *Apodemus sylvaticus*.

Moreover, a high diversity in this layer, a low percentage of synanthropic species and the presence of five species of chiropters indicate a low human presence at this moment (7401-7308 cal BP) in Cova Bonica.

At the Late Neolithic (4835 - 4711 cal BP), the MER analysis shows mild temperatures and low precipitation. Moreover, at this layer have been registered the presence of *Iberomys cabrerae*, whose requirements are strictly Mediterranean. For this reason, the Layer XIX of Cova Bonica shows that, had climatic characteristic of the aridification phase after “Holocene Climate Optimum”.

From 4800-5000 cal BP the Iberian Peninsula landscape suffers big changes produced mainly by anthropic pressure on the environment, but the palaeoenvironmental data obtained from the small-mammals assemblage of the Layer XIX of Cova Bonica indicate that the woodland covers practically the surrounding landscape of the cavity.

Another aspect to consider is the first appearance of *Mus spretus* in the north Iberian at Neolithic period.

# 3.3. SITE DESCRIPTION: Balma del Gai

Balma de Gai is a rockshelter located at about 760 m a.s.l. in the left margin of the Gai ravine, in Moià (Barcelona, Spain) (Fig.3.3.1). The cavity is part of the high plateau of Moianés in the south-eastern margin of the Ebro basin. This plateau is composed by sandstone and calcareous of Eocene and Oligocene (García-Argüelles et al., 2010).

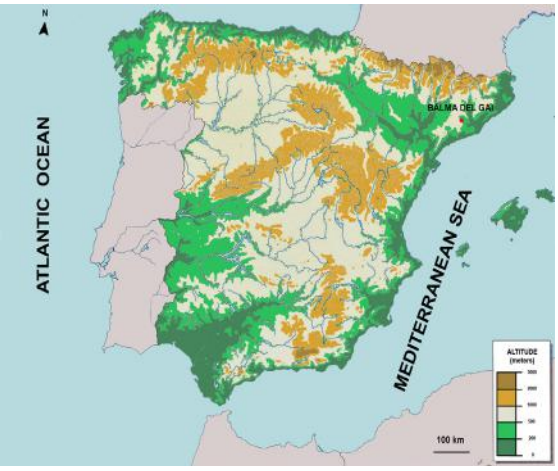


**Figure.3.3.1**. Location of Balma del Gai site in the Iberian Peninsula.

This site was discovered at 1974-1975 by Joan Surroca. In these years carried out small excavations. However, seemed that there were no sediment well preserved, with the exception of the most marginal areas of rockshelter. This was caused mainly by agricultural transformations, but also because it was built on the site a small stone house that had been transformed many times. During 1977 and 1978, a french-catalan team led by Miguel Llongueras and Jean Guilaine, conducted the first archaeological interventions. From these early interventions, numerous studies appeared in several specialized papers. In 1994, interventions carried out by members of the group SERP (*Seminari d'Estudis I Recerques Prehistòrics*) University of Barcelona, started and continued until 2014 (García-Argüelles et al., 2010).

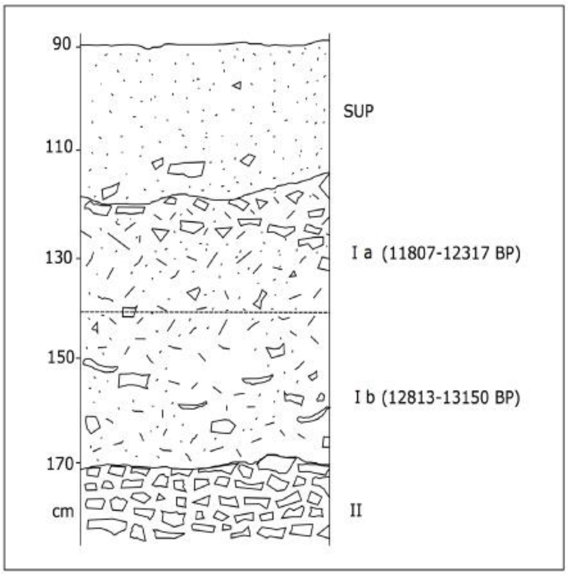


**Figure. 3.3.2.** Stratigraphy context of Balma del Gai and the radiocarbon dates (modified to Bergedá, 1998)

In the stratigraphy of the Balma del Gai, they have differentiated three geological layers: layer 2, layer 1 and a surface layer (Fig. 3.3.2):

Layer 2: composed of relatively large fragments of angular calcareous, without matrix between them. Its origin could be related to the weathering of the wall and roof of the rockshelter in a cold environment. This level could have its origin in the final phase of Pleistocene human occupation would have primary position.

Layer 1: consisting of fine sand and fragments of Rockshelter wall. It is the moment of maximum rockshelter occupancy by the Epipaleolithic hunters. This occupation has been divided into two facies, one would correspond to Epipaleolithic microlaminar (Layer 1B) (13150-12813 cal BP) and another to the geometric Epipaleolithic (Layer 1A) (10189-9786 cal BP) of Filador type (Fortea, 1973; García-Argüelles et al., 2010) (Fig.3.3.2). This distinction has been made from the lithic typology and datings performed (Fig.3.3.3).

Surface layer: consists of silty sands and presents many current and subactual biological activities. This level presents Epipaleolithic materials mixed with prehistoric and historic material culture.

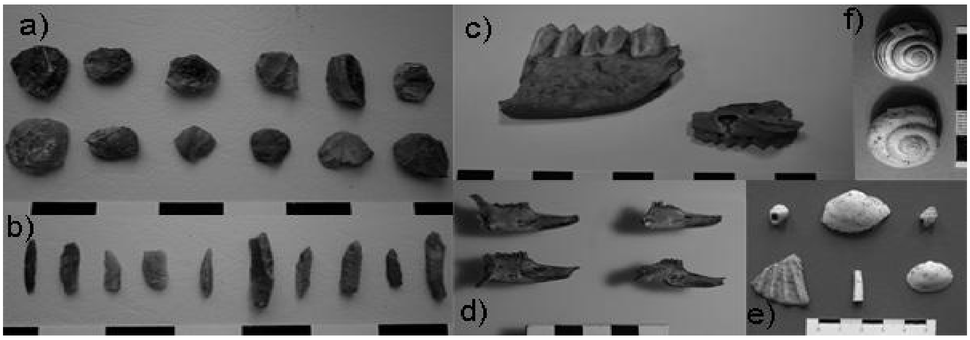
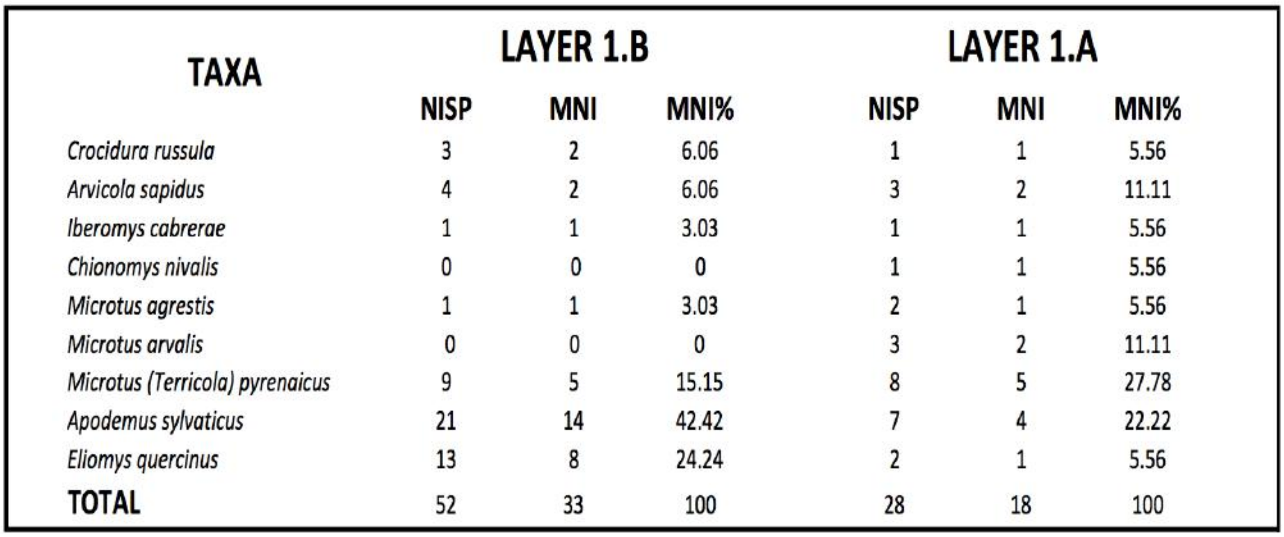


**Figure 3.3.3.** Archaeological material: a) and b) lithic artefacts; c) large mammals; d) mandibules of rabbit; e) marine malacofauna, and f) terrestrial malacofauna.

There are numerous studies that have been conducted on materials from the Balma of Gai. Furthermore, these studies cover a variety of disciplines: Malacology (Estrada et al., 2004, 2010), raw materials (Mangado and Nadal, 2006), lithic assemblages (García-Argüelles et al., 2009a, 2009b), Zooarcheology (Nadal et al., 2003, 2005), charcoals (Allué et al., 2007), pollen, seeds and phitolits (Estrada et al., 2011, García-Argüelles et al., 2010).

### 3.3.1. RESULTS

The analysed small mammals of Balma del Gai, belong to layer 1.B and layer 1.A. From these layers, 80 remains (NISP) have been identified, with a minimum number of individuals (MNI) of 51. Nine small-mammal taxa have been identified (APPENDIX 1): *Crocidura russula*, *Arvicola sapidus*, *Iberomys cabrerae*, *Chionomys nivalis*, *Microtus arvalis*, *Microtus agrestis*, *Microtus (Terricola) pyrenaicus*, *Apodemus sylvaticus* and *Eliomys quercinus* (Table. 3.3.1).



| TAXA | LAYER 1.B | | | LAYER 1.A | | |
|---|---|---|---|---|---|---|
| | NISP | MNI | MNI% | NISP | MNI | MNI% |
| *Crocidura russula* | 3 | 2 | 6.06 | 1 | 1 | 5.56 |
| *Arvicola sapidus* | 4 | 2 | 6.06 | 3 | 2 | 11.11 |
| *Iberomys cabrerae* | 1 | 1 | 3.03 | 1 | 1 | 5.56 |
| *Chionomys nivalis* | 0 | 0 | 0 | 1 | 1 | 5.56 |
| *Microtus agrestis* | 1 | 1 | 3.03 | 2 | 1 | 5.56 |
| *Microtus arvalis* | 0 | 0 | 0 | 3 | 2 | 11.11 |
| *Microtus (Terricola) pyrenaicus* | 9 | 5 | 15.15 | 8 | 5 | 27.78 |
| *Apodemus sylvaticus* | 21 | 14 | 42.42 | 7 | 4 | 22.22 |
| *Eliomys quercinus* | 13 | 8 | 24.24 | 2 | 1 | 5.56 |
| **TOTAL** | 52 | 33 | 100 | 28 | 18 | 100 |

**Table.3.3.1.** Distribution of the small-mammal remains of Balma del Gai by Layer 1.B and Layer 1.A. Number of identified specimens (NISP), Minimum number of individuals (MNI) and the percentage of minimum number of individuals (MNI%).

### Layer 1.B (Latest Pleistocene)

In this layer have been studied 52 remains (NISP) and have been identified a minimum number of individuals (MNI) of 33, belong to seven small-mammal taxa (APPENDIX 1): *Crocidura russula*, *Arvicola sapidus*, *Iberomys cabrerae*, *Microtus agrestis*, *Microtus (Terricola) pyrenaicus*, *Apodemus sylvaticus* and *Eliomys quercinus*; and the most represented taxa is *Apodemus sylvaticus* (42.42%) (Table. 3.3.1).The percentage of synanthropic species in this layer is low (33.33%) and the Simpson index indicates a high diversity (0.73).

The palaeoenvironmental reconstruction, indicates a predominance of wooded grounds (68.18 %). Besides the woodland, a variety of landscapes have been observed "Open Humid meadow" (22.73 %) which indicates evergreen meadowland with pastures and dense topsoil, "Open Dry meadow" (3.03 %) which consists of meadowland subject to seasonal climate change and "Water"(6.06 %) areas along streams, lakes and ponds (Fig.3.3.4).

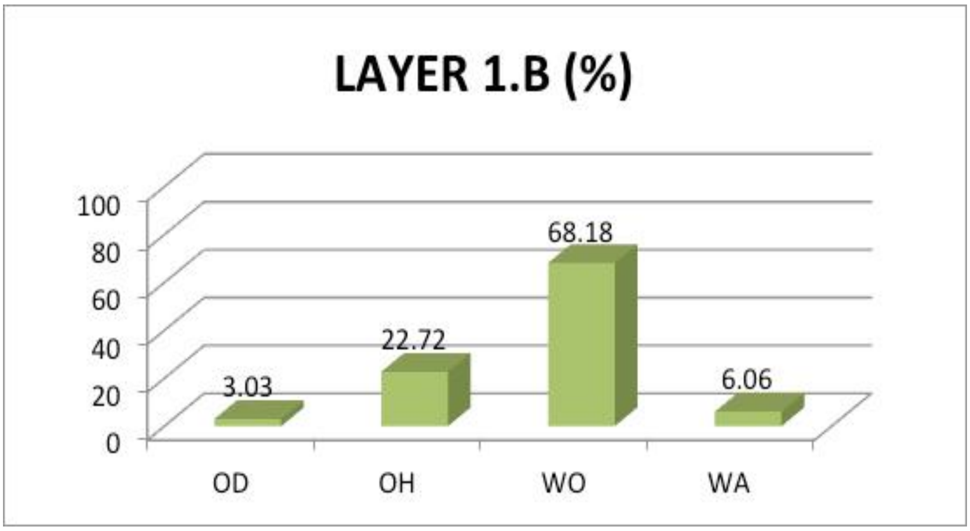
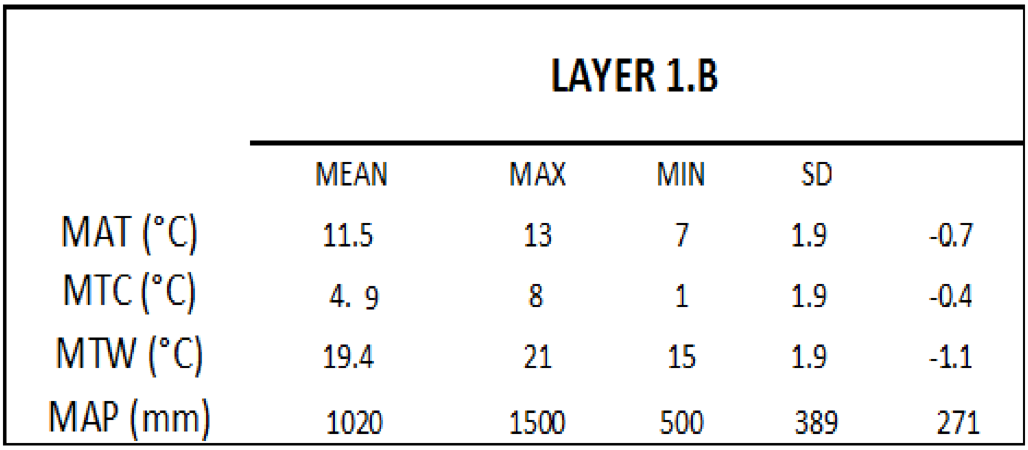


**Figure 3.3.4.** Distribution of small mammals from the layer 1.A of Balma del Gai according to their habitat preferences. We divided the habitats into four categories: OD (Open Dry meadow), OH (Open Humid meadow), WO (Woodland) and WA (Water).

The palaeoclimate obtained results are very similar than current climatic data of Moia (Climate-data.org). The mean annual temperature (MAT) is 11.5 ºC, 0.75 % lower than nowadays (12.3 °C), the mean temperature of the warmest month (MTW) is 19.4 ºC, 1.15 ºC lower than nowadays (20.6°C) and finally the mean temperature of the coldest month (MTC) is 4.9 ºC, 0.4 ºC lower than nowadays (5.3 °C) (Table.3.3.2). The Continentality index of *Gorczynski*, indicates that these climatic conditions are typically of Oceanic climate (Ic=17). On the other hand, the MAP (mean annual precipitation) is 1020 mm, 271mm higher than nowadays (749 mm), and the Rainfall Index of *Lang*, indicates a semi-humid event (L =88).



| | LAYER 1.B | | | | |
|---|---|---|---|---|---|
| | MEAN | MAX | MIN | SD | |
| MAT (°C) | 11.5 | 13 | 7 | 1.9 | -0.7 |
| MTC (°C) | 4. 9 | 8 | 1 | 1.9 | -0.4 |
| MTW (°C) | 19.4 | 21 | 15 | 1.9 | -1.1 |
| MAP (mm) | 1020 | 1500 | 500 | 389 | 271 |

**Table.3.3.2.** Relation of temperatures and precipitation obtained using the MER (Mutual Ecogeographic Range) method of layer 1.B. MAT: mean annual temperature; MTC: mean temperature of the coldest month; MTW: mean temperature of the warmest month; MAP: mean annual precipitation; 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; Δ: difference between the current mean for Moià (climate-data.org) and that obtained for the small mammals.

The chorotypes analysis shows that the most represented species (66.67%) were the generalist species (CH-3), the Euro-Siberian species (CH-1) represents 18.18 %, and the Mediterranean species (CH-4) represent the 15.15 % of the assemblage (Fig.3.3.5).

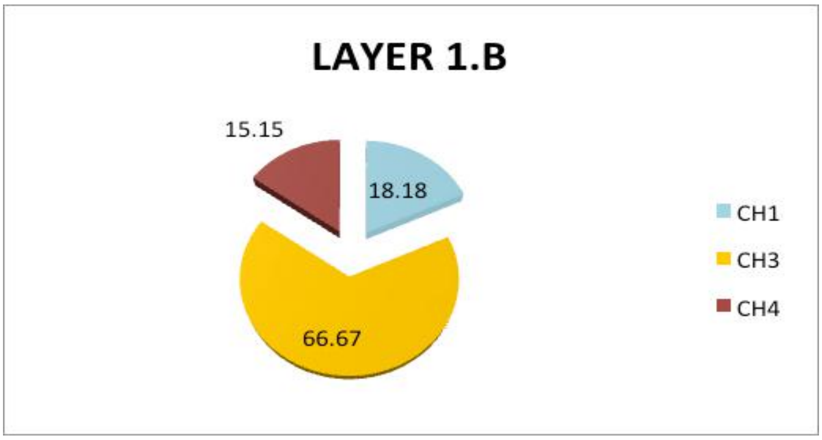


**Figure 3.3.5**. Percentage of chorotypes at layer 1.B of Balma del Gai. Representation of the chorotypes: CH-1 (chorotype 1, Eurosiberian species), CH-3 (chorotype 3, Generalist species), CH-4 (chorotype 4, Thermo-Mediterranean species).

### Layer 1.A (Earliest Holocene)

In this layer have been studied 28 remains (NISP) and have been identified a minimum number of individuals (MNI) of 18, belong to nine small-mammal taxa (APPENDIX 1): *Crocidura russula*, *Arvicola sapidus*, *Iberomys cabrerae*, *Chionomys nivalis*, *Microtus arvalis*, *Microtus agrestis*, *Microtus (Terricola) pyrenaicus*, *Apodemus sylvaticus* and *Eliomys quercinus* (Table.3.3.1). This assemblage presents a very high (0.84) diversity (*Simpson index*) and a low percentage (22.22%) of species that are adapted to conditions created or modified by human activities (synanthropic species).The most represented taxa is *Microtus (Terricola) pyrenaicus* (27.78%).

In order to reconstruct the environment, the method of habitat weightings shows a predominance of “Woodland” (52.78%), namely ranges from leafy forests to woodland margins, with moderate vegetation cover, but also indicate a high variety of landscape closely to the rockshelter. “Open Humid meadow” (22.22 %) which indicates evergreen meadowland with pastures and dense topsoil, “Open Dry meadow” (8.33 %) which consists of meadowland subject to seasonal climate change, “Rocky” (5.56 %) refer to rocky habitats without vegetation cover and “Water” (11.11 %) areas along streams, lakes and ponds (Fig.3.3.6).

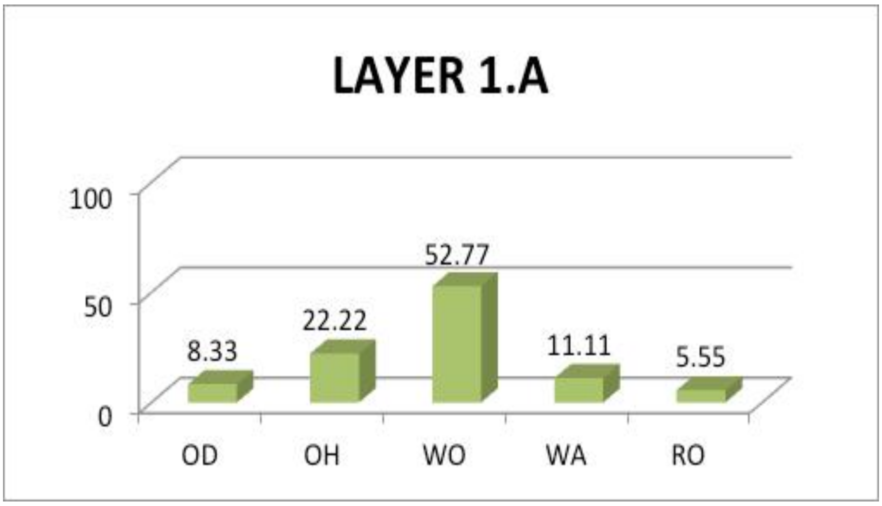
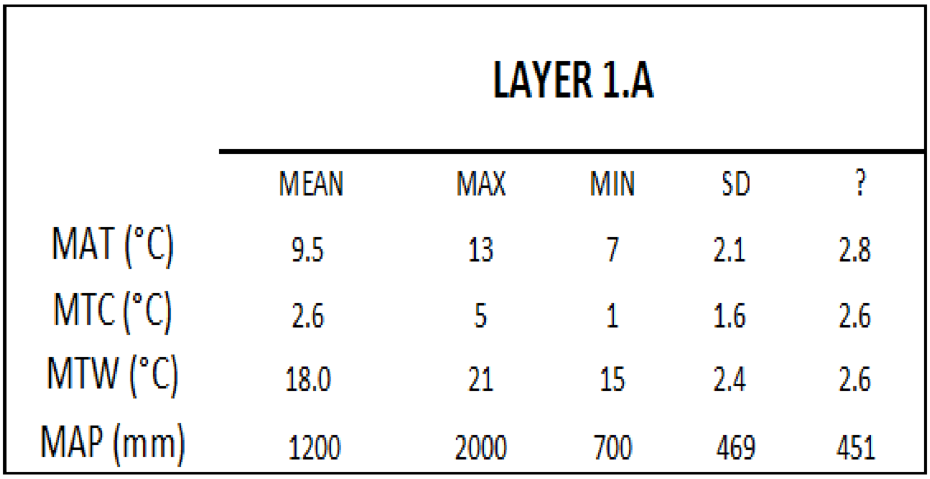


**Figure 3.3.6**. Distribution of small mammals from the layer 1.A of Balma del Gai according to their habitat preferences. We divided the habitats into four categories: OD (Open Dry meadow), OH (Open Humid meadow), WO (Woodland) ,WA (Water) and RO (Rocky).

The results of the MER (Mutual Ecogeographic Range) analysis by means of the small-mammal intersections provides a mean annual temperature (MAT) of 9.5 ºC, 2.8 ºC lower than nowadays

(12.3°C), a mean temperature of the warmest month (MTW) of 18 ºC, 2.6 ºC lower than nowadays (20.6 °C) and finally a mean temperature of the coldest month (MTC) of 2.7 ºC, 2.6 ºC lower than nowadays (5.3°C). On the other hand, the MAP (mean annual precipitation) is 1200 mm, 451 mm higher than nowadays (749 mm) (Table.3.3.3). Comparing the precipitation and the temperatures with the Rainfall Index of *Lang*, it indicates humid conditions (L =126), whereas, the Continentality index of *Gorczynski*, indicates Oceanic climate (Ic =19) equal to nowadays.



LAYER 1.A

| | MEAN | MAX | MIN | SD | ? |
|---|---|---|---|---|---|
| MAT (°C) | 9.5 | 13 | 7 | 2.1 | 2.8 |
| MTC (°C) | 2.6 | 5 | 1 | 1.6 | 2.6 |
| MTW (°C) | 18.0 | 21 | 15 | 2.4 | 2.6 |
| MAP (mm) | 1200 | 2000 | 700 | 469 | 451 |

**Table.3.3.3**. Relation of temperatures and precipitation obtained using the MER (Mutual Ecogeographic Range) method of layer 1.B. MAT: mean annual temperature; MTC: mean temperature of the coldest month; MTW: mean temperature of the warmest month; MAP: mean annual precipitation; 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; Δ: difference between the current mean for Moià (climate-data.org) and that obtained for the small mammals.

The chorotypes analysis shows that the Euro-Siberian taxa (CH-1) were the most represented species (50%), and the Mediterranean species (CH-4) represent the 22.22 %, while the generalist species (CH-3) represents 27.78 % of the assemblage (Fig.3.3.7).

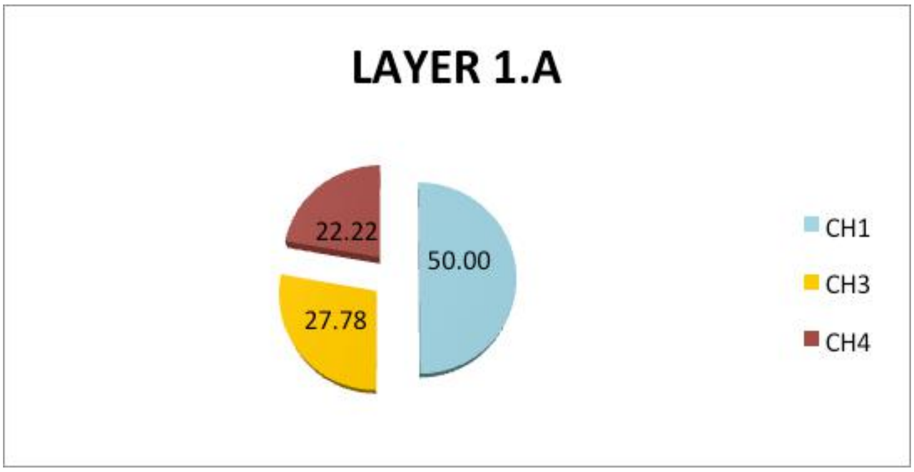


**Figure 3.3.7**. Percentage of chorotypes at layer 1.A of Balma del Gai. Representation of the chorotypes: CH-1 (chorotype 1, Eurosiberian species), CH-3 (chorotype 3, Generalist species), CH-4 (chorotype 4, Thermo-Mediterranean species).

## 3.3.2. DISCUSSION : Balma del Gai

### Layer 1.B (Latest Pleistocene)

The results obtained from small-mammals study, indicate warm and humid climatic conditions. The radiocarbon dates obtained(13150-12813 cal BP) have allowed us to place, these climatic conditions during Bølling–Allerød interstadial that is overall a relatively warm period (García-Alix et al., 2014). The MER (Mutual Ecogeographic Range) analysis shows temperatures very similar to current data. The mean annual temperature (MAT) obtained belong to small mammals is 11.5 ºC, only 0.75 ºC lower than nowadays (12.3 ºC) (Table.3.3.2). Moreover, the continentality index of *Gorczynski* indicates an Oceanic Climate (Ic =17) as the Köppen-Geiger classification of Moia climate (Cfb) (Climate-data.org).

Pollen data of western Mediterranean region shows temperature and precipitation values comparable to those of the Holocene and the development of the forest during the entire Bølling–Allerød (Fletcher et al.,2010). The Habitat Weighting allow us to observe a high percentage of woodland (68.18%) in detriment of open areas, (36.36 %) (Fig.3.3.4). The most abundant species in this layer are *Apodemus sylvaticus* (42.42%) and *Eliomys quercinus* (24.24%) (Table.3.3.1).

### Layer 1.A (Earliest Holocene)

The warm conditions detected during the Bølling-Allerød were truncated by a short but very cold period, the Younger Dryas. The chorotypes analysis shows that the most represented chorotype is CH-1 (50%), namely Euro-Siberian species (Fig.3.3.7) and the most abundant species is *Microtus (Terricola) pyrenaicus* (27.78%). However, the presence of *Iberomys cabrerae*, although is scarce (Table.3.3.1), indicates that this cool conditions are not very harsh yet, because this arvicolinae is a strictly thermo-mediterranean species. Besides, the MER (Mutual Ecogeographic Range) analysis shows cool temperatures, the MAT are 2.8 ºC lower than nowadays (12.3 °C) (Table.3.3.3). The dry climate regime recorded at the beginning of the Younger Dryas was gradually substituted by wet conditions (Baldini et al., 2015; Bartolomé et al., 2015; Oliva et al., 2016), and these conditions are similar those obtained with our small-mammals data. The MER indicates a mean annual precipitation of 1200 mm, 451 mm higher than current data (749 mm)(Climate-data.org) (Table.3.3.3), and Rainfall Index shows “humid” conditions (L =126). Moreover, the sedimentology analysis indicates a humid and cool event too, with the presence of fine sand with fragments of wall shelter (Bergedà, 1998)

The Younger Dryas period is characterized by the decrease of *Pinus sylvestris* in Iberian Peninsula (Carrión et al., 2015). The decrease of *Pinus sylvestris* has been also observed from the anthracological analysis in Balma del Gai. In this case could be related to intensification of human occupations which it had caused the vegetal biomass reduction for the fuel exploitation of the immediate environment (Allué et al., 2007). The Habitat Weighting analysis shows a reduction of woodland lanscape (52.78%) respect to previous layer (66.67%), but not an important reduction (Fig.3.3.6). Despite, the Simpson index indicates a very high diversity (0.84), and it usually shows a low human impact. The most frequently cited explanations for patterns of elevational diversity relate climatic factors as a principal influence on trends in diversity (Lomolino, 2001; McCain, 2004). Moreover numerous continental records show high variability in the response of vegetation, which is not always synchronous (Cacho et al., 2010).

### 3.3.3. CONCLUSIONS

In Balma del Gai during the Latest Pleistocene (13150-12813 cal BP), we have detected the Bølling–Allerød interstadial. This period has been characterised by warm and humid climatic conditions through small-mammals assemblages. Moreover, the MER (Mutual Ecogeographic

Range) analysis shows temperatures very similar to current data, and the continentality index of *Gorczynski* indicates an Oceanic Climate (Ic =17) as the Köppen-Geiger classification of Moià climate (Cfb) (Climate-data.org), while the environment have been characterised by a high percentage in woodland formations.

These warm conditions detected during the Bølling-Allerød in Balma del Gai were truncated by the Younger Dryas, a short but very cold period. The MER (Mutual Ecogeographic Range) results of Layer 1.A (10189-9786 cal BP) shows cool temperatures. The chorotypes analysis show that the most represented species in the assemblage were Euro-Siberian species, but the presence of *Iberomys cabrerae*, species with requirements strictly thermo-Mediterranean, indicates cool conditions but not very harsh. Moreover, the mean annual precipitations are higher than nowadays data and the Rainfall Index indicates “humid” conditions. Despite, the Habitat Weighting analysis, shows a reduction of woodland (52.78%) respect to previous layer (66.67%), but not an important reduction. This reduction could be related with the human impact on the landscape, but low human pressure because the Simpson index indicates a very high diversity.

# 3.4. SITE DESCRIPTION: Grottina dei Covoloni del Broion

The Grottina dei Covoloni del Broion is a narrow cave located in the Colli Berici (Vicenza, North-Eastern Italy), at about 120 m a.s.l. (Fig.3.4.1). This site is inside calcareous massif of Lumignano valley, in the Longare village, and takes its name from the Broion village which is closer to the famous cave that represents the only investigated stratigraphic sequence recovered in the lowland Venetian area that covers the Latest Pleistocene and Early-Middle Holocene time span (Ligabue, 1973).

**Figure 3.4.1**. Location of Grottina dei Covoloni del Broion site in the Italian Peninsula.

At the bottom of the cave was located a small cave, where microliths were found in surface. This small cave ends in a small corridor (1.80 m) silted by heavy depositions of calcite leading to an inner chamber (3.40 x 1.70 m) communicating at one end with a small orthographic hall about 2 m, which even today is at ground level, during use would be found hanging on the wall. In 1973-74 and 1976-77 the University of Ferrara carried out the first excavations. During these fieldworks, eight stratigraphy levels dated from the late Pleistocene to the Copper Age were identified. The lowest layers (from 8 to 6) are composed of brownish yellow silt sediment rich in coarse clasts. Layers 7 and 6 contained respectively a Sauveterrian and Castelnovian lithic complex. A radiocarbon date for layer 6 is available: 7832-7686 cal BP (R-892) (Fig.3.4.2). The upper layers to 1 are characterized by heavy depositions of calcite and include human remains and material culture related to the use of the cave as burial site during the Copper Age. The layer 5 has few bones remains, whereas the layer 4 is composed by stalagmite plate up to 30 cm thick containing skeletal remains and cultural result of the funerary use of the cavity.

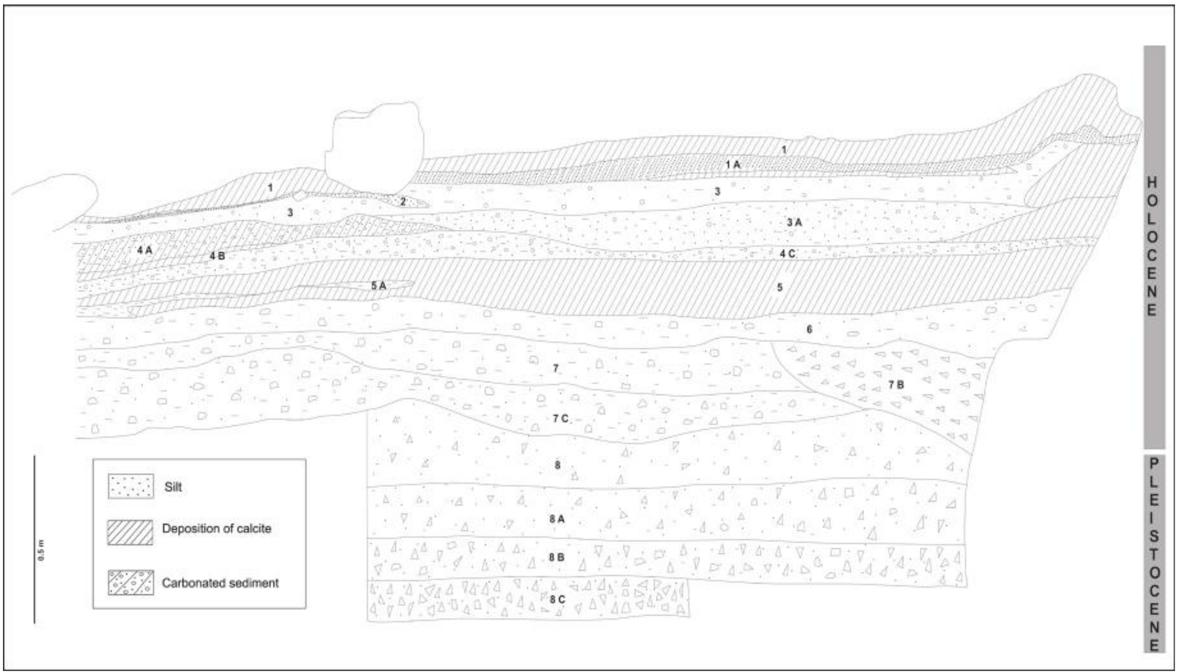


**Figure.3.4.2**. Stratigraphy and chronological position of Grottina dei Covoloni del Broion ( modified from Cattani, 1977).

All remains found on the inside of cave belonging to layer 4 are understood as part of the grave goods, are attributed to the 3rd millennium BC (Bagolini, 1984; Bianchin Citton and Guerreschi, 1988) among which are instruments made of flint, pottery and large mammals, as well as numerous human remains. These human remains are composed of bones and teeth under various conditions of conservation and distribution attributed about 40 individuals. Including adults of both sexes of different age groups and all anatomical regions are distinguished (Fig.3.4.3).

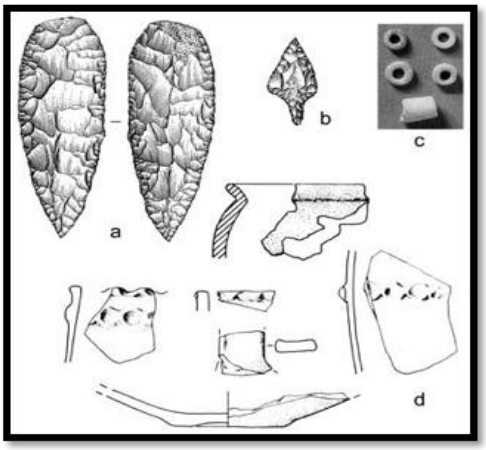


**Figure.3.4.3**. Archeological material of layer 4. A: flint blade; B: flint arrowhead; C: ornamental elements; D: fragment of pottery (Fedele and Guerreschi, 1976).

There have also been pollen studies at the entire sequence. The 8d level, pollen species found represents the padano climate, with the presence of *Picea* or fir European common, soon disappears to make way for a discrete range of herbaceous of different environments (understory, meadow and marshland). On the other hand in layer 7c is observed a decline in tree pollen. From layer 7 to 5, the pollen indicates an arid environment with small wetter oscillations that favors the expansion of the forest. Already the layers 4a-4c were sterile, and the remains belonging to the layer 6 are scarce, but the other levels have allowed an approximate environmental and climatic approach (Cattani, 1977).

### 3.4.1. METHODOLOGY

In order to reconstruct the palaeoclimate, we used the Mutual Ecogeographic Range (MER) (Blain, 2005; Blain et al., 2007, 2009, 2010; Agustí et al., 2009; López-García et al., 2010a, Blain et al., 2016). The case of Grottina dei Covoloni del Broion is different, because there are no studies on the geographical distribution of species in the Italian Peninsula and we cannot use this method and we used the Bioclimatic Model (BM). This is a method for palaeoclimatic reconstruction built on the assumption that exists a significant correlation between climate and mammal community composition, but in the case of small mammals, especially those of rodents, have been considered as a suitable climatic indicator for qualitative and climatic reconstructions (Hernádez-Fernández, 2001).

Taking into account, the matrix of species for each location climates created by Hernádez-Fernández (2001), when the species inhabits this climatic zone the value is determined by Climatic Restriction Index (CRI), and the sum of the different kind of CRI equals to 1. This index corresponds to the following formula:

$$CRIi=1/n$$

n: the number of bioclimatic zones inhabited for each species

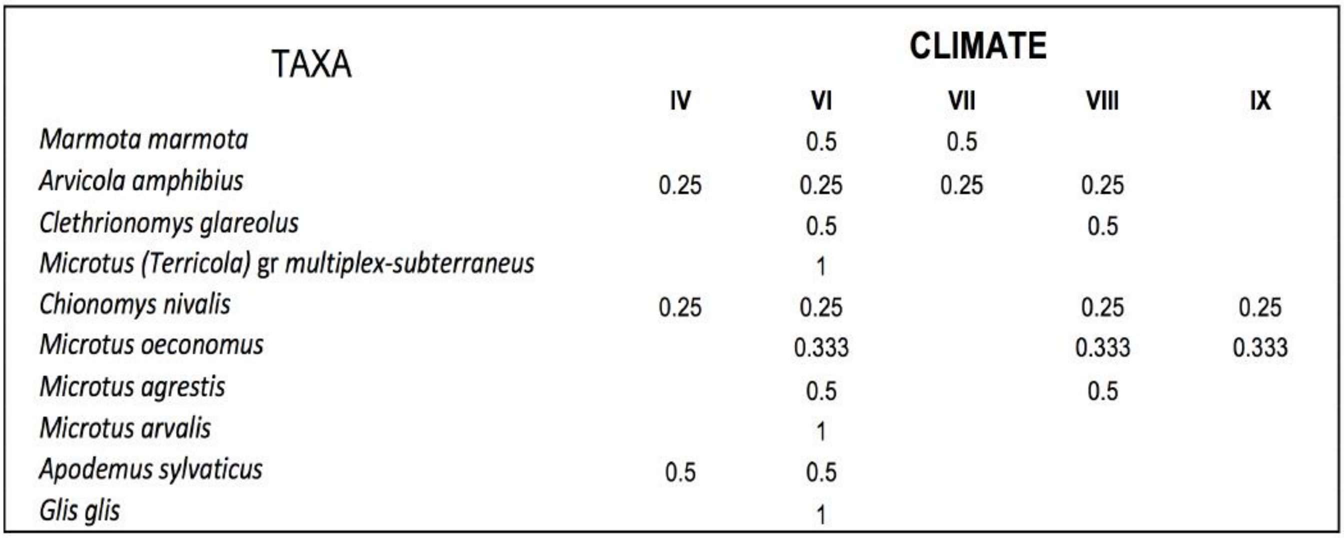
i: climate zone in which appears the species.

The number of climatic zones inhabited by one species is determined by the proportion of its geographic range. The criteria used for this climate allocation species were adopted after a preliminary chorologic examination of the species considered. In this study the term Bioclimatic Component (BC), which is the representation in a specific location of each of the ten existing climates, is used. The CRI of each species are calculated and placed in the corresponding BCs that species occupy. Each value of the BCs of the locality is calculated according to the following formula:

$$BCi = (\Sigma\ CRIi)\ 100/S$$

In this formula "i" is the climate zone "i" and "S" is the number of species in the locality.

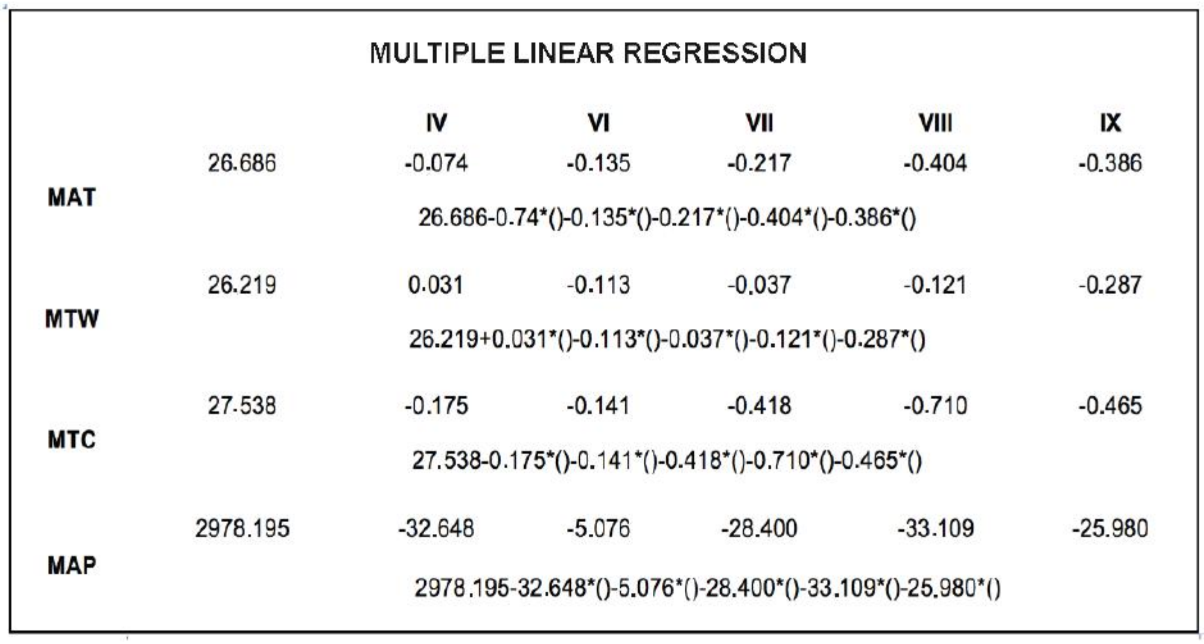
The group of values of the BCs of a locality are the bioclimatic spectrum. It could be considered that the value of each BC is the relative frequency of the species in the locality occupying the corresponding climate zone (Table.3.4.1).



| TAXA | CLIMATE | | | | |
|---|---|---|---|---|---|
| | IV | VI | VII | VIII | IX |
| *Marmota marmota* | | 0.5 | 0.5 | | |
| *Arvicola amphibius* | 0.25 | 0.25 | 0.25 | 0.25 | |
| *Clethrionomys glareolus* | | 0.5 | | 0.5 | |
| *Microtus (Terricola) gr multiplex-subterraneus* | | 1 | | | |
| *Chionomys nivalis* | 0.25 | 0.25 | | 0.25 | 0.25 |
| *Microtus oeconomus* | | 0.333 | | 0.333 | 0.333 |
| *Microtus agrestis* | | 0.5 | | 0.5 | |
| *Microtus arvalis* | | 1 | | | |
| *Apodemus sylvaticus* | 0.5 | 0.5 | | | |
| *Glis glis* | | 1 | | | |

**Table.3.4.1.** Distribution of rodents belongs to Grottina dei Covoloni del Broion to their climate preferences according to Hernández-Fernández (2001).

Taking into account the rodent assemblage of Grottina dei Covoloni del Broion, five of the ten different climates are represented: IV, *Subtropical* with winter rains and summer droughts; VI, *Typical temperate* with winters that are cold but not very long, but summers that are cool; VII, *Arid-temperate* with large temperature contrasts between winter and summer; VIII, *Cold-temperate* with cool summers and long cold winters (boreal) and IX, *Polar* with very low temperatures and very short summers (Hernádez-Fernández, 2001, Hernádez-Fernández et al 2007).



MULTIPLE LINEAR REGRESSION

| | | IV | VI | VII | VIII | IX |
|---|---|---|---|---|---|---|
| MAT | 26.686 | -0.074 | -0.135 | -0.217 | -0.404 | -0.386 |
| | | 26.686-0.74*()-0.135*()-0.217*()-0.404*()-0.386*() | | | | |
| MTW | 26.219 | 0.031 | -0.113 | -0.037 | -0.121 | -0.287 |
| | | 26.219+0.031*()-0.113*()-0.037*()-0.121*()-0.287*() | | | | |
| MTC | 27.538 | -0.175 | -0.141 | -0.418 | -0.710 | -0.465 |
| | | 27.538-0.175*()-0.141*()-0.418*()-0.710*()-0.465*() | | | | |
| MAP | 2978.195 | -32.648 | -5.076 | -28.400 | -33.109 | -25.980 |
| | | 2978.195-32.648*()-5.076*()-28.400*()-33.109*()-25.980*() | | | | |

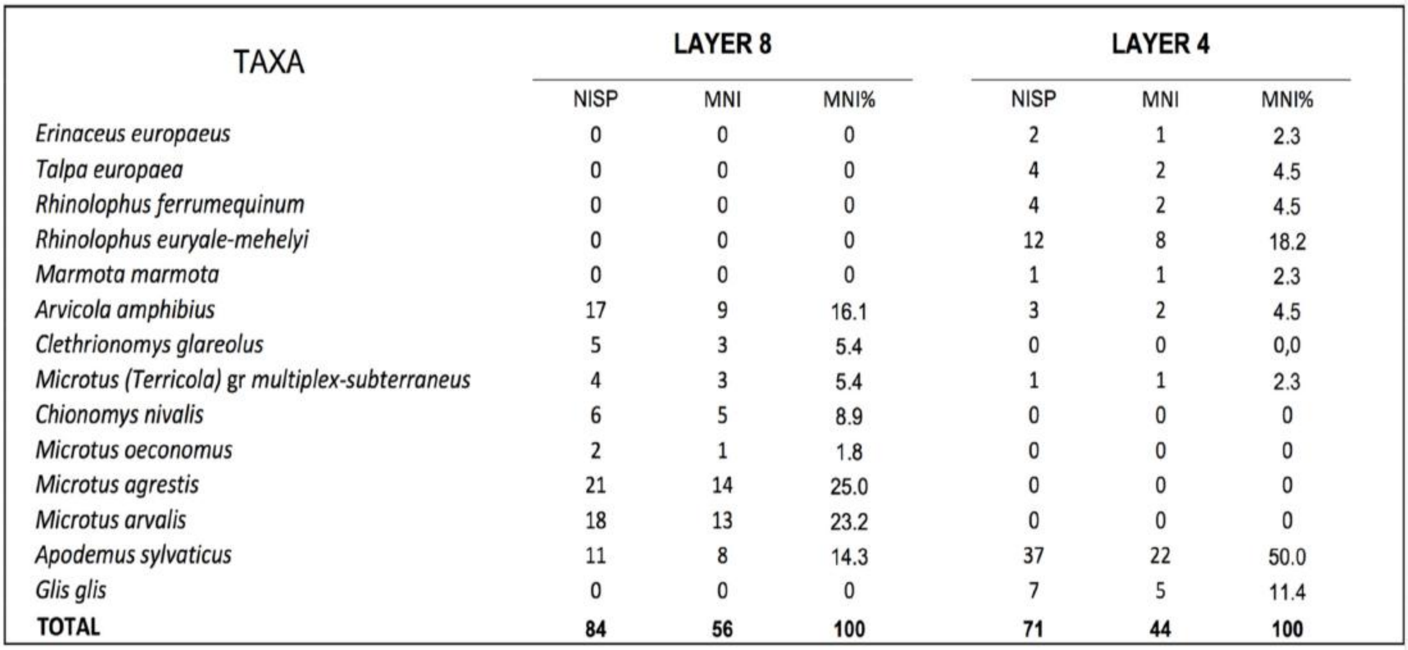
**Table 3.4.2.** Multiple Linear Regression formula according to the rodent assemblage of layer 8 and 4 (according to Hernádez-Fernández, 2001, Hernádez-Fernández et al., 2007).

Finally, we are able to estimate 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) with a multiple linear regression formula established by Hernádez-Fernández (2001, 2007) (Table. 3.4.2).

Moreover, these climatic data obtained from rodents have been compared with current climatic data from a location near the site, Longare, which has a MAT of 13.4ºC, a MTC of 2.9ºC, a MTW of 23.7ºC, and a MAP of 921 mm (Climate-data.org).

### 3.4.2. RESULTS

This study is focused on layers 8 (Latest Pleistocene) and layer 4 (Copper Age), because the others do not have yielded enough small mammals remains. We have studied 155 remains (NISP) with a total minimum number of individuals (MNI) of 100, and have been identified thirteen small mammal species (APPENDIX 1): *Erinaceus europaeus*, *Talpa europaea*, *Rhinolophus ferrumequinum*, *Rhinolophus euryale-mehelyi*, *Marmota marmota*, *Arvicola amphibius*, *Chionomys nivalis*, *Clethrionomys glareolus*, *Microtus (Terricola)* gr. multiplex*-subterraneus*, *Microtus oeconomus*, *Microtus agrestis*, *Microtus arvalis*, *Apodemus sylvaticus* and *Glis glis* (Table.3.4.3).



| TAXA | LAYER 8 | | | LAYER 4 | | |
|---|---|---|---|---|---|---|
| | NISP | MNI | MNI% | NISP | MNI | MNI% |
| *Erinaceus europaeus* | 0 | 0 | 0 | 2 | 1 | 2.3 |
| *Talpa europaea* | 0 | 0 | 0 | 4 | 2 | 4.5 |
| *Rhinolophus ferrumequinum* | 0 | 0 | 0 | 4 | 2 | 4.5 |
| *Rhinolophus euryale-mehelyi* | 0 | 0 | 0 | 12 | 8 | 18.2 |
| *Marmota marmota* | 0 | 0 | 0 | 1 | 1 | 2.3 |
| *Arvicola amphibius* | 17 | 9 | 16.1 | 3 | 2 | 4.5 |
| *Clethrionomys glareolus* | 5 | 3 | 5.4 | 0 | 0 | 0,0 |
| *Microtus (Terricola) gr multiplex-subterraneus* | 4 | 3 | 5.4 | 1 | 1 | 2.3 |
| *Chionomys nivalis* | 6 | 5 | 8.9 | 0 | 0 | 0 |
| *Microtus oeconomus* | 2 | 1 | 1.8 | 0 | 0 | 0 |
| *Microtus agrestis* | 21 | 14 | 25.0 | 0 | 0 | 0 |
| *Microtus arvalis* | 18 | 13 | 23.2 | 0 | 0 | 0 |
| *Apodemus sylvaticus* | 11 | 8 | 14.3 | 37 | 22 | 50.0 |
| *Glis glis* | 0 | 0 | 0 | 7 | 5 | 11.4 |
| **TOTAL** | **84** | **56** | **100** | **71** | **44** | **100** |

**Table.3.4.3.** Distribution of the small-mammal remains of Layer 8 and Layer 4. Number of identified specimens (NISP), Minimum number of individuals (MNI) and the percentage of minimum number of individuals (MNI%).

### Layer 8 (Latest Pleistocene)

In this layer, we have studied 84 remains (NISP) and 56 minimum number of individuals (MNI). We have identified, using the methods of systematic paleontology (APPENDIX 1), eight small mammal: *Arvicola amphibius*, *Chionomys nivalis*, *Clethrionomys glareolus*, *Microtus (Terricola)* gr. multiplex-*subterraneus*, *Microtus oeconomus*, *Microtus agrestis*, *Microtus arvalis* and *Apodemus sylvaticus*. The most represented taxa is *Microtus agrestis* (25% MNI) (Table.3.4.2). Moreover, the diversity has been measured using the Simpson index, and we can registered a very high diversity (0.82).

The palaeoenvironmental reconstruction shows the diversity of the habitats exists closed to the cave. The most represented habitat is the woodland (47.32%) and with higher percentage of Open Humid meadow (32.14%), "wet meadow" that indicates evergreen meadowland with pastures and dense topsoil. Finally, the Open Dry meadow habitat, meadowland subject to seasonal climate change, represents the 11.61 %, while the Rocky, habitats without vegetation cover, is the 8.93% of the total (Fig.3.4.4).

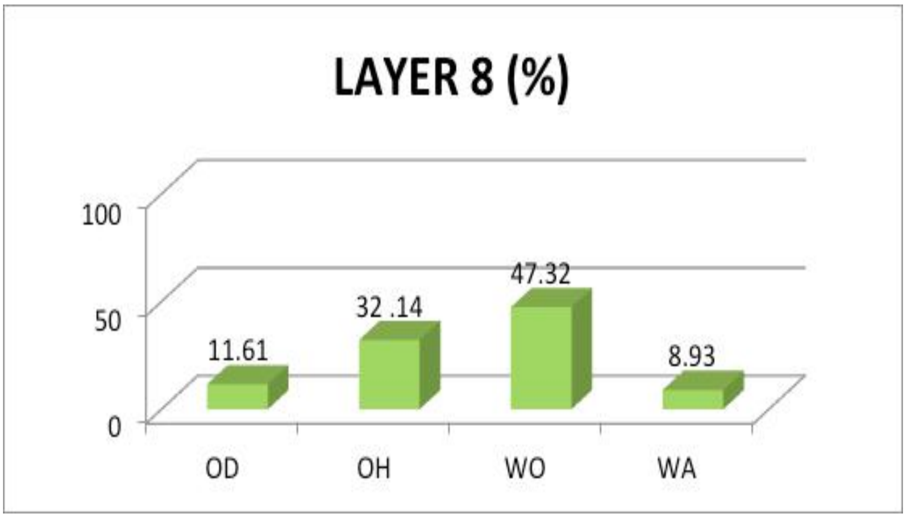
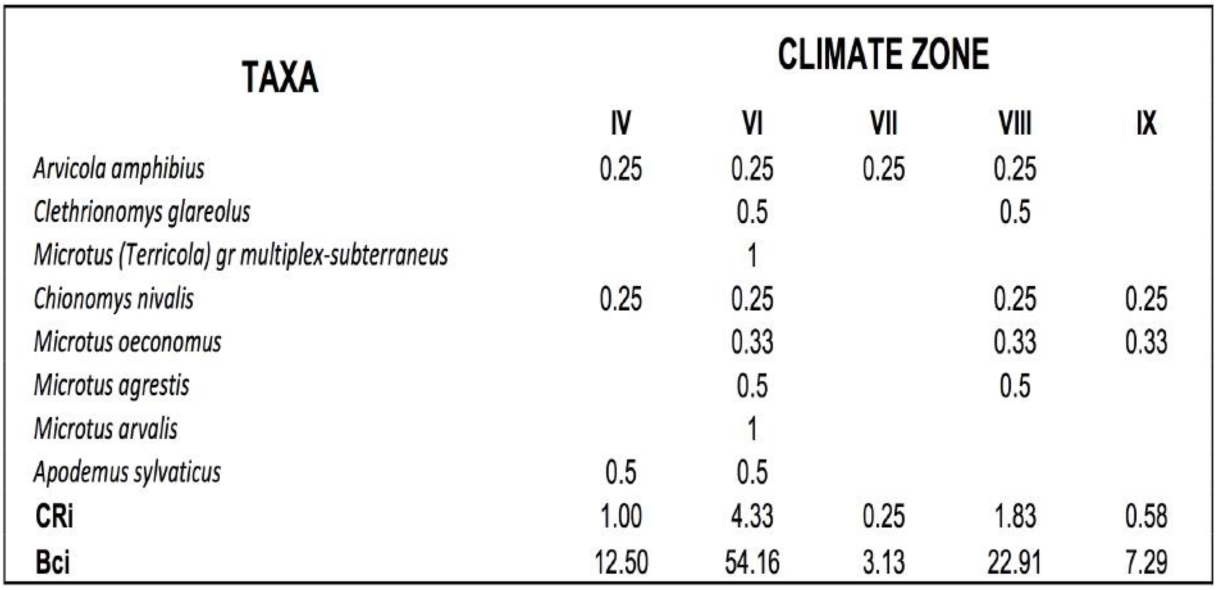


**Figure.3.4.4**. Distribution of small mammals according to their habitat preferences. We divided the habitats into four categories: OD (Open Dry meadow), OH (Open Humid meadow), WO (Woodland) and WA (Water).

The most represented bioclimatic zones is "VI" (54.16%), typical temperate climate and nemoral broadleaf-decidious forest and the second is "VIII" (22.91%), cold-temperate climate and boreal coniferous forest (Table.3.4.4).



| TAXA | CLIMATE ZONE | | | | |
|---|---|---|---|---|---|
| | IV | VI | VII | VIII | IX |
| *Arvicola amphibius* | 0.25 | 0.25 | 0.25 | 0.25 | |
| *Clethrionomys glareolus* | | 0.5 | | 0.5 | |
| *Microtus (Terricola) gr multiplex-subterraneus* | | 1 | | | |
| *Chionomys nivalis* | 0.25 | 0.25 | | 0.25 | 0.25 |
| *Microtus oeconomus* | | 0.33 | | 0.33 | 0.33 |
| *Microtus agrestis* | | 0.5 | | 0.5 | |
| *Microtus arvalis* | | 1 | | | |
| *Apodemus sylvaticus* | 0.5 | 0.5 | | | |
| **CRi** | 1.00 | 4.33 | 0.25 | 1.83 | 0.58 |
| **Bci** | 12.50 | 54.16 | 3.13 | 22.91 | 7.29 |

**Table.3.4.4**. Distribution of rodents belongs to layer 8 according to their habitat preferences.

The MAT (mean annual temperature) is 5.7 ºC, 7.7 ºC lower than nowadays (13.4 °C), the MTW(mean temperature of the warmest month) is 15.5º C, 8.2 ºC lower than nowadays (23.7 °C) and the MTC (mean temperature of the coldest month) is -3.2 ºC, 6.2 ºC lower than nowadays (2.9 °C). Whereas the MAP (mean annual precipitation) is 1258mm, 337 mm more than nowadays (921 mm) (Table.3.4.5).The Rainfall Index of *Lang*, indicates a very humid event (L =221) and the Continentality index of *Gorczynski*, indicates a continental climate (Ic =25).

| | MAT | MTW | MTC | MAP |
|---|---|---|---|---|
| **MEAN** | 5.7 | 15.5 | 3.2 | 1258 |
| Δ | 7.7 | 8.2 | 6.1 | 337 |

**Table.3.4.5**. Relation of temperatures and precipitation obtained using the Bioclimatic Model. MAT: mean annual temperature; MTC: mean temperature of the coldest month; MTW: mean temperature of the warmest month; MAP: mean annual precipitation; MEAN: mean of the values obtained; Δ: difference between the current mean for Longare (climate-data.org) and that obtained from the rodents of layer 8.

Moreover, the chorological test, indicates that the Euro-Siberian species (CH-1) represents the 83.36 %, and the generalist species (CH-3) represent the 19.64 % of the assemblage (Fig.3.4.5).

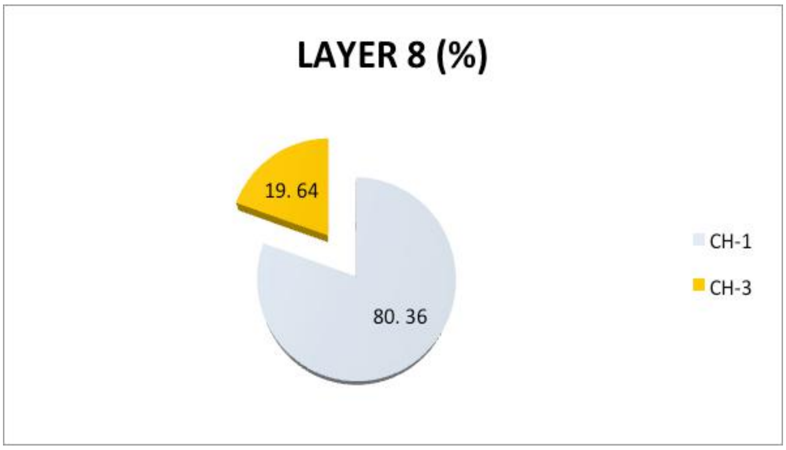


**Figure.3.4.5**. The chorotypes representation of layer 8: CH-1 (chorotype 1, Euro-Siberian species) and CH-3 (chorotype 3, Generalist species).

### Layer 4 (Copper Age)

In this layer, we have studied 71 remains (NISP) and 44 minimum number of individuals (MNI). We have identified, using the methods of systematic palaeontology (APPENDIX 1), nine small mammal: *Erinaceus europaeus*, *Talpa europaea*, *Rhinolophus ferrumequinum*, *Rhinolophus* *euryale-mehelyi*, *Marmota marmota*, *Arvicola amphibius*, *Microtus (Terricola)* gr. multiplex-*subterraneus*, *Apodemus sylvaticus* and *Glis glis*.The most represented taxa is *Apodemus sylvaticus* (50% MNI) (Table.3.4.3). Besides,we have registered a high diversity (0.70) using the Simpson index .

In this layer, the species related with the woodland landscape represents 78.41% of the assemblage. The others habitat represented are the Open Humid meadow (15.91%), that indicates evergreen meadowland with pastures and dense topsoil, and finally Open Dry meadow habitat, meadowland subject to seasonal climate change, represents the 5.68 % (Fig.3.4.6).

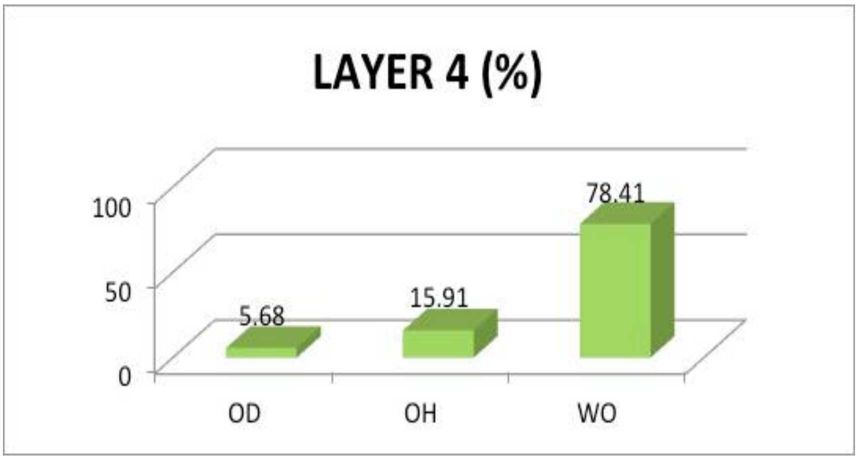
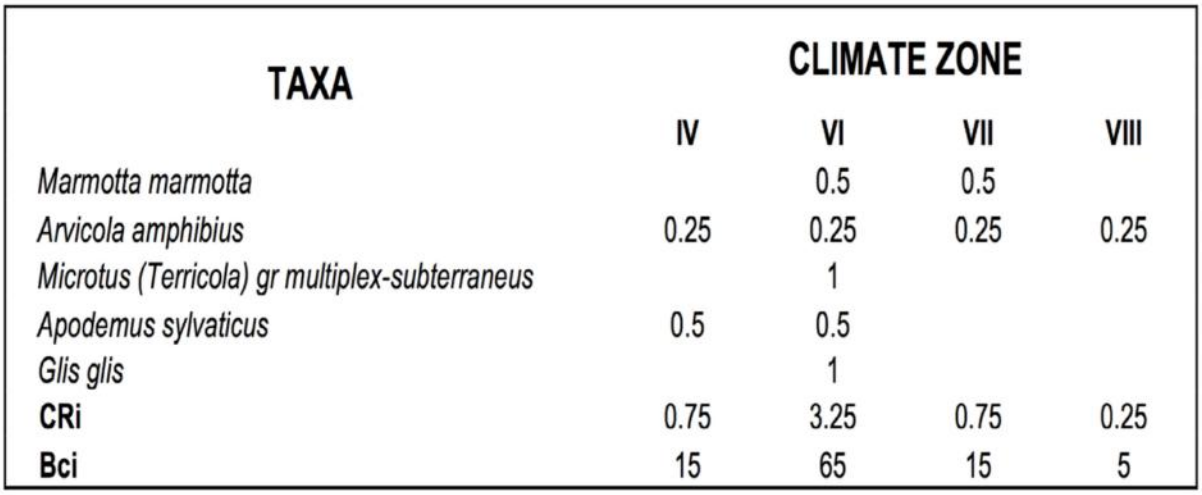


**Figure.3.4.6**. Distribution of small mammals according to their habitat preferences. We divided the habitats into four categories: OD (Open Dry meadow), OH (Open Humid meadow) and WO (Woodland).

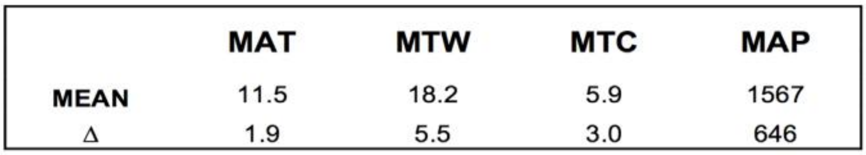
The palaeoclimatic reconstruction shows that the most represented bioclimatic zones is “VI” (65%), typical temperate climate and nemoral broadleaf-decidious forest and with the same percentage (15%) bioclimatic zones “IV” Winter rain and summer drought climate and sclerophyllous woody plants and “VII” arid-temperate climate and steppe to cold desert (Table.3.4.6).



| TAXA | CLIMATE ZONE | | | |
|---|---|---|---|---|
| | IV | VI | VII | VIII |
| *Marmotta marmotta* | | 0.5 | 0.5 | |
| *Arvicola amphibius* | 0.25 | 0.25 | 0.25 | 0.25 |
| *Microtus (Terricola) gr multiplex-subterraneus* | | 1 | | |
| *Apodemus sylvaticus* | 0.5 | 0.5 | | |
| *Glis glis* | | 1 | | |
| **CRi** | 0.75 | 3.25 | 0.75 | 0.25 |
| **Bci** | 15 | 65 | 15 | 5 |

**Table.3.4.6.** Distribution of rodents belongs to layer 4 according to their habitat preferences.

The MAT (mean annual temperature) is 11.5 ºC, 1.9ºC lower than nowadays (13.4 °C), the MTW (mean temperature of the warmest month) is 18.2 ºC, 5.5ºC lower than nowadays (23.7 °C)and the MTC (mean temperature of the coldest month) is 5.9 ºC, 3.0 ºC higher than nowadays (2.9 °C). Whereas, the MAP (mean annual precipitation) is 1567 mm, 646 mm higher than nowadays (921 mm) (Table.3.4.7). The Rainfall Index of *Lang*, indicates a humid event (L =136) and the Continentality index of *Gorczynski,* indicates a hyperoceanic climate (Ic =9).



| | MAT | MTW | MTC | MAP |
|---|---|---|---|---|
| MEAN | 11.5 | 18.2 | 5.9 | 1567 |
| Δ | 1.9 | 5.5 | 3.0 | 646 |

**Table 3.4.7.** Relation of temperatures and precipitation of layer 8 obtained using the Bioclimatic Model. MAT: mean annual temperature; MTC: mean temperature of the coldest month; MTW: mean temperature of the warmest month; MAP: mean annual precipitation; MEAN: mean of the values obtained; Δ: difference between the current mean for Longare (climate-data.org) and that obtained for the small mammals.

Moreover, we have done the chorological test, shows that the generalist species (CH-3) represents the 77.27 %, and the Euro-Siberian species (CH-1) represents the 18.18 %, whereas the only 4.55 % refers to Euro-Siberian species that nonetheless tolerate Mediterranean conditions (CH-2) (Fig.3.4.7).

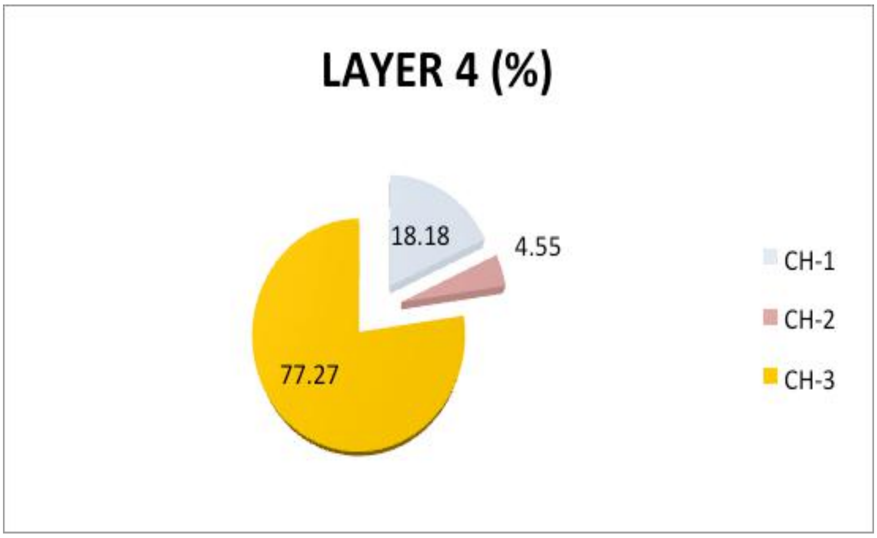


**Figure 3.4.7**. The chorotypes representation of layer 4: CH-1 (chorotype 1, Euro-Siberian species), CH-2 (chorotype 2, Euro-Siberian species that nonetheless tolerate Mediterranean conditions), CH-3 (chorotype 3, Generalist species).

### 3.4.3. DISCUSSION: Grottina dei Covoloni del Broion

#### 3.4.3.1. Layer 8 (Latest Pleistocene)

The palaeoclimatic reconstruction using the small-mammals assemblage belongs to layer 8 indicates cool and humid climatic conditions. The bioclimatic model (Hernández-Fernández, 2001) show a higher representation of typical temperate climate (54.2%), but with an important percentage of cold climates, as cold-temperate conditions (22.9%) and the presence of artic climate (7.3%) (Table.3.4.3). Besides, the mean annual temperature inferred with this method is 5.7 ºC, 7.7 ºC lower than nowadays (13.4 °C) (Table.3.4.4). Moreover, the most represented chorotype is the CH-1 (83.36%) (Fig.3.4.5), that refers to species with Euro-Siberian requirements; this implies a mean summer temperature lower than 20 ºC, a mean annual temperature that should be between 10 ºC and 12 ºC, and a mean annual precipitation higher than 800 mm (López-García et al. 2010b). The chorotype includes the species *Microtus agrestis* as the most represented taxa (25%), and the presence of *Chionomys nivalis* (8.93%) and *Microtus oeconomus* (1.79%) (Table.3.4.2). Additionally, the pollen analysis shows a mountain climate with cold winters (Cattani, 1977), for these reasons this level may be probably related with a cool moment from the end of the latest Pleistocene, probably at the end of the Younger

Dryas and in earliest Holocene when the conditions remained relatively cold and rock glacier systems developed in the European Alps (Ivy-Ochs et al., 2009).

Thus, the palaeoenvironmental analysis shows a higher percentage of open environments (52.68 %), especially "Open Humid meadow" (32.14%) or evergreen meadowland with pastures and dense topsoil (Fig.3.4.4). Furthermore, the pollen analysis indicates the decline of woodland formations from the layer 7 and a discrete proliferation of herbaceous variety of different environments (Cattani, 1977).This kind of habitat has been favoured by high record of precipitation, 337 mm higher than nowadays (921 mm), in fact, according to the *Lang* index,the rainfall rate is very humid (L =221). These data of precipitation and the cool temperatures has favored this environment.

### 3.4.3.2. Layer 4 (Copper Age)

On the other hand , the small-mammal assemblages indicate that the level 4 is dominated by mild and humid climatic conditions (Table.3.4.3). Taking into account, that in this level has been found human remains and material culture belonging to the Copper Age, we could be framed it in the middle Holocene. The Bioclimatic Model (Hernández-Fernández, 2001), shows that typical temperate climate is the most represented (65%) and temperatures are similar to nowadays (the difference is only 1.9 ºC), but the precipitation are higher than nowadays, 646 mm (Table.3.4.4). This rate of precipitation has been considered "humid" (136) by the rainfall index of *Lang.* The continentality index of *Gorczynski* (Ic =9), that analyzed the temperatures and the precipitation indicates that the layer 4 has "Hyperoceanic" characteristics.

During the Chalcolithic period in the northwest Mediterranean forest decreases (Heinz et al., 2004) and in the Central Alps this reduction was observed from 5000 to 3000 BP (Moe et al., 2007). The anthropogenic indicator taxa during this chronology exist, but the human pressure is different in every zone. In the Pre-Alps human impact on vegetation was absent (Finsinger and Tinner, 2006). In fact, this happens in G. C. Broion, where the woodland is the highest represented habitat (78.41 %) (Fig.3.4.6).

Moreover, the numerous burials found in the cave and other results suggest that the cave was temporarily disabled by humans. There are a higher percentage of chiropters (22%) (Table.3.4.2) and in general, bats do not cohabit with humans (Cuenca-Bescós et al., 2008). Additionally, we have observed a relatively high diversity index (0.70). All of these results have been associated with the low human impact.

### 3.4.4. CONCLUSIONS

The layer 8 (Latest Pleistocene) of Grottina dei Covoloni del Broion have been characterized by cool and humid climate with the Bioclimatic Model method, placed at the end of the Younger Dryas. This method shows that the climate represented in this layer was principally typical temperate climate, but an important percentage of cold climates, as Boreal and Artic climate are represented. Moreover, the mean annual temperature inferred with this method is 5.7 ºC, 7.7 ºC lower than nowadays (13.4 °C). Finally, the Euro-Siberian taxa were the most represented species, such as *Microtus agrestis*, *Chionomys nivalis* and *Microtus oeconomus*.

In this layer have been registered a high values of precipitation, 337 mm higher than nowadays (921 mm) and a very humid rainfall index. This precipitation has favored a higher percentage of Open Humid environments or evergreen meadowland with pastures and dense topsoil.

The small-mammal assemblages of the Copper Age layer (Layer 4) show a mild and humid climate, with "Hyperoceanic" characteristics. The Bioclimatic Model indicates that typical temperate climate is the most represented and temperatures are similar than today, but the precipitation are more elevated than nowadays, together with a humid rainfall index of *Lang*.

The woodland landscape is the most abundant habitat represented in layer 4 and we have registered a high diversity index. Within this high diversity, the percentage of chiropters is important. This event could be related with temporarily disabled by humans. The numerous burials have been registered in the cave in this layer.

# CHAPTER 4:

# GENERAL DISCUSSION

# 4. GENERAL DISCUSSION

In this chapter we separated the data into two main parts. In the first part we are going to explain the most important palaeoclimatic and palaeoenvironmental moments that we are detected from our small-mammal analysis, and in the second part we going to discuss the main anthropization events that we have observed with our small-mammal assemblages.

## 4.1.PALAEOENVIRONMENTAL AND PALAEOCLIMATIC RECONSTRUCTION

In general, the climatic oscillations have been the main factors controlling vegetation changes in Iberia and elsewhere in Europe from Last Glacial Maximum (Carrión et al., 2007; Morales-Molino et al., 2011).

### 4.1.1.LATEGLACIAL

The Lateglacial period ca. 15000–11000 BP was characterized by the major changes in climate. The North Atlantic region experienced abrupt variations in climate during this period, including rapid warming phases at the beginning of the Bølling–Allerød (14600 cal BP) and abrupt cooling as the Heinrich Events 1 (since 16000 to14000 cal BP) and the beginning of the Younger Dryas (12700 cal BP) (Fletcher and Sánchez-Goñi, 2008; Heiri et al., 2014) (Fig.4.1.1).

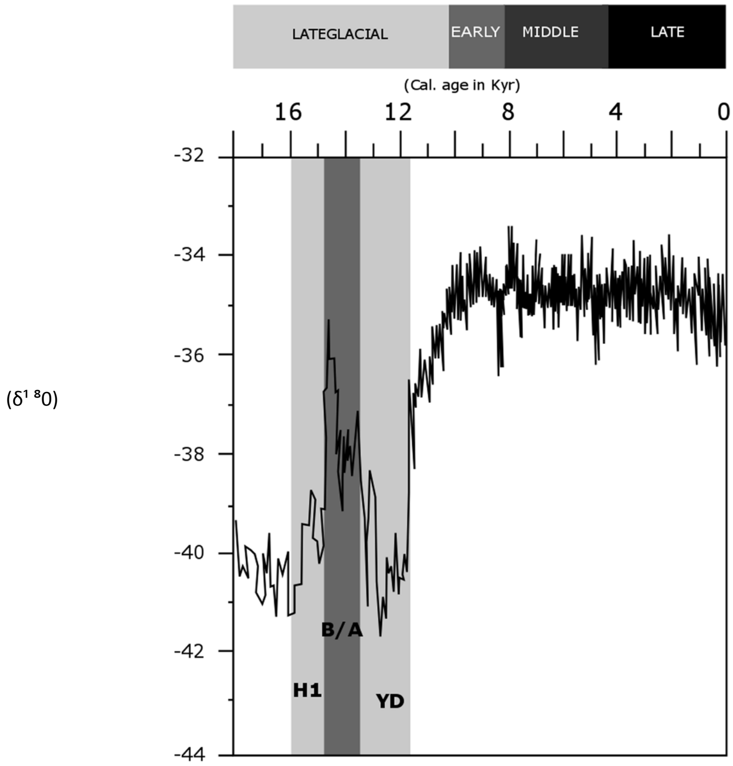


**Figure 4.1.1.** Main climatic events registered with our small-mammal analysis, located in the alkenone sea surface temperature from marine core MD95-2043 of Alboran Sea (Cacho et al., 1999). H1: Heinrich Event 1; B/A: Bölling/Allërod; YD: Younger Dryas.

#### 4.1.1.1. Heinrich event 1

The palaeoclimatic data obtained from the small-mammal assemblage show that in MIR51 (El Mirador, Sierra de Atapuerca, northern Iberian Peninsula) the MAT are 7.9 ºC, 2.2 ºC lower than currently in Burgos (Climate-Data.org). These climatic characteristics could be related with a cool period of the Lateglacial, probably a Heinrich event. The Heinrich events are abrupt changes in the Laurentide Ice Sheet associated with millennial-scale cooling in the Northern Hemisphere. Fresh water from the melting icebergs is thought to have interrupted the Atlantic meridional over turning circulation, thus minimizing heat transport into the northern North Atlantic (Roberts et al., 2014, Lynch-Stieglitz et al., 2014). In the surroundings of the Iberian Peninsula they have been also detected Heinrich events from marine core: MD95-2042 (south-western) (Cayre, 1999), MD95-2043 (south-east) (Cacho et al., 1999) and MD99-2331(north-western) (Naughton et al., 2009). Taking into account the absolute dating for this layer 15100-13180 cal BP (Bañuls-Cardona et al., 2014), this cool period could correspond to Heinrich Event 1 (H1), dated to between 16000 and 14000 cal yr BP (Fletcher and Sánchez-Goñi, 2008).

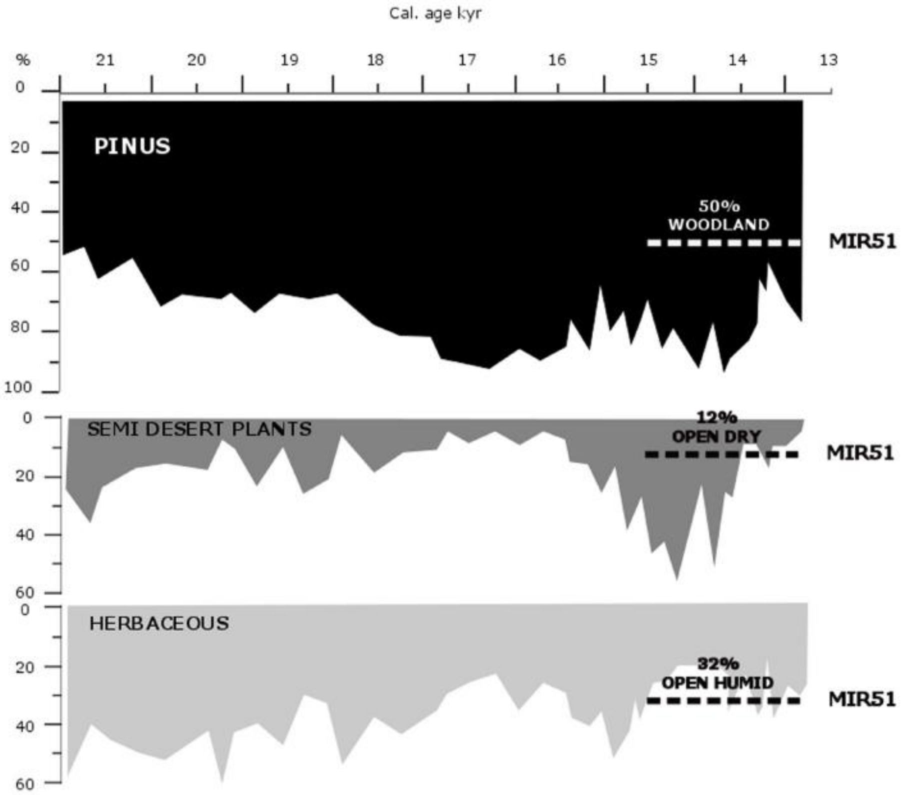


**Figure 4.1.2**. Correlation of the pollen data from Alboran sea core (Kageyama et al., 2005) with the Habitat Weighting data obtained from small-mammal assemblage of MIR51 (15100-13180 cal BP).

In general, the Lateglacial period has been characterised by the expansion of semi-desert vegetation (Kageyama et al., 2005) and particularly at H1 there was a major reduction in arboreal pollen (Fletcher and Sánchez-Goñi, 2008). The small-mammal assemblage shows a high percentage of woodland (50%) in MIR51, but we observe an increase in woodland at MIR50 (59%) (Fig.4.1.2).

However, a high MAP is observed with the small-mammal assemblage, 400 mm higher than nowadays. In fact, the *Lang* rainfall index characterises these pluviometric data as humid, and not as pertaining to a semi-arid Mediterranean climate as is currently characteristic of Burgos. These humid conditions suggest that during the Lateglacial in the North of Iberian Peninsula the climatic conditions were slightly more humid than the rest of Europe (Kageyama et al., 2005; Peyron et al., 1998; Fletcher and Sánchez-Goñi, 2008).

#### 4.1.1.2. Bølling–Allerød interstadial

The Bølling-Allerød interstadial (14600–12900 cal BP) is marked by a synchronous progressive increase of ocean and atmospheric temperatures and precipitation (Naughton et al., 2016). Moreover, from the beginning of the Bølling and culminating in the Allerød period, occurred a major gradual increase in humidity (Moreno et al., 2010).

The radiocarbon dates (13150-12813 cal BP) and the palaeoclimatic data of Layer 1.B (Balma del Gai, Moià, north-eastern Iberian Peninsula) have allowed us to place it at the end of the Bølling-Allerød interstadial, characterised by progressive atmospheric warming (Naughton et al., 2016) (Fig.4.1.1). The MER (Mutual Ecogeographic Range) analysis shows temperatures similar to current data and the continentality index of *Gorczynski* indicates an Oceanic Climate (Ic =17) as the Köppen-Geiger classification of Moià climate nowadays (Cfb) (Climate-data.org).

The palaeoenvironmental conditions in the western Mediterranean region shows a development of the forest during the Bølling–Allerød (Fletcher et al., 2010). In the NE, a general increase of arboreal and shrub taxa have been detected (mainly *Pinus* and *Juniperus* ), including a timid spread of varied mesophytes (Pérez-Sanz et al., 2013; González-Sampériz et al., 2016).While during the Allerød in the NW Iberia, the *Pinus* values increase, the pollen concentration of *Betula* fluctuates and the pollen percentages and concentrations of deciduous and sclerophylous trees also increase (Jalut et al., 2010).

The most abundant species in Layer 1.B (Balma del Gai, Moià, north-eastern Iberian Peninsula) are *Apodemus sylvaticus* and *Eliomys quercinus*, species associated with arboreal landscapes and the Habitat Weighting shows a high percentage of woodland (68.18%)(Fig.4.1.3).

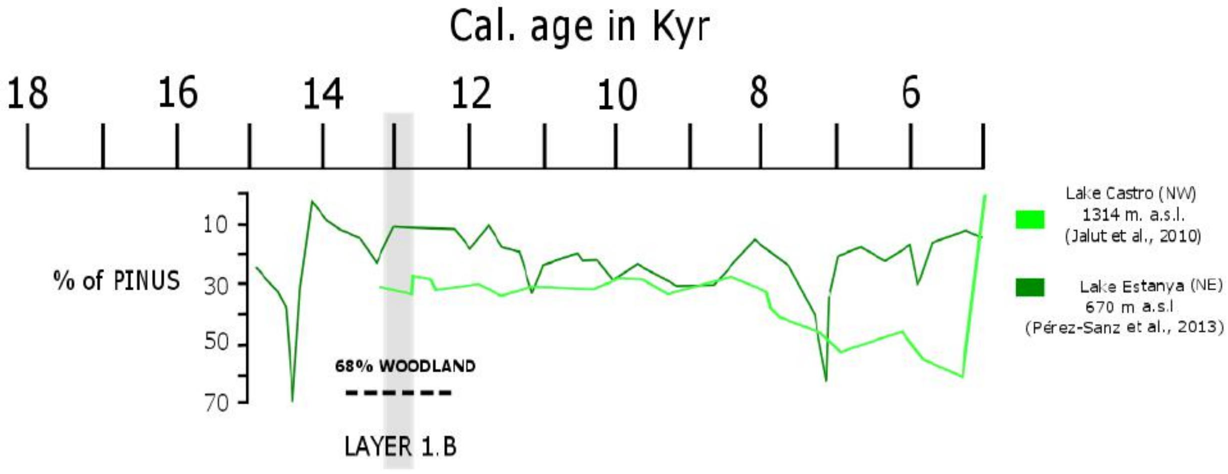


**Figure 4.1.3**. Correlation of the *Pinus* percentages registered in Lake Castro (Jalut et al., 2010) and Lake Estanya (Pérez-Sanz et al., 2013) with the woodland data registered from small-mammal assemblage of Layer 1.B (13150-12813 cal BP) of Balma del Gai.

### 4.1.1.3. Younger Dryas

The warm conditions detected during the Bølling-Allerød were truncated by a short cold period. This period is the Younger Dryas (YD), which was a relatively short cold period between approximately 12900-11700 cal BP (Rasmussen et al., 2014). Some proxies indicate the return of a glacial environment (Morellón et al., 2009; Pérez-Sanz et al., 2013; Montes et al., 2016).

The transition in climatic conditions between the Allerød and the YD was extremely abrupt (Moreno, 2014). The beginning of the Younger Dryas was characterized by cold conditions in all available sequences in the Iberian Peninsula (Montes et al., 2016), but in the European Alps from the end of the Younger Dryas to earliest Holocene the conditions remained relatively cold and rock glacier systems developed (Ivy-Ochs et al., 2009). The available climatic data of Layer 8 of Grottina dei Covoloni del Broion (Vicenza, north-eastern Italian Peninsula)shows cold conditions. We have applied to the rodents assemblage the Hernandez-Fernández (2001) climate method and we have observed an important percentage of cold climates, and, moreover, the most represented species have Euro-Siberian climate requirements, such as *Microtus agrestis*, *Chionomys nivalis* and *Microtus oeconomus* (López-García et al. 2010b). Additionally, the pollen analysis shows a mountain climate with cold winters (Cattani, 1977). At Layer 1.A (12300-11800 cal BP) of Balma del Gai (Moià, north-eastern Iberian Peninsula) we registered cool climatic conditions with the MER method (Mutual Ecogeographic Range) (2.8 ºC lower than nowadays) that could be related with Younger Dryas (Fig.4.1.1). Moreover, the sedimentology analysis has registered a cool and event humid in this layer also, have been detected fine sand with fragments of wall shelter (Bergedà, 1998). Additionally, a humid conditions have been registered with the Rainfall Index (L =126). Nevertheless the most abundant species is *Microtus (Terricola) pyrenaicus*, Euro-Siberian species, but the presence of *Iberomys cabrerae*, strictly thermo-mediterranean species, indicates that this cool conditions were not very harsh, climatic conditions that characterize the last pulsations of the Younger Dryas.

In the Iberian Peninsula, the YD is characterized by dry conditions with the shrub expansion (García-Ruíz et al., 2016) and xerophytes taxa (Carrión et al., 2010). However, the Habitat Weighting analysis of Layer 1.A of Balma del Gai (Moià, north-eastern Iberian Peninsula) assemblage, shows a little reduction of woodland formations (52.78%) respect to previous layer (66.67%). Is pointed above, our association could be framed within the last pulsations of the YD, for this reason we could observed about the start recovery of the arboreal cover, which occurred especially in the early Holocene.

### 4.1.2. HOLOCENE

The Holocene starts around 11.200 cal BP when the high summer insolation was registered in the Nothern Hemisfere, due to a coincidence of the precession and obliquity cycles (Wanner et al., 2008). Althought in this period a clear cyclicity was not found, and the spatiothermal variability of temperature and humidity/precipitation was very high (Fig.4.1.4.).

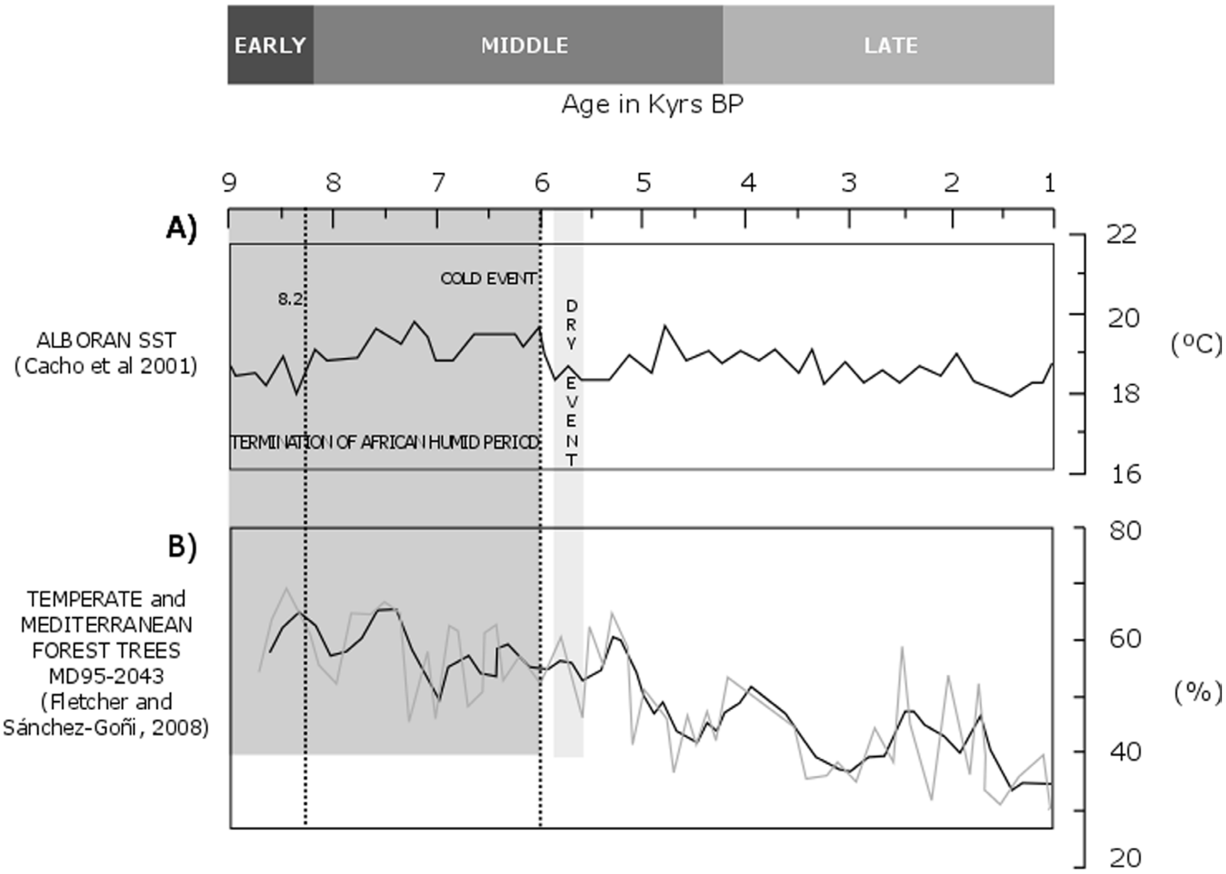


**Figure 4.1.4**. Main climatic events registered with our small-mammal analysis placed with the sea surface temperatures (Cacho et al., 2001) and the percentage of temperate and Mediterranean forest trees (Fletcher and Sánchez-Goñi, 2008) obtained from core MD95-2043 of Alboran sea.

These features have been registered in our small-mammal assemblages. The analysis of different methodologies has allowed us to characterize the palaeoenvironment and palaeoclimate from middle to late Holocene in the north of Iberian Peninsula with the data of El Mirador, El Portalon, Balma del Gai and Cova Bonica (Fig.4.1.5). Moreover, the study of small-mammal assemblage of Grottina dei Covoloni del Broion (North-eastern Italian Peninsula) has allowed us to show a little representation of late Holocene palaeoenvironmental and palaeoclimatic data of Italian Peninsula.

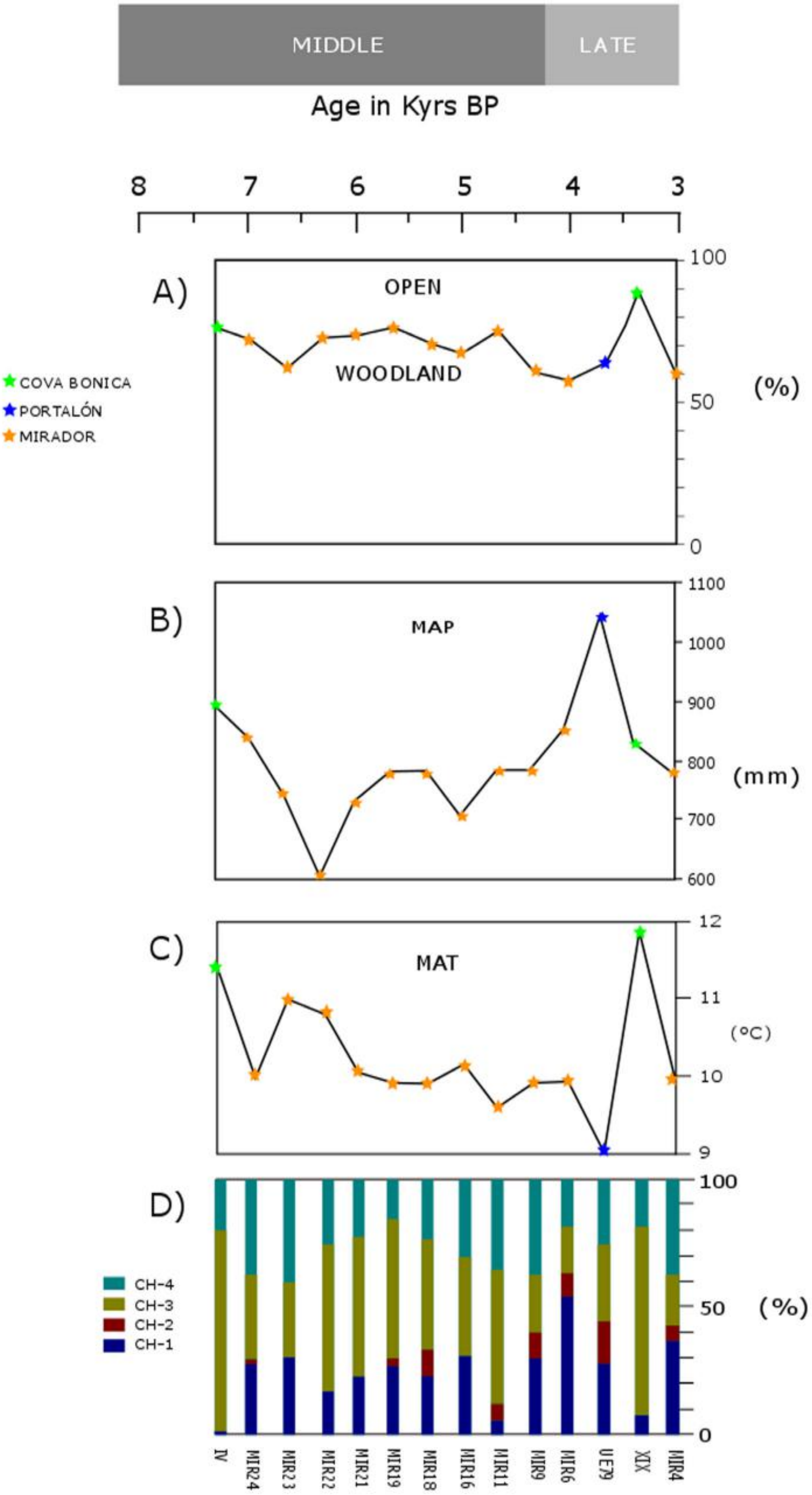


**Figure 4.1.5**. Comparison (A) Habitat Weighting data, (B) Mean Annual Precipitation, (C) Mean Annual Temperatures, (D) and Chorotypes of Holocene studied layers with dates.

### 4.1.2.1. MIDDLE HOLOCENE

Walker et al. (2012) proposed that the 8.2 ka BP event should mark the boundary between Early and Middle Holocene, because is a major short-lived cooling episode that is clearly reflected in the isotopic signal in Greenland ice cores. This cold event was characterised by cooler temperatures in Polar Regions (Mayewski et al., 2004) and drier conditions in mid to low latitudes (González-Sampériz et al., 2009; Gómez-Paccard et al., 2013).

#### A)Climate and landscape recovery from 8.2 event

The Holocene warm period occurs approximately between 8200 and 5600 cal BP (Steig et al., 2009) and in the Iberian Peninsula, warm and wet climatic conditions also were documented at this period (Tarroso et al., 2014).

In the layer IV (7401-7308 cal yr BP) of Cova Bonica (Vallirana, north-eastern Iberian Peninsula) and in MIR24 (7030-6870 cal yr BP) of El Mirador (Sierra de Atapuerca, northern Iberian Peninsula) the temperatures obtained with the MER method (Mutual Ecogeographic Range) have registered milder climatic conditions, and this data coincide with the results of core MD95-2043 of Alboran Sea (Fletcher et al., 2010) (Fig.4.1.4).

These milder climatic conditions could be related with a transition from the cold conditions of the previous 8.2 event to a warm and humid climate as pointed by Leira (2005), in 7300 cal BP, in north-western of Iberian Peninsula. Moreover, in the layer IV of Cova Bonica (Vallirana), we have found *Iberomys cabrerae*, whose requirements are strictly Mediterranean. Futhermore, the Continentality index indicate values between a climate with oceanic and a climate with continental influence, all of these values indicates a climate transition.

Together with this temperature recovery after the cold event, the environmental data obtained from Habitat Weighting suggest a clear predominance of woodland landscape and high percentage of *Apodemus sylvaticus,* more than 50 % in Cova Bonica (north-eastern Iberian Peninsula) and El Mirador cave (northern Iberian Peninsula). Moreover, this great development of forest masses has been observed with pollen analysis in other areas of the Iberian Peninsula (Muñóz-Rodrigo et al., 2005, Carrión et a.,l 2010 and Pérez-Sanz et al., 2013), in the western Mediterranean (Jiménez-Moreno et al., 2013), in the Ebro Valley (González-Sampériz et al., 2009; Gómez-Paccard et al., 2013), and in the south of the Iberian Peninsula (Fernández et al., 2007).

### B) African Humid period

The African Humid Period started as early as 14.5 cal ka BP following the fully glacial hyperarid conditions during the latest Pleistocene and consists in humid conditions attributed to a strengthening of the African monsoon due to gradual orbital increases in summer season insolation (de Menocal et al., 2000). However, the onset and termination of this humid period (9000-6000 cal yr BP) were very abrupt and were recorded moments of great droughts (Rensen et al., 2003).

In El Mirador has recorded an important increase in the temperatures from 7400 to 7000 cal BP (MIR23-22), the highest values in El Mirador sequence. Moreover, in MIR22 have been registered a semi-arid level of precipitation. These characteristics were probably related with the abrupt end of the African Humid Period.

### C) Cool event

From ca. 7000 to 5000 yr BP in several regions of Europe (Leira, 2005; Kalis et al., 2003) and North Africa (Mercuri et al., 2011) have been registered a decrease in temperatures and an increase in precipitation. These conditions are observed in El Mirador from 7200-6600 cal yr BP (MIR19, MIR18 and MIR17), when the palaeoclimatic data shows an increase in precipitation and a little decrease of the temperatures in comparison to MIR21. Moreover, a similar cool event is detected at Cova Colomera (Sant Esteve de la Sarga, north-eastern Spain) in the layers CE13-14 (7060 cal yr BP) and CE12 (6870 cal yr BP) where the most represented species have Eurosiberian requeriments, specially, *Chionomys nivalis* (snow vole) (Bañuls-Cardona and López-García, 2009).

At 6000 yr BP these slightly cooler conditions were increased (Bond et al., 1997; Kalis et al., 2003; Mayewski et al., 2004; Pérez-Sanz et al., 2013), there was a decline of solar insolation in Northern Hemisphere that brought global cooling with alpine glacier advances (Davis et al., 2003). These climatic conditions have been identified in El Mirador at 6300-5940 cal BP (MIR11), where we have recorded the lowest temperatures in the Holocene sequence of El Mirador cave (Atapuerca, northern Iberian Peninsula). Moreover, in this moment in El Mirador, a change in livestock management was registered, the importance of goats and sheep decreases while the presence of equids, whose origin is likely to be wild, becomes more significant in this layer (Martín et al., 2016a).

### D) Dry event

During the Holocene various dry events have been detected (Jalut et al., 2000; Carrión et al., 2010). In Iberian Peninsula at ca. 5800-5600 BP an important dry event occurred (Domínguez-Villar et al., 2012; Tarroso et al., 2014), concretely, in the Iberian Meseta around 5740 cal BP (Pérez-Olbiol et al., 2010). In El Mirador cave we detected this dry event in 5940-5660 cal BP (MIR9). A decrease in MAP from 867 mm in MIR10 to 794 mm in MIR9 has been observed. Moreover, the palaeoenvironmental analysis shows a clear change in the landscape with an important decrease in woodland formations in MIR9.

Neverthless, these data could be caused by two different events. On one hand, in 5940-5660 cal BP (MIR9) the best-represented taxa is *C. russula*, a thermo-Mediterranean shrew. This high presence of *C. russula* is probably related with the incipient establishment of Mediterranean climate that occurred in the area around El Mirador cave before ca. 5000 yr BP (Pérez-Olbiol et al., 2010). On the other hand, some studies explain that the agricultural intensification caused a deterioration in landscape in the Iberian Peninsula (Fletcher and Sánchez-Goñi, 2008; Pérez-Sanz et al., 2013). The first agricultural intensification has been observed in the Iberian Peninsula in general after ca. 5000 yr BP (Badal et al., 1994; Carrión, 2002; Fletcher and Sánchez-Goñi, 2008; Martínez-Cortizas et al., 2009; López-Merino et al., 2012; Tarroso et al., 2014; Pérez-Díaz et al., 2014; Aranbarri et al., 2015; Revelles et al., 2015; Lillios et al., 2016), but this agricultural intensification have been registered from 5630-5350 cal yr BP in El Mirador cave (MIR6), where we observed with small-mammal analysis a substantial increase in precipitation (73 mm higher than in MIR9), although there is no gain in forest cover. Moreover, around El Mirador cave the pollen studies have registered a significant increase in crops (Expósito et al., 2017).

### E) Expansion Mediterranean climate

Before 5000 cal BP near 41°North Jalut et al. (2000) placed the expansion of the Mediterranean climate, and this event carried on an important climatic and environmental changes. From 5200 to 4711 cal BP with our small-mammal analysis we have registered temperate and humid climatic conditions in the units UE79 (5200-4800 cal BP) and UE85 of El Portalón cave (Sierra de Atapuerca, northern Iberian Peninsula) and layer XIX (4835-4711 cal BP) of Cova Bonica (Vallirana, northeastern Iberian Peninsula), as show palynological studies of northern Iberian Peninsula (Pérez-Díaz et al., 2014) and at eastern Mediterranean from oxygen and carbon isotopic record in a speleothem (Bar-Mathews and Ayalon, 2011).

Nevertheless, we detected the expansion of the Mediterranean climate with the chorotypes analysis.

The two units of El Portalón (Atapuerca, north-western Spain) shows the change of the importance in the percentage of the CH-1 (Eurosiberian species) in the UE79 (5200-4800 cal yr BP) by CH-2 (Euro-Siberian species that tolerate Mediterranean conditions) in the UE85. Moreover, in the layer XIX (4835-4711 cal yr BP) of Cova Bonica (Vallirana, north-eastern Spain) we found *Iberomys cabrerae*, species whose climatic requirements are strictly Mediterranean.

Since the Chalcolithic the forest decreases in the north-western Mediterranean (Heinz et al., 2004) and in the Central Alps this reduction was observed from 5000 to 3000 cal BP (Moe et al., 2007), but the climatic change favoured the woodland expansion in other parts. In the Pre-Alps, the human impact on vegetation was absent (Fisinger and Tinner, 2006), in the north of Iberian Peninsula the pollen analysis indicates a woodland expansion from 5000 cal BP (Santos et al., 2000, Muñoz Sobrino et al., 2005), concretely, between 5250 and 4100 cal BP disappearance of cereal signs in the Atlantic zone (Pérez-Olbiol et al., 2016). We have registered a predominance of the woodland in palaeoenvironmental data obtained with the small-mammal analysis of the units UE79 (5200-4800 cal BP) and UE85 of El Portalón cave (Atapuerca, northern Iberian Peninsula), layer XIX (4835-4711 cal BP) of Cova Bonica (Vallirana, north-eastern Iberian Peninsula) and Layer 4 of Grottina dei Covoloni del Broion (Vicenza, north-eastern Italian Peninsula). In every one of these small mammals assemblages the most represented species is *Apodemus sylvaticus* (species with woodland requirements) and we detected that this is a trend of the other small-mammal assemblages with the same chronology in the Iberian Peninsula. In the small-mammal studies of layer III (5288-4881 cal BP) of Peña Larga (Álava, northern Iberian Peninsula) (Rofes et al., 2013), layer 8 (4680 cal BP) of El Mirón (Ramales de Victoria, northern Iberian Peninsula) (Cuenca-Bescós et al., 2008), layer VUU (5130 cal BP) of Valdavara-1 (Becerreá, north-western Iberian Peninsula) (López-García et al., 2011) and layer III of Cova Bolumini (Benimeli-Beniarbeig, eastern Iberian Peninsula) (Guillem-Calatayud, 1999) the most abundant taxa are species related with forest requeriments as *Apodemus sylvaticus*, *Apodemus flavicolis*, *Eliomys quercinus*, and *Glis glis*.

#### 4.1.2.2. LATE HOLOCENE

Walker et al. (2012) published that the Middle–Late Holocene boundary should be placed at 4.2 ka BP as defined by a mid/low-latitude aridification event that is reflected in proxy records such as pollen, solar variability and sedimentology from North America, through the Middle East to China, Africa, parts of South America, Antarctica and the Iberian Peninsula (Jalut et al., 2000; Carrión, 2002; Mayewski et al., 2004; Martín-Puertas et al., 2008).

### A) Intensification Human groups impact

In El Mirador cave (Sierra de Atapuerca, northern Iberian Peninsula) we detected an incipient process of aridification with the MER method in MIR4 (3700-3000 cal BP). We registered a slight decrease in precipitation of MIR4 respect to MIR5, moreover, we have detected a high percentage of Eurosiberian species as *M. arvalis* and *M. agrestis*, in MIR4. This data coincide with increase in xerophytic and cold taxa in detriment of Mediterranean species as manifestation of this slight cooling and increased dryness that some authors have published (Murelaga et al., 2009; Ruíz-Zapata et al., 2010; Domínguez-Villar et al., 2012; Pérez-Sanz et al., 2013).

On the other hand, in that chronology, cereal-growing and livestock-keeping are widely documented in all deposits of human groups (Revelles et al., 2015). The archaeobotanical studies based on pollen, charcoal, seeds and phytoliths of El Mirador cave have confirmed the presence of herbaceous plants related to the development of agriculture and livestock in MIR4 (3700-3000 cal BP) (Rodríguez and Buxó, 2008; Cabanes et al., 2009; Expósito et al., 2017) and with small-mammal analysis we observed an increase in open dry environments.

## 4.2. HUMAN IMPACT AND BIODIVERSITY

The Biodiversity have been defined as "a state or attribute of a site or area and specifically refers to the variety within and among living organisms, assemblages of living organisms, biotic communities, and biotic processes, whether naturally occurring or modified by humans" (DeLong, 1996). During the Holocene the climate and the human impact on vegetal species are indiscriminately mentioned as causes of rapid oscillations in the environment, efforts to disentangle the specific causes of this process are complicated yet (Jalut et al., 2009; Mercuri et al., 2011; Jimenez-Moreno et al., 2012).

The climatic changes affect the small-mammals ethology, their small size makes them more sensitive to minor variations in climate and environment than large and medium-sized mammal populations (López-García et al., 2013; Porras et al., 2016). Moreover, small-mammal accumulation in a site is produced when the human presence is low, especially in the case of the bats (Cuenca-Bescós et al., 2008), but the synanthropic species have adapted their ethology to conditions created or modified by human activities (Mistrot, 2000). These species have the capacity for adaptation to these new conditions, enabling them to modify their climatic and environmental requirements (McKinney, 1997).

At the beginning of the Holocene, climatic factors are the principal influence on trends in diversity

(Lomolino, 2001; McCain, 2004), while in the mid-Neolithic and Bronze Age, by contrast, the richness and diversity of species have been associated with the human impact (Carrión et al., 2010; López-García et al., 2013). The expansion of the first farming societies and the practice of an intensive agriculture implied impact on the landscape across Europe. The Neolithisation process, starting in south-eastern Europe in 9000 cal. BP (Kouli and Dermitzakis, 2008; Marinova et al., 2012) and reaching the opposite extreme of the continent at the beginning of 6000 cal. BP (O'Connell and Molloy, 2001; Woodbridge et al., 2012). In the Iberian Peninsula, palaeobotanical studies documented the first human landscape modifications around 6000 cal BP (Carrión et al., 2010a). However, the clear intensification of farming activities in the landscape started around 2000 cal BP (Martínez-Cortizas et al., 2009; Iriarte, 2009).

Some palaeoenvironmental evidences demonstrate that agriculture was early adopted in Mediterranean coastal (Badal et al., 1994; Zapata et al., 2013; Bernabeu et al., 2016). Zilhão (2001) indicates an east–west pattern in the agriculture adoption, although controversy exists regarding the timing. Recent studies (Peña Chocarro et al., 2005; Rojo-Guerra et al., 2008; Alday, 2011; Utrilla et al., 2013) have changed the traditional view of marginal and secondary colonization in inner Iberia during Neolithisation, and these studies have revealed the presence of Neolithic settlements during 7350 cal BP. We explain the effect of the Neolithisation process on small mammals in the two main regions of Iberian Peninsula: Mediterranean region and Inner Iberian Peninsula.

### 4.2.1. MEDITERRANEAN REGION

The first signs of domestication in Iberia appear in the Early Neolithic around 7650 cal BP at sites located in Catalonia such as El Cavet (Oms et al., 2014) and southern Valencia region such as Cova de les Cendres, Abric de la Falguera and Cova de l'Or (García Atienzar, 2009; Bernabéu and Molina, 2009; Martí, 2011; Bernabéu, 2006; García Borja et al., 2012; García Puchol et al., 2009).

As it was pointed previously, Zilhão (2001) indicates an east–west pattern in the agriculture adoption, but Manen et al. (2007) and García-Atiénzar (2010) suggest that it should also consider another possible route of neolithization from North Africa.

Related with the last hypothesis, in our assemblage we have identified *Mus spretus* in Cova Bonica (North-eastern, Iberian Peninsula). The oldest *Mus spretus* fossils have been found in North Africa at Middle Pleistocene in Morocco (Darviche et al., 2006). In more recent chronologies is found in El Harhoura 2 cave (Rabat-Témara, Morocco) from the beginning of the Late Pleistocene, around 120 to 5.8 kyr BP (Stoetzel et al., 2013) and during the Holocene in Genfouda cave (Jerada, Morocco) which has been dated around 5000 BP (López-García et al., 2013b).

The first appearance of *Mus spretus* out of Africa was in Bolumini cave (Beniarbeig, eastern Iberian Peninsula) (Guillem-Calatayud, 1999) at 6950-5350 BP. Other site where the species have been found was in a Neolithic layers (5593-5386 BP) at Cendres cave (Teulada, eastern Iberian Peninsula) (Guillem-Calatayud, 1999) and at 4711-4835 cal BP in Cova Bonica. Afterwards, in the Bronze Age appears in more sites, such as Cova 120 (4859-4656 cal BP) (Sales de Llierca, Girona) (Alcalde, 1986), Rafal Rubí (3450-3350 cal BP) (Alaior, Menorca), La Encantada (3530-3490 cal BP) (Granátula de Calatrava, Ciudad Real) and Cuesta del Negro (3350 cal BP) (Purullena, Granada) (Morales Muñiz et al., 1995) (Fig.4.2.1). The geographical distribution of *Mus spretus* is restricted to a small region of the north of Africa, eastern of Iberian Peninsula and the southeastern of France.

**Figure 4.2.1.** *Mus spretus* current distribution in red colour. 1: El Harhoura 2 cave, 2: Genfouda cave, 3: Bolumini cave, 4: Cendres cave, 5: Cova Bonica, 6: Cova 120, 7: La Encantada, 8: Rafal Rubí, 9: Cuesta del Negro. Green mouse : Late Pleistocene, Blue: Neolithic sites; Pink: Bronze age sites.

*Mus spretus* (Algerian mouse), it is not a commensal species, is a synanthropic species. This species prefers inhabits a variety of grasslands, scrubland, agroecosystems and cereals fields (Gosàlbez, 1987; Palomo et al., 2009), for this reason, *Mus spretus* have been associated to the expansion of the Neolithization.

Nevertheless, we observed that the distribution of *M. spretus* in Iberian Peninsula is related with the Mediterranean climate, it does not appear in the northern sites (Gosàlbez, 1987; Palomo et al., 2009). It is occurs because *M. spretus* has low capacity of thermoregulation (Górecki et al., 1990) and low adaptation to the dryness (Stoetzel et al., 2011). One example of this question, is El Mirón, where the cereal use have been documented in the Neolithic (Peña-Chocarro et al., 2005), but Cuenca-Bescós et al., (2008) did not find *Mus spretus* along the sequence of El Mirón from late Mosterian to Medieval occupation. Moreover, the presence of this rodent have not documented in Mediterranean sites located at more than 500 m.a.s.l. as in Cova Colomera (northeastern Iberian Peninsula) (670 m.a.s.l)(Bañuls-Cardona and López-García, 2009) or Cova Fosca (easthern Iberian Peninsula) (900 m.a.s.l) (Sesé, 2011).

### 4.2.2. INNER IBERIAN PENINSULA

During the Neolithic occurs an important transformation in the strategies for obtaining resources, as the agriculture and livestock, and with them a new human interaction on the landscape (García-Martínez de Lagrán, 2013). Besides the big diversity of landscapes and ecological conditions in the Iberian Peninsula (Zapata et al., 2004), is important to understand the degree of human response and/or adaptation to environmental changes in different sites and periods (Montes et al., 2016), especially at recent prehistoric times in mountainous areas (Carrión et al., 2010; Tarroso et al., 2014). The small-mammals study of El Mirador cave and El Portalón cave has proved to be a useful tool to identifying the human impact during the middle-late Holocene of the northern of the Iberian Peninsula.

#### A) Anthropogenic transformations in El Mirador cave

El Mirador cave is particularly valuable in this context because it has a sequence with a well-documented human occupation from 7200 to 3000 cal. BP. The records of Spanish Central System are scarce in Holocene period and the most of them are short-term pollen records extend back beyond the last 6000 years BP (López-Sáez et al., 2014).

The study of diversity and synanthropic species of El Mirador allow us to identify two phases of human impact. In the first phase (7000-5900 cal. BP) changes in diversity were associated with the human impact, the small-mammal assemblage and zooarcheological remains of El Mirador cave have indicated an important use of pastoralism in detriment of agricultural strategies. The most represented species in these layers is *Apodemus sylvaticus*, which prefers non-tilled soils (Noguerales, 2013), do not live in the agriculture environment (Tarjuelo et al., 2010). Moreover, Martín et al., (2016b) registered an increased of herds and / or the higher intensity of the occupation of the cave due to its use as a sheepfold (a large number of remains, large number of perinatal individuals) in MIR16 and MIR18. While in MIR11 the importance of goats and sheep decreases but the presence of equids, whose origin is likely to be wild, is more important in this layer (Martín et al., 2016a).

On contrary, from 5900 to 3000 cal BP we have documented the dominance of microtines that could indicate an increase in cultivated lands to the detriment of herding practices (Burel et al., 2004) specially with the dominance of *Microtus arvalis* (Fisher et al., 2011) in MIR6 (5600-5300 cal BP) and MIR4 (3700-3300 cal BP) (Fig.4.2.2).

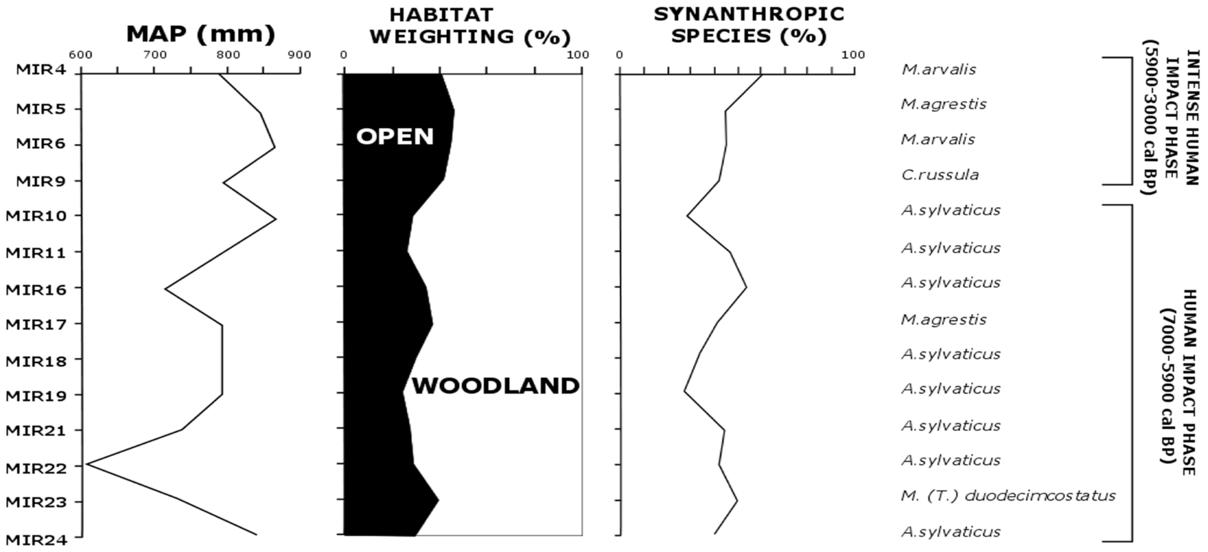


**Figure 4.2.2**. Two phases of human impact identified in El Mirador cave.

Moreover the evidence from other studied proxies as pollen, charcoal, seeds and phytoliths, (Cabanes et al., 2009; Euba et al., 2015; Expósito and Burjachs, 2016; Rodríguez et al., 2016) have confirmed the forest degradation, which is most likely due to intensified human activity. Concretely, the pollen analyses of MIR4 (Bronze Age) show higher values of anthropogenic signatures related to human activities (Expósito et al., 2017) and the highest value of synanthropic species (60%).

**B) Seasonal anthropic occupation**

Other important question in the human occupation of Central Iberia is the topography, with two sub-plateaus surrounded by high mountains ranges. This peculiar topography has allowed humans to implement mobile pastoralism practices to exploit available pastures in every season (López-Sáez et al., 2014). This hypothesis has been observed in El Mirador cave, where the palaeoclimatic and palaeoenvironmental data obtained through the small-mammal study shows typically summer and autumn climatic conditions in El Mirador cave. Furthermore, zooarchaeological studies indicate that in some levels of El Mirador cave foetal remains from the final days of the third gestational trimester have been identified, and in all levels foetal remains from the final weeks of gestation have been recovered. These data testify to the very likely use of the cave as a breeding and birthing space for ovicaprines, at least during the end of winter and early spring (Martín et al., 2015).

## CHAPTER 5:

# GENERAL CONCLUSIONS

# 5. GENERAL CONCLUSIONS

## 5.1.PALAEOENVIRONMENTAL AND PALAEOCLIMATIC RECONSTRUTION

### 5.1.1.LATEGLACIAL

1.- The cold conditions detected in MIR51 [15100-13180 cal BP] (El Mirador cave) have been related with the Heinrich event 1.

2.- The climatic data (MER and Continentality) documented in layer 1.B [13150-12813 cal BP] (Balma del Gai) are similar to current data coinciding with the Bölling-Ällerod characteristics.

3.- The conditions of Younger Dryas have been detected in our small-mammals assemblage. Cool temperatures (Bioclimatical Model) have been recorded in layer 8 (Grottina dei Covoloni del Broion), as a high percentage of Eurosiberian species (*M.agrestis*, *Ch.nivalis* and *M.oeconomus*). While in layer 1.A [12300-11800 cal BP] have been documented cool conditions with arboreal cover recovery, these conditions corresponds to the characteristics of end to the Younger Dryas and the onset of the Holocene period.

### 5.1.2. HOLOCENE

1.- The climate and landscape suffer a recovery after the cold event occurred at 8200 cal BP, in the layer IV [7401-7308cal BP] (Cova Bonica) and MIR24 [7030-6870 cal BP] (El Mirador).

2.- The semi-arid characteristics recorded in MIR22 and MIR23 [7400 to 7000 cal BP] (El Mirador) could be related to the termination of the African Humid Period.

3.- Cool event has been registered from MIR19 to MIR17 [7200-6600 cal BP] (El Mirador), but these cool conditions increase at MIR11 [6300-5940 cal BP] (El Mirador).

4.- A dry event has been detected in MIR9 [5940-5660 cal BP] (El Mirador) probably consequence of the incipient establishment of Mediterranean climate and the first agricultural intensification.

5.-The expansion of Mediterranean climate supposed temperate and humid conditions that favored the woodland expansion in UE79 [5200-4800 cal BP], UE85 (El Portalón), layer XIX [4835-4711 cal BP] (Cova Bonica) and layer 4 (Grottina dei Covoloni del Broion).

6.- Human groups intensification on landscape is recorded from Late Holocene, we observed an increase in open dry environments in MIR4 [3700-3000 cal BP] (El Mirador) that they do not related with the climatic conditions.

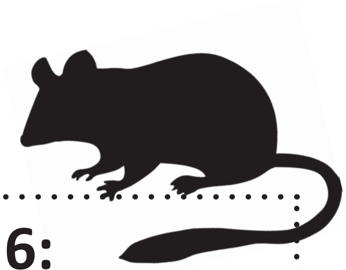
## 5.2. HUMAN IMPACT AND BIODIVERSITY

1.- The first appearance of *Mus spretus* in the north of Iberian Peninsula during the Neolithic is documented in Cova Bonica [4835-4711 cal BP]. The distribution of *Mus spretu*s from North Africa to Iberian Peninsula during the Neolithic could be related with another possible way of the neolithization.

2.- The Anthropogenic transformations in El Mirador cave have been divided in two phases. The first phase (7000-5900 cal BP) presents characteristics related with the pastoralism practices and the second phase (5900-3000 cal BP) presents environmental changes related with the use of the landscape by the agricultural practices.

3.- We have detected a phase with low human pressure in the major part of the Iberian Peninsula from 5200 to 4000 cal BP.

4.- The anthropic occupation of the Inner Iberian Peninsula has a seasonal character.

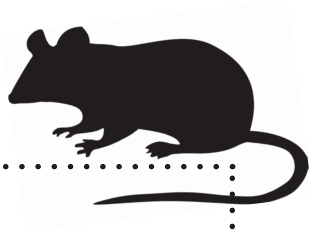


# CHAPTER 6:
# FUTURE PERSPECTIVES

# 6. FUTURE PERSPECTIVES

For many reasons, we could not be done some interesting analysis for this Ph.D. thesis, but we want to continue this study with these objectives:

- The usewear study of molars belonging to rodents provides information about their diet that allows us to establish patterns in agricultural intensification.
- To study the entire sequence of El Portalón as it has done with El Mirador, to see the differences and similarities of occupation in these neighbouring cavities.
- Expand the sample studied to observe the climatic and environmental changes at the regional context.
- To deepen the study of the Mediterranean climate expansion.



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# APPENDIX 1

# A.1.1. NOMENCLATURE

The craneal bones and teeth (also post-craneal bones in some species) of small mammals present specific morphologic characteristics that allow us to distinguish the species. The nomenclature of these characters has been uniformed in order, family or subfamily.

We used the terminology of Butler (1948) for family Erinaceidae, Reumer (1984) for family Soricidae and Talpidae, in the case of the order Chiroptera Bruijn and Rumke (1974) and Menu (1985) for teeth and Felten et al. (1973) for humerus, for the family Sciuridae, Cuenca.Bescós, 1985, the subfamily Arvicolinae we used the terminology of van der Meulen (1972), for the teeth description of the family Muridae we used the terminology of Pasquier (1974) and finally for the for the family Gliridae we used the nomenclature establish to Damms (1981).

## Order Eulipotyphla GREGORY, 1910

## Family Erinaceidae FISCHER VON WALDHEIM, 1817

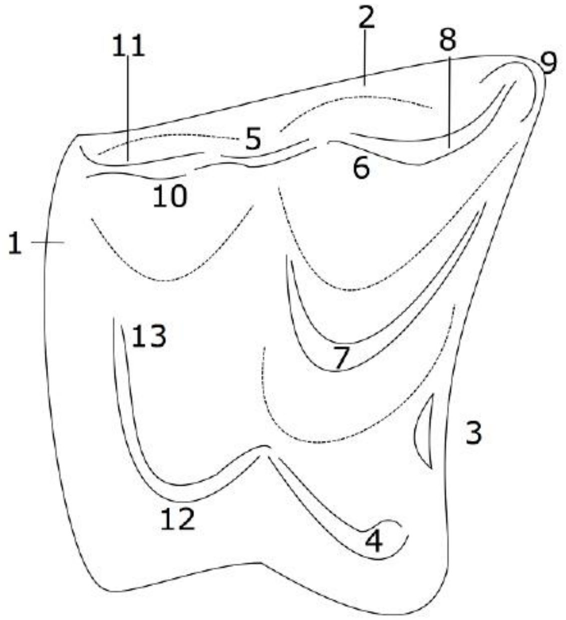

**Fig.1.** First left upper molar (M1) of *Erinaceus europaeus*. 1. Anterior cingulum, 2. Labial cingulum, 3. Posterior cingulum, 4. Hypocone, 5. Mesostyle, 6. Metacone, 7. Metaconulid, 8. Metacristid, 9. Metastyle, 10. Paracone, 11. Paracristid, 12. Protocone, 13. Prtoconulid (According to Butler, 1948)

## Family Soricidae FISHER, 1817

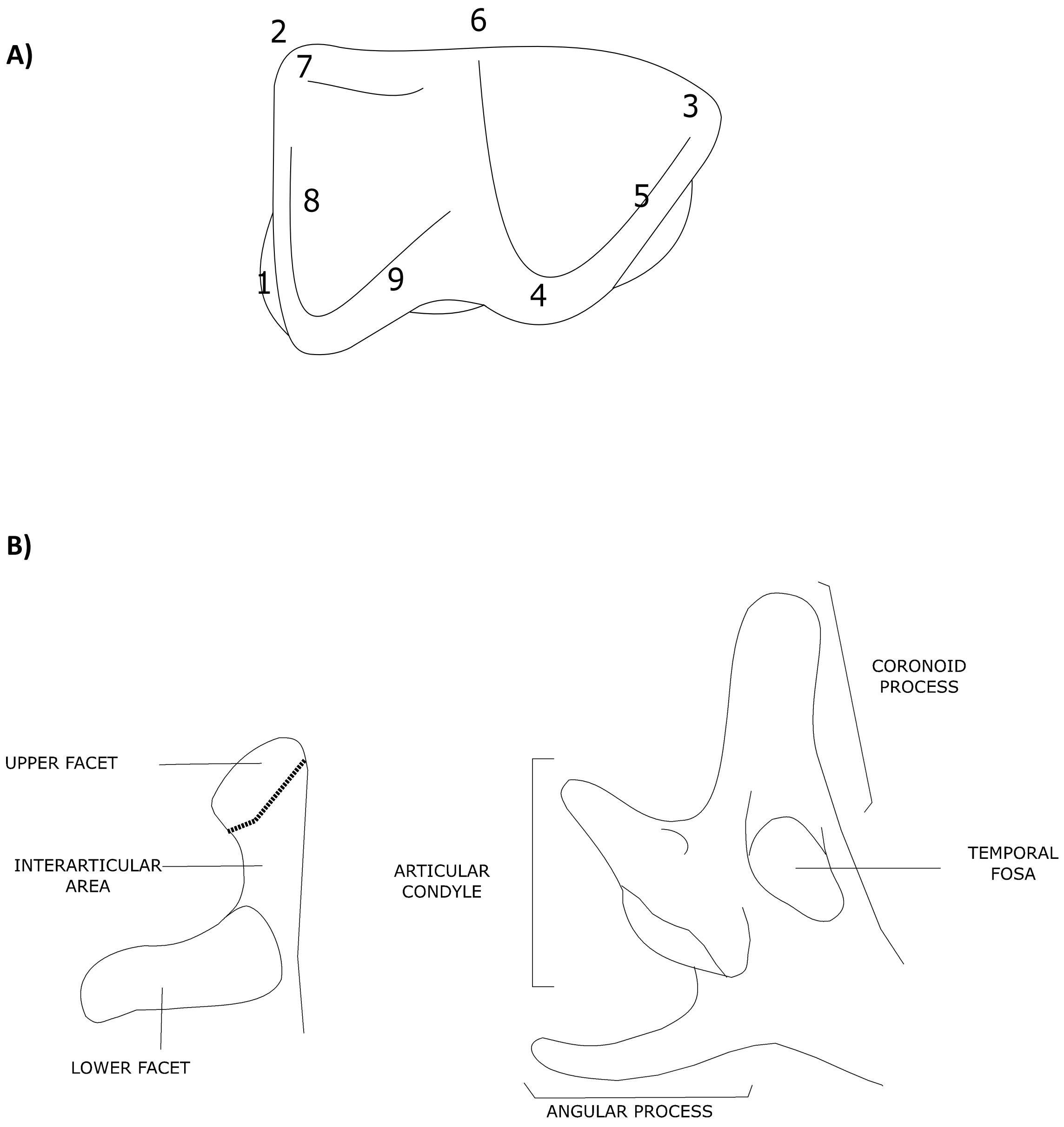

**Fig.2. A)** First right lower molar (m1) of *Crocidura russula*. 1. Labial cingulum, 2. Entoconid, 3.Paraconid, 4.Protoconid, 5.Paralofid, 6.Metaconid, 7.Entostilid, 8.Hipolofid, 9. Hipoconid **B)** Posterior part of *Crocidura russula* mandible (According to Reumer, 1984).

## Family Talpidae FISCHER, 1817

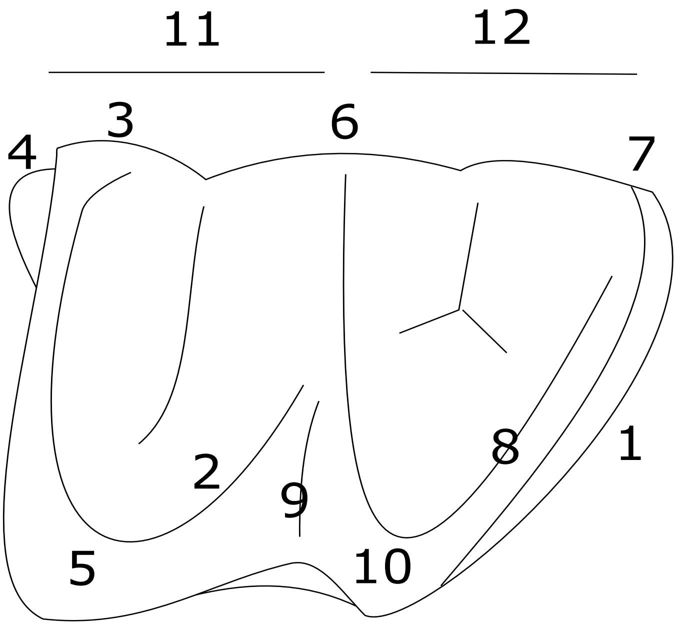

**Fig.3.** First right lower molar (m1) of *Talpa europaea***.** 1. Labial cingulum, 2. Oblique cristid, 3. Entoconid, 4. Entostylid, 5. Hipoconid, 6. Metaconid, 7. Paraconid, 8. Paralofid, 9. Parastylid, 10. Protoconid, 11. Talonid, 12. Trigonid (According to Reumer, 1984).

# Order Chiroptera BLUMENBACH, 1779

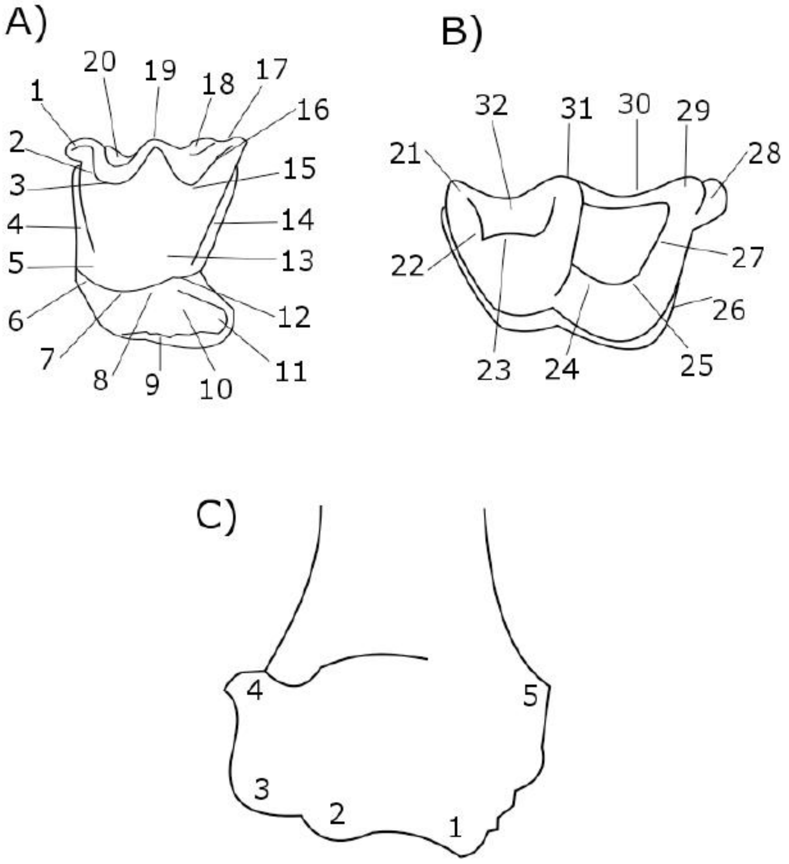

**Fig.4. A)** Right second upper molar (M2) of *Myotis myotis-blythii*. 1. Parastyle, 2. Preparacristid, 3. Paraconid, 4. Anterior cingulum, 5. Paralofid, 6. Paraconulid, 7. Protoconid, 8. Postparacristid, 9. Lingual cingulum, 10. Hipoconid, 11. Heel, 12. Metaconulid, 13.Metalofid, 14.Distal cingulum, 15. Metaconid, 16. Postmetacristid, 17. Metastyle, 18. Labial cingulum of metaflex, 19. Mesostyle, 20. Labial cingulum of paraflex. **B)** Left second lower molar (m2) of *Myotis myotis-blythii*. 1. Paraconid, 22.Paralofid, 23.Protoconid, 24.Oblique cristid, 25.Hipoconid, 26.Distal cingulum, 27.Postcristid, 28.Hypoconulid, 29.Entoconid, 30.Entocristid, 31.Metaconid, 32.Trigonid labial cingulum .**C)** Humerus distal epiphysis of *Myotis myotis-blythii* (posterior view). 1. Styloid process, 2. Troclea, 3. Condyle, 4. Epicondyle, 5. Epitroclea (According to Bruijn and Rumke, 1974; Menu, 1985; Felten et al. 1973).

## Order Rodentia BOWDICH, 1821
## Family Sciuridae FISHER, 1817

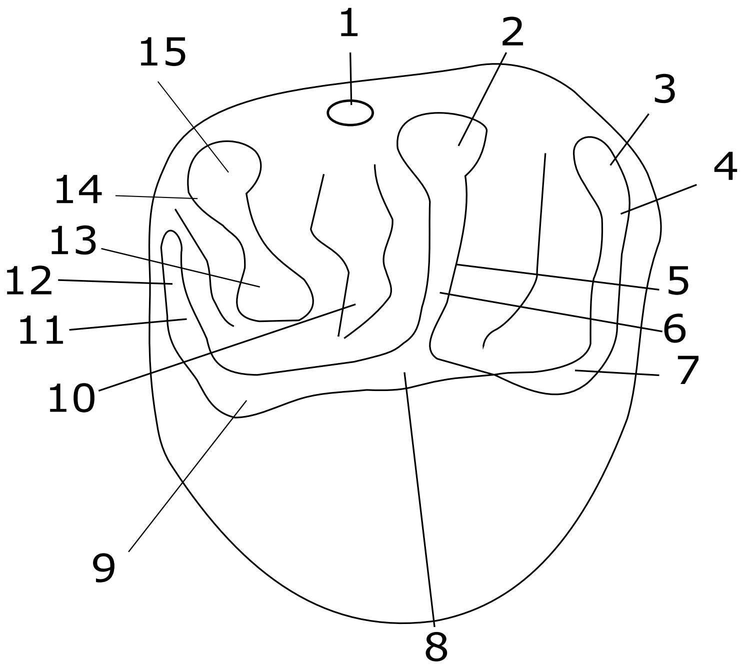

**Fig.5.** Left first lower molar (m1) of *Marmota marmota.* 1. Mesostyle, 2. Paraconid, 3. Parastyle, 4. Anterolofid, 5. Protolofid, 6. Protoconulid, 7. Anteroconulid, 8. Protoconid, 9. Hipocone, 10. Central valley, 11. Hypoconulid, 12. Posterolofid, 13. Metaconulid, 14. Metalofid, 15. Metaconid (According to Cuenca-Bescós, 1985)

## Family Cricetidae FISHER, 1817
## Subfamily Arvicolinae GRAY, 1821

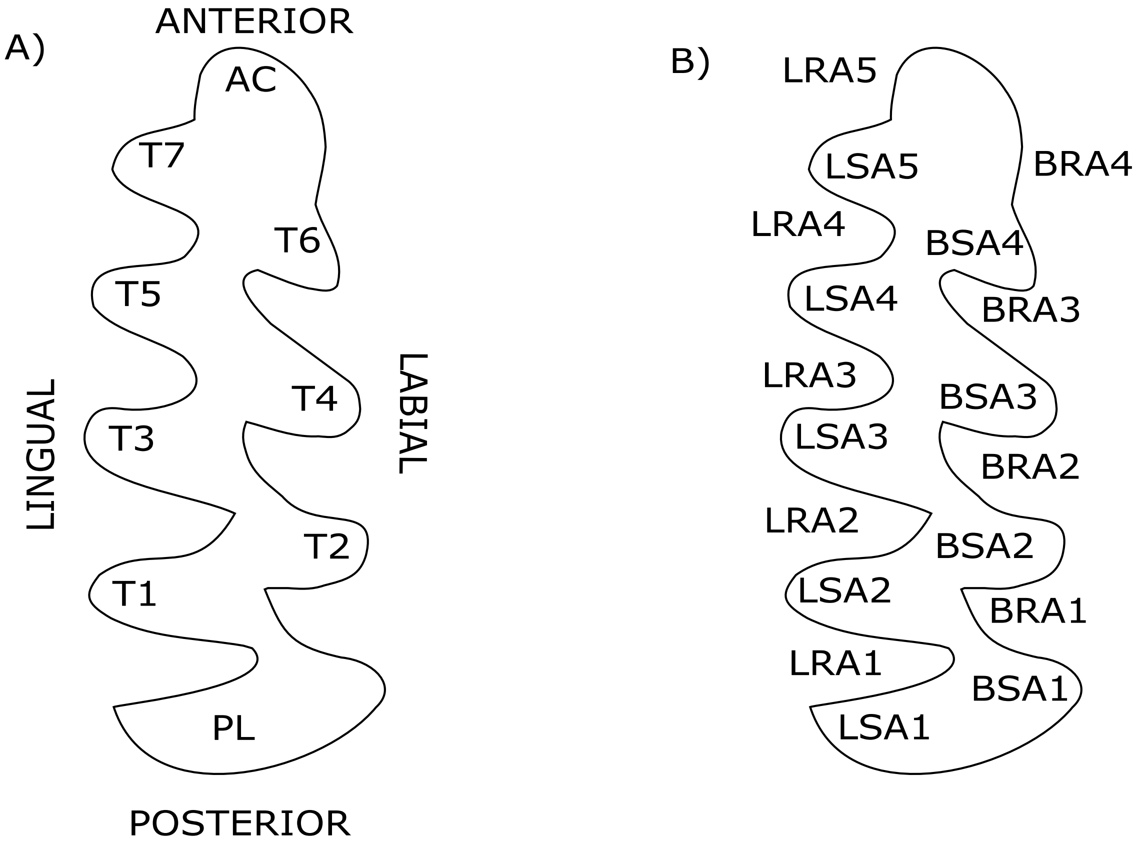

**Fig.6.** First right lower molar (m1) of *Microtus (Terricola) duodecimcostatus*. **A)** AC: Anteroconid complex, PL: Posterior lobular, T: Triangle; **B)** BRA: Bucal re-entrant angle, BSA: Bucal salient angle, LRA: Lingual re-entrant Angle, LSA: Lingual salient angle (According to Van der Meulen, 1972).

# Family Muridae ILLIGER, 1811
# Subfamily Murinae ILLIGER, 1811

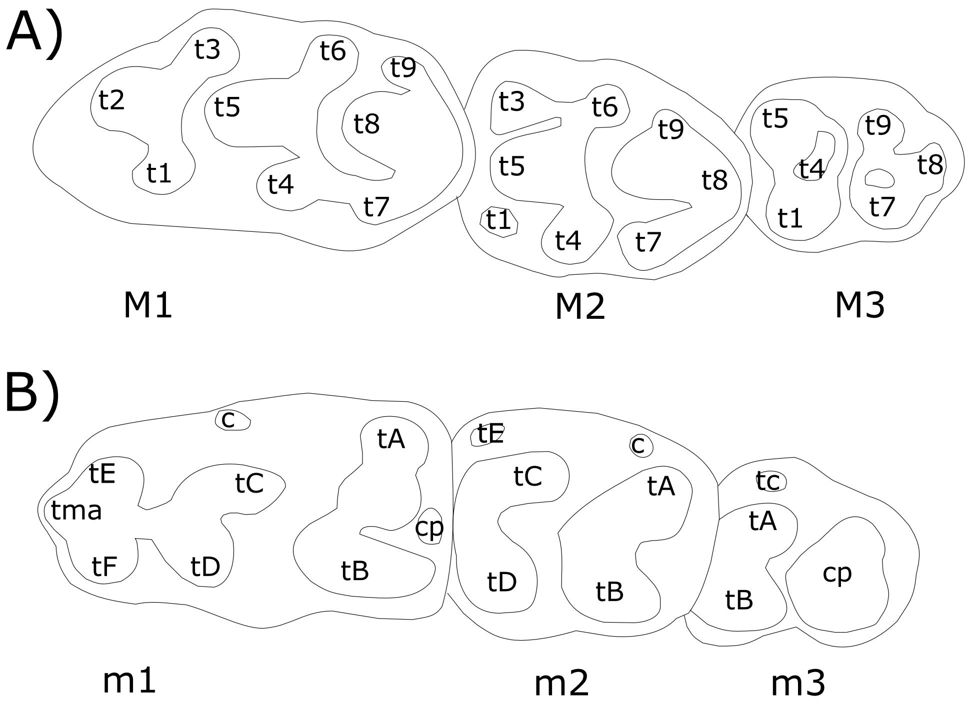

**Fig.7.** Dentition of *Apodemus sylvaticus*. **A)** Right superior molars. T (1-9). Tubercle , t5. protoconid, t6. paraconid, t8. pseudohipoconid o hipoconid, t9. metaconid **B)** Right inferior molars, C. labial accessory tubercles, cp. posterior accessory tubercles, tma. medium tubercle anterior, tF. principal tubercle antero-lingual, tE. principal tubercle antero-labial, tD. metaconid, tC. protoconid, tB. entoconid, tA. Hipoconid (According to Pasquier, 1974).

# Family *Gliridae* THOMAS, 1897

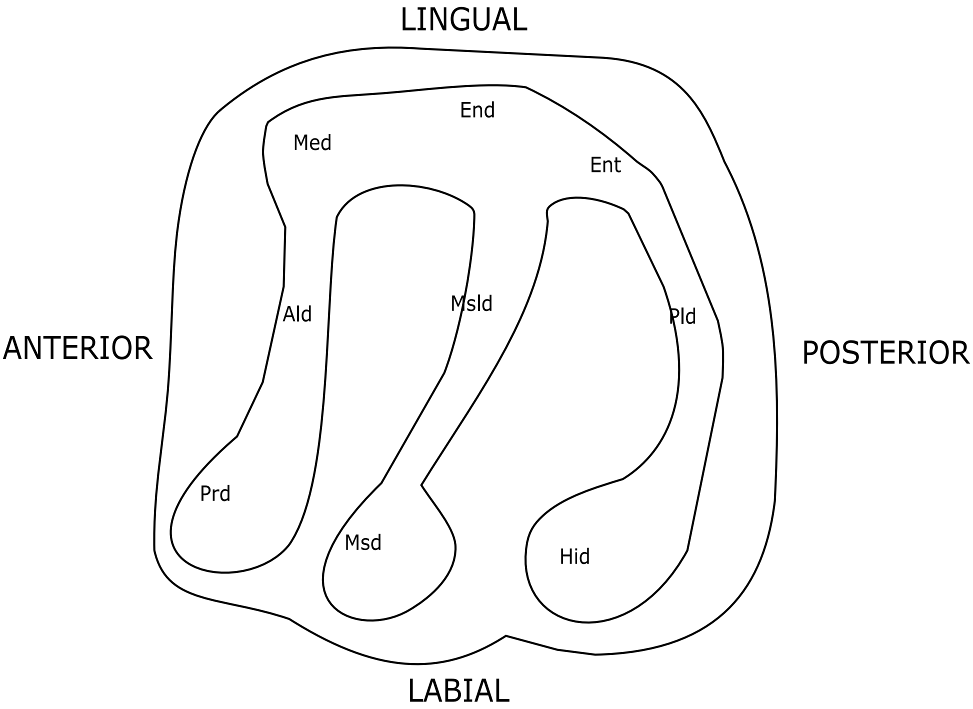

**Fig.8.** First right lower molar (m1) of *Eliomys quercinus*. Ald. anterolofid, End. endolophyd, Ent. entoconid, Hid. hipoconid, Med. metaconid, Msd. mesoconid, Msld. mesolofid, Pld. posterolofid, Prd. Protoconid (According to Damms, 1981).

# A.1.2.SYSTEMATIC PALEONTOLOGY

Class MAMMALIA LINNAEUS, 1758

Order Eulipotyphla DOUADY, 2001

Family Erinaceidae FISCHER VON WALDHEIM, 1817

Genus *Erinaceus* LINNAEUS, 1758

***Erinaceus europaeus*** LINNAEUS, 1758

**Fig.6.** First left upper molar (M1) of *Erinaceus europaeus* in occlusal view from Grottina dei Covoloni del Broion. Scale 1mm.

### MATERIAL

**Grottina dei Covoloni del Broion (4):** 1 second lower premolar (p2) and 1 first upper molar (M1).

### DESCRIPTION

The fourth premolar (p4) presents in labial view well separated paraconid from the protoconid and in the first upper molar (M1) we can observe a large paralofid and a thick regular cingulum (Corbet, 1988), and these characteristics allow us to identify our material as *Erinaceus europaeus*.

## HABITAT

*Erinaceus europaeus* thrives in a variety of man-made habitats including orchards, vineyards, farmland, parks and gardens, including those in urban areas. It also occurs in deciduous woodland, woodland edge and grasslands, although it is less common in these areas .It is typically found at altitudes of up to 600 m, although it can reach 1,500-2,000 m in the Alps (Lapini 1999; Amori, 2016).

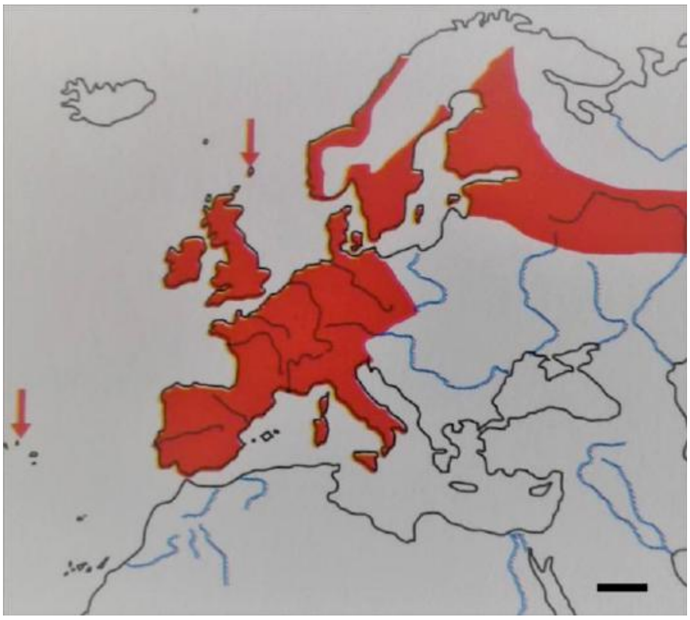

**Fig.7.** Current geographycal distribution of *Erinaceus europaeus*. Scale 100 km (Aulagnier et al.,2015)

## Family Soricidae FISHER, 1817
## Genus *Sorex* LINNAEUS, 1758

### ***Sorex coronatus*** MILLET, 1828

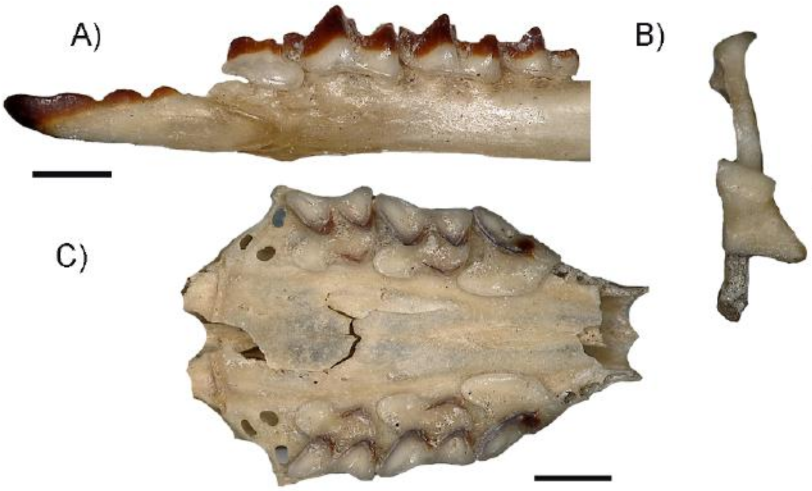

**Fig.8.** Mandible and maxilla of *Sorex coronatus* from El Portalón. A) Left mandible (i-m3) in labial view. B) Articular condyle of left mandible in posterior view. C) Complet maxilla (P4-M3) in occlusal view. Scale 1mm.

## MATERIAL

**El Portalón (UE79):** 13 mandibles and 6 maxilla; **(UE85):** 96 mandibles and 43 maxilla.

### ***Sorex* gr. *coronatus -araneus*** LINNAEUS, 1758

**Fig.9.** Complet maxilla (I2-M3) in occlusal view of *Sorex* gr.*coronatus-araneus* from El Mirador. Scale 1mm.

## MATERIAL

**EL Mirador (MIR49):** 1 first lower molar (m1)**,** 16 mandibles and 14 maxilla; **(MIR24):** 4 mandibles and 1 maxilla**; (MIR19):** 1 first lower molar (m1) and 5 mandibles; **(MIR18):** 1 first lower molar (m1), 25 mandibles, 1 second upper molar (M2) and 17 maxilla; **(MIR17):** 12 mandibles ; **(MIR11)**: 1 mandible; **(MIR10)**: 1 mandible; **(MIR9):** 3 mandibles and 4 maxilla**; (MIR6)**: 1 maxilla**; (MIR5)**: 2 mandibles and 3 maxilla; **(MIR4):** 8 mandibles and 4 maxilla.

## DESCRIPTION

Reumer (1998) described that the genus *Sorex* and genus *Crocidura* can be distinguished by the coloration of the dentition; the teeth in the genus *Sorex* are red, while in the genus *Crocidura* the teeth are white. In the genus *Sorex* the articular condyle is graceful (more large than wide) and presents two separate facets by the interarticular area*,* whose length and width may vary.

The assemblage registered in El Portalón has been identified as *Sorex coronatus.* The mandibles with a developed articular condyle inclined, the coronoid process slightly inclined to distal part and the temporal fosa presents an ovoide morphology.

The material of El Mirador is characterized by being medium-sized and by the pigmentation of the molars, typical of the genus *Sorex*, but we cannot distinguish which species *S. araneus* or *S. coronatus,* the morphology is not clear.

## HABITAT

*Sorex coronatus* inhabits a variety of habitats with dense vegetation at ground level, including woods, hedges, abandoned or unmown meadows, and marshes. It is scarce in intensively cultivated areas, and tends not to occur near to human habitation. Its vertical range is from 0 to 2.200 m (Hausser, 1999; Palomo and Gisbert, 2002; Meinig and Aulagnier, 2016). *Sorex araneus* prefers cool, damp and shady habitats with dense vegetation, such as riparian forests and reed beds. However, it tolerates a broad range of habitats, and it is present in drier areas such as woodland, scrub, road verges, hedges in farmland, and even sand dunes. There are isolated populations in the Pyrenees and the Massif Central (France). It is recorded from sea level to 2.500 m (Hausser *et al.* 1990; Anděra 1999, Hutterer and Kryštufek, 2016).

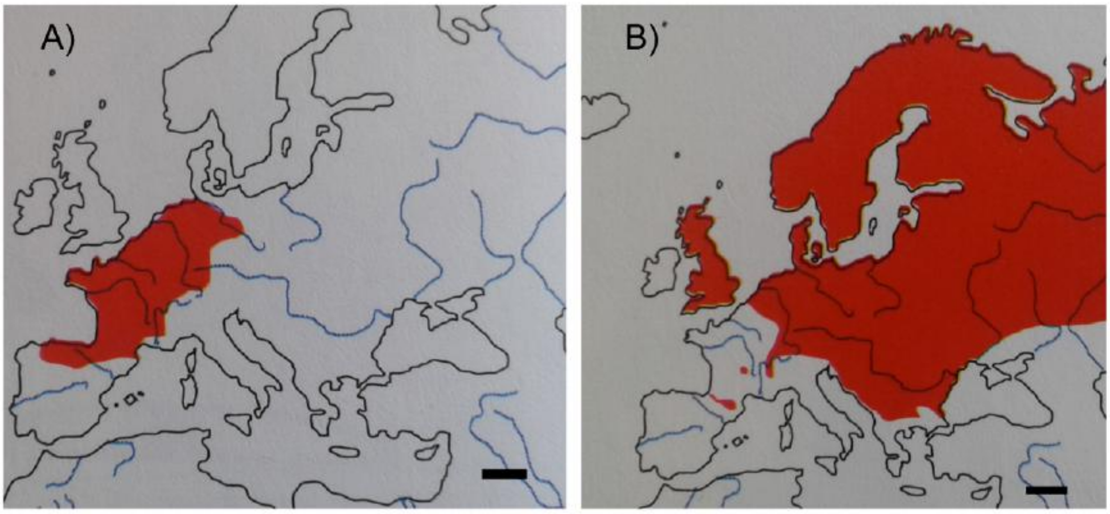

**Fig.10.** Current geographycal distribution of *Sorex coronatus* (A) and *Sorex araneus* (B). Scale 100 km (Aulagnier et al.,2015).

## Genus *Neomys* KAUP, 1829

### ***Neomys anomalus*** CABRERA, 1907

**Fig.11.** Mandible of *Neomys anomalus* from El Mirador. A) Left mandible (i and m2-3) in labial view. B) Articular condyle of left mandible in posterior view. Scale 1mm.

### MATERIAL

**EL Mirador (MIR49):** 1 mandible (i m1 m2).

**El Portalón (UE79):** 1 mandibule (m1) and 1 maxilla (P4 M1); **(UE85):** 1 mandibule (i p4 m1-2-3)

### DESCRIPTION

The coloration of the dentition is red as in the genus *Sorex*, but the difference with this genus is observed in the interarticular area where the upper and lower facets are connected, the articular condyle is extended and strait and the teeth are robust and the lower incisive is straight (Reumer, 1998). Whithin the genus *Neomys*, our material presents a more graceful and small morphology, for this reason we have identified it as *Neomys anomalus*.

## HABITAT

*Neomys anomalus* inhabits lush vegetation next to slow-flowing or still eutrophic waters (marshes, swamps, lakes, rivers, and streams). In general, is less aquatic than *Neomys fodiens* and can colonise areas away from water. It is recorded from sea level to 1,850 m (Spitzenberger 1999; Huterer et al., 2016).

**Fig.12.** Current geographycal distribution of *Neomys anomalus*. Scale 100 km (Aulagnier et al.,2015).

## Subfamily Crocidurinae WAGLER, 1832

## Genus *Crocidura* WAGLER, 1832

### ***Crocidura russula*** HERMANN**,** 1780

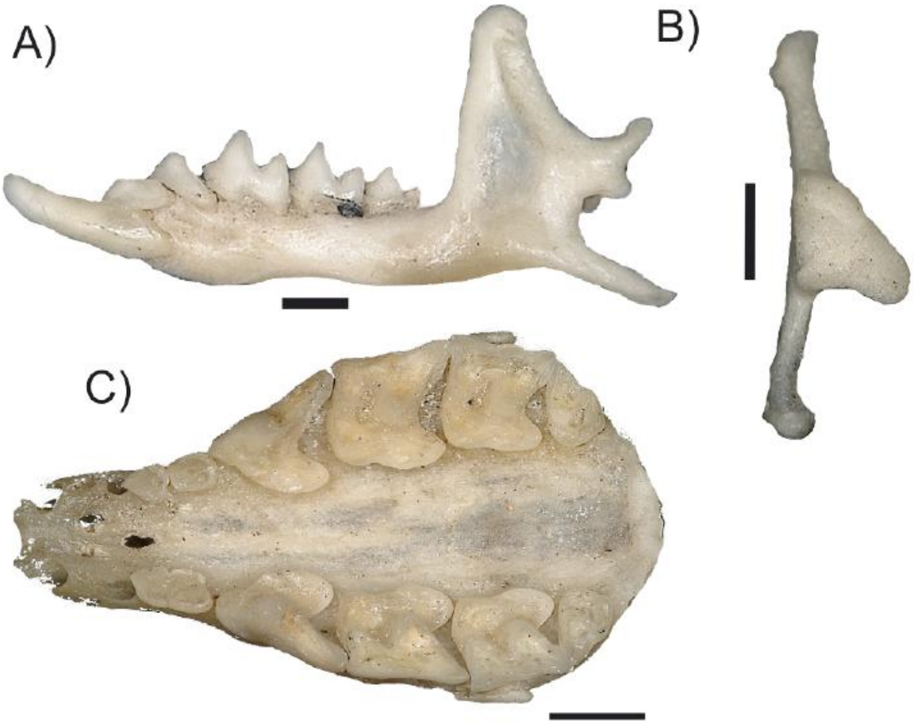

**Fig.13.** A) Left mandible (i-m3) in labial view of *Crocidura russula* from Balma del Gai. B) Articular condyle of left mandible of *Crocidura russula* in posterior view from Balma del Gai. C) Complet maxilla (I3-M3) in occlusal view of *Crocidura russula* from El Portalón. Scale 1mm.

### MATERIAL

**Balma del Gai (1.B):** 1 mandible; **(1.A):** 2 mandibles and 1 maxilla.

**Cova Bonica (IV):** 28 mandibles and 2 maxilla; **(XIX):** 39 mandibles and 19 maxilla**.**

**El Portalón (UE79):** 20 mandibles and 8 maxilla**; (UE85):** 85 mandibles and 49 maxilla.

**EL Mirador (MIR50):** 1 mandible and 1maxilla; **(MIR49):** 47 mandibles and 17 maxilla; **(MIR24):** 9 mandibles and 3 maxilla; **(MIR22):** 1 mandible; **(MIR19):** 9 mandibles and 2 maxilla; **(MIR18):** 28 mandibles and 9 maxilla; **(MIR17):** 18 mandibles and 3 maxilla; **(MIR16):** 2 mandibles; **(MIR11):** 1 maxilla; **(MIR9):** 18 mandibles and 11 maxilla; **(MIR5):** 5 mandibles and 2 maxilla; **(MIR4):** 26 mandibles and 8 maxilla.

## DESCRIPTION

The main characteristics of the genus *Crocidura* are the white color of the teeth, the straight shape of the lower incisive and the completely or partially fusion of the lower and upper facets of articular condyle. Moreover, in *Crocidura russula* the mandibular corpus is robust and thinner coronoid process especially the upper half. The articular surface of the condyle has different outlines, and the ventral emargination of the upper sigmoid notch is much more pronounced (Reumer, 1998). Our assemblage of Balma del Gai, Cova Bonica, El Mirador and El Portalón present these characteristics.

## HABITAT

*Crocidura russula* live in a wide range of habitats including shrubland (maquis), open habitats, forest edges with abundant ground vegetation, cultivated fields, urban areas, gardens, farms, mountainous areas and land adjacent to rivers and streams. It typically occurs from sea level to 1,200 m, but has also been found as high as 2,000 m, particularly in Mediterranean landscapes (Palomo and Gisbert 2002; Aulagnier et al., 2016).

**Fig.14.** Current geographycal distribution of *Crocidura russula*. Scale 100 km (Aulagnier et al.,2015).

## Family Talpidae FISCHER, 1817
## Subfamily Talpinae FISCHER, 1817
## Genus *Talpa* LINNAEUS, 1758

### ***Talpa europaea*** LINNAEUS, 1758

**Fig.15.** Left mandible (c and m1-3) of *Talpa europaea* from El Portalón. A) Left mandible in labial view. B) Left mandible in occlusal view. Scale 1mm.

### MATERIAL

**El Portalón (UE79):** 1 femur; **(UE85):** 1 mandible**,** 1 femur and 1 ulna.

**Grottina dei Covoloni del Broion (4):** 3 mandibles and 1 humerus.

### DESCRIPTION

We have identified our assemblage as *Talpa europaea* because the mandible is elongated and it has the angular and coronoid process robust, contrasting with a delicate, simple and cylindrical articular condyle. Moreover this species presents a big canine characterized by the forward inclination and two roots. The most important characteristic of this species is the robustness of its anterior members as the humerus that presents a peculiar blade shape (Van Cleef-Roders and van den Hoek Ostende, 2001).

## HABITAT

*Talpa europae* is present in most habitats where there is sufficiently deep soil to permit the construction of its extensive burrows. It prefers meadows, pastures, arable land, gardens and parks, and is rarely found in coniferous forests, or habitats with sandy, stony or permanently waterlogged soils. It is found from sea level to 2,400 m (Kryštufek, 1999; Amori et al., 2008 ).

**Fig.16.** Current geographycal distribution of *Talpa europae*. Scale 100 km (Aulagnier et al.,2015).

## Order Chiroptera BLUMENBACH, 1779
## Suborder Microchiroptera DOBSON, 1875
## Family Rhinolophidae GRAY 1866

## Genus *Rhinolophus* LACÉPÈDE, 1779

### ***Rhinolophus ferrumequinum*** SCHREBER, 1774

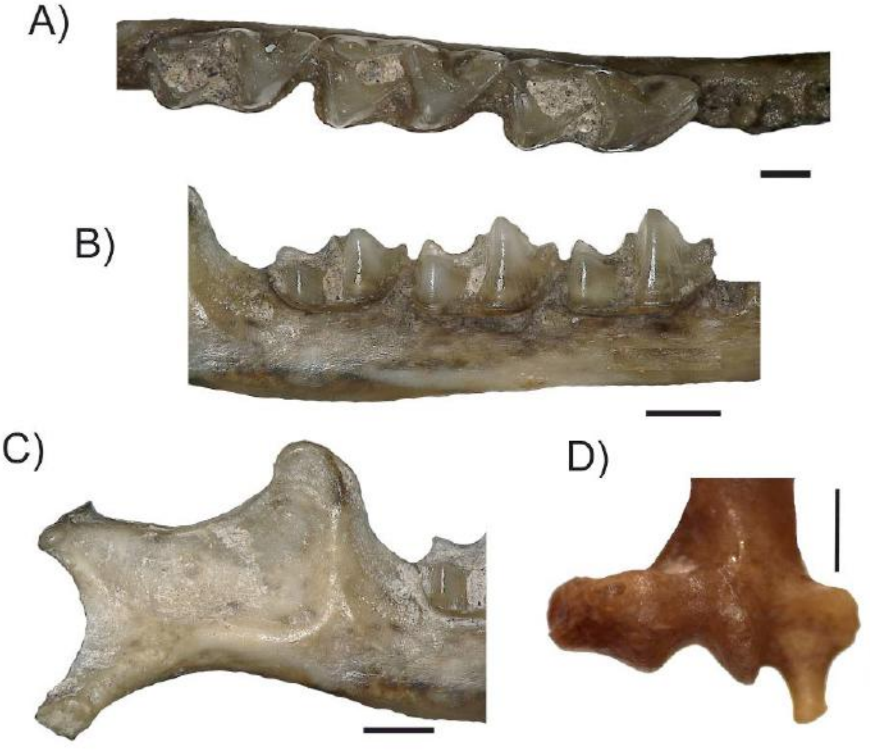

**Fig.17.** Craneal and postcranial remains of *Rhinolophus ferrumequinum* from El Portalón. A) Right mandible in occlusal view. B) Right mandible (m1-3) in labial view. C) Angular process in labial view. D) Left humerus in posterior view of *Rhinolophus ferrumequinum* from El Portalón. Scale 1mm.

## MATERIAL

**Cova Bonica (IV)**: 3 mandibles and 1 humerus.

**El Portalón (UE79)**: 1 humerus; **(UE85)**: 6 mandibles, 1 maxilla and 1 humerus.

**El Mirador (MIR49)**: 1 first lower molar (m1) and 1 mandible.

**Grottina dei Covoloni del Broion (4)**: 2 first lower molar (m1), 1 mandible and 1 humerus (Table 1).

|  | **Dentition** |
|---|---|
| **MANDIBLES** | c p4 m1-2-3 |
|  | p4 m1-2-3 |
|  | p4 m2 |
|  | m1-2-3 |
|  | without |

**Table 1.** Dentition present in the analyzed mandibles of *Rhinolophus ferrumequinum*. Abbreviations: c, canine; p4, fourth lower premolar; m1, first lower molar; m2, second lower molar; m3, third lower molar.

## DESCRIPTION

This genus (*Rhinolophus*) is characterized by the presence of the hypoconulid connected with entoconid in lower molars (m1), morphology called "nyctalodont". The canine lower (c) presents a crown bigger in the labial view than in the lingual. The cingulum is continuous, but in the lingual view is thicker in the distal part and finer in the proximal part. The fourth lower premolar (p4) has two roots, one cusp in the middle of the tooth and a continuous cingulum thicker in the distal and in the mesiolingual part. In the first lower molar (m1), the trigonid is open and the paralofid developed and presents cingulum in the lingual view with regular wide, while in the labial view is finer. The second lower molar (m2) has similar characteristics of first lower molar (m1), but the trigonid is less open and the paralofid is less developed. In the third lower molar (m3) we detected that the trigonid has not cingulum and the talonid is reduced and the cingulum in the distal part of the talonid is not reduced. The distal epiphysis of the humerus has a robust styloid process turned to the inside part; the epitroclea and styloid process are separated by a marked constriction (Sevilla, 1988). All of these characteristics have been observed in our specimens.

## HABITAT

*Rhinolophus ferrumequinum* forages in pastures, deciduous temperate woodland, Mediterranean and sub-mediterranean shrubland and woodland. The requirements for hibernation appear to be within limited confines of temperature and humidity, but vary with age, sex and condition (Hutson *et al.* 2001; Piraccini, 2016).

**Fig.18.** Current geographycal distribution of *Rhinolophus ferrumequinum*. Scale 100 km (Aulagnier et al.,2015).

## ***Rhinolophus* gr. *euryale-mehelyi***

**Fig.19.** Craneal and postcraneal remains of *Rhinolophus* gr*. euryale-mehelyi* from Cova Bonica. A) Right mandible (m1-3) in occlusal view. B) Right mandible in labial view. C) Left humerus in posterior view. Scale 1mm.

## MATERIAL

**Cova Bonica (IV)**: 5 mandibles and 2 humerus.

**El Mirador (MIR49)**: 5 mandibles.

**Grottina dei Covoloni del Broion (4)**: 4 mandibles and 5 humerus (Table 2 ).

| | **Dentition** |
|---|---|
| **MANDIBLES** | c p4 m1-2-3 |
| | p4 m1-2-3 |
| | p4 m1-2 |
| | p4 m2 |
| | m1-2-3 |
| | m1-2 |
| | m2-3 |
| | without |

**Table 2.** Dentition present in the analized mandibles of *Rhinolophus euryale-mehelyi*. Abbreviations: c, canine; p4, fourth lower premolar; m1, first lower molar; m2, second lower molar; m3, third lower molar.

## DESCRIPTION

We have observed a fine lingual and labial cingulum in the first and second lower molar, present a fine and irregular cingulum. Moreover, in lower molars the hypoconulid is connected with entoconid, this morphology is called "nyctalodont". The upper canine is robust and p4 is trapezoidal with a slight cusp. The trigonid is open in the first lower molar (m1), in the second lower molar (m2) is a little more closed and more in the third lower molar (m3). In the first lower molar (m1) we have registered a paralofid with a curved entocristid, and in the second lower molar (m2) the entocristid is curved too. The third lower molar not presents lingual cingulum in the trigonid and a reduced talonid. The mandible without teeth is thickened. The coronoideus process is a vertical thin triangular blade with the tip slightly flattened towards posterior side and the angular process is an isosceles triangle with a rounded tip. The distal epiphysis of the humerus has a relatively long and thin styloid process turned to the inside part; the epitroclea and styloid process are separated by a marked constriction (Sevilla, 1988).
This morphology is representative of genus *Rhinolophus* and within this genus. Our fossil bats have characteristics of medium size *Rhinolophus*, as *Rhinolophus euryale* or *Rhinolophus mehelyi,* but these species have a very similar morphology and we cannot distinguish them.

## HABITAT

*Rhinolophus euryale* forages in Mediterranean and sub-Mediterranean shrubland and woodland. In Italy, preferred foraging habitats are broadleaved woodland and riparian vegetation; coniferous woodland is avoided, and shrubland is rarely used. In Spain, foraging activities take place mostly in woodland edges and isolated trees. It is widely distributed over its range, and is found from sea level to 1,360 m (Russo et al. 2002; Goiti et al. 2008; Juste and Alcalde, 2016 ). *Rhinolophus mehelyi* forages in Mediterranean shrubland and woodland, in dry steppes and particularly link to water bodies. Winter hibernacula are in colder underground sites (usually large caves with a constant microclimate) (Salsamendi et al. 2012; Alcalde et al 2016).

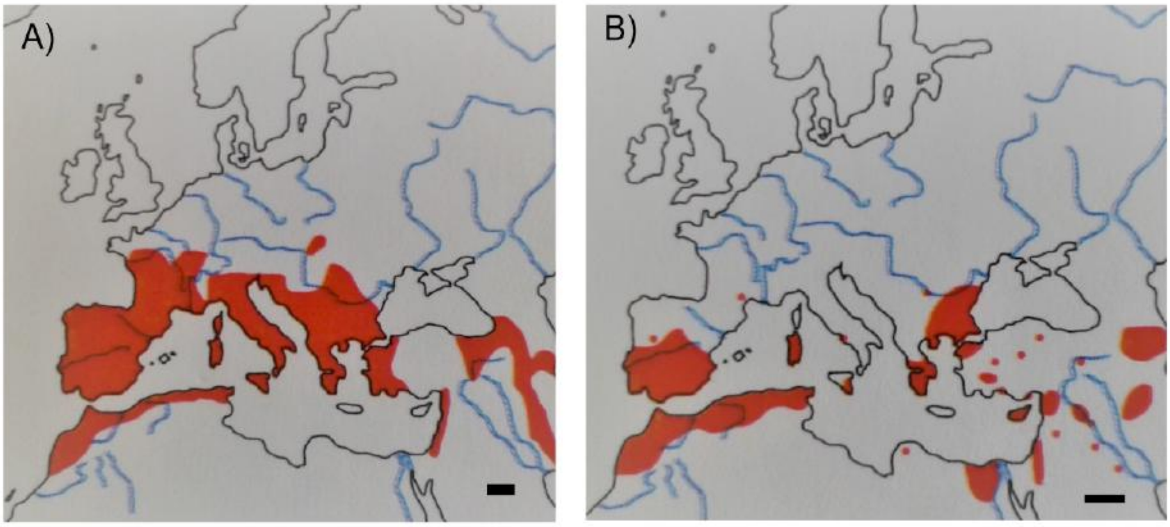

**Fig.20.** Current geographycal distribution of *Rhinolophus euryale* (A) and *Rhinolophus mehelyi* (B). Scale 100 km (Aulagnier et al.,2015).

## Family Miniopteridae DOBSON, 1875
## Genus *Miniopterus* BONAPARTE, 1837

### ***Miniopterus schreibersii*** **KUHL, 1817**

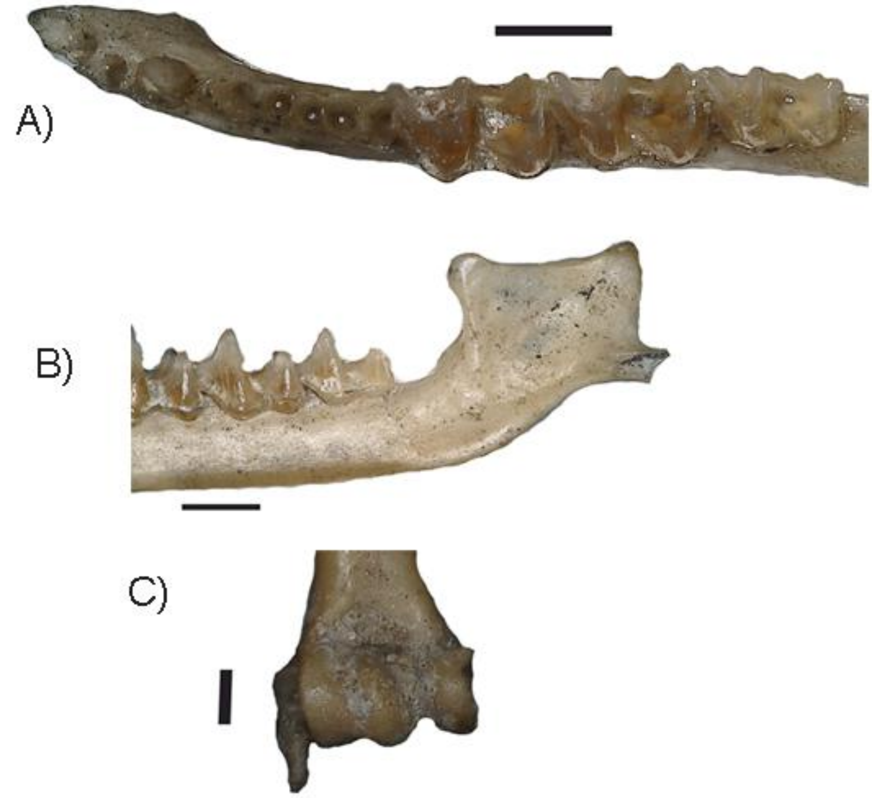

**Fig.21.** Craneal and postcraneal remains of *Miniopterus schreibersii* from Grottina dei Covoloni del Broion. A) Left mandible (m1-3) in occulsal view. B) Left mandible in labial view. C) Right humerus in posterior view. Scale 1mm.

## MATERIAL

**Cova Bonica (IV)**: 3 mandibles and 2 humerus.

**El Portalón (UE79)**: 1 humerus; **(UE85)**: 6 mandibles, 1 maxilla and 1 humerus.

**El Mirador (MIR49)**: 3 mandibles; **(MIR24)**: 2 mandibles; **(MIR19)**: 1 mandible; **(MIR18)**: 1 first lower molar (m1); **(MIR9)**: 2 mandibles (Table 3).

|  | **Dentition** |
|---|---|
| **MANDIBLES** | p3-p4 m1-2-3 |
|  | p3-p4 m1 |
|  | p4 m1-2-3 |
|  | p4 m1-2 |
|  | p4 m1-3 |
|  | p4 m1 |
|  | m1-2-3 |
|  | m1-2 |
|  | m2-3 |
|  | without |

**Table 3.** Dentition present in the analyzed mandibles of *Miniopterus schreibersii*. Abbreviations: p3, third lower premolar; p4, fourth lower premolar; m1, first lower molar; m2, second lower molar; m3, third lower molar.

## DESCRIPTION

These teeth present an irregular cingulum and “nyctalodont” pattern (hypoconulid connected with entoconid) in lower molars. In the first (M1) and second (M2) upper molars we have observed a fine cingulum in the mesial and lingual part but this cingulum is thicker in the heel. Moreover the parastyle is developed and the metastyle is curved slightly. The third upper molar (M3) presents three roots, an isolated and fine cingulum in the mesial part of the protoconid, and a parastyle more developed than in M1 and M2. In the third lower premolar (p3) has two roots, characteristic of the genus *Miniopterus*. In the third (p3) and fourth (p4) lower premolar we have registered a continuous cingulum is is thicker in the lingual. The first (m1) and second (m2) lower molar presents a fine cingulum, thick in the protoconid and a curved entocristid. Although trigonid is regular in the first lower molar (m1) and closed in the second lower molar (m2). Finally in the first lower molar (m3) we have observed a fine cingulum more regular than in the m1 and m2, a curved entocristid and closed trigonid. Moreover, in the mandibles we can observe that coronoid process is a thick blade exteriorly directed, terminally rounded; angular process is short, with a tip turned up towards exterior; in dorsal view. The distal epiphysis of the humerus has a long styloid process in the shape of a hook; the epitroclea is not very wide, and the condyle and epicondyle are separated by a marked constriction (Sevilla, 1988). These characteristics allow us to identify our material as *Miniopterus schreibersii.*

## HABITAT

*Miniopterus schreibersii* forages in a variety of open and semi-open natural and artificial habitats, including suburban areas. Large warm caves are preferred during the nursing season. In winter it hibernates in underground sites (usually large caves with a constant microclimate) (Hutterer et al. 2005; Hutson et al., 2008).

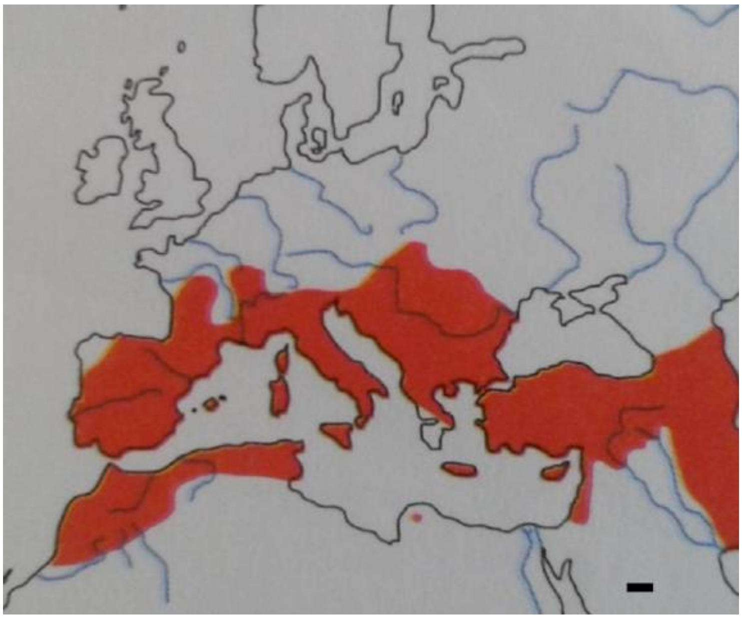

**Fig.22.** Current geographycal distribution of *Miniopterus schreibersii*. Scale 100 km (Aulagnier et al.,2015).

## Genus *Plecotus* GEOFFROY, 1818

### ***Plecotus auritus*** LINNAEUS, 1758

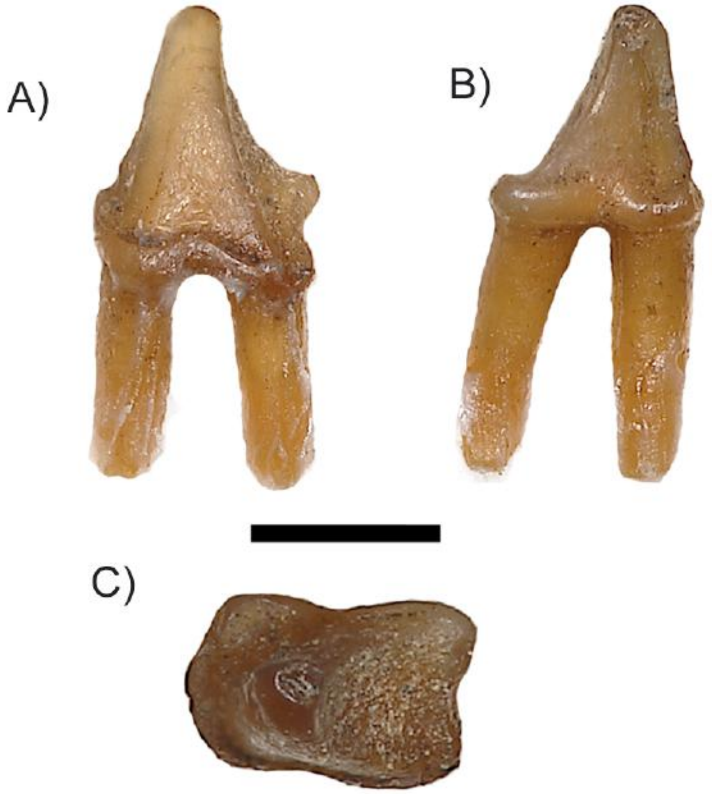

**Fig.23.** Fourth lower premolar (p4) of *Plecotus auritus* from El Mirador. A) p4 in lingual view. B) p4 in labial view. C) p4 in occulsal view. Scale 1mm.

### MATERIAL

**Mirador (MIR49):** fourth lower premolar (p4).

### DESCRIPTION

The fourth lower premolar (p4) has a trapezoidal profile with one cusp in the middle of the teeth. This cusp presents three sides; the distal side is concave, the labial side is convex and the lingual side is concave in his anterior half and convex in his posterior half. The cingulum is continuous (Sevilla, 1988). For these reasons we considered that this fourth lower premolar belongs to *Plecotus auritus.*

### HABITAT

*Plecotus auritus* forages in the vicinity of the roost in deciduous and coniferous woodlands, along hedgerows, and in isolated trees. In winter it hibernates in caves, mines, buildings and occasionally trees (Gaisler *et al.* 2003; Hutson et al., 2008).

**Fig.24.** Current geographycal distribution of *Plecotus auritus*. Scale 100 km (Aulagnier et al.,2015).

## Genus *Nyctalus* BOWDICH, 1825

### ***Nyctalus noctula*** SCHREBER, 1774

**Fig.25.** Mandible (p4 and m2) of *Nyctalus noctula* from El Mirador. A) Right mandible in occlusal view. B) Right mandible in labial view. Scale 1mm.

### MATERIAL

**Mirador (MIR49):** 1 mandible with fourth lower premolar (p4) and second lower molar (m2)

### DESCRIPTION

We have scarce material but we identified this mandible as *Nyctalus noctula* because second lower molar presents an irregular cingulum and “nyctalodont” pattern. In the mandible we have observed an elliptical symphysis with a well-defined distal projection, “mental foramen” under the anterior margin of p3 and one-rooted p3. Moreover it has a thin mandibular ramus centrally, concave towards angular process; coronoid process is like a triangular blade, with a rounded tip and slightly directed to anterior part (Sevilla, 1988).

## HABITAT

*Nyctalus noctula* forages over wetland, woodland and pasture. Summer colonies are in tree holes, sometimes in buildings. Winter hibernacula are in rock crevices, caves, occasionally artificial structures (Csorba et al., 2016).

**Fig.26.** Current geographycal distribution of *Nyctalus noctula*. Scale 100 km (Aulagnier et al.,2015)

## Family Vespertilionidae GRAY, 1821
## Subfamily Vespertilioninae GRAY, 1821
## Genus *Myotis* KAUP, 1829

### ***Myotis* gr. *myotis-blythii***

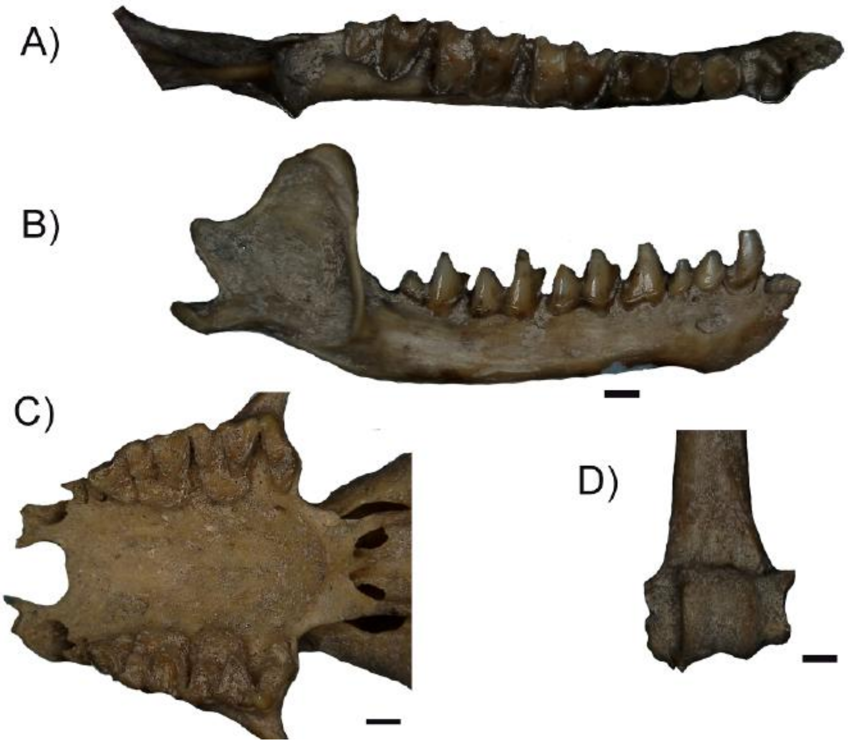

**Fig.27.** Craneal and postcraneal remains of *Myotis* gr. *myotis-blythii* from Cova Bonica and from El Mirador. A) Right mandible (c-m3) in oclusal view. B) Right mandible in labial view. C) Complet maxilla (P4-M3) in occlusal view. D) Right humerus in posterior view. Scale 1mm.

## MATERIAL

**Cova Bonica (IV)**: 1 fourth lower premolar (p4), 2 first lower molar (m1), 1 second lower molar (m2), 73 mandibles, 25 maxilla and 19 humerus.

**El Portalón (UE79)**: 1 mandible, 1 maxilla and 1 humerus; **(UE85)**: 3 first lower molar (m1),1 second lower molar (m2), 8 mandibles, 1 second upper molar (M2), 1 maxilla and 1 humerus.

**El Mirador (MIR51)**: 1 humerus **(MIR50)**: 10 mandibles, 2 first upper molar (M1) ,1 second upper molar (M2) and 2 maxilla **(MIR49)**: 1 second lower molar (m2), 23 mandibles, 1 first upper molar (M1) and 23 maxilla **(MIR24)**: 2 mandibles **(MIR22)**: 1 mandible and 1 second upper molar (M2) **(MIR18)**: 2mandible and 1 maxilla **(MIR10)**: 1maxilla **(MIR9)**: 1 mandible and 2 maxilla (Table 4 and 5).

| | **Dentition** |
|---|---|
| **MANDIBLES** | c p2-3-4 m1-2-3 |
| | c p2-3-4 m1-3 |
| | c p2-3-4 m2-3 |
| | c p4 m1-2-3 |
| | p2-3-4 m1-2-3 |
| | p2-4 m1-2-3 |
| | p3-4 m1-2-3 |
| | p3-4 m2-3 |
| | p3-4 m3 |
| | p4 m1-2-3 |
| | p4 m1-2 |
| | p4 m2-3 |
| | p4 m1 |
| | p4 m3 |
| | p4 |
| | m1-2-3 |
| | m1-2 |
| | m2-3 |
| | m1 |
| | m2 |
| | m3 |
| | without |

**Table 4.** Dentition present in the analyzed mandibles of *Myotis* gr. *myotis-blythii*. Abbreviations: c, canine; p2,second lower premolar; p3, third lower premolar; p4, fourth lower premolar; m1, first lower molar; m2, second lower molar; m3, third lower molar.

| | **Dentition** |
|---|---|
| **MAXILLA** | P3-4 M1-2-3 |
| | P3 M1 |
| | P3 |
| | P4 M1-2-3 |
| | P4 M2-3 |
| | P4 M1 |
| | P4 |
| | M1-2-3 |
| | M2-3 |
| | M2 |

**Table 5.** Dentition present in the analyzed maxilla of *Myotis* gr. *myotis-blythii*. Abbreviations: P3, third upper premolar; P4, fourth upper premolar; M1, first upper molar; M2, second upper molar; M3, third upper molar.

## DESCRIPTION

The material that we have identified as *Myotis* gr. *myotis-blythii*, present a typical features of the genus *Myotis.* The mandibular ramus is wide and the coronoid process is higher in relation to the articular process. The lower molars are myotodont (hypoconulid clearly separated from the entoconid), the thick and quite irregular cingulum present in all teeth. In the upper molars we have not observed heel neither hipoconid, also the third upper molar is reduced. The distal epiphysis of the humerus has a reduced styloid process and the proximal edge of the epitroclea does not reach the epiphyseal border (Sevilla, 1988).

All of these features together with the large size of this specimens indicated that these remains could be *M. myotis* or *M. blythii*, but both species are difficult to distinguish from each other due to the morphology extremely similar.

## HABITAT

*Myotis myotis* forages over deciduous woodland edge, open deciduous woodland and pasture Occasionally it forms small colonies in trees. It is an occasional migrant (Simon *et al.,* 2004; Coroiu et al., 2016). *Myotis blythii* forages in scrub and grassland habitats, including farmland and gardens. It hibernates in winter in underground sites with a relatively constant temperature of 6-12ºC (Hutterer *et al.* 2005; Juste and Paunović, 2016).

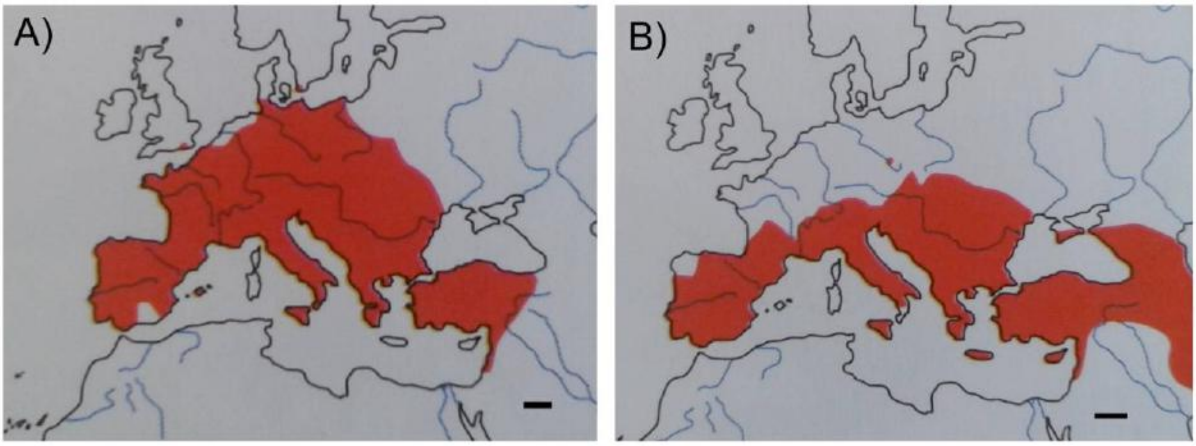

**Fig.28.** Current geographycal distribution of *Myotis myotis* and *Myotis blythii*. Scale 100 km (Aulagnier et al.,2015).

## ***Myotis nattereri*** KUHL, 1817

**Fig.29.** Right mandible of *Myotis nattereri* from Cova Bonica. A) Mandible in occlusal view. B) Mandible in labial view. Scale 1mm

### MATERIAL

**Cova Bonica (IV)**: 3 mandibles and 1 maxilla **(Table 6).**

| | Dentition |
|---|---|
| **MANDIBLES** | p4 m1-2-3 |
| | m1-2-3 |
| **MAXILLA** | P4 M1-2-3 |
| | P4 M2-3 |

**Table 6.** Dentition present in the analyzed mandibles and maxilla of *Myotis nattereri*. Abbreviations: p4, fourth lower premolar; m1, first lower molar; m2, second lower molar; m3, third lower molar; P4, fourth upper premolar; M1, first l upper molar; M2, second upper molar; M3, third upper molar.

### DESCRIPTION

The p4 is characterized in occlusal view by its rectangular outline and a single cusp rising at the centre of the crown, with three faces: the distal and lingual ones slightly convex, and the labial one concave. In labial view the cingulum is thick and continuous along the whole perimeter of the tooth. The lower molars are characterized in occlusal view by a myotodont pattern (hypoconulid clearly separated from the entoconid), also the cingulum is thick and irregular in the labial view and present a small lingual cingulum in the trigonid. The first lower molar has a regular trigonid, the protoconid and the metaconid are separated and the entocristid is straight, and the lingual cusps are aligned in m1 and m2. The m2 and m3 have a closed trigonid (forming a V-shape). The P4 presents a trapezoidal outline with a mesial part concave and a continuos cingulum except in the distal part, but the thickness is regular. The M1 and M2 is characterized by possessing a subrectangular outline; the parastyle highly developed, forming an angle with the preparacristid; the metastyle less developed and slightly curved; the cingulum disappears in the base of the protoconid and is small in the mesolingual base (Sevilla, 1988). These characteristics representative of *Myotis nattereri* allow us to identify our specimens.

## HABITAT

*Myotis nattereri* forages in woodland (Mediterranean pine and oak forest), shrubland and parkland, sometimes over water, pasture, and road verges. It occurs in humid areas, and in dry areas it is dependant on water bodies (Hutson et al. 2008).

**Fig.30.** Current geographycal distribution of *Myotis nattereri*. Scale 100 km (Aulagnier et al.,2015).

## ***Myotis bechsteinii*** KUHL, 1818

**Fig.31.** Left mandible of *Myotis bechsteinii* from El Mirador. A) Mandible in occlusal view. B) Mandible in labial view. Scale 1mm.

### MATERIAL

**Mirador (MIR49)**: 7 mandibles (Table 7).

| | **Dentition** |
|---|---|
| **MANDIBLES** | p3-p4 m1-2-3 |
| | p4 m1-2-3 |
| | p4 m2-3 |
| | m1-2-3 |
| | m1-2 |
| | m3 |

**Table 7.** Dentition present in the analyzed mandibles of *Myotis bechsteinii*. Abbreviations: p3, third lower premolar; p4, fourth lower premolar; m1, first lower molar; m2, second lower molar; m3, third lower molar.

## DESCRIPTION

Our material identified as *Myotis bechsteinii* presents in p4 a rectangular outline with one cusp and a cingulum thick and continuous. In the m1 the trigonid is regular and presents lingual cingulum; entocristid is straight; in the lingual view the metaconid is taller than other lingual cusps. The m3 has a trigonid regular too, but without cingulum and hypoconulid and talonid are reduced (Sevilla, 1988).

## HABITAT

*Myotis bechsteinii* has specialized habitat requirements and is largely dependent on mature natural forests. In Europe, it tends to prefer mature deciduous woodland of beech and oak with a high proportion of old trees. Densities of this species are highest in forests that are managed according to environmental (rather than strictly economic) principles. It is occasionally found in artificial hábitats such as pasture, plantations (especially orchards) and rural gardens (Paunović, 2016).

**Fig.32.** Current geographycal distribution of *Myotis bechsteinii*. Scale 100 km (Aulagnier et al.,2015).

## Order Rodentia BOWDICH, 1821
## Family Sciuridae FISHER, 1817
## Subfamily Xerinae OSBORN, 1910
## Genus *Marmota* BLUMENBACH, 1779

### ***Marmota Marmota*** LINNAEUS, 1758

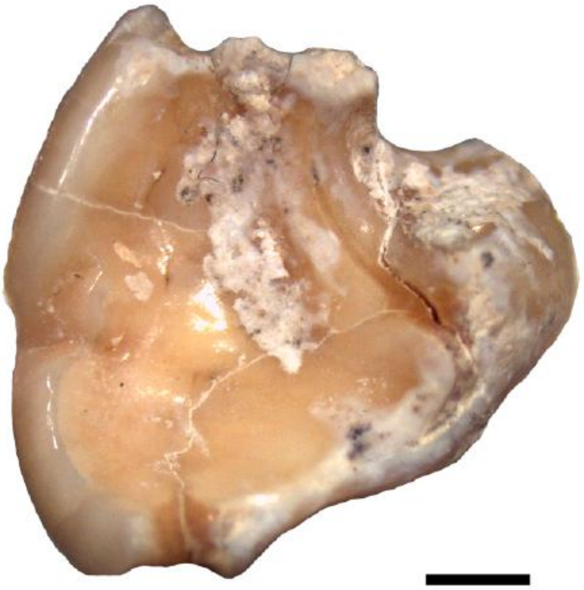

**Fig.33.** Third left upper molar (M3) in occlusal view of *Marmota marmota* from Grottina dei Covoloni del Broion. Scale 1mm.

## MATERIAL

**Grottina dei Covoloni del Broion (4):** third upper molar (M3)

## DESCRIPTION

This third upper molar (M3) presents three extern tubercles and one inner, the anterior crest is more developed than the posterior and the proximal part of the tooth is forward extended (Chaline, 1972), representative morphology of *Marmota marmota*.

## HABITAT

*Marmota marmota* inhabits alpine meadows and high-altitude pastures, typically on south facing slopes from 1,200-3,000 m (although it is occasionally found at lower altitudes). Colonies inhabit deep burrow systems in alluvial soil or rocky areas (Cassola, 2016).

**Fig.34.** Current geographycal distribution of *Marmota marmota*. Scale 100 km (Aulagnier et al., 2015)

## Family Cricetidae FISHER, 1817

## Subfamily Arvicolinae GRAY, 1821

## Genus *Clethrionomys* TILESIUS, 1850

### ***Clethrionomys glareolus*** SCHREBER, 1780

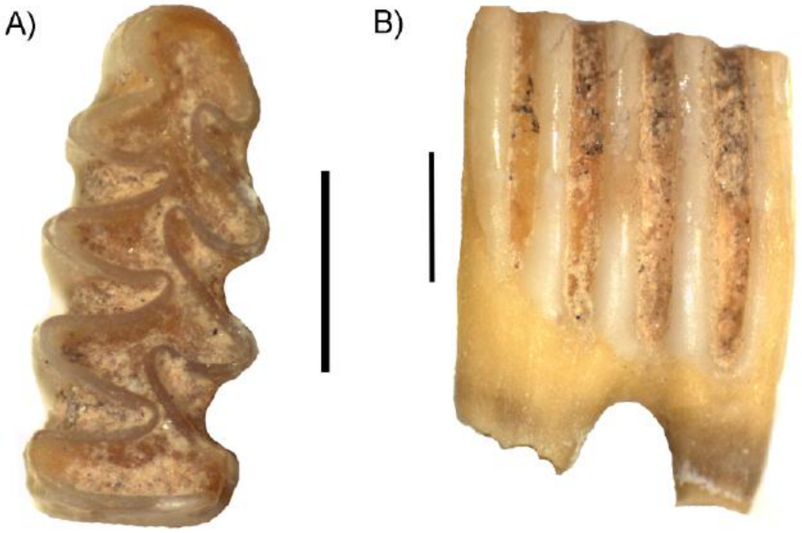

**Fig.35.** First right lower molar (m1) of *Clethrionomys glareolus* from Grottina dei Covoloni del Broion. A) Occlusal view, B) Labial view. Scale 1mm.

### MATERIAL

**EL Mirador (MIR49):** 1 mandible**.**

**Grottina dei Covoloni del Broion (8):** 2 first lower molar (m1) and 3 mandibles**.**

### DESCRIPTION

*C. glareolus* is the only current arvicolid with roots and cement in the lingual and labial re-entrant angles, and it has confluent angles and continuos wide enamel in the occlusal view (Chaline, 1972). These characteristics have been observed in our specimens.

## HABITAT

*C. glareolus* inhabits all kinds of woodland, preferring densely-vegetated clearings, woodland edge, and river and stream banks in forests. It is also found in scrub, parkland, and hedges (Hutterer et al., 2016).

**Fig.36.** Current geographycal distribution of *Clethrionomys glareolus*. Scale 100 km (Aulagnier et al., 2015)

## Genus *Arvicola* LACEPÈDE, 1799

### ***Arvicola sapidus*** MILLER, 1908

**Fig.37.** First left lower molar (m1) in occlusal view of *Arvicola sapidus* from Balma del Gai. Scale 1mm.

### MATERIAL

**Balma del Gai (1.B):** 3 first lower molar (m1)**; (1.A):** 3 mandibles and 1 maxila.

**El Portalón (UE79):** 1 first upper molar (M1).

### DESCRIPTION

This genus is characterized by large size and by having five isolated triangles and the cement is present in all species. *Arvicola sapidus* has an angular anteroconid complex (AC). Moreover, *Arvicola sapidus* have enamel "*Arvicola* or *Mimomys*" type thinner in the leading edges than the trailing edges of the triangles (Chaline, 1972). For these reasons we can identify the material of Balma del Gai and El Portalón as *Arvicola sapidus.*

## HABITAT

*Arvicola sapidus* prefers small freshwater lakes, ponds and slow-moving rivers and streams with dense riparian vegetation. It sometimes occurs in drainage ditches and wet fields. Abundant hydrophilic vegetation and shorelines suitable for water vole burrowing activity seem to be essential characteristics of water vole habitat (Rigaux et al., 2016).

**Fig.38.** Current geographycal distribution of *Arvicola sapidus*. Scale 100 km (Aulagnier et al., 2015)

## ***Arvicola amphibius*** LINNAEUS, 1758

**Fig.39.** First right lower molar (m1) in occlusal view of *Arvicola amphibius* from Grottina dei Covoloni del Broion. Scale 1mm.

### MATERIAL

**El Portalón (UE85):** 1 first lower molar (m1) and 2 first upper molar (M1).

**El Mirador (MIR49):** 1 first lower molar (m1) and 3 mandibles**.**

**Grottina dei Covoloni del Broion (8):** 12 first lower molar (m1), 4 mandibles and 1 first upper molar (M1)**; (4):** 3 first lower molar (m1).

### DESCRIPTION

We can point that these teeth belong to *Arvicola amphibius,* because presents five isolated triangles with cement, a rounded anteroconid complex (AC) and enamel *"Microtus"* type*,* thinner in the trailing edges than the leading edges of the re-entrant angles (Chaline, 1972).

### HABITAT

*Arvicola amphibius* is adaptable and survives in a range of habitats around rivers, streams and marshes in the lowlands and the mountains. It occurs around streams and irrigation ditches (Batsaikhan et al., 2016).

**Fig.40.** Current geographycal distribution of *Arvicola amphibius*. Scale 100 km (Aulagnier et al.,2015)

## Genus *Chionomys* MILLER, 1908

### ***Chionomys nivalis*** MARTINS, 1842

**Fig.41.** First right lower molar (m1) in occlusal view of *Chionomys nivalis* from Grottina dei Covoloni del Broion. Scale 1mm.

### MATERIAL

**Balma del Gai (1.B):** 1 first lower molar (m1).

**EL Mirador (MIR51):** 1 mandible; **(MIR49):** 1 first lower molar (m1).

**Grottina dei Covoloni del Broion (8):** 1 first lower molar (m1) and 5 mandibles.

### DESCRIPTION

According to Chaline (1972), we can observe in our specimens that the first lower molar have four salient closed angles (LSA2, BSA2, LSA3, BSA3) and the salient angle of T5 (LSA4) is more or less open to anteroconid complex. The morphology of anteroconid complex (AC) is characteristic, it has rounded form inclinated to labial part. The enamel is *Microtus* type and it has cement. All of these characteristics are representative of *Chionomys nivalis.*

## HABITAT

Nowadays, *Chionomys nivalis* lives mountain areas with south direction, in open areas with scarce vegetation cover, rocky areas, typically above the tree-line (Amori, 1999; Krystufek, 2016).

**Fig.42.** Current geographycal distribution of *Chionomys nivalis*. Scale 100 km (Aulagnier et al.,2015)

## Genus *Iberomys* CHALINE, 1972

### ***Iberomys cabrerae*** THOMAS, 1906

**Fig.43.** Left mandible in occlusal view of *Iberomys cabrerae* from Cova Bonica.Scale 1mm.

## MATERIAL

**Cova Bonica (IV)**: 21 first lower molar (m1) and 80 mandibles; **(XIX)**: 4 first lower molar (m1) and 2 mandibles.

**Balma del Gai (1.B)**: 1 first lower molar (m1); **(1.A)**: 1 first lower molar (m1).

## DESCRIPTION

*Iberomys* was described by Chaline in 1972 as a subgenus of *Microtus*. Althought Cuenca-Bescós *et al.* (2014) observed morphological, genetic, biological and ecological differences that allow *Iberomys* to be established as a genus, and that it should include the species *I. huescarensis*, *I. brecciensis* and *I. cabrerae*.

*Iberomys cabrerae* is characterized by big and wide first lower molars (m1), by the reduction of the anteroconid complex angles, salient lingual angles that are markedly longer in a latero-medial direction, and an anteroconid complex that is triangular-quadrangular in shape, with abundant cement in the synclines. These morphologic characteristics allow us to identify our specimens as *Iberomys cabrerae*.

## HABITAT

*Iberomys cabrerae* is currently an endemic species of the Iberian Peninsula. It is a typically Mediterranean species, which is specifically adapted to withstand high summer temperatures. This species occurs mainly at medium altitudes, in brushwood near small streams, in riverside areas with sedges or rushes or in fields of tall grass, and is frequently associated with oak *Quercus* sp. woods (Santos et al. 2006).

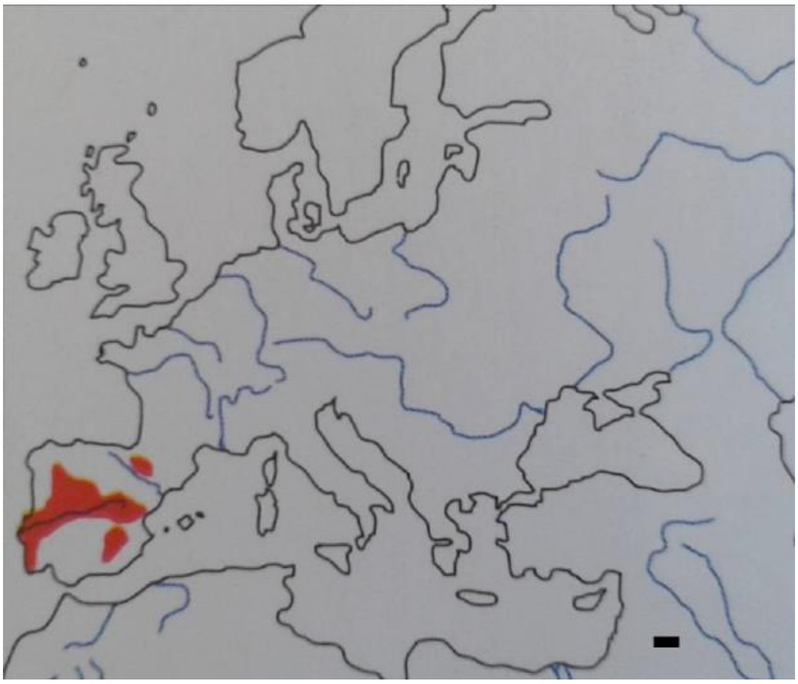

**Fig.44.** Current geographycal distribution of *Iberomys cabrerae*. Scale 100 km (Aulagnier et al.,2015)

## Genus *Microtus* SCHRANK, 1798

### ***Microtus oeconomus*** PALLAS, 1776

**Fig.45.** First left lower molar (m1) in occlusal view of *Microtus oeconomus* from Grottina dei Covoloni del Broion. Scale 1mm.

#### MATERIAL

**EL Mirador (MIR51):** 4 first lower molar (m1) and 2 mandibles; **(MIR49):** 1 mandible.

**Grottina dei Covoloni del Broion (8):** 2 mandibles.

#### DESCRIPTION

The main morphologic characteristic of this genus is that the salient angles T4 (BSA3) and T5 (LSA4) of the first lower molar are closed, besides has four angles in the lingual part. Moreover the genus *Microtus* and *Chionomys*, and the subgenus *Terricola*, have a characteristic enamel, "*Microtus"* type. This enamel is wider in the mesial part than distal part of the molars oclusal angles (Chaline, 1972).

We can observe the morphologic characteristics of *Microtus oeconomus* in our specimens. The dentition is the biggest in the genus *Microtus*. The first lower molar have three salient closed angles (LSA2, BSA2, LSA3), with T4 (BSA3) and T5 (LSA4) alternates but T5 (LSA4) is confluent with T7 (BSA4) and the anteroconid complex. The anterior complex is asymmetric, and the T6 is reduced (Chaline, 1972).

## HABITAT

*Microtus oeconomus* typically inhabits damp, densely-vegetated areas along the edges of lakes, streams and marshes; may be found in tundra, taiga, forest-steppe, and even semi-desert. Wet meadows, bogs, fens, riverbanks and flooded shores are all important habitats (van Apeldoorn 1999; Linzey et al., 2016).

**Fig.46.** Current geographycal distribution of *Microtus oeconomus*. Scale 100 km (Aulagnier et al.,2015)

## ***Microtus agrestis*** LINNAEUS, 1761

**Fig.47.** First right lower molar (m1) in occlusal view of *Micortus agrestis* from El Mirador. Scale 1mm.

### MATERIAL

**Balma del Gai** (**1.B): 2** first lower molar (m1); **(1.A):** 1 first lower molar (m1).

**El Portalón (UE79):** 10 first lower molar (m1) and 1 mandible; **(UE85):** 24 first lower molar (m1) and 2 mandibles.

**EL Mirador (MIR51):** 10 first lower molar (m1) and 3 mandibles **; (MIR50)**: 6 first lower molar (m1) and 2 mandibles; **(MIR49):** 63 first lower molar (m1) and 3 mandibles **; (MIR24):** 29 first lower molar (m1); **(MIR23):** 1 first lower molar (m1); **(MIR21):** 6 first lower molar (m1); **(MIR19):** 28 first lower molar (m1) and 2 mandibles **; (MIR18):** 59 first lower molar (m1) and 2 mandibles; **(MIR17):** 39 first lower molar (m1) and 4 mandibles; **(MIR16):** 2 first lower molar (m1); **(MIR10):** 2 first lower molar (m1); **(MIR9):** 11 first lower molar (m1) and 6 mandibles; **(MIR6):** 4 first lower molar (m1); **(MIR5):** 61 first lower molar (m1) and 2 mandibles; **(MIR4):** 22 first lower molar (m1) and 3 mandibles.

**Grottina dei Covoloni del Broion (8):** 10 first lower molar (m1) and 11 mandibles.

## ***Microtus arvalis*** LINNAEUS, 1761

**Fig.48.** First right lower molar (m1) in occlusal view of *Micortus arvalis* from El Mirador. Scale 1mm.

### MATERIAL

**Balma del Gai** (**1.B):** 2 first lower molar (m1) and 1 mandible.

**El Portalón (UE79):** 13 first lower molar (m1); **(UE85):** 32 first lower molar (m1) and 15 mandibles.

**EL Mirador (MIR51):** 11 first lower molar (m1) and 2 mandibles **; (MIR50)**: 4 first lower molar (m1); **(MIR49):** 501 first lower molar (m1) and 24 mandibles **; (MIR24):** 35 first lower molar (m1) and 2 mandibles; **(MIR23):** 1 first lower molar (m1); **(MIR22):** 2 first lower molar (m1); **(MIR21):** 3 first lower molar (m1); **(MIR19):** 15 first lower molar (m1) and 2 mandibles **; (MIR18):** 23 first lower molar (m1) and 2 mandibles; **(MIR17):** 28 first lower molar (m1) and 2 mandibles; **(MIR16):** 2 first lower molar (m1); **(MIR10):** 2 first lower molar (m1); **(MIR9):** 4 first lower molar (m1) and 1 mandibles; **(MIR6):** 3 first lower molar (m1) and 1 mandible; **(MIR5):** 37 first lower molar (m1) and 1 mandibles; **(MIR4):** 34 first lower molar (m1) and 4 mandibles.

**Grottina dei Covoloni del Broion (8):** 6 first lower molar (m1) and 13 mandibles.

### ***Microtus* gr. *agrestis-arvalis***

**Fig.49.** First left lower molar (m1) in occlusal view of *Microtus* gr. *agrestis-arvalis* from El Mirador.Scale 1mm.

## MATERIAL

**EL Mirador (MIR49):** 1 mandible; **(MIR19):** 1 first lower molar (m1); **(MIR18):** 2 first lower molar (m1); **(MIR6):** 2 first lower molar (m1); **(MIR5):** 33 first lower molar (m1); **(MIR4):** 40 first lower molar (m1) and 1 mandible.

**Grottina dei Covoloni del Broion (8):** 1 first lower molar (m1) and 2 mandibles.

## DESCRIPTION

According to Chaline (1972), we can observe in these two species that the first lower molars have five closed angles in the posterior part but the anteroconid complex is different in everyone. *Microtus arvalis* have the salient angles T6 (LSA5) and T7 (BSA4) more or less opposite and confluents in the anteroconid complex which morphology is rounded, while *Microtus agrestis* the salient angles T6 (LSA5) and T7 (BSA4) are alternates and confluents in the anteroconid complex which morphology is more angular. Normally, we can distinguish

*Microtus agrestis* and *Microtus arvalis*, but we cannot distinguish these two species in all our material, for this reason we have used *Microtus* gr. *agrestis-arvalis*.

## HABITAT

*Microtus agrestis* occurs in a wide range of habitats including grasslands, woods, upland heaths, dunes, marshes, peatbogs and river-banks, tending to prefer damp areas. It occurs in anthropogenic habitats but is absent from heavily grazed areas (Zima, 1999; Kryštufek et al., 2016). *Microtus arvalis* lives in a wide variety of open habitats including moist meadows, pastures, forest steppe, moist forest and sometimes agricultural areas, rarely in forest plantations. It is a serious agricultural pest in some areas (Zima, 1999; Yigit et al., 2016).

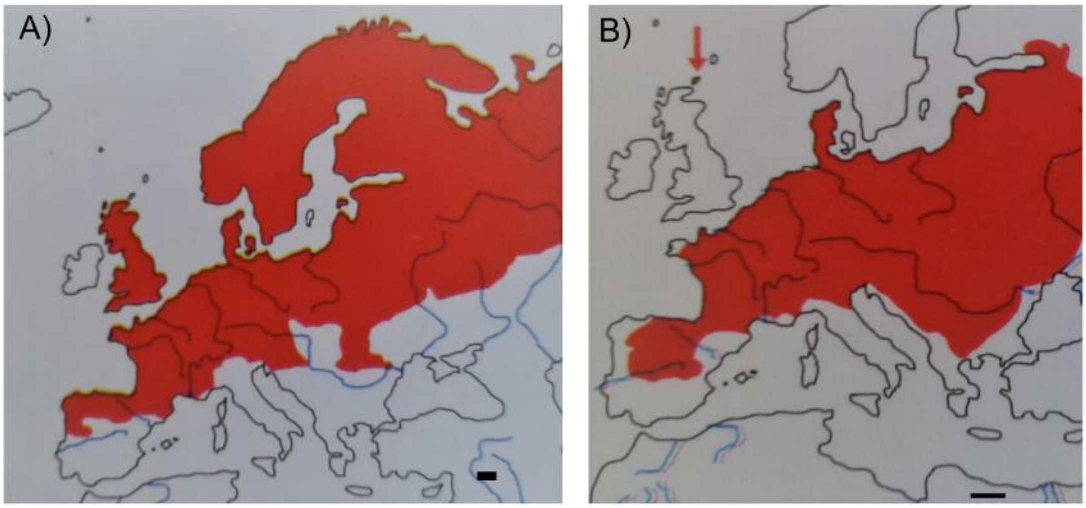

**Fig.50.** Current geographycal distribution of *Microtus agrestis* (A) and *Microtus arvalis* (B). Scale 100 km (Aulagnier et al.,2015)

## Subgenus *Terricola* FATIO, 1867

### ***Microtus* (*Terricola*) *duodecimcostatus*** DE SÉYS-LONGCHAMPS, 1839

**Fig.51.** First left lower molar (m1) in occlusal view of *Microtus* (*Terricola*) *duodecimcostatus* from El Mirador. Scale 1mm.

**MATERIAL**

**Cova Bonica (IV):** 21 first lower molar (m1) and 34 mandibles.

**EL Mirador (MIR51):** 1 first lower molar (m1) and 1 mandible **; (MIR50):** 14 first lower molar (m1); **(MIR49):** 601 first lower molar (m1) and 27 mandibles; **(MIR24):** 44 first lower molar (m1) and 5 mandibles; **(MIR23):** 1 first lower molar (m1); **(MIR22):** 2 first lower molar (m1) and 1 mandible; **(MIR21):** 4 first lower molar (m1); **(MIR19):** 20 first lower molar (m1); **(MIR18):** 41 first lower molar (m1) and 4 mandibles; (**MIR17):** 29 first lower molar (m1) and 7 mandibles; **(MIR11):** 3 first lower molar (m1) and 2 mandibles; **(MIR10):** 3 first lower molar (m1) and 2 mandibles; **(MIR9):** 1 first lower molar (m1); **(MIR6):** 2 first lower molar (m1) and 2 mandibles; **(MIR5):** 20 first lower molar (m1) and 4 mandibles; **(MIR4):** 31 first lower molar (m1) and 1 mandible.

## DESCRIPTION

The subgenus *Terricola* have a characteristic enamel , "*Microtus"* type, more wide in the mesial part than distal part of the molars oclusal angles, also subgenus *Terricola* is characterized by T4 (BSA3) open in the first lower molar (m1) and T4 (BSA3) and T5 (LSA4) are broadly confluent forming the so-called "pitymyan rhombus" (Chaline, 1972).

In our specimens, we identified *Microtus* (*Terricola*) *duodecimcostatus.* These teeth have the salient angles T6 (BSA4) open broadly confluent with T7 (LSA5) forming a second "pitymyan rhombus" in the first lower molar (m1) (Chaline, 1972).

## HABITAT

*Microtus* (*Terricola*) *duodecimcostatus* is a typical thermo-mediterranean species that lives in open habitats with relatively deep, loose soil, where it constructs underground burrows. It occurs in a number of anthropogenic habitats, including pastures, arable land, and orchards. It is also found in shrubland (le Louarn and Quéré, 2003; Aulagnier, 2016 ).

**Fig.52.** Current geographycal distribution of *Microtus* (*Terricola*) *duodecimcostatus*. Scale 100 km (Aulagnier et al., 2015)

## ***Microtus* (*Terricola*) *pyrenaicus*** SCHREBER, 1780

**Fig.53.** First right lower molar (m1) in occlusal view of *Microtus* (*Terricola*) *pyrenaicus* from Balma del Gai. Scale 1mm.

### MATERIAL

**Balma del Gai (1.B):** 6 first lower molar (m1) and 2 mandibles; **(1.A):** 4 first lower molar (m1) and 5 mandibles.

**El Portalón (UE79):** 8 first lower molar (m1)**; (UE85)** 26 first lower molar (m1) and 1 mandible**.**

### DESCRIPTION

*Microtus* (*Terricola*) *pyrenaicus* presents a T4 very open in the first lower molar (m1) and T4 (BSA3) and T5 (LSA4) are confluent forming the so-called “pitymyan rhombus”. Moreover a salient angle of T6 (BSA4) open and inclined towards the distal part of the tooth and the salient angles of T6 (BSA4) and T7 (LSA5) are in asymmetric position (Chaline, 1972). All of these characteristics allow us to identify as *Microtus* (*Terricola*) *pyrenaicus* in our small-mammals material.

## HABITAT

*Microtus* (*Terricola*) *pyrenaicus* is an endemism of France and Iberian Peninsula that lives at lower altitudes, it is found in pastures and arable land, whereas in the mountains it inhabits grassland and rocky woodland edges. Relatively cool (15° - 16° annual medium temperature) and dry areas are preferred (Palomo and Gisbert, 2002; Cassola, 2016).

**Fig.54.** Current geographycal distribution of *Microtus* (*Terricola*) *pyrenaicus*. Scale 100 km (Aulagnier et al.,2015)

## ***Microtus* (*Terricola*) *multiplex*** FATIO, 1905/ **(*Terricola*) *subterraneus*** DE SÉYS-LONGCHAMPS, 1836

**Fig.55.** First right lower molar (m1) in occlusal view of *Microtus* (*Terricola*) gr. *multiplex-subterraneus* from Grottina dei Covoloni del Broion. Scale 1mm.

### MATERIAL

**Grottina dei Covoloni del Broion (8):** 1 first lower molar (m1) and 3 mandibles**; (4):** 1 mandible.

### DESCRIPTION

The teeth from Grottina dei Covoloni del Broion presents a anterior cusp constricted in the first lower molar (m1), the salient angle of T4 (BSA3) is open and T4 (BSA3) and T5 (LSA4) are confluent forming the so-called "pitymyan rhombus" (Chaline, 1972). In this case we cannot distinguish *Microtus* (*Terricola*) *multiplex* and *Microtus* (*Terricola*) *subterraneus* because their morphology is very similar, for this reason we used *Microtus* (*Terricola*) gr. *multiplex-subterraneus.*

## HABITAT

*Microtus* (*Terricola*) *multiplex* inhabits pastures, meadows, open woodland and woodland clearings, preferring open areas with dense herbaceous vegetation to mature forest. In the high mountains and in the coastal lowlands it occurs in dry meadows, vineyards, and hedgerows (Hausser, 1995; Amori and Aulagnier, 2016). *Microtus* (*Terricola*) *subterraneus* is found in a broad range of habitats including broadleaf and coniferous woodlands, meadows and pastures, and rocky areas in the high mountains. It tolerates both dry and damp conditions (Kryštufek, 1999; Amori et al., 2016).

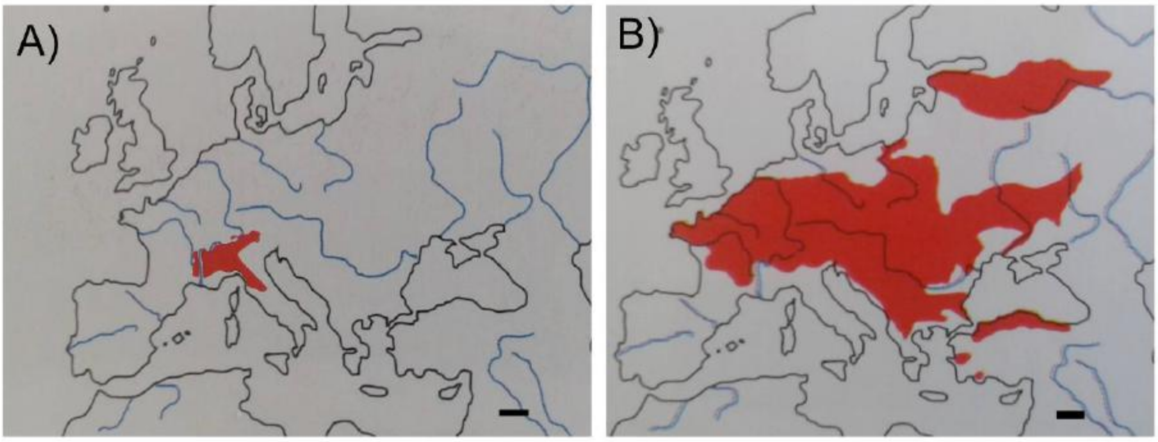

**Fig.56.** Current geographycal distribution of *Microtus (Terricola) multiplex* (A) and *Microtus (Terricola) subterraneus* (B). Scale 100 km (Aulagnier et al.,2015)

## Family Muridae ILLIGER, 1811
## Subfamily Murinae ILLIGER, 1811
## Genus *Apodemus* KAUP, 1829

## ***Apodemus sylvaticus*** LINNAEUS, 1758

**Fig.57.** First and second lower left molar of *Apodemus sylvaticus* in occlusal view from Grottina dei Covoloni del Broion. Scale 1mm.

### MATERIAL

**Balma del Gai (1.B):** 2 first lower molar (m1)**,** 4 mandibles and 1 maxilla; **(1.A):** 2 first lower molar (m1)**,** 17 mandibles and 2 maxilla.

**Cova Bonica (IV):** 17 first lower molar (m1), 3 second lower molar (m2), 10 third lower molar (m3)**,** 427 mandibles**,** 8 first upper molar (M1), 1 second upper molar (M2) and 139 maxilla; (**XIX):** 1 first lower molar (m1), 1 second lower molar (m2)**,** 134 mandibles**,** 2 first upper molar (M1) and 118 maxilla.

**El Portalón (UE79):** 2 first lower molar (m1)**,** 16 mandibles**,** 1 second upper molar (M2) and 17 maxilla; **(UE85):** 8 first lower molar (m1), 1 second lower molar (m2)**,** 150 mandibles**,** 4 first upper molar (M1) and 103 maxilla.

**EL Mirador (MIR51):** 3 mandibles and 1maxilla; **(MIR50):** 4 first lower molar (m1), 3 mandibles**,** 2 first upper molar (M1), 3 second upper molar (M2) and 8 maxilla; **(MIR49):** 42 first lower molar (m1), 8 second lower molar (m2), 4 third lower molar (m3)**,** 665 mandibles**,** 40 first upper molar (M1), 3 second upper molar (M2), 2 third upper molar (M3) and 418 maxilla; **(MIR24):** 16 first lower molar (m1), 1 second lower molar (m2), 3 third lower molar (m3), 48 mandibles**,** 6 first upper molar (M1), 4 second upper molar (M2), 1 third upper molar (M3) and 32 maxilla; **(MIR23)** 2 first lower molar (m1), 1 second lower molar (m2)**,** 3 mandibles**,** 2 first upper molar (M1), 1 second upper molar (M2)**; (MIR22):** 1 first lower molar (m1) and 6 mandibles**; (MIR21):** 1 mandible and 2 maxilla**; (MIR19):** 10 first lower molar (m1), 6 second lower molar (m2), 3 third lower molar (m3)**,** 15 mandibles**,** 9 first upper molar (M1), 2 second upper molar (M2), 1 third upper molar (M3) and 12 maxilla**; (MIR18):** 28 first lower molar (m1), 11 second lower molar (m2), 3 third lower molar (m3)**,** 43 mandibles**,** 21first upper molar (M1), 6 second upper molar (M2), 1 third upper molar (M3) and 32 maxilla**; (MIR17):** 8 first lower molar (m1), 2 second lower molar (m2)**,** 28 mandibles**,** 6 first upper molar (M1), 1 third upper molar (M3)**,** 17 maxilla**; (MIR16):** 2 first lower molar (m1) and 3 mandibles; **(MIR11):** 4 mandibles and 8 maxilla; **(MIR10):** 3 mandibles and 5 maxilla**; (MIR9):** 1third lower molar (m3)**,** 7 mandibles**,** 1 first upper molar (M1) and 3 maxilla; **(MIR6):** 2 mandibles; **(MIR5):** 4 first lower molar (m1), 1 second lower molar (m2), 1 mandibles, 1 first upper molar (M1) and 3 maxilla; **(MIR4):** 3 first lower molar (m1), 13 mandibles**,** 5 first upper molar (M1) and 14 maxilla**.**

**Grottina dei Covoloni del Broion (8):** 10 mandibles and 1 maxilla**; (4):** 2 first lower molar (m1)**,** 23 mandibles**,** 2 first upper molar (M1) and 10 maxilla**.**

## DESCRIPTION

We can observe in the first lower molar (m1) of our assemblage present five main tubercles, the anterolingual and anterolabial tubercles (tF, tE, tD, tC) confluent in X shape. In the first upper molars (M1) we observed the confluence of tubercles 4 (t4) and 7 (t7) and a development of the tubercle 9 (metaconid) in the upper second molars (M2). Acording Cuenca-Bescós et al., ( 1997), these are the representative morphology of *A.sylvaticus*.

## HABITAT

*A.sylvaticus* is a very adaptable species, inhabiting a wide variety of semi-natural habitats including all types of woodland, moorland, steppe, arid Mediterranean shrubland, and sand dunes. It is also found in many man-made habitats including suburban and urban parks, gardens and wasteland, pastures and arable fields, and forestry plantations (Montgomery, 1999; Schlitter et al., 2016).

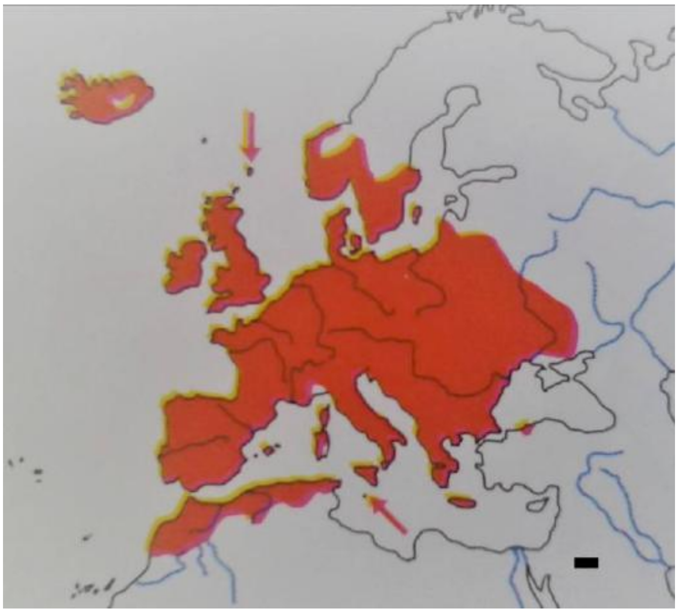

**Fig.58.** Current geographycal distribution of *Apodemus sylvaticus*. Scale 100 km (Aulagnier et al.,2015)

## Genus *Mus* LINNAEUS, 1758

### ***Mus spretus*** LATASTE, 1883

**Fig.59.** Right mandible (m1-2) of *Mus spretus* in occlusal view from Cova Bonica.Sacle 1mm

## MATERIAL

**Cova Bonica (XIX):** 2 mandibles and 4 maxilla.

## DESCRIPTION

The teeth of *Mus spretus* are composed by tubercles as *Apodemus sylvaticus*. The first upper molar (M1) has three groups of tubercles, the first (t1, t2 and t3) and second (t4, t5 and t6) groups situated in the anterior part has three tubercles and the last group has two tubercles (t7 and t9), also M1 presents three roots (*Apodemus sylvaticus* 5 roots). In the first lower molar (m1), we can observe in the anterior part of the molar, 4 tubercles (tE, tF, tC and tD) which the principal tubercle antero-labial (tE) is more developed than *Mus musculus,* forming a perfect shape X*;* the second group has two tubercles (tA and tB) and in the posterior part of the molar has the posterior accessory tubercle (cp) (Darviche et al., 2006).These characteristics allow us to identify these remains as *Mus spretus*.

## HABITAT

*Mus spretus* lives in grasslands, dry shrubland, cereal fields and open woodland. It is absent from dense forest, and tends to avoid human settlements. Their limited water requirements (half that of the house mouse) allows them to inhabit drier areas than other mice (Palomo and Gisbert 2002; Aulagnier, 2016).

**Fig.60.** Current geographycal distribution of *Mus spretus*. Scale 100 km (Aulagnier et al.,2015)

## Family *Gliridae* THOMAS, 1897

## Subfamily *Leithinae* LYDEKKER, 1896

## Genus *Eliomys* WAGNER, 1840

### ***Eliomys quercinus*** LINNAEUS, 1766

**Fig.61.** Left mandible (m1-2) of *Eliomys quercinus* in occlusal view from Cova Bonica.Scale 1mm

**MATERIAL**

**Balma del Gai (1.B):** 1 second lower molar (m2) and 1 second upper molar (M2)**; (1.A):** 1 lower premolar (p4), 2 first lower molar (m1), 8 mandibles and 1 second upper molar (M2).

**Cova Bonica (IV):** 1 first lower molar (m1), 2 second lower molar (m2)**,** 109 mandibles and 14 maxilla; **(XIX):** 1 lower premolar (p4), 1 first lower molar (m1), 1 second lower molar (m2)**,** 16 mandibles and 2 first upper molar (M1).

**El Portalón (UE79):** 1 maxilla; **(UE85):** 1 second lower molar (m2), 5 mandibles and 11 maxilla.

**EL Mirador (MIR49):** 1 second lower molar (m2), 7 mandibles and 2 maxilla; **(MIR23):** 1 second lower molar (m2) and 2 mandibles; **(MIR19)**: 2 first lower molar (m1), 3 second lower molar (m2) and 1 mandible; **(MIR18)**: 1 first lower molar (m1) and 3 second lower molar (m2); **(MIR17)**: 1 second lower molar (m2); **(MIR9)**: 1 mandible; **(MIR4)**: 1 second lower molar (m2).

## DESCRIPTION

*Eliomys quercinus* is characteristic by a wide perforated foramen in the distal part of the mandible. The teeth present a concave occusal surface where protoconid (Prd), mesoconid (Msd) and hipoconid (Hid) are more developed (Cuenca.Bescós et al., 2008). These characteristics have been observed in our specimens.

## HABITAT

*Eliomys quercinus* is a commensal species that its main habitat is woodland (coniferous, deciduous, and mixed), although it is sometimes found in orchards and gardens. It is less arboreal than some other dormice, and is often found on the ground in rocky areas, cracks in stone walls, and even in houses .It cannot lives at more than 2000 m asl (Bertolino et al., 2008).

**Fig.62.** Current geographycal distribution of *Eliomys quercinus*. Scale 100 km (Aulagnier et al.,2015)

## Subfamily *Glirinae* THOMAS, 1897

### Genus *Glis* BRISON, 1762

### ***Glis glis*** LINNAEUS, 1766

**Fig.63.** First right lower molar (m1) of *Glis glis* in oclusal view from Grottina dei Covoloni del Broion. Scale 1mm.

## MATERIAL

**Cova Bonica (IV):** 1 first lower molar (m1) and 1 mandible; **(XIX):** 2 first lower molar (m1), 5 second lower molar (m2)**,** 1 mandibles and 1 maxilla.

**Grottina dei Covoloni del Broion (4):** 6 mandibles and 1 maxilla.

## DESCRIPTION

*Glis glis* have rectangular or square teeth with occlusal surface flat that present three accesory crests interspersed with the four main cusps. These crests have a continuos development labio-lingual. In the lower molars the crests are inclined to anterior part and in the upper molars are inclined to posterior part (Cuenca-Bescós et al., 2008). All of these characteristics allow us to identify as *Glis glis* in our small-mammals material.

## HABITAT

*Glis glis* is found in mature deciduous and mixed woodland, where it frequents the canopy, although it also occurs in maquis and shrubland on rocky areas along the Mediterranean coast. Man-made habitats such as gardens and orchards are sometimes used, and the species often enters buildings (Kryštufek, 1999; Amori et al., 2016).

**Fig.64.** Current geographycal distribution of *Glis glis*. Scale 100 km (Aulagnier et al.,2015).

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# APPENDIX 2

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# Climatic and environmental conditions from the Neolithic to the Bronze Age (7000–3000 BP) in the Iberian Peninsula assessed using small-mammal assemblages

## *Les conditions climatiques et environnementales du Néolithique à l'âge du bronze (7000–3000 BP) dans la péninsule Ibérique évaluées en utilisant les petits mammifères*

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ABSTRACT

We have analyzed the palaeoenvironment and palaeoclimate of the beginning of the Holocene in the Iberian Peninsula on the basis of the small-mammal assemblages from three sites within the geography of the Iberian Peninsula: Mirador (Sierra de Atapuerca, Burgos), Colomera (Sant Esteve de la Sarga, Lleida) and Valdavara-1 (Becerreá, Lugo). These associations reveal that the palaeoenvironment was more humid than today in the sites under study, and the landscape was dominated by woodland and woodland margins in all the studied layers. Further, the climatic conditions were stable, but with winters colder than at present, above all in the Mediterranean area. Finally, our data have been compared with other environmental and climatic proxies, showing that human activities exerted little impact on the palaeoenvironmental conditions that occurred from 7000 to 3000 BP in the Iberian Peninsula.

RÉSUMÉ

Nous avons analysé le paléoenvironnement et le paléoclimat du début de l'Holocène dans la péninsule Ibérique, sur la base des assemblages de petits mammifères provenant de trois sites situés dans celle-ci : Mirador (Sierra de Atapuerca), Colomera (Sant Esteve de la Sarga, Lleida) et Valdavara-1 (Becerreá, Lugo). Ces associations révèlent que le paléoenvironnement était plus humide qu'aujourd'hui dans les sites étudiés, et le paysage dominé par des forêts et marges de forêts dans tous les niveaux étudiés. En outre, les conditions

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climatiques étaient plus ou moins stables, mais avec des hivers plus froids qu'à l'heure actuelle, surtout dans la région méditerranéenne. Finalement, nos données ont été comparées avec d'autres, environnementales et climatiques, ce qui a permis d'établir que les activités humaines avaient peu d'influence sur les conditions paléoenvironnementales entre 7000 à 3000 BP dans la péninsule Ibérique.

## 1. Introduction

The Holocene climate in the Iberian Peninsula is known mainly from different scientific studies (palaeobotany, sedimentology, mineralogy, isotopes, solar variability), which can obtain new palaeoenvironmental and palaeoclimatic data either from continental records alone (Bastida et al., 2013; Carrión, 2002; Carrión et al., 2010a,b; Domínguez-Villar et al., 2011; Fletcher and Sánchez-Goñi, 2008; Fletcher and Zielhofer, 2013; García-Amorena et al., 2011; Gómez-Paccard et al., 2013; Jiménez-Moreno et al., 2013; López Sáez et al., 2005; López-Merino et al., 2012; Luzón et al., 2011; Pérez-Lambán et al., 2014; Perez-Obiol et al., 2011; Sancho et al., 2011) or from continental records in conjunction with marine records (Cacho et al., 2001; Fletcher and Zielhofer, 2013; Mayewski et al., 2004). This period is characterized by major changes in the vegetation and rapid oscillations in the climate (Cacho et al., 2001; Domínguez-Villar et al., 2012; Fletcher and Zielhofer, 2013; Jiménez-Moreno et al., 2013; Mayewski et al., 2004).

However, the Holocene is understudied in the Iberian Peninsula, especially in terms of small-mammal studies, and for this reason we want to provide a broader reference framework for interpreting the Holocene in the region (Fig. 1).

Recently, studies of small mammals in the Holocene have started to become more abundant. These studies have involved palaeoenvironmental and palaeoclimatic reconstructions (Bañuls-Cardona and López-García, 2009; Bañuls-Cardona et al., 2013; Cuenca-Bescós et al., 2009; López-García et al., 2011), which have been useful for characterizing the small changes that occurred at the beginning of the Holocene.

In this paper, our study of small mammals is focused chronologically on the Early and Middle Holocene. The aim is to characterize the environmental and climatic conditions of the period by the study of small mammals, and compare our results with other data in order to establish natural or human causes that influenced these results.

To this end, the small-mammal data chosen belong to archaeological sites situated in different climatic zones of the Iberian Peninsula. We have taken new small-mammal data from the Neolithic layers of Mirador cave and the data from the Bronze Age layer (MIR4) published in Bañuls-Cardona et al. (2013), as well as other small-mammal data published from Colomera cave (Sant Esteve de la Sarga, Lleida) (Bañuls-Cardona and López-García, 2009; López-García et al., 2010) and Valdavara-1 cave (Becerreá, Lugo) (López-García et al., 2011). The faunal assemblages used here are included in the small-mammal studies of three Middle Holocene sites (from the Early Neolithic to the Bronze Age) that correspond to 11 different layers dated to between 7000 and 3000 ka BP: six layers from the Early Neolithic (MIR24, MIR19, MIR18 and MIR17 of Mirador cave, CE12 and CE13-14 of Colomera cave), two layers from the Middle-Late Neolithic (MIR9 and MIR5 of Mirador cave) and finally three layers from the Bronze Age (MIR4 of Mirador, VUU of Valdavara-1 and EE1 of Colomera cave).

## 2. Material and methods

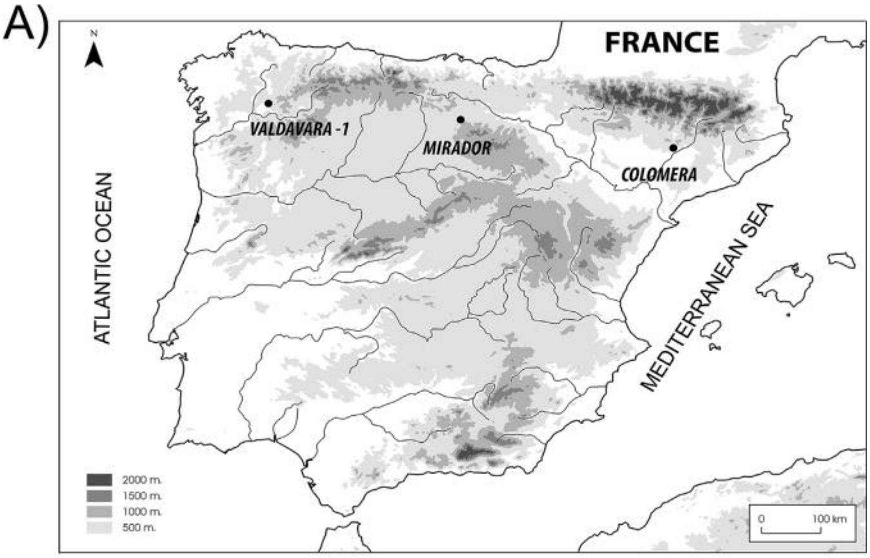
The new data of this paper are from Mirador cave (Sierra de Atapuerca, Burgos). For this paper, layers MIR5, MIR9, MIR17, MIR18, MIR19 and MIR24 have been analyzed. From these layers, 1154 remains (NR) have been identified, with a minimum number of individuals (MNI) of 706. Nine small-mammal taxa have been identified: *Sorex* gr. *coronatus-araneus*, *Crocidura russula*, *Myotis myotis-blythii*, *Miniopterus schreibersii*, *Microtus arvalis*, *Microtus agrestis*, *Microtus* (*Terricola*) *duodecimcostatus*, *Apodemus sylvaticus* and *Eliomys quercinus* (Table 1).

### 2.1. Palaeontological study

The small mammals belonging to levels MIR5, MIR9, MIR17, MIR18, MIR19 and MIR24 of Mirador cave (Sierra de Atapuerca, Burgos) have been identified by systematic palaeontology. For Soricidae, we used mandibles and isolated teeth (Cuenca-Bescós et al., 2008; López-García, 2008; Reumer, 1984); for chiropters, the mandibles, isolated teeth and humeri (Bruijn and Rumke, 1974; Menu and Popelard, 1987; Sevilla, 1988); for Arvicolinae, the first lower molars (Cuenca-Bescós et al., 2008; López-García, 2008, van der Meulen, 1973); while for *Apodemus sylvaticus* and *Eliomys quercinus* identification relied on isolated teeth (Cuenca-Bescós et al., 2008; López-García, 2008; Damms, 1981; Pasquier, 1974).

### 2.2. Palaeoenvironmental reconstruction

To produce the palaeoenvironmental reconstruction, we used the Habitat Weighting method (Andrews, 2006; modified by Blain et al., 2008; López-García et al., 2011). We took into account the geographical location of each species today, as all of them still exist in the Iberian Peninsula. We ascertained a percentage distribution for the habitat(s) preferentially occupied by each taxon, dividing the habitats into five categories defined according to a series of highly concrete environmental features: dry meadow, wet meadow, woodland, rocky areas and watercourse areas. "Dry meadow" consists of meadowland subject to seasonal climate change; "wet meadow" indicates evergreen meadowland with pastures and dense topsoil; "woodland"



B)

| LAYER | Laboratory number | Measured Radiocarbon age | 2σ calibrated result BP | Mean of 2σ calibrated result BP |
|---|---|---|---|---|
| MIR4 (top) | Beta-154894 | 3020±40 | 3350-3140 | 4026 |
| MIR4 (bass) | Beta-153366 | 3380±40 | 3720-3560 | |
| MIR9 | Beta-220912 | 5050±40 | 5920-5730 | 5825 |
| MIR18 | Beta-208132 | 6090±40 | 7180-7110 /7100-6880 | 7067 |
| MIR19 | Beta-182040 | 6130±50 | 7180-6870 | 6990 |
| MIR24 | Beta-220914 | 6080±40 | 7160-7120 /7030-6870 | 7880 |
| | Beta-197386 | 7030±40 | 7960-7800 | |
| EE1 | Beta-241704 | 3630±40 | 4080-3840 | 3980 |
| CE12 | Beta-248523 | 6020±50 | 6990-6740 | 6870 |
| CE13-14 | Beta-240551 | 6120±40 | 7170-6940 | 7060 |
| VUU | Beta-235727 | 4490±40 | 5340-4980 | 5130 |

**Fig. 1.** **A)** Geographic location of the sites under study. **B)** Radiocarbon dates measured of the layers chosen from each site, the calibrated dates 2$\sigma$ ($P$ = 95%) and the mean of the calibrated dates.

**Fig. 1.** **A)** Situation géographique des sites étudiés. **B)** Datations radiocarbone mesurées sur des couches choisies pour chaque site, datations radiocarbone calibrées 2$\sigma$ ($p$ = 95 %) et moyenne des datations calibrées.

ranges from leafy forests to woodland margins, with moderate vegetation cover; "rocky areas" refer to rocky habitats without vegetation cover; and "watercourse areas" include streams, lakes and ponds (Table 2).

### 2.3. Palaeoclimatic reconstruction

For the palaeoclimatic reconstruction, we used the Mutual Ecogeographic Range method (MER) (Blain, 2005; Blain et al., 2010; Blain et al., 2016). With this method, we defined the current distribution area of the faunal association, superimposing current distribution maps divided into 10 × 10 km UTM grids (Palomo and Gisbert, 2005). The resulting intersection indicates an area where the climatic characteristics are similar to those of our association. On the basis of this intersection, we calculated the MAT (mean annual temperature), MTC (mean temperature of the coldest month) and the MTW (mean temperature of the warmest month), as well as the MAP (mean annual precipitation). These climatic characteristics are obtained using current data relating to temperature and precipitation, collected between 1982 and 2012 (Climate_Data.org). The data obtained were compared with the present-day climate of this region of the Iberian Peninsula, enabling us to note the changes in temperature and precipitation with respect to this point of the Holocene period.

We have omitted certain taxa from the palaeoclimatic reconstruction. This applies to chiropters, because studies of chiropteran distribution are currently very scarce; in many cases their mobility makes it difficult to ascertain their present geographical distribution, which could thus falsify our data.

Moreover, we have used a classification of taxa according to chorotypes established by Sans-Fuentes and Ventura (2000), Real et al. (2003) and López-García et al. (2010b). A chorotype can be defined as a group of species whose distributions in space overlap more than expected at random. Chorotype 1 (CH-1) refers to species with Euro-Siberian requirements; this implies a mean summer temperature lower than 20 °C, a mean annual temperature that should be between 10 and 12 °C, and a mean annual precipitation higher than 800 mm. Chorotype 2 (CH-2) refers to Euro-Siberian species that nonetheless tolerate Mediterranean conditions, with a mean annual precipitation greater than

**Table 1**
Minimum number of individuals (MNI) and percentage of minimum number of individuals (MNI%).
**Tableau 1**
Nombre minimum d'individus (MNI) et pourcentage du nombre minimum d'individus (MNI %).

| Taxa | Mirador | | | | | | | | | | | | | | Colomera | | | | | | Valdavara-1 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | MIR4 | | MIR5 | | MIR9 | MIR17 | | | MIR18 | | MIR19 | | MIR24 | | EE1 | | CE12 | | CE13-14 | | VUU | |
| | NMI | NMI% | NMI | NMI% | NMI | NMI% | NMI | NMI% | NMI | NMI% | NMI | NMI% | NMI | NMI% | NMI | NMI% | NMI | NMI% | NMI | NMI% | NMI | NMI% |
| *Crocidura russula* | 19 | 19.8 | 6 | 6.7 | 17 | 32.1 | 16 | 12.5 | 21 | 11.4 | 6 | 5.1 | 8 | 6.0 | 1 | 2.3 | 3 | 4.3 | 2 | 2.4 | 2 | 3.4 |
| *Sorex coronatus-araneus* | 6 | 6.3 | 4 | 4.5 | 5 | 9.4 | 9 | 7.0 | 21 | 11.4 | 4 | 3.4 | 3 | 2.2 | | | | | | | | |
| *Sorex sp.* | | | | | | | | | | | | | | | | | | | | | 1 | 1.7 |
| *Erinaceus europaeus* | | | | | | | | | | | | | | | | | | | | | 1 | 1.7 |
| *Talpa occidentalis* | | | | | | | | | | | | | | | | | | | | | 4 | 6.8 |
| *Rhinolophus sp.* | | | | | | | | | | | | | | | | | | | | | 1 | 1.7 |
| *Myotis myotis* | | | | | 2 | 3.8 | | | 3 | 1.6 | | | 4 | 3.0 | | | | | | | | |
| *Myotis nattereri* | | | | | | | | | | | | | | | | | | | | | 1 | 1.7 |
| *Miniopterus schreibersii* | | | | | 2 | 3.8 | | | 1 | 0.5 | 1 | 0.9 | 2 | 1.5 | | | | | | | | |
| *Arvicola sapidus* | | | | | | | | | | | | | | | | | | | | | 2 | 3.4 |
| *Iberomys cabrerae* | | | | | | | | | | | | | | | 1 | 2.3 | 2 | 2.9 | 1 | 1.2 | 2 | 3.4 |
| *Clethrionomys glareolus* | | | | | | | | | | | | | | | | | | | | | 1 | 1.7 |
| *Micromys minutus* | | | | | | | | | | | | | | | | | | | | | 1 | 1.7 |
| *Chionomys nivalis* | | | | | | | | | | | | | | | 6 | 14.0 | 11 | 15.9 | 24 | 28.9 | 1 | 1.7 |
| *Microtus arvalis* | 21 | 21.9 | 20 | 22.5 | 3 | 5.7 | 18 | 14.1 | 16 | 8.6 | 9 | 7.7 | 22 | 16.4 | 5 | 11.6 | 4 | 5.8 | 4 | 4.8 | 1 | 1.7 |
| *Microtus agrestis* | 14 | 14.6 | 37 | 41.6 | 13 | 24.5 | 34 | 26.6 | 26 | 14.1 | 22 | 18.8 | 15 | 11.2 | 3 | 7.0 | 7 | 10.1 | 7 | 8.4 | 1 | 1.7 |
| *Microtus (Terricola) lusitanicus* | | | | | | | | | | | | | | | | | | | | | 17 | 28.8 |
| *Microtus (Terricola) duodecimcostatus* | 17 | 17.7 | 14 | 15.7 | 1 | 1.9 | 18 | 14.1 | 21 | 11.4 | 11 | 9.4 | 24 | 17.9 | 1 | 2.3 | 4 | 5.8 | 5 | 6.0 | | |
| *Apodemus sylvaticus* | 18 | 18.8 | 8 | 9.0 | 1 | 1.9 | 32 | 25.0 | 73 | 39.5 | 58 | 49.6 | 56 | 41.8 | 22 | 51.2 | 32 | 46.4 | 36 | 43.4 | 16 | 27.1 |
| *Glis glis* | | | | | | | | | | | | | | | | | | | | | 6 | 10.2 |
| *Eliomys quercinus* | 1 | 1.0 | | | 9 | 17.0 | 1 | 0.8 | 3 | 1.6 | 6 | 5.1 | | | 4 | 9.3 | 6 | 8.7 | 4 | 4.8 | 1 | 1.7 |
| Total | 96 | 100 | 89 | 100 | 53 | 100 | 128 | 100 | 185 | 100 | 117 | 100 | 134 | 100 | 43 | 100 | 69 | 100 | 83 | 100 | 59 | 100 |

**Table 2**
Distribution of the taxa by habitat: the abbreviations are as follows: R, Rocky; WA, Water; OD, Open Dry; OH, Open Humid; WO, Woodland. Distribution of the taxa by chorotype: CH-1, Chorotype 1 (species with Euro-Siberian requirements); CH-2, Chorotype 2 (Euro-Siberian species that nonetheless tolerate Mediterranean conditions); CH-3, Chorotype 3 (species with strictly Mediterranean requirements); CH-4, Chorotype 4 (generalist species).
**Tableau 2**
Répartition des taxons par habitat. Les abréviations sont les suivantes : R, milieux rocheux ; WA, milieux aquatiques ; OD, milieux ouverts et secs ; OH, milieux ouverts et humides et WO, forêts. Répartition des taxons par chorotype. Les abréviations sont les suivantes : CH-1, chorotype 1 (espèces ayant des exigences euro-sibériennes) ; CH2, chorotype 2 (espèces euro-sibériennes qui tolèrent néanmoins des conditions méditerranéennes) ; CH-3, chorotype 3 (espèces strictement méditerranéennes) et CH-4, chorotype 4 (espèces généralistes).

| Taxa | Habitat weighting | | | | | Chorotypes | | | |
|---|---|---|---|---|---|---|---|---|---|
| | OD | OH | WO | RO | WA | CH-1 | CH-2 | CH-3 | CH-4 |
| *Crocidura russula* | 0.5 | | 0.5 | | | | | | X |
| *Sorex coronatus-araneus* | | 0.5 | 0.5 | | | | X | | |
| *Erinaceus europaeus* | | 0.5 | 0.5 | | | | | X | |
| *Talpa occidentalis* | | 0.5 | 0.5 | | | | X | | |
| *Talpa europaea* | | 0.5 | 0.5 | | | | X | | |
| *Myotis myotis* | 0.25 | 0.25 | 0.5 | | | | | X | |
| *Myotis nattereri* | 0.25 | 0.25 | 0.5 | | | | | X | |
| *Miniopterus schreibersii* | 0.25 | 0.25 | 0.5 | | | | | | X |
| *Arvicola sapidus* | | | | | 1 | | | | |
| *Iberomys cabrerae* | | 0.5 | 0.5 | | | | | | X |
| *Cletrionomys glareolus* | | | 1 | | | X | | | |
| *Chionomys nivalis* | | | | 1 | | X | | | |
| *Microtus arvalis* | 0.5 | | 0.5 | | | X | | | |
| *Microtus agrestis* | | 0.5 | 0.5 | | | X | | | |
| *Microtus (Terricola) lusitanicus* | | 0.5 | 0.5 | | | | | X | |
| *Microtus (Terricola) duodecimcostatus* | | 0.5 | 0.5 | | | | | | X |
| *Apodemus sylvaticus* | | | 1 | | | | | X | |
| *Micromys minutus* | | | 1 | | | | X | | |
| *Eliomys quercinus* | | | 0.5 | 0.5 | | | | X | |
| *Glis glis* | | | 1 | | | X | | | |

600 mm. Chorotype 3 (CH-3) denotes generalist species, and finally Chorotype 4 (CH-4) denotes species with strictly Mediterranean requirements (Table 2).

## 3. Results and discussion

The Holocene is a warm and wet period, with some episodes with increased aridity and global climatic pulsations. However, there are many regional differences. Little is known about Holocene climatic variability from the continental records of Europe, and there is a need to gather more information from terrestrial sources whose reach across Europe is well known (Bernárdez et al., 2008; Leira and Santos, 2002). In the Iberian Peninsula, the detailed examination of high-frequency climatic variability in the present interglacial has focused mainly on ice cores and marine or continental records. Studies such as the Alboran sea (MD95-2043) core record off the Mediterranean coast have been carried out on marine deep-sea cores, using oxygen isotope curves (Cacho et al., 2001), while the record from core SMP02-3 from the Galician continental shelf off the NW Iberian Peninsula (Bernárdez et al., 2008) has also been used to understand the vegetation response to climate variability in the Holocene (Carrión, 2002; Fletcher and Zielhofer, 2013; Fletcher et al., 2008; Jiménez-Moreno et al., 2013; Morellón et al., 2009) (Fig. 2).

Our study focuses chronologically in particular on the Early and Middle Holocene, and in order to characterize this period climatically and environmentally on the basis of a small-mammal study, we have chosen sites with special geographic characteristics, because the Iberian Peninsula represents one of the largest and most diverse areas of Mediterranean-type climate in the Mediterranean region (Moreno et al., 2007).

### a) Northern Spanish Meseta

Mirador cave (Sierra de Atapuerca, Burgos) is located 1033 m above sea level on the northeastern edge of the northern Spanish Meseta (Fig. 1), which currently has a continental Mediterranean climate or Cfb climate (according to the Köppen-Geiger system), with special characteristics: long, cold winters with moderate rainfall and short, warm summers (Kottek et al., 2006).

According to our taphonomic study of the small mammals from Mirador cave, the remains analyzed present slight signs of digestion. From these results, it can be surmised that the main animal responsible for the accumulation in the cave was a category 1 predator, a nocturnal bird of prey that displays an opportunistic trophic pattern and produces slight modifications of the bones it ingests (Andrews, 1990). The small mammals form an assemblage of great taxonomic variety, indicating that it was the work of an opportunistic hunter.

The results obtained from Mirador cave by the MER method show that the same climatic characteristics prevailed throughout the Holocene period, because the species represented in the layers studied did not undergo great changes. The temperatures are seen to undergo minimal changes of less than one degree Celsius throughout the sequence, and the same applies when we compare our data with current climate data. However, the precipitation is higher (between 200–252 mm) than at present. Moreover, the study of chorotypes shows some climatic changes.

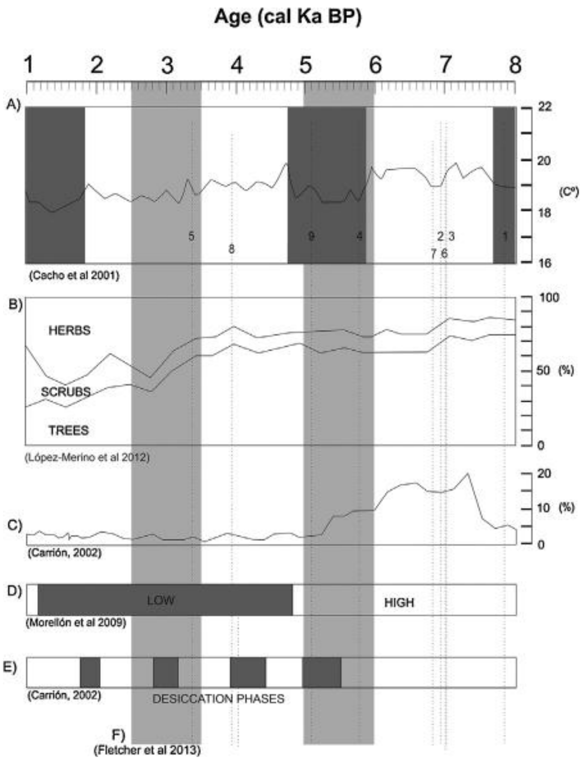


**Fig. 2.** Relation between the dating of each of the layers under study and other palaeoenvironmental and palaeoclimatic studies: **A)** the Alboran sea (MD95-2043) isotope curve showing cooling events (Cacho et al., 2001), **B)** percentages of trees, shrubs and herbs in the northwest (López-Merino et al., 2012), **C)** percentages of deciduous trees in the southeast (Carrión, 2002), **D)** level of water in Lake Estanya, northeast (Morellón et al., 2009), **E)** level of water in Lake Siles, southeast (Carrión, 2002), **F)** cold periods (Fletcher and Zielhofer, 2013). The abbreviations are as follows: 1: MIR24 (7880 ka BP); 2: MIR19 (6990 ka BP); 3: MIR18 (7067 ka BP); 4: MIR9 (5825 ka BP); 5: MIR4 (4026 ka BP); 6: CE13-14 (7060 ka BP); 7: CE12 (6870 ka BP); 8: EE1 (3980 ka BP); 9: VUU (5130 ka BP).

**Fig. 2.** Relation entre la datation de chacun des niveaux étudiés et d'autres études paléoenvironnementales et paléoclimatiques : **A)** en mer d'Alboran (MD95-2043) courbe isotopique montrant les événements de refroidissement (Cacho et al., 2001), **B)** pourcentages d'arbres, d'arbustes et d'herbes dans le Nord-Ouest (López-Merino et al., 2012), **C)** pourcentages d'arbres feuillus dans le Sud-Est (Carrión, 2002), **D)** niveau de l'eau dans le lac Estanya, au nord-est (Morellón et al., 2009), **E)** niveau de l'eau dans le lac Siles, au Sud-Est (Carrión, 2002), **F)** périodes froides (Fletcher and Zielhofer, 2013). Les abréviations sont les suivantes : 1 : MIR24 (7880 ka BP); 2 : MIR19 (6990 ka BP) ; 3 : MIR18 (7067 ka BP) ; 4 : MIR9 (5825 ka BP) ; 5 : MIR4 (4026 ka BP) ; 6 : CE13-14 (7060 ka BP) ; 7 : CE12 (6870 ka BP) ; 8 : EE1 (3980 ka BP) ; 9 : VUU (5130 ka BP).

The percentages of Euro-Siberian species are significant in the Middle-Late Neolithic and Bronze Age layers, particularly in MIR5 (64.0%), while in the Early Neolithic (MIR24, MIR19, MIR18) generalist species (CH-3) are more abundant (Fig. 4).

Within the sequence of Mirador cave, however, various singular characteristics are seen to occur. During the Early Neolithic (MIR24, MIR19, MIR18), climatic conditions are warmer than in the rest of the sequence, generalist species occupying 43–54% of the total sample due to the high presence of *Apodemus sylvaticus* in these layers (from 40 to 50%). This warm period breaks off in MIR17, with a sharp increase (20%) in Euro-Siberian species, in this case with a high proportion (26.6%) of *M. agrestis* (Fig. 4). In the Middle Neolithic (MIR9), we registered an increase of 10% in CH-4, Mediterranean species, especially manifest in the figure of 32.1% for *Crocidura russula* (Fig. 4). These data suggest a slight thermal recovery with respect to MIR17. They could also be due to the incipient establishment of a Mediterranean climate that occurred in the Mirador area before 5000 BP (Jalut et al., 1997), but until all the layers have been analyzed, it will not be possible to say for sure. This mild climate persisted until the Bronze Age (MIR4), when there was another very slight increase (5%) in Euro-Siberian species, with the typical conditions of a continental Mediterranean climate prevailing in the northern Meseta, i.e. long, cold winters with short, warm summers (Kottek et al., 2006). However, these mild conditions were interrupted in MIR5. In this layer, another increase in the percentage of Euro-Siberian species (64.0%) is observed, corresponding to the cold period registered at this time in the Alboran sea (MD95-2043) core record (Cacho et al., 2001; Fletcher and Zielhofer, 2013) (Fig. 2).

The Habitat Weighting study shows a gradual increase in open areas to the detriment of woodland areas (Fig. 4); this is observed especially in MIR9 and MIR4, where the percentage of open dry areas reaches 20%. In MIR4 there is also a small decrease in rainfall of 52 mm with respect to MIR5. Fletcher and Zielhofer (2013) refer to an increase in dry conditions in the intervals lasting from 6000 – 5000 and 3500–2500 ka BP, as also observed in the record (SMP02-3) from the Galician continental shelf (NW Iberian Peninsula) from 4700 to 3300 ka BP (Bernárdez et al., 2008). However, this could be due to the major human impact on the environment, as indicated by archaeobotanical studies based on pollen, charcoal, seeds and phytoliths at the Mirador site (Cabanes et al., 2009; Rodríguez and Buxó, 2008). These studies have confirmed the presence of herbaceous plants related to the development of agriculture and livestock. On the other hand, García-Antón et al. (2011) have indicated that the human impact on the environment in this area of the northern Meseta was not intense in the first millennium B.C.

### b) Pyrenees area

Colomera cave (Sant Esteve de la Sarga, Lleida) is located at an altitude of 670 m above sea level, on the southern face of the Pyrenees (Fig. 1) in a continental Mediterranean zone or Cfb climate (Köppen-Geiger system). Such a location is generally characterized by very cold winters and warm summers, and, unlike the northern Meseta, by very low rainfall (Kottek et al., 2006).

The chorotype study shows a predominance of chorotype 3 or generalist species (48–60%) such as *Apodemus sylvaticus*, which exceeds 40% in all layers. But despite this, there is a notable percentage of Euro-Siberian species throughout the sequence, mainly represented by *Chionomys nivalis*, which lives in strictly Euro-Siberian climatic zones, especially in CE13-14, with a substantial percentage of 28.9%. Nonetheless, Colomera also shows the greatest variety of Mediterranean species, with *C. russula*, *M. (T.) duodecimcostatus* and especially *Iberomys cabrerae*, which live in strictly Mediterranean climate zones and are not found in Euro-Siberian climates (Fig. 4). These percentages indicate abrupt changes in temperatures, because we do not find species belonging to CH-2, i.e. Euro-Siberian species that nonetheless tolerate Mediterranean conditions. Together, these climatic characteristics are typical of a continental Mediterranean climate, generally characterized by very cold winters and warm summers (Kottek et al., 2006). These typical characteristics can be seen especially in layers CE12 and EE1, because within the sequence, we see small changes in the percentages of chorotypes that indicate an improving climate from the early Neolithic (CE12), similar to during the Bronze Age (EE1). We also observe an increase of 10% in the percentage of thermo-Mediterranean taxa, which increases from 57.8% in CE12 to 68.1% in CE13-14.

The climatic characteristics deduced from the MER study, when compared with current data, indicate that the temperatures during the Holocene were 2.4 °C lower than at present and that the precipitation was higher than at present (557 mm). Temperatures are observed to be 1 °C lower for the MTC, while for the MTW they were less than 1 °C lower.

Our study of the habitat reveals a minor increase in open dry areas to the detriment of open humid areas, and the level of precipitation is shown to be the same in all the layers. The zooarchaeological data also attest a scarce presence of ovicaprids, which would indicate the presence of pastures, suggesting that herds might have been stabled inside the cavity (fumier). From archaeobotanical data, agricultural practices are evidenced by the significant presence of cereals and legumes, but this presence is likewise scarce (Oms et al., 2008, 2009).

This low pressure on the environment is reflected in the predominance of woodland in all layers of Colomera cave, increasing towards more recent layers. This could be due to the type of cave occupation. The human communities that frequented Colomera cave were probably nomadic, since the narrow circumstances of the cave (in the middle of a gorge) do not seem appropriate for the establishment of a camp of shepherds or an agricultural holding around the cave (Oms et al., 2008, 2009). This was common in mountain areas at the time, where occupations have been found to occur later than in the plains (Tarroso et al., 2014).

*c) Northwest area*

Valdavara-1 cave is located in the Iberian Massif at an altitude of 600 m above sea level (Becerreá, Lugo) (Fig. 1). This site represents a continental Mediterranean climate, with influences from an Atlantic climate or Csb climate (Köppen-Geiger system). The summers are dry, as in the previous case, but precipitation is more abundant and occurs mainly in winter, with the arrival of fronts from the Atlantic (influence of the temperate zone), and in the winter the temperatures are mild (Font Tullot, 2000).

The MER analysis of the small-mammal assemblages in the Bronze Age (VUU) of Valdavara-1 cave indicates mild temperatures (Fig. 3): i.e. the MTC is 5 °C, the highest of the sites studied in this paper, and the MTW is 17.20 °C, the lowest of the sites studied in this paper (Table 3). These low temperatures in the warmer months (MTW) could be related to a cold climate period in the Iberian Peninsula, as observed in the temperature curve of the Alboran sea (MD95-2043) core record (Cacho et al., 2001; Fletcher and Zielhofer, 2013) (Fig. 2). At the same time, the precipitation for this layer is very high (1690 mm), the highest in our study.

These features are also observed in the study of the chorotypes from Valdavara-1 cave (Becerreá, Lugo). Similar percentages of Mediterranean and Euro-Siberian species tolerant to Mediterranean conditions are seen, while the percentage of Euro-Siberian species *sensu stricto* is negligible (Fig. 4).

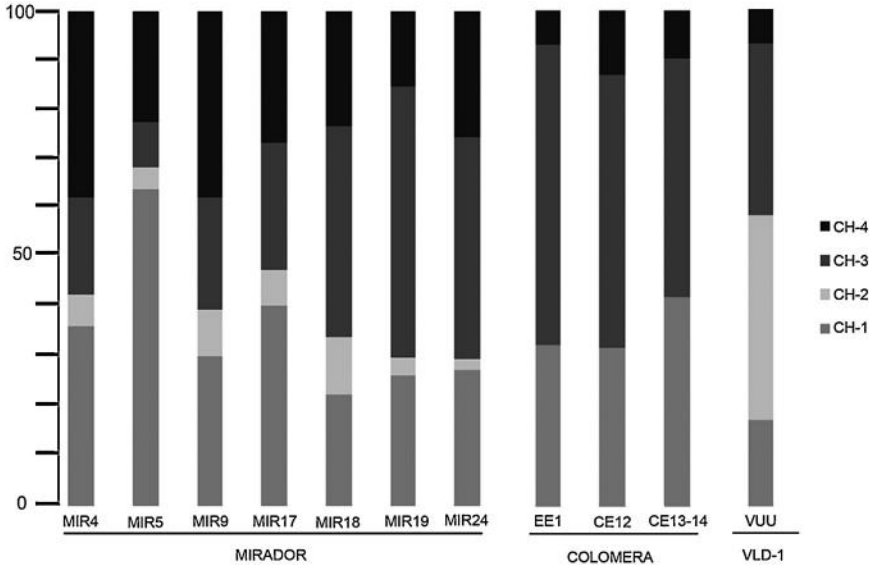


**Fig. 3.** Percentage of chorotypes at each of the sites under study.

**Fig. 3.** Pourcentage de chorotypes dans chacun des sites étudiés.

**Table 3**
Relation of temperature and precipitation, obtained by the MER (Mutual Ecogeographic Range) analysis of the small mammals at each of the sites studied: MAT (mean annual temperature); MTW (mean temperature of the warmest month); MTC (mean temperature of the coldest month) and MAP (mean annual precipitation). SD (standard deviation): Max (maximum); Min (minimum); Δ (difference in relation to the current means at the meteorological stations).

**Tableau 3**
Relation entre température et précipitations, obtenue en utilisant la méthode MER (domaine écogéographique commun) à partir des micromammifères pour chacun des sites étudiés : MAT (température moyenne annuelle) ; MTW (température moyenne du mois le plus chaud) ; MTC (température moyenne du mois le plus froid) et le MAP (précipitations moyennes annuelles). SD (écart-type) : Max (maximum) ; Min (minimum) ; Δ (différence par rapport à la moyenne actuelle des stations météorologiques).

| Sites | Layers | MAT | | | MTW | | | MTC | | | MAP | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Mean | SD | Δ | Mean | SD | Δ | Mean | SD | Δ | Mean | SD | Δ |
| Mirador | MIR4 | 9.9 | 1.5 | −0.2 | 18.5 | 1.4 | −0.2 | 2.5 | 1.2 | 0.0 | 794 | 221 | 200 |
| | MIR5 | 10.0 | 1.6 | −0.1 | 18.6 | 1.4 | −0.1 | 2.6 | 1.2 | 0.1 | 846 | 284 | 252 |
| | MIR9 | 9.9 | 1.5 | −0.2 | 18.5 | 1.4 | −0.2 | 2.5 | 1.2 | 0.0 | 794 | 221 | 200 |
| | MIR17 | 9.9 | 1.5 | −0.2 | 18.5 | 1.4 | −0.2 | 2.5 | 1.2 | 0.0 | 794 | 221 | 200 |
| | MIR18 | 9.9 | 1.5 | −0.2 | 18.5 | 1.4 | −0.2 | 2.5 | 1.2 | 0.0 | 794 | 221 | 200 |
| | MIR19 | 9.9 | 1.5 | −0.2 | 18.5 | 1.4 | −0.2 | 2.5 | 1.2 | 0.0 | 794 | 221 | 200 |
| | MIR24 | 10.0 | 1.6 | −0.1 | 18.6 | 1.4 | −0.1 | 2.6 | 1.2 | 0.1 | 846 | 284 | 252 |
| Colomera | EE1 | 8.0 | 1.0 | −2.4 | 18.6 | 1.9 | −0.6 | 1.5 | 1.3 | −1.0 | 971 | 349 | 88 |
| | CE12 | 8.0 | 1.0 | −2.4 | 18.6 | 1.9 | −0.6 | 1.5 | 1.3 | −1.0 | 971 | 349 | 88 |
| | CE13–14 | 8.0 | 1.0 | −2.4 | 18.6 | 1.9 | −0.6 | 1.5 | 1.3 | −1.0 | 971 | 349 | 88 |
| Valdavara-1 | VUU | 11.4 | 1.2 | −0.2 | 17.2 | 1.3 | −1.9 | 5.0 | 1.7 | −0.2 | 1690 | 575 | 749 |

Mild temperatures are thus indicated by the MER and the chorotypes, and the temperatures are a little higher nowadays than in the Holocene, above all the MTW, with temperatures 1.9 °C higher (Table 3). The same results are shown by the record (SMP02-3) from the Galician continental shelf (NW Iberian Peninsula). This record indicates a warm and dry period characterized by low nutrient levels and productivity, as also revealed by planktonic foraminifera (Bernárdez et al., 2008).

The palaeoenvironmental reconstruction has revealed a high percentage of woodland (67.9%) (Fig. 5). Some authors have confirmed the persistence of pine forest in NW Iberia until the Late Holocene (Morales-Molino et al., 2011). However, a considerable percentage of open areas (26%) can also be observed. These results coincide with other palaeobotanical analyses, which have confirmed that shrubland expansion was significant by around ca. 5500 BP in the Iberian Peninsula in general (Carrión, 2002; Carrión et al., 2010b), but particularly in the Northwest, where the study by López-Merino et al. (2012) recorded an increase in shrubs to the detriment of trees (Fig. 3).

In summary, it has been observed that in all the studied sites, despite the regional variations resulting from their different geographic locations, the climatic evolution

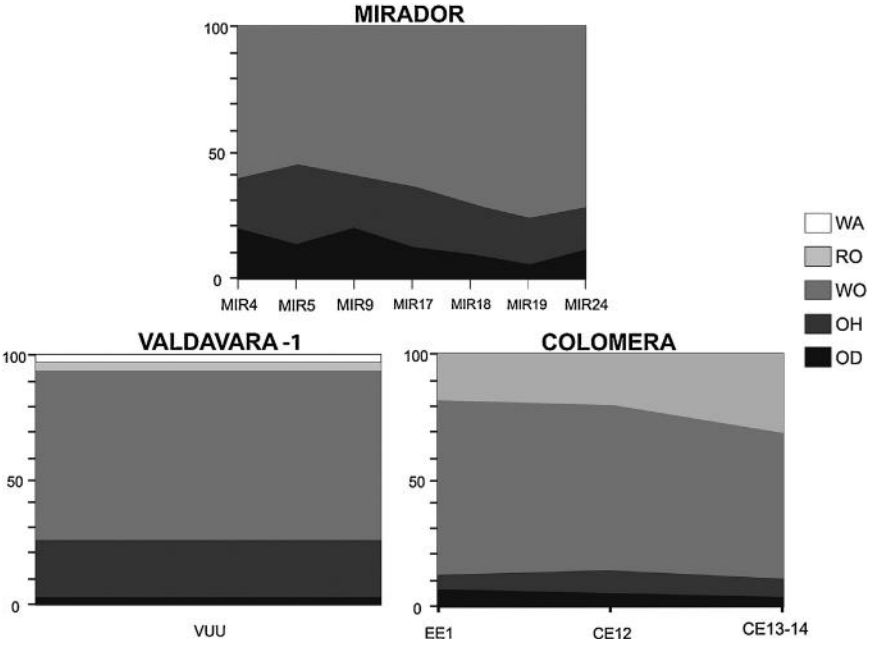


**Fig. 4.** Percentage of the habitats represented at each site. The abbreviations are as follows: R, Rocky; WA, Water; OD, Open Dry; OH, Open Humid; WO, Woodland.

**Fig. 4.** Pourcentage des habitats représentés dans chaque site. Les abréviations sont les suivantes : R, milieux rocheux ; WA, milieux aquatiques ; OD, milieux ouverts et secs ; OH, milieux ouverts et humides et WO, milieux forestiers.

followed the same pattern. From the Early Neolithic to the Bronze Age, the temperature and rainfall were maintained stable at Colomera and Mirador caves. The study of the palaeoenvironment showed slight variation between the studied sequences which are not related to the palaeoclimatic data. For this reason, we think that some landscape variations are related to the human impact, though this impact is slight. We recovered synanthropic species (taxa adapted to the conditions created or modified by human activities) such as *M.* (*Terricola*) *duodecimcostatus*, *M.* (*Terricola*) *lusitanicus*, *M. arvalis*, *E. quercinus* and *C. russula* (Mistrot, 2000). However, we did not find commensal species (e.g., *Mus musculus domesticus*) in any of the sites studied. Such species would have indicated a strong human impact. The pattern of expansion of these species through the Mediterranean basin suggests that they did not colonise the Iberian Peninsula until the first millennium BC (Cucchi et al., 2005).

## 4. Conclusions

From the Early Neolithic to the Bronze Age (ca. 7000–3000 BP) of the Iberian Peninsula, the evolution of the palaeoenvironment was conditioned not only by palaeoclimatic conditions, but was also linked to human activity.

In general, the climatic conditions in this period were more or less stable. The MER analysis shows winters that were colder than nowadays, above all in the Mediterranean area (Colomera), while in the northern Meseta (Mirador), we observe lower temperatures in the warmer months, and in the northwest (Valdavara-1) the temperatures were similar to today. As regards precipitation during the Holocene, in the northwestern site of Valdavara-1 this was lower than at present, whereas in the other studied sites it was higher.

The chorotype study shows that the dominant species in most of the studied layers were generalist species, but despite this we have detected a small weather pulse that occurred at different times in each study area. These changes could be related to the establishment of the Mediterranean climate in each area from ca. 7000 BP.

The landscape is dominated by woodland, with a gradual increase in open dry meadows in the major part of the studied sites during the Bronze Age. In some cases, this increase in open dry areas is linked to rising temperatures and declining rainfall, as is the case for Valdavara-1, while in Colomera and above all Mirador one notices a change in the landscape that follows a different dynamic, possibly caused by human activity. While the reduction in arboreal cover has been linked to the start of anthropogenic activity after ca. 4500 BP, in Mirador cave and Valdavara-1 cave, we see a decrease in woodland, but in Colomera cave there was an increase in woodland. Although some synanthropic species are represented in the studied sites, a strong human impact cannot be ascertained, because there is no evidence of the presence of commensal species.

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# APPENDIX 3

Palaeogeography, Palaeoclimatology, Palaeoecology 471 (2017) 71–81

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# Lateglacial to Late Holocene palaeoclimatic and palaeoenvironmental reconstruction of El Mirador cave (Sierra de Atapuerca, Burgos, Spain) using the small-mammal assemblages

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## ABSTRACT

El Mirador is a cave in the Sierra de Atapuerca (northern Iberian Peninsula) that contains 27 archaeological layers from the Lateglacial to the Late Holocene. A total of 4436 small-mammal remains have been analysed from these layers, and 19 taxa have been identified (three insectivores, seven chiropters and nine rodents). The palaeoenvironmental reconstruction based on a small-mammal analysis suggests that the entire sequence is dominated by a woodland landscape. Our climatic analysis characterises the climate in terms of an evolution from a cool and arid period in the Pleistocene layers (16,000 to 14,000 cal yr BP), probably related to Heinrich Event 1, to humid conditions and temperatures similar to nowadays in the Holocene layers in general. In MIR23 and MIR22 (7300 to 6800 cal yr BP) we detect an increase in temperature to levels above current values and an important decrease in rainfall. These climatic characteristics could be related to the end of the African Humid Period. Moreover, a short, slightly cooler event is registered in MIR11 (ca. 6300 to 5900 cal yr BP), coinciding with a change in the economic pattern in El Mirador. The results obtained on the basis of small-mammal studies are compared with multiproxy terrestrial data (pollen, charcoal, phytoliths, geochemistry, large mammals) and the Greenland ice-core record, as well as various other core records closer to the coasts of the Iberian Peninsula (MD95-2042, MD99-2331, MD95-2043 and SMP02-3). These comparisons show the agreement of the palaeoenvironmental and palaeoclimatic results with all the previous multiproxy and core-record data.

## 1. Introduction

During the last glacial period a sensitive response by Mediterranean vegetation to rapid climate variability has been detected in studies of the Alborán Sea core MD95-2043, with rapid woodland development during interstadials and the spread of semi-desert vegetation during Dansgaard-Oeschger events and Heinrich Events (Sánchez Goñi et al., 2002; Kageyama et al., 2005; Fletcher and Sanchez-Goñi, 2008). By contrast, the Holocene was in general a warm and wet period, with episodes of increased aridity and global climatic pulsations, but with many regional differences, whose reach across Europe is well known (Bond et al., 1997; Davis et al., 2003; Kalis et al., 2003; Mayewski et al., 2004; Jalut et al., 2009; Mercuri et al., 2011; Aranbarri et al., 2014). Although the Holocene has been defined as a relatively stable period in comparison to the Pleistocene, diverse climate and environmental changes have been widely recognized (Morellón et al., 2009). From 11,000 to 9000 cal yr BP, in the Northern Hemisphere dry and cool conditions persisted, while the beginning of the mid-Holocene (9000–5000 cal yr BP) was characterised by warm and moister conditions in the northern mid-to-high latitudes (Wanner et al., 2008; Morellón et al., 2009; Aranbarri et al., 2014). Within this period, a short-lived cold event was recorded, the event of 8200 cal yr BP (Mercuri et al., 2011). This was followed by a transition phase (ca.7000–5500 yr BP) known as the Holocene Climate Optimum, characterised by a period of climate stability, but this stability was interrupted by the end of the African period, characterised by an abrupt decrease in precipitation and an increase in temperatures (de Menocal et al., 2000). Finally there was a phase (ca. 5500 yr BP) of drier conditions with major environmental changes (Carrión et al., 2010a, 2010b; Jiménez-Moreno and Anderson, 2012; Aranbarri et al., 2014; Morales-Molino and García-Antón, 2014). These changes were linked to climate variability but also to human

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activities, a consequence of the incorporation of new agricultural and livestock techniques that conditioned the subsequent evolution of the potentialities of the landscape ecosystems (López Sáez et al., 2005; Carrión, 2002; Tarroso et al., 2014; Revelles et al., 2015).

In this paper we use the study of small mammals to undertake a palaeoclimatic and palaeoenvironmental reconstruction. This proxy is not generally used for Holocene sequences, since until recently small mammals have mainly been important for their contribution to biochronology. Fortunately, these preferences have recently been changing, and palaeoenvironmental and palaeoclimatic reconstructions have been carried out from small-mammal studies of the Holocene (Laplana Conesa and Cuenca-Bescós, 1995; Murelaga et al., 2007; Oms et al., 2009; Cuenca-Bescós et al., 2009; Bañuls-Cardona and López-García, 2009; López-García et al., 2011; Cuenca-Bescós and García Pimienta, 2012; Rofes et al., 2013; Bañuls-Cardona et al., 2013). These studies have provided interesting palaeoclimatic and palaeoenvironmental information on the Iberian Peninsula. On account of their size, small mammals are more sensitive in detecting small changes in the surrounding environment (López-García et al., 2013).

Our study analyses climatic pulsations and their relation to environmental changes in the Iberian Peninsula on the basis of the small-mammal assemblages of El Mirador cave. These range from the Lateglacial to the Late Holocene (15,000 to 3000 cal yr BP). In El Mirador cave, a complete sequence from the Lateglacial to the Early Bronze Age has been documented. This is of great significance for characterising the Pleistocene-Holocene transition in northern Iberia.

In addition, the results obtained are supported with other palaeoenvironmental data acquired from El Mirador cave, such as pollen (Expósito and Burjachs, 2016), anthracology (Euba et al., 2015), carpology (Rodríguez et al., 2016), phytoliths (Cabanes et al., 2009) and large-mammal remains (Martín et al., 2014; 2015). Further, marine core studies using oxygen isotope curves in the Alboran Sea (MD95-2043) (Cacho et al., 2001) and core SMP02-3 from the Galician continental shelf (Bernárdez et al., 2008) have also been used to understand the response of vegetation to the climate variability of the Lateglacial and Late Holocene.

## 2. El Mirador cave

El Mirador cave is situated in the south of the Sierra de Atapuerca (Ibeas de Juarros, Burgos, Spain). The site is located at an altitude of 1033 m a. s. l., and its geographical coordinates are 42° 20′ 58″ N, 03° 30′ 33″ E (Fig. 1). In 1999 drilling work was started on an area of 6 $m^2$ in the central part of the cave, on the basis of which the stratigraphic sequence was established. This is composed of a total of 27 layers that display high lateral and vertical variability due to the sedimentary characteristics of the cave and the post-depositional processes that took place there, such as the collapse of blocks and anthropic spatial organization, as well as bioturbation (Fig. 1). For this reason, it was decided that the naming and excavation should be in assemblages, distinguishing between the characteristic facies in the anthropized units (Vergès et al., 2002). There are a total of 17 radiocarbon dates for the sequence of El Mirador cave, which range from the Lateglacial to the Bronze Age (Vergès et al., 2002, Vergés et al., 2016; Angelucci et al., 2009) (Fig. 2).

The Pleistocene deposit is composed of 14 m of metric and decimetric limestone blocks with no sedimentary matrix in between. It is the result of the collapsed roof (MIR51/4 and MIR51/1) and contains two intercalated levels: MIR51/3, a shallow, archaeologically sterile level composed of wind-borne sediment, and MIR51/2, with the same sedimentary characteristics but with evidence of human activity: remains of a hearth, and lithic and faunal materials (Vergés et al., 2016). The 6-m-thick Holocene sedimentary layers rest directly on top of MIR51. Four meters are attributed to Neolithic occupations (levels MIR24 to MIR6) (Vergès et al., 2008), while the remaining two meters are from the Middle Bronze Age (MIR4 and MIR3A) (Vergès et al., 2002). These Holocene levels were essentially formed as a result of the use of the cave as a livestock pen. The activities related to animal husbandry left sedimentary layers of dung, which was piled together and burned at regular intervals in order to reduce its volume and to eliminate parasites (Angelucci et al., 2009). These burned layers alternate with partially burnt and unburned layers of manure and nodules of ash from burned dung. An artefact record related to domestic occupations is often present in these levels. This kind of deposit is known as “fumier” (Vergés et al., 2016).

Archaeological remains are abundant in this site, and many scientific papers on them have been published. These include analyses of ceramic and lithic artefacts (Vergès et al., 2002, 2008; Vergés et al., 2016), archaeobotanical studies (Allué and Euba, 2008; Cabanes et al., 2009; Euba et al., 2015; Expósito and Burjachs, 2016; Rodríguez et al., 2016), studies of human remains (Cáceres et al., 2007; Ceperuelo et al., 2015; Lozano et al., 2015) and of large mammals (Martín et al., 2009; Martín et al., 2014; Martín et al., 2016a, 2016b), and also preliminary studies of small-mammal remains (López-García, 2008; Bañuls-Cardona et al., 2013).

## 3. Material and methods

The small mammals analysed for this manuscript belong to seventeen layers (MIR51, MIR50, MIR49, MIR24, MIR23, MIR22, MIR21, MIR19, MIR18, MIR17, MIR16, MIR11, MIR10, MIR9, MIR6, MIR5 and MIR4).

### 3.1. Palaeontological study

In order to obtain the small-vertebrate remains, a system of water screening was used with sieves of decreasing mesh size (1 cm, 0.5 cm and 0.05 cm). Once the microfossils were separated from the now dry sediment, we proceeded to identify each species. This was based on both cranial and post-cranial diagnostic elements from the small-vertebrate skeletons.

The small mammals were identified using the methods of systematic paleontology. For the identification of chiropters, mandibles and isolated teeth were used (Reumer, 1984; Cuenca-Bescós et al., 2008; López-García, 2008); for insectivores, mandibles, isolated teeth and humeri were used (Bruijn and Rumke, 1974; Menu and Popelard, 1987; Sevilla, 1988); for Arvicolinae, the first lower molars (Meulen van der, 1973; Cuenca-Bescós et al., 2008; López-García, 2008); while for *Apodemus sylvaticus* and *Eliomys quercinus* identification was based on isolated teeth (Pasquier, 1974; Damms, 1981; Cuenca-Bescós et al., 2008; López-García, 2008).

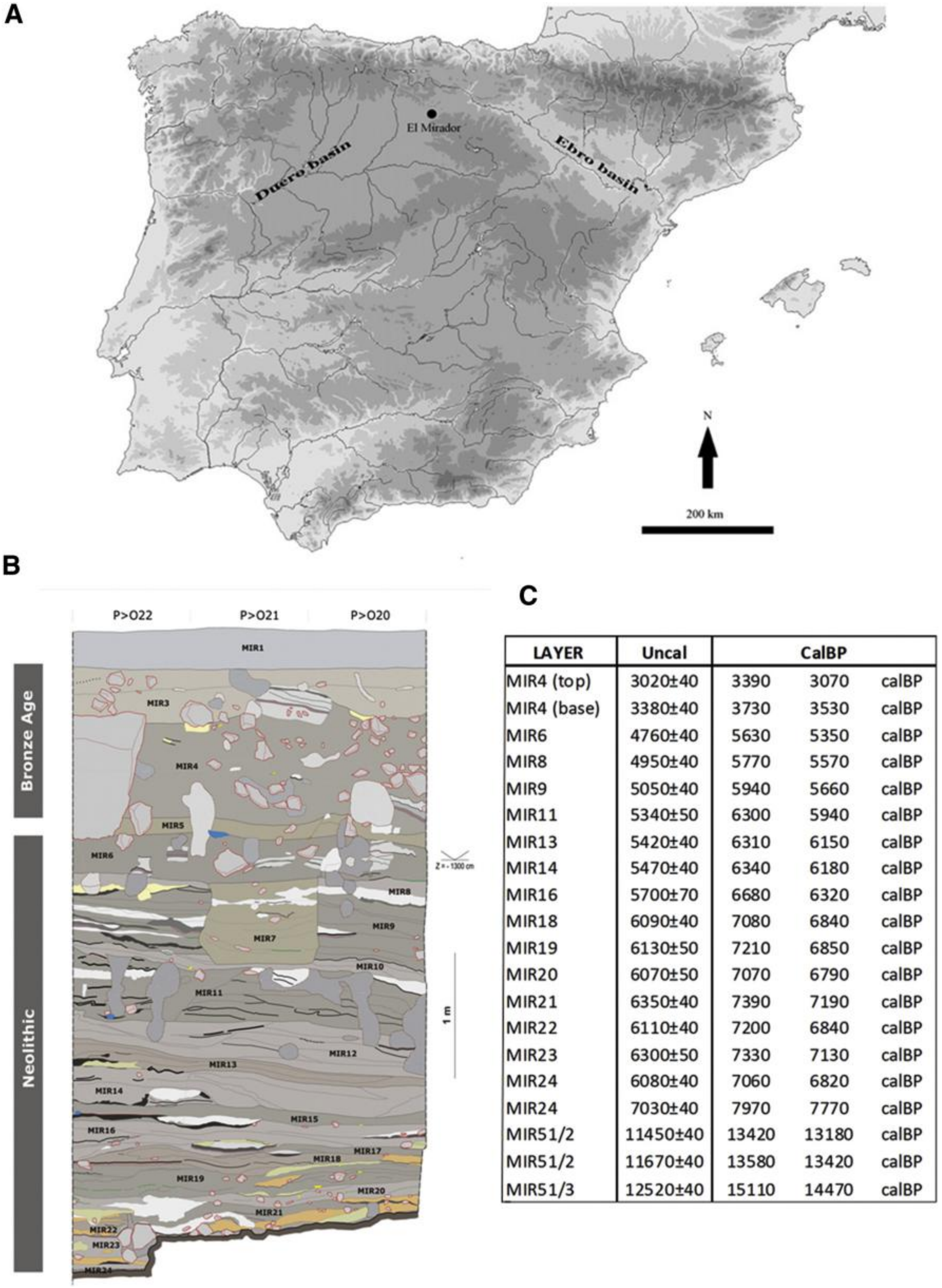
### 3.2. Habitat weighting method

We used the habitat weighting method (Evans et al., 1981; Andrews, 2006; modified by Blain et al., 2008, López-García et al., 2011) for the palaeoenvironmental reconstruction. This method involves ascertaining a percentage distribution for the habitat or habitats preferentially occupied by each taxon at present. We divided the habitats into four categories, defined according to a series of highly concrete environmental features: dry meadow, wet meadow, woodland and rocky areas: “dry meadow” consists of meadowland subject to seasonal climate change; “wet meadow” indicates evergreen meadowland with pastures and dense topsoil; “woodland” ranges from leafy forests to woodland margins, with moderate vegetation cover; and “rocky areas” refer to rocky habitats without vegetation cover (Table 2).

### 3.3. Bioclimatical approach

#### 3.3.1. Mutual Ecogeographic Range method (MER)

In order to reconstruct the features of the climate, we used the Mutual Ecogeographic Range method (MER) (Blain, 2005; Blain et al., 2010;



| LAYER | Uncal | CalBP | | |
|---|---|---|---|---|
| MIR4 (top) | 3020±40 | 3390 | 3070 | calBP |
| MIR4 (base) | 3380±40 | 3730 | 3530 | calBP |
| MIR6 | 4760±40 | 5630 | 5350 | calBP |
| MIR8 | 4950±40 | 5770 | 5570 | calBP |
| MIR9 | 5050±40 | 5940 | 5660 | calBP |
| MIR11 | 5340±50 | 6300 | 5940 | calBP |
| MIR13 | 5420±40 | 6310 | 6150 | calBP |
| MIR14 | 5470±40 | 6340 | 6180 | calBP |
| MIR16 | 5700±70 | 6680 | 6320 | calBP |
| MIR18 | 6090±40 | 7080 | 6840 | calBP |
| MIR19 | 6130±50 | 7210 | 6850 | calBP |
| MIR20 | 6070±50 | 7070 | 6790 | calBP |
| MIR21 | 6350±40 | 7390 | 7190 | calBP |
| MIR22 | 6110±40 | 7200 | 6840 | calBP |
| MIR23 | 6300±50 | 7330 | 7130 | calBP |
| MIR24 | 6080±40 | 7060 | 6820 | calBP |
| MIR24 | 7030±40 | 7970 | 7770 | calBP |
| MIR51/2 | 11450±40 | 13420 | 13180 | calBP |
| MIR51/2 | 11670±40 | 13580 | 13420 | calBP |
| MIR51/3 | 12520±40 | 15110 | 14470 | calBP |

**Fig. 1.** A. Geographical location of El Mirador cave. B. Stratigraphy of El Mirador cave (Angelucci et al., 2009). C. Radiocarbon datings of studied layers. Uncal: Mean of the radiocarbon dates. CalBP: 2σ range of the calibrated dates in cal yr BP.

Blain et al., 2016). We removed *Microtus oeconomus* and the chiropters from the sample remains. *Microtus oeconomus* is not currently found in the Iberian Peninsula (Pokines, 1998). In spite of this, its environmental requirements are taken into account in the general interpretation of the work. The omission of the chiropters is due to the fact that in many cases their mobility makes it difficult to ascertain their present geographical distribution, which could thus result in a distortion of the data.

The method involves defining the current distribution area of the faunal association, superimposing current distribution maps divided into 10 × 10 km UTM grids (Palomo and Gisbert, 2005). The resulting

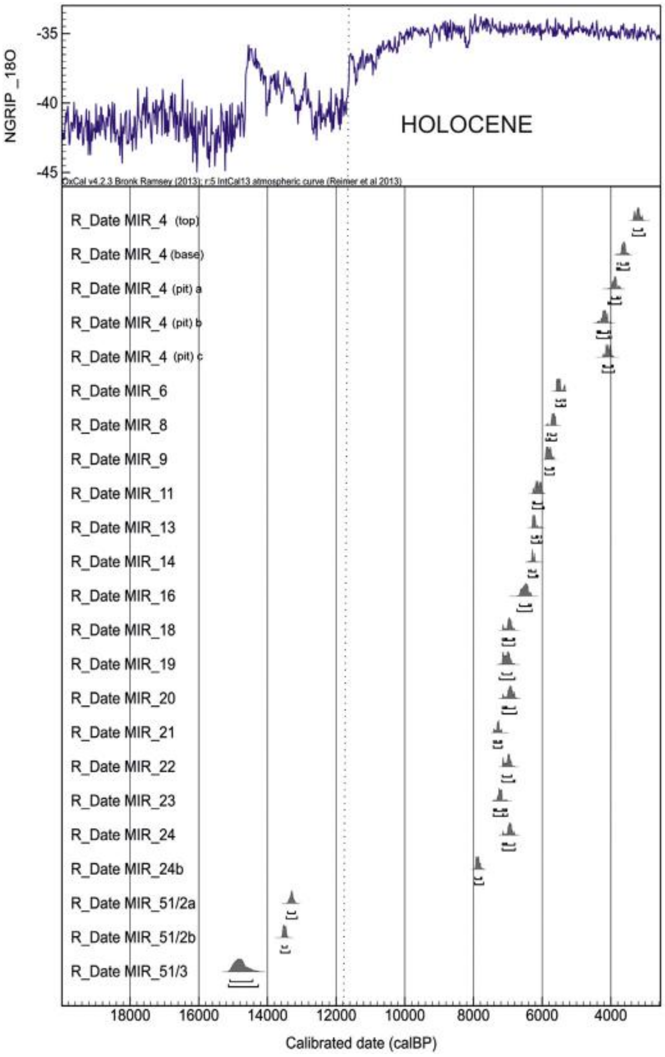


**Fig. 2.** Radiocarbon age of El Mirador cave calibrated by Oxcal v4.2.3 (Bronk Ramsey et al., 2013) placed in relation to the IntCal13 atmospheric curve (Reimer et al., 2013).

intersection indicates an area where the climatic characteristics are similar to those of our association. On the basis of this intersection we calculated the MAT (mean annual temperature), MTC (mean temperature of the coldest month), MTW (mean temperature of the warmest month), and MAP (mean annual precipitation). These climatic characteristics are obtained using current maps of temperature and precipitation (Climate-Data.org). The data obtained were compared with the present-day climate of this region of the Iberian Peninsula, enabling us to note the changes in temperature and precipitation in relation to the various points of the Pleistocene and the Holocene (Table 3).

### 3.3.2. Continentality index: Gorczynski (1920)

Continentality is one of the basic characteristics of climate. It reflects how much a particular area is influenced by the ocean or by large expanses of land. It is a result of the impact of climatic elements such as temperature, precipitation, solar radiation and cloudiness (Mikolášková, 2009). Gorczynski (1920) suggested estimating the continentality of a region on the basis of the amplitude of the annual temperature oscillation and the latitude of the place (Mineti, 1989). The values of the lowest-ranking units are classified as hyperoceanic with the index of continentality (*Ic*) lower than 11, as oceanic with *Ic* between 11 and 21, and as continental with *Ic* higher than 21 (Rivas Martínez et al., 2011).

$$Ic = 1.7 * (\mathrm{Mi} - \mathrm{mi}) / \sin(\mathrm{Lat} + 10) - 14$$

Mi: mean temperature of the warmest month
mi: mean temperature of the coldest month
Lat: latitude where the site is located

### 3.3.3. Rainfall index: Lang (1915)

Aridity refers to when there is insufficient water in the soil and the atmosphere, and it occurs when precipitation is lower than evaporation. It thus depends on the relationship between precipitation and temperature, which largely determines the evaporation of water. Lang relates the precipitation (mm) to the temperature (°C) to determine whether or not there is a shortage of water in a place (Capel Molina, 1963). In this classification a climate is defined as arid with *L* values lower than 40, as humid with *L* between 40 and 160, and as perhumid with *L* values higher than 160 (Lang, 1915; Quan et al., 2013).

$$L = \mathrm{P}/\mathrm{T}$$

P: mean annual precipitation
T: mean annual temperature

## 4. Results

From these seventeen layers (MIR51, MIR50, MIR49, MIR24, MIR23, MIR22, MIR21, MIR19, MIR18, MIR17, MIR16, MIR11, MIR10, MIR9, MIR6, MIR5 and MIR4), 4374 remains (NISP) have been analysed, with a minimum number of individuals (MNI) of 2283 (Table 1). Nineteen small-mammal taxa have been identified: *Sorex* gr. *coronatus-araneus*, *Neomys anomalus*, *Crocidura russula*, *Myotis myotis-blythii*, *Myotis bechsteinii*, *Miniopterus schreibersii*, *Rhinolophus ferrumequinum*, *Rhinolophus euryale-mehelyi*, *Nyctalus noctula*, *Plecotus austriacus*, *Arvicola amphibius*, *Clethrionomys glareolus*, *Chionomys nivalis*, *Microtus oeconomus*, *Microtus arvalis*, *Microtus agrestis*, *Microtus* (*Terricola*) *duodecimcostatus*, *Apodemus sylvaticus* and *Eliomys quercinus* (Fig. 3).

The remains analysed present slight signs of digestion. From these results, it can be surmised that the main animal responsible for the accumulation in the cave was a category 1 predator, a nocturnal bird of prey that displays an opportunistic trophic pattern and produces slight modifications of the bones it ingests (Andrews, 1990). The small mammals form an assemblage of great taxonomic variety, indicating that it was the work of an opportunistic hunter.

### 4.1. Lateglacial: MIR51(15100–13,180 cal yr BP), MIR50 and MIR49

### 4.1.1. Palaeontological study

From the small-mammal assemblages of MIR51, MIR50 and MIR49, 2708 remains (NISP) have been analysed, with a minimum number of individuals (MNI) of 1420 (Table 1). Nineteen small-mammal taxa have been identified: *Crocidura russula*, *Sorex* gr. *coronatus-araneus*, *Neomys anomalus*, *Myotis myotis-blythii*, *Myotis bechsteinii*, *Miniopterus schreibersii*, *Rhinolophus ferrumequinum*, *Rhinolophus euryale-mehelyi*, *Nyctalus noctula*, *Plecotus austriacus*, *Arvicola amphibius*, *Clethrionomys glareolus*, *Chionomys nivalis*, *Microtus oeconomus*, *Microtus arvalis*, *Microtus agrestis*, *Microtus* (*Terricola*) *duodecimcostatus*, *Apodemus sylvaticus* and *Eliomys quercinus* (Fig. 3).

### 4.1.2. Palaeoenvironmental analysis

In MIR51 (15100–13,180 cal yr BP) the most highly represented taxon is *M. agrestis*. This is probably related to the high percentage of open environments (50%). In MIR50, *Microtus* (*Terricola*)

**Table 1**
Distribution of the small-mammal remains of El Mirador cave by layers. Minimum number of individuals (MNI) and number of identified specimens (NISP).

| TAXA | MIR4 | MIR5 | MIR6 | MIR9 | MIR10 | MIR11 | MIR16 | MIR17 | MIR18 | MIR19 | MIR21 | MIR22 | MIR23 | MIR24 | MIR49 | MIR50 | MIR51 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Crocidura russula* | 19 | 6 | | 17 | | 1 | 2 | 16 | 21 | 6 | | 1 | | 8 | 33 | 2 | |
| *Sorex gr.coronatus-araneus* | 6 | 4 | 1 | 5 | 1 | 1 | | 9 | 21 | 4 | | | | 3 | 23 | | 1 |
| *Neomys anomalus* | | | | | | | | | | | | | | | 1 | | |
| *Myotis gr.myotis-blythii* | | | | 2 | 1 | | | | 3 | | | 2 | | 4 | 30 | 7 | 1 |
| *Myotis bechsteinii* | | | | | | | | | | | | | | | 4 | | |
| *Rhinolophus ferrumequinum* | | | | | | | | | | | | | | | 2 | | |
| *Rhinolophus euryale-mehelyi* | | | | | | | | | | | | | | | 3 | | |
| *Nyctalus noctula* | | | | | | | | | | | | | | | 1 | | |
| *Miniopterus schreibersii* | | | | 2 | | | | | 1 | 1 | | | | 2 | 3 | 1 | |
| *Plecotus auritus* | | | | | | | | | | | | | | | | | |
| *Arvicola amphibius* | | | | | | | | | | | | | | | 2 | | |
| *Clethrionomys glareolus* | | | | | | | | | | | | | | | 1 | | |
| *Chionomys nivalis* | | | | | | | | | | | | | | | 1 | 1 | 2 |
| *Microtus oeconomus* | | | | | | | | | | | | | | | 1 | | 4 |
| *Microtus arvalis* | 21 | 20 | 3 | 3 | 1 | 1 | 2 | 18 | 16 | 9 | 1 | 2 | | 22 | 280 | 4 | 7 |
| *Microtus agrestis* | 14 | 37 | 3 | 13 | 2 | | 2 | 34 | 26 | 22 | 1 | 2 | 3 | 15 | 36 | 5 | 12 |
| *Microtus (Terricola) duodecimcostatus* | 17 | 14 | 2 | 1 | 3 | 5 | 2 | 18 | 21 | 11 | 2 | 5 | 4 | 24 | 320 | 10 | 2 |
| *Apodemus sylvaticus* | 18 | 8 | 2 | 9 | 6 | 8 | 4 | 32 | 73 | 58 | 4 | | 2 | 56 | 604 | 8 | 2 |
| *Eliomys quercinus* | 1 | | | 1 | | 1 | 1 | 1 | 3 | 6 | 1 | | 1 | | 6 | | |
| Total MNI | 96 | 89 | 11 | 53 | 14 | 17 | 13 | 128 | 185 | 117 | 9 | 12 | 10 | 134 | 1351 | 38 | 31 |
| Total NISP | 280 | 193 | 17 | 77 | 19 | 19 | 14 | 230 | 376 | 154 | 17 | 15 | 15 | 240 | 2591 | 76 | 41 |

*duodecimcostatus* is the most highly represented taxon, and in this layer we have registered a minor increase in woodland with respect to MIR51. Finally, in MIR49 the trend of *Apodemus sylvaticus* predominating over the rest of the species, with a mainly woodland landscape, begins.

### 4.1.3. Palaeoclimatical approach

The results of the continentality index indicate climatic conditions characteristic of an oceanic climate in MIR51 (15100–13,180 cal yr BP) and MIR50, but characteristic of a hyperoceanic climate in MIR49. As regards the mean annual temperatures (MAT), in MIR51 we have

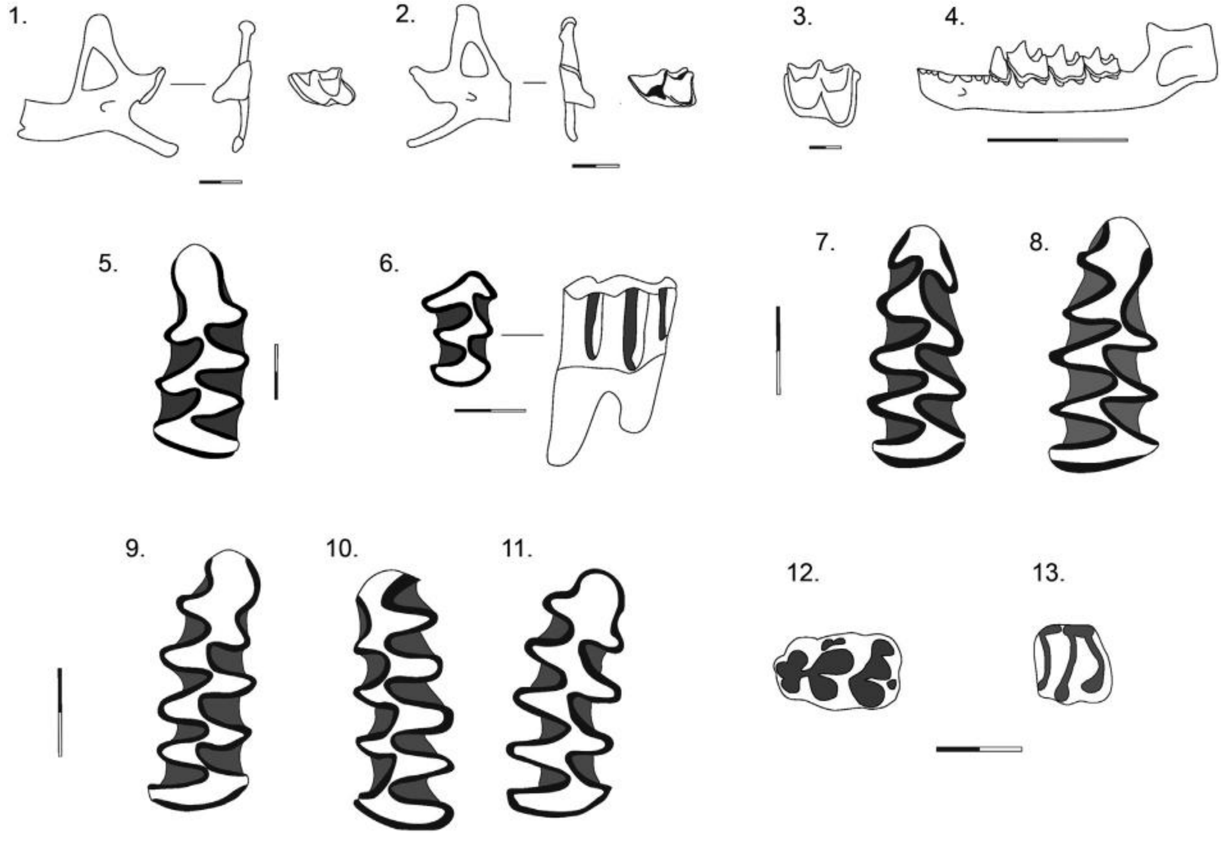


**Fig. 3.** Small-mammal fossil remains from layer MIR4 of El Mirador cave. From left to right: 1. *Crocidura russula*, right mandible (lingual and posterior view) and right m2 (occlusal view); 2. *Sorex* gr. *coronatus-araneus*, left mandible (lingual and posterior view) and left m1 (occlusal view); 3. *Myotis* gr. *myotis-blythii*, first right molar (occlusal view); 4. *Miniopterus schreibersii*, right mandible (labial view); 5. *Arvicola amphibius*, first right molar (occlusal view); 6. *Clethrionomys glareolus*, first right molar (occlusal view and labial view); 7. *Chionomys nivalis*, first right molar (occlusal view); 8. *Microtus oeconomus*, first right molar (occlusal view); 9. *Microtus agrestis*, left m1 (occlusal view); 10. *Microtus arvalis*, right m1 (occlusal view); 11. *Microtus (Terricola) duodecimcostatus*, right m1 (occlusal view); 12. *Apodemus sylvaticus*, right m1 (occlusal view); 13. *Eliomys quercinus*, left m2 (occlusal view). Scale bars = 1 mm.

registered the lowest temperatures in the sequence, 7.9 °C, related with the cool event, while in MIR49 we have registered 10.2 °C.

The results obtained from the rainfall index show wet and temperate climatic conditions, but the MER method reveals a difference of 200 mm between the MAP of MIR51–50 (1013–1067 mm) and MIR49 (1200 mm).

### *4.2. Middle Holocene (7060–5350 cal yr BP)*

#### *4.2.1. Palaeontological study*

From the small-mammal assemblages of MIR24, MIR23, MIR22, MIR21, MIR19, MIR18, MIR17, MIR16, MIR11, MIR10, MIR9, MIR6, and MIR5, 1386 remains (NISP) have been analysed, with a minimum number of individuals (MNI) of 792 (Table 1). Nine small-mammal taxa have been identified: *Crocidura russula*, *Sorex* gr. *coronatus-araneus*, *Myotis myotis-blythii*, *Miniopterus schreibersii*, *Microtus arvalis*, *Microtus agrestis*, *Microtus* (*Terricola*) *duodecimcostatus*, *Apodemus sylvaticus* and *Eliomys quercinus* (Fig. 3).

#### *4.2.2. Palaeoenvironmental analysis*

The most highly represented taxon is *Apodemus sylvaticus*. The presence of this species is directly related with the predominant representation of woodland in the Middle Holocene sequence. Woodland percentages range from 54% to 74% of the entire landscape around the cave. This is the general trend, but we have detected variations at specific times that should be noted. One of them took place at 7300–7100 cal yr BP (MIR23). In this layer, we have documented a decrease in woodland from 71% (MIR24) to 60% (MIR23), associated with the predominance of *Microtus (Terricola) duodecimcostatus* to the detriment of *Apodemus sylvaticus*. Starting from 6800 cal yr BP, there is another decrease in the percentage of arboreal cover around El Mirador. This decrease is from 70% in MIR18 to 62% in MIR17, and in this case it is associated with the increase in the presence of *Microtus agrestis*. Finally, we have observed from 6000 cal yr BP (MIR9) a decrease in woodland of 13% with respect to MIR10, and this trend continues until the end of the Middle Holocene in El Mirador cave. Moreover this trend is accompanied by the complete replacement of *A. sylvaticus* as the predominant species.

#### *4.2.3. Palaeoclimatic approach*

The continentality index in the Middle Holocene indicates climatic conditions characteristic of an oceanic climate. We have detected only two exceptions, with the climatic characteristics showing a hyperoceanic climate at 5900 cal yr BP (MIR10) and at 5600–5300 cal yr BP (MIR6). However, the MER analysis has revealed thermal oscillations that we consider important. During the Middle Holocene of El Mirador, we have observed that the mean annual temperature averages 10 °C, but this trend is interrupted at two points. From 7000 to 6800 cal yr BP (MIR23-MIR22), we have recorded an increase of 1 °C with respect to MIR24, while in MIR11 (6300–5900 cal yr BP) the general trend of 10 °C drops to 9.6 °C. This is not a sharp decrease, but it is the lowest temperature recorded in the Holocene sequence of El Mirador. Moreover, after this decrease the general trend (10 °C) is recovered through to the end of the Middle Holocene.

As regards the results obtained from the rainfall index for the Middle Holocene, these indicate pluviometric values characteristic of a warm and temperate climate, with the exception of MIR22 (7200–6800 cal yr BP), where the pluviometric values indicate a semi-arid climate.

By means of the MER climatic analysis, we have observed that the MAP (mean annual precipitation) generally ranges from 790 to 870 mm, with slight variations throughout the Middle Holocene. Nevertheless, we have documented a short arid period lasting from 7300 to 6800 cal yr BP (MIR23-MIR21). During this short period, the precipitation was 100 mm lower in MIR23 and MIR21, while in MIR22 it decreased by 200 mm with respect to MIR24. Another important decrease is recorded in MIR16 (6600–6300 cal yr BP), from 794 mm in MIR17 to 715 mm in MIR16.

### *4.3. Late Holocene (4330–3070 cal yr BP)*

#### *4.3.1. Palaeontological study*

From the small-mammal assemblage of MIR4, 280 remains (NISP) have been analysed, with a minimum number of individuals (MNI) of 71 (Table 1). Seven small-mammal taxa have been identified: *Crocidura russula*, *Sorex* gr. *coronatus-araneus*, *Microtus arvalis*, *Microtus agrestis*, *Microtus* (*Terricola*) *duodecimcostatus*, *Apodemus sylvaticus* and *Eliomys quercinus* (Fig. 3).

#### *4.3.2. Palaeoenvironmental analysis*

In this layer the predominant landscape is woodland (59%), following the trend of the Middle Holocene.

#### *4.3.3. Palaeoclimatic approach*

The climatic values for MIR4 are similar to those obtained for the Middle Holocene layers. The continentality index indicates climatic conditions characteristic of an oceanic climate, with a mean annual temperature of 9.9 °C, i.e. almost the same as the Middle Holocene layers. The rainfall index reveals pluviometric values for this layer that are characteristic of a warm and temperate climate, with a mean annual precipitation of 794 mm.

## **5. Discussion**

In the Iberian Peninsula, major changes in the vegetation and rapid oscillations in the climate have been identified between the Lateglacial and the Late Holocene (Mayewski et al., 2004; Kageyama et al., 2005; Pérez-Sanz et al., 2013). This is shown by studies such as the ice-core record from Greenland (Johnsen et al., 1972), marine core records closer to the coasts of the Iberian Peninsula such as marine core MD95-2042 off the southwestern coast of Portugal (Shackleton et al., 2000), MD99-2331 off the coast of Galicia (Naughton et al., 2007; Bernárdez et al., 2008), and MD95-2043 from the Alboran Sea (Kageyama et al., 2005), as well as continental cores from Padul (Sierra Nevada) (Pons and Reille, 1988) and core SMP02-3 retrieved from the Galician shelf (NW Iberian Peninsula) (Bernárdez et al., 2008). Furthermore, these changes in vegetation have also been seen from the pollen sequences of the Iberian Peninsula from the Lateglacial to the Early Holocene (Fletcher and Sanchez-Goñi, 2008; Carrión et al., 2010a, 2010b; Jiménez-Moreno et al., 2013; Aranbarri et al., 2014).

### *5.1. Lateglacial (15100–13,180 cal yr BP)*

The palaeoclimatic data obtained from the small-mammal assemblage show that in layer MIR51 the MAT is 7.9 °C, 2.2 °C lower than currently in Burgos (Climate-Data.org). This may well be related with a cool period from the end of the Lateglacial. The MD95-2042 record (southwestern Spain) has detected phases comprising a significant cooling of ocean surface waters caused by the influx of icebergs as far as Iberian shores (Shackleton et al., 2000). These phases have been called Heinrich Events (Fig. 2) (Sánchez-Goñi and d'Errico, 2005). Taking into account the absolute dating for this layer to between 15,100 and 13,180 cal yr BP, this cool period could correspond to Heinrich Event 1 (H1), dated to between 16,000 and 14,000 cal yr BP (Fletcher and Sanchez-Goñi, 2008).

Expansions of semi-desert vegetation also characterised the Lateglacial (Kageyama et al., 2005; Fletcher and Sanchez-Goñi, 2008), although we do not observe arid conditions from MIR51 to MIR49. A high MAP is registered with the small-mammal assemblage, between 400 and 600 mm higher than nowadays (Table 2). In fact, the Lang rainfall index characterises these pluviometric data as humid, and not as pertaining to a semi-arid Mediterranean climate as is currently

**Table 2**
Distribution of the minimum number of individuals (MNI) of small mammals from the different layers of El Mirador cave sequence according to their habitat preferences. We divided the habitats into four categories: OD, dry meadow; OH, wet meadow; WO, woodland; RO, rocky areas.

| Layers | MIR4 | MIR5 | MIR6 | MIR9 | MIR10 | MIR11 | MIR16 | MIR17 | MIR18 | MIR19 | MIR21 | MIR22 | MIR23 | MIR24 | MIR49 | MIR50 | MIR51 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| OD | 20.8 | 14.6 | 11.8 | 20.8 | 5.4 | 5.9 | 15.4 | 13.3 | 10.5 | 6.6 | 5.6 | 16.7 | 0.0 | 12.3 | 12.4 | 13.8 | 12.1 |
| OH | 19.8 | 30.9 | 32.4 | 20.8 | 23.2 | 20.6 | 19.2 | 24.2 | 19.7 | 18.6 | 22.2 | 12.5 | 40.0 | 16.8 | 15.3 | 25.0 | 31.5 |
| WO | 59.4 | 54.5 | 55.9 | 58.5 | 71.4 | 73.5 | 65.4 | 62.4 | 69.7 | 74.8 | 72.2 | 70.8 | 60.0 | 70.9 | 72.3 | 58.8 | 50.0 |
| RO | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.1 | 2.5 | 6.5 |

characteristic of Burgos (Table 3). These records show that during the Lateglacial the Iberian Peninsula was characterised by conditions that were slightly more humid than the rest of Europe (Kageyama et al., 2005; Peyron et al., 1998; Fletcher and Sanchez-Goñi, 2008).

During H1 there was a major reduction in arboreal pollen (Fletcher and Sanchez-Goñi, 2008). From the small-mammal assemblage we observe an increase in woodland, rising from MIR51 (50%) to MIR50 (59%) and particularly MIR49 (72%) (Fig. 2).

## 5.2. Holocene

In general, small-mammal accumulations were produced when the cave was inhabited, but during the Holocene El Mirador cave was a site with human occupation throughout its sequence. Zooarchaeological studies indicate that in some levels of El Mirador cave foetal remains from the final days of the third gestational trimester have been identified, and in all levels foetal remains from the final weeks of gestation have been recovered. These data testify to the very likely use of the cave as a breeding and birthing space for ovicaprines, at least during the end of winter and early spring (Martín et al., 2016a). The palaeoclimatic and palaeoenvironmental results for the Holocene sequence of El Mirador cave thus represent summer and autumn conditions.

### 5.2.1. Middle Holocene

At 8200 yr BP a cold event took place, characterised by cooler temperatures (Mayewski et al., 2004) and by drier conditions (Sáez et al., 2008; González-Sampériz et al., 2009; Gómez-Paccard et al., 2013). This event is most clearly recorded as a marked shift in oxygen isotope records from the Greenland Ice Sheet, and for this reason it has been used to signal the beginning of the Middle Holocene (Walker et al., 2012).

*5.2.1.1. PHASE I: 8000–6000 cal yr BP.* After this cold climatic event, however, the cores of the North Atlantic Ocean indicate warm temperatures from ca. 8000 to 5000 yr BP (Steig et al., 2009). At 7030–6870 cal yr BP (MIR24), we find mild and humid conditions. According to the Lang rainfall index, the climate of this layer was semi-humid; the MER method reveals the MAT to be 0.1 °C lower than nowadays, while the MAP is 252 mm higher than at present in the Burgos area. Even the pollen record of Padul in southeastern Spain shows signs of the onset of warm and humid conditions at ca. 8000 yr BP (Pons and Reille, 1988). We also observe in this layer a clear predominance of woodland (70. 9%) (Fig. 4) due to the high level of precipitation (865 mm) within the Holocene sequence of El Mirador (Table 2). This is not a local case. Palaeobotanical studies (Fernández et al., 2007; Jiménez-Moreno and Anderson, 2012) have shown that in this period there were wetter conditions and a substantial increase in the percentage of arboreal pollen in the western Mediterranean (Jiménez-Moreno et al., 2013), in the Ebro Valley (González-Sampériz et al., 2009; Gómez-Paccard et al., 2013), and in the south of the Iberian Peninsula (Fernández et al., 2007).

The highest temperatures in the El Mirador sequence (Table 3) are recorded from 7400 to 7000 cal yr BP (MIR23-22). In these layers the MAT exceeds the current level by 1 °C (Table 3). However, the MAP of these layers is the lowest in the entire sequence. The MAP in MIR23 is 148 mm higher than at present, while in the case of MIR22 the MAP is 608 mm, only 14 mm higher than nowadays (Table 2). According to the Lang index, MIR22 presents a semi-arid level of precipitation similar to present-day data (Table 3). Nevertheless, these lower levels of precipitation had no immediate effect on the palaeoenvironmental conditions of these layers: the percentage of arboreal cover in MIR22 is 71%, and in MIR23 it is 60% (Table 2). In terms of vegetation cover, dry conditions have been recorded in northern Iberia in general (Muñoz-Sobrino et al., 2007; Santos et al., 2000).

These conditions could be related to the end of the African Humid Period (ca. 9000–6000 cal yr BP). In fact, humid conditions had started

**Table 3**
Relation of temperatures and precipitation obtained using the MER (Mutual Ecogeographic Range) method. MAT: mean annual temperature; MTC: mean temperature of the coldest month; MTW: mean temperature of the warmest month; MAP: mean annual precipitation; n: number of 10 × 10 km UTM squares forming the intersection obtained for micromammals; mean ± SD: mean and standard deviation of the values obtained; min: minimum of the values obtained; max: maximum of the values obtained: Δ difference between the current mean for Burgos weather station over 30 years and that obtained for the small mammals.

| Layers | MAT | | | | | MTC | | | | | MTW | | | | | MAP | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | MAX | MIN | MEAN | SD | Δ | MAX | MIN | MEAN | SD | Δ | MAX | MIN | MEAN | SD | Δ | MAX | MIN | MEAN | SD | Δ |
| MIR4 | 13 | 5 | 9.94 | 1.5 | 0.2 | 5 | 0 | 2.54 | 1.2 | 0.06 | 22 | 15 | 18.53 | 1.4 | 0.2 | 1500 | 500 | 794 | 221 | −200 |
| MIR5 | 13 | 5 | 10.03 | 1.6 | 0.1 | 7 | 0 | 2.65 | 1.2 | −0.05 | 23 | 15 | 18.60 | 1.4 | 0.1 | 2500 | 500 | 846 | 284 | −252 |
| MIR6 | 13 | 5 | 9.97 | 1.5 | 0.1 | 7 | 0 | 2.64 | 1.2 | −0.04 | 22 | 15 | 18.49 | 1.3 | 0.2 | 2000 | 500 | 867 | 277 | −273 |
| MIR9 | 13 | 5 | 9.94 | 1.5 | 0.2 | 5 | 0 | 2.54 | 1.2 | 0.06 | 22 | 15 | 18.53 | 1.4 | 0.2 | 1500 | 500 | 794 | 221 | −200 |
| MIR10 | 13 | 5 | 9.97 | 1.5 | 0.1 | 7 | 0 | 2.64 | 1.2 | −0.04 | 22 | 15 | 18.49 | 1.3 | 0.2 | 2000 | 500 | 867 | 277 | −273 |
| MIR11 | 13 | 5 | 9.62 | 1.8 | 0.5 | 5 | 0 | 2.46 | 1.2 | 0.14 | 23 | 15 | 18.70 | 1.3 | 0.0 | 2000 | 500 | 792 | 238 | −198 |
| MIR16 | 13 | 5 | 10.17 | 1.5 | −0.1 | 5 | 0 | 2.62 | 1.0 | −0.02 | 23 | 15 | 18.97 | 1.5 | −0.3 | 1500 | 400 | 715 | 230 | −121 |
| MIR17 | 13 | 5 | 9.94 | 1.5 | 0.2 | 5 | 0 | 2.54 | 1.2 | 0.06 | 22 | 15 | 18.53 | 1.4 | 0.2 | 1500 | 500 | 794 | 221 | −200 |
| MIR18 | 13 | 5 | 9.94 | 1.5 | 0.2 | 5 | 0 | 2.54 | 1.2 | 0.06 | 22 | 15 | 18.53 | 1.4 | 0.2 | 1500 | 500 | 794 | 221 | −200 |
| MIR19 | 13 | 5 | 9.94 | 1.5 | 0.2 | 5 | 0 | 2.54 | 1.2 | 0.06 | 22 | 15 | 18.53 | 1.4 | 0.2 | 1500 | 500 | 794 | 221 | −200 |
| MIR21 | 13 | 5 | 10.07 | 1.6 | 0.0 | 5 | 0 | 2.57 | 1.1 | 0.03 | 23 | 15 | 19.05 | 1.4 | −0.3 | 1500 | 400 | 740 | 249 | −146 |
| MIR22 | 15 | 5 | 10.83 | 1.5 | −0.7 | 7 | 0 | 2.96 | 1.1 | −0.36 | 25 | 15 | 20.17 | 1.5 | −1.5 | 2500 | 300 | 608 | 233 | −14 |
| MIR23 | 15 | 5 | 11.02 | 2.1 | −0.9 | 9 | 0 | 3.37 | 1.8 | −0.77 | 25 | 15 | 19.79 | 1.8 | −1.1 | 1500 | 400 | 742 | 233 | −148 |
| MIR24 | 13 | 5 | 10.03 | 1.6 | 0.1 | 7 | 0 | 2.65 | 1.2 | −0.05 | 23 | 15 | 18.60 | 1.4 | 0.1 | 2500 | 500 | 846 | 284 | −252 |
| MIR49 | 11 | 9 | 10.20 | 1.2 | −0.1 | 3 | 1 | 2.20 | 1.2 | 0.40 | 17 | 17 | 17.00 | 0.0 | 1.7 | 1500 | 1000 | 1200 | 289 | −606 |
| MIR50 | 10 | 7 | 8.63 | 1.4 | 1.5 | 3 | 0 | 1.38 | 1.0 | 1.23 | 21 | 15 | 17.63 | 2.1 | 1.1 | 1500 | 700 | 1013 | 293 | −419 |
| MIR51 | 10 | 6 | 7.89 | 1.6 | 2.2 | 3 | 0 | 1.44 | 1.1 | 1.16 | 21 | 17 | 18.33 | 1.6 | 0.4 | 1500 | 700 | 1067 | 331 | −473 |

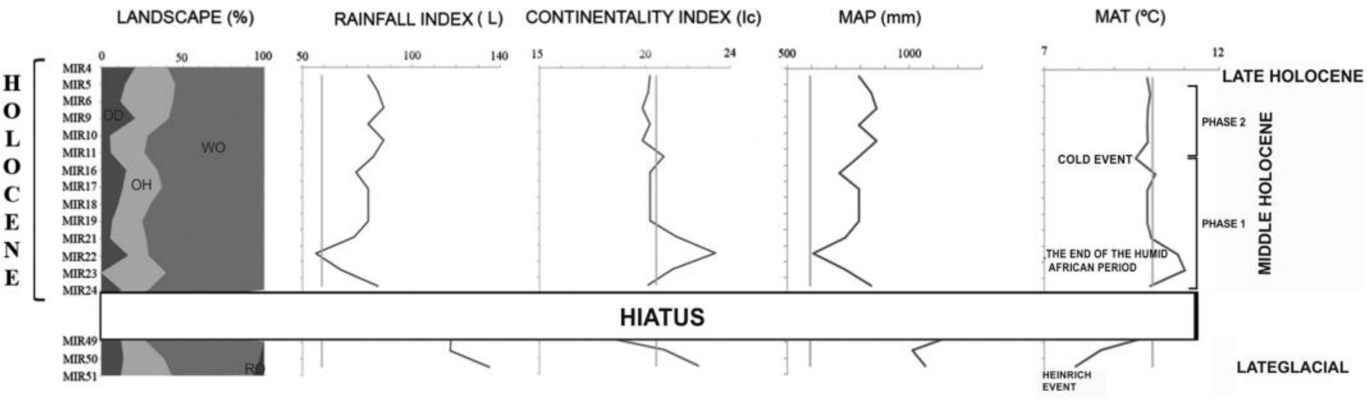


**Fig. 4.** Climatic and environmental comparisons between various proxies used throughout the El Mirador cave sequence. From left to right: Habitat interpretation for the El Mirador cave based on the habitat weighting method. Reconstruction of the rainfall index (Lang). Reconstruction of the continentality index (Gorczynski). Mean annual precipitation (MAP) and mean annual temperature (MAT) of the El Mirador cave sequence. Grey bar in rainfall index, continentality index, MAP and MAT represents the current values.

as early as ca. 14.5 cal ka BP following the fully glacial hyperarid conditions during the latest Pleistocene. This event has been attributed to a strengthening of the African monsoon due to gradual orbital increases in summer season insolation. However, the onset and termination of this humid period were very abrupt (deMenocal et al., 2000).

As regards the percentage representation of the small mammals, in most of the El Mirador cave sequence the most representative species is *A. sylvaticus*, a generalist species, whereas in MIR23 the most highly represented taxon (40%) is *M.*(*T*). *duodecimcostatus*, a thermo-Mediterranean taxon (Table 1).

After the African Humid Period the climatic conditions were more similar to present-day conditions in the Iberian Peninsula (Fig. 2) (Ruiz-Zapata et al., 2010). In fact, the MER method reveals that the MAT from 7390 to 7190 cal yr BP (MIR21) is equal to current data, although the MAP is 146 mm higher than now (Table 2). However, from ca. 7000 to 5000 yr BP, a decrease in temperature and an increase in precipitation are recorded in several regions of Europe (Leira, 2005; Kalis et al., 2003) and North Africa (Mercuri et al., 2011). These conditions are observed from 7200 to 6600 cal yr BP in MIR19, MIR18 and MIR17. Palaeoclimatic analysis shows an increase in precipitation in comparison to MIR21, for the MAP is 54 mm higher, and the temperatures are lower: a decrease of 0.5 °C is recorded in the mean of the coldest months (MTC) (Table 2).

After this slight cooling, from 6600 to 6300 cal yr BP (MIR16) the temperatures returned to levels similar to nowadays, with the MAT 0.1 °C higher than today (Table 2), and a significant decrease of 79 mm in rainfall is observed with respect to MIR17. Despite the climate changes revealed by MER, the landscape is virtually unchanged in relation to MIR17 (Table 2), and the Lang rainfall index lies within the parameters of a semi-humid interval, like MIR17 (Table 3).

At 6000 yr BP there was a steep decline in Northern Hemisphere solar insolation that brought global cooling with alpine glacier advances (Davis et al., 2003). The result was a short, slightly cooler and humid period (Bond et al., 1997; Kalis et al., 2003; Mayewski et al., 2004; Pérez-Sanz et al., 2013). These slightly cooler conditions have been identified in El Mirador at 6300–5940 cal yr BP (MIR11). With the MER we see the MAT (9.6 °C) at its lowest in the Holocene sequence of El Mirador cave, 0.5 °C lower than at present, mainly due to the low MTC (2.4 °C) (Table 2). Moreover, these results could be associated with a change in herding strategies at this point in El Mirador. The importance of goats and sheep decreases while the presence of equids, whose origin is likely to be wild, becomes more significant in this layer (Martín et al., 2016a). This change in livestock management may in part have been influenced by the low temperatures shown by the small-mammal study. Furthermore, this period was characterised by a wet event, with a general trend towards more humid conditions (Carrión, 2002; Tarroso et al., 2014). The climatic data obtained from the small mammals of El Mirador suggest that the MAP in MIR11 (792 mm) underwent an increase in relation to the pluviometric data for MIR16 (715 mm).

*5.2.1.2. PHASE II: 6000–5000 cal yr BP.* As well as several short cooling events detected throughout Europe within relatively stable climatic conditions (Mayewski et al., 2004), dry events have also been detected during the Holocene (Fig. 2) (Jalut et al., 2000; Carrión et al., 2010a, 2010b). Such a stage of marked aridity has been identified in Europe (Mercuri et al., 2011), and in the Iberian Peninsula such an event occurred towards ca. 5800–5600 yr BP (Domínguez-Villar et al., 2012; Tarroso et al., 2014). More concretely, in the Iberian Meseta it occurred at around 5740 cal yr BP (Perez-Obiol et al., 2011). In El Mirador we detect one of these dry events in 5940–5660 cal yr BP (MIR9). This level shows a decrease in MAP from 867 mm in MIR10 to 794 mm in MIR9 (Table 2).

The palaeoenvironmental analysis shows a clear change in the landscape with respect to the lower layers. A major decrease in woodland formations is observed from 71% in MIR10 to 58% in MIR9 (Fig. 4). The pollen remains indicate a significant increase in crops around the cave (Expósito et al., 2017). The agricultural intensification caused a deterioration in landscape throughout the Iberian Peninsula (Fletcher and Sanchez-Goñi, 2008; Pérez-Sanz et al., 2013).

Moreover, some studies have described this event as preceding the development of a dry Mediterranean climate, corresponding to the expansion of sclerophyllous woodlands (Carrión et al., 2010a, 2010b; Pérez-Sanz et al., 2013; Tarroso et al., 2014). In MIR9 the best-represented small mammal taxon is a thermo-Mediterranean species, *C. russula* (32%) (Table 1). This suggests a slight thermal recovery with respect to MIR10. It could also be due to the incipient establishment of a Mediterranean climate that occurred in the area around El Mirador before ca. 5000 yr BP (Perez-Obiol et al., 2011). As regards the temperatures, by contrast, no change is observed from MIR10, and this trend is to persist until the Bronze Age.

After the dry event of MIR9 (5940–5660 cal yr BP), an increase in humidity and woodland expansion has been observed in the Iberian Peninsula (Fig. 4) (Carrión et al., 2010a, 2010b), although there are regional areas where forest cover is reduced and shrub vegetation expands (López-Merino et al., 2012). From 5630 to 5350 cal yr BP (MIR6 and MIR5), we observe a substantial increase in precipitation (73 mm more than in MIR9) (Table 2), although there is no gain in forest cover. On the contrary, we observe a major increase in open wet meadows (10% with respect to MIR9), which in both layers results in the highest percentages in El Mirador cave (Fig. 4).

The palaeoenvironmental and palaeoclimatic conditions of these layers (5630–5350 cal yr BP) of El Mirador cave suggest that there was probably another factor that contributed to the decline in woodland

(Fig. 4). In central Europe, adaptation to the forest ecosystem was abandoned during the Early Neolithic in favour of an agricultural system (Kalis et al., 2003). Some authors claim that the landscape in the Iberian Peninsula after ca. 5000 yr BP is likely to have been influenced by non-natural ecosystem changes due to the spread of human activities, first in the lowlands and expanding to mountainous environments (Carrión et al., 2010a; Tarroso et al., 2014). Other authors believe that the first evidence of a human impact on the landscape of the Iberian Peninsula was produced during this time period (Badal et al., 1993; Carrión, 2002; Fletcher and Sanchez-Goñi, 2008; Martínez-Cortizas et al., 2009; López-Merino et al., 2012; Tarroso et al., 2014; Pérez-Díaz et al., 2015; Aranbarri et al., 2014; Revelles et al., 2015; Lillios et al., 2016).

### 5.2.2. Late Holocene

This was characterised by an increase in temperature but with slight fluctuations, and by irregular rainfall with summers undergoing mild droughts and very rainy winters (Fig. 3) (Mariscal, 1993)

Palaeoclimatic studies have claimed that the period from ca. 4300–3400 yr BP was an arid, cool phase in MIR4 (Fig. 4) (Jalut et al., 2000; Carrión, 2002; Mayewski et al., 2004; Martín-Puertas et al., 2010). Other authors have pointed to a slight cooling and increased dryness manifested by an increase in xerophytic and cold taxa at the expense of Mediterranean species (Murelaga et al., 2007; Ruiz-Zapata et al., 2010; Domínguez-Villar et al., 2012; Pérez-Sanz et al., 2013). In the case of MIR4, a high percentage of *M. arvalis*, a Eurosiberian taxon (Table 1), is recorded. The MER method indicates a minor decrease in temperatures and in precipitation with respect to MIR5 (Table 2). The results obtained by the MER method for MIR 4 concur with those obtained from palaeobotanical studies in the same layer (Vergès et al., 2002; Cabanes et al., 2009) and from other pollen studies within the Iberian Peninsula (López Sáez et al., 2005), which indicate a mixed environment and an expansion of pine forests. However, the habitat weighting method in MIR4 shows an increase in open dry to the detriment of open humid ecosystems (Table 2).

This increase in open dry environments could be related with the MER results that indicate a small decrease in precipitation, or it could be linked to the human impact on the landscape. In the Bronze Age, cereal-growing and livestock-keeping are widely documented in all deposits of human groups (Aranbarri et al., 2014; Revelles et al., 2015). On the other hand, García-Antón et al. (2011) have suggested that the human impact on the environment in this area of the northern Meseta was not intense in the first millennium B.C. However, the human impact on the environment is indicated by archaeobotanical studies based on pollen, charcoal, seeds and phytoliths at El Mirador site (Rodríguez and Buxó, 2008; Cabanes et al., 2009). These studies have confirmed the presence of herbaceous plants related to the development of agriculture and livestock.

All these data thus indicate that this part of the Bronze Age is characterised by temperatures that are similar to, or slightly lower than, present-day ones, and levels of mean annual precipitation that are slightly higher than present-day ones, suggesting the start of the climatic conditions typical of the Mediterranean climate (Terral and Mengüal, 1999).

## 6. Conclusions

The palaeoclimatic data obtained by means of the small-mammal assemblage of the Lateglacial in general show humid and cool climate conditions. Within this context, it should be noted that layer MIR51 represents a cool period that may well be related with Heinrich Event 1. The palaeoenvironmental analysis indicates the greatest reductions in woodland in the lowest layers of the sequence and an increase in MIR49 with respect to MIR51and MIR50.

In the Holocene layers of El Mirador cave, we observe seasonal anthropic occupation. The palaeoclimatic and palaeoenvironmental data obtained from the study of small mammals represent typical climatic conditions registered in summer and autumn.

During the Middle Holocene we detect important climatic events. From 7000 to 6800 (MIR 23 and MIR22), we register climatic characteristics that could be related to the end of the African Humid Period, namely an increase in temperatures and a progressive reduction in arboreal cover as a result of a decrease in precipitation. The temperatures exceeded current levels by 1 °C, especially in MIR23, where the most highly represented taxon is a thermo-Mediterranean species, *M.* (*T.*) *duodecimcostatus*. After this period, the climatic conditions became more similar or equal to present-day conditions, while the precipitation decreased but always remained above current levels. When this warm period finished, the temperatures from MIR19 to MIR17 underwent a slight decline and there was a slight increase in precipitation. This was associated with a minor increase in open landscape to the detriment of woodland. After this slight cooling, at 6600–6300 cal yr BP (MIR16) the temperatures recorded again become higher than nowadays, and a significant increase in aridification is observed.

In MIR11 (6300–5940 cal yr BP) a short, slightly cooler event is recorded. The temperature in this period is the lowest in the Holocene sequence of El Mirador cave, 0.5 °C lower than nowadays.

On the other hand, there is a significant increase in precipitation in MIR10 (867 mm). Moreover, in this layer a period of thermal stability begins, which could be related with the incipient establishment of a Mediterranean climate, corresponding to the expansion of Mediterranean species such as *C. russula* (32%) in MIR9.

From MIR9 to MIR 4 we note a significant palaeoenvironmental change. In MIR6 (5630–5350 cal yr BP) and MIR5 there is an increase in precipitation, but the reduction in woodland continues, with a major increase in open humid landscapes. This indicates that there was probably another factor that contributed to the decline in woodland, such as an agricultural system that exploited the environment. This trend was to persist until the Bronze Age.

In the Late Holocene, the application of the MER method to the small-mammal assemblage of level MIR4 (4330–3070 cal yr BP) of El Mirador cave reveals a rather cool, arid phase with a high percentage of *M. arvalis*, a Eurosiberian taxon. Moreover, the palaeoenvironmental analysis indicates an increase in open dry landscapes to the detriment of open humid landscapes. This increase could be associated with the MER results, which indicate a minor decrease in precipitation, or it could be related with the human impact on the landscape, as in MIR5 and MIR6.

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# APPENDIX 4

Research paper

# Human impact on small-mammal diversity during the middle- to late-Holocene in Iberia: The case of El Mirador cave (Sierra de Atapuerca, Burgos, Spain)

The Holocene
1–11

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**Abstract**

The human impact on the environment in the Holocene has usually been characterized on the basis of palaeobotanical records, but attempts to distinguish the anthropogenic impact from natural events in landscape evolution have been the subject of much debate in recent years. The aim of this paper is to analyse small-mammal diversity and the presence of synanthropic species, whose small size makes them more sensitive to any changes in their environment that may occur. This study has allowed us to characterize palaeoclimatic and palaeoenvironmental changes, recording small changes whether resulting from a human influence or otherwise. Our object of study is El Mirador cave, which has a sequence with a well-documented human occupation extending from 7200 to 3000 cal. BP. The study has led us to differentiate two phases. In one phase, we can see small changes in diversity related to climatic oscillations from ca. 7200 to 6800 cal. BP, while in the second phase, lasting from ca. 6800 to 3000 cal. BP, the changes in diversity and in the assemblage of synanthropic species are associated with human economic strategies. Moreover, we distinguish which kinds of economic activity (crop and livestock farming) have influenced these changes, because some small-mammal species are influenced, positively or negatively, by environmental changes based on crop farming and animal husbandry. All this information is contrasted with other archaeological proxies, such as the large-mammal and palaeobotanical assemblages from El Mirador cave. Furthermore, this integrative analysis has made it possible to identify the existence of altered environments more generally throughout the Iberian Peninsula from ca. 6000 cal. BP. It additionally confirms the theory of low human occupation intensity in the northern Meseta and in high mountainous areas during the early Neolithic.

**Keywords**
anthropogenic impact, Bronze Age, diversity, Neolithic, paleoclimate, palaeoenvironment, small mammals

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## Introduction

The climate during the Holocene was warm and wet with some arid episodes, but with many regional differences of which we know their reach across Europe (Aranbarri et al., 2014; Bond et al., 1997; Davis et al., 2003; Jalut et al., 2009; Kalis et al., 2003; Mayewski et al., 2004; Mercuri et al., 2011). All these climatic characteristics contributed to modifying the landscape, but so did the human use of the territory for economic purposes (Heinz et al., 2004; Morales-Molino et al., 2011; Pérez-Díaz et al., 2015; Tarroso et al., 2014). In fact, human disturbances have been considered the major agent of vegetation change in the Iberian Peninsula for at least the last 7500 years (Pérez-Obiol et al., 2011).

El Mirador is situated in the northwest of the Iberian Peninsula where the climate is typically Mediterranean, whereas in the northern areas variability is primarily in tune with central European climatic oscillations (Rivas-Martínez et al., 2011). In this area, the palaeoecological studies have registered the influence of anthropogenic activity on natural vegetation for ca. 6000 years (Iriarte, 2009; Tarroso et al., 2014). This influence has continuously increased over several millennia of human occupation of these environments, with the resulting fire and grazing pressure (López-Merino et al., 2012; Morales-Molino et al., 2011; Santos et al., 2000).

In this study, we have included the small mammals' samples and the environmental (*habitat weighting*) and climatic (*mutual ecogeographic range* (MER)) conditions exposed in Bañuls-Cardona et al.

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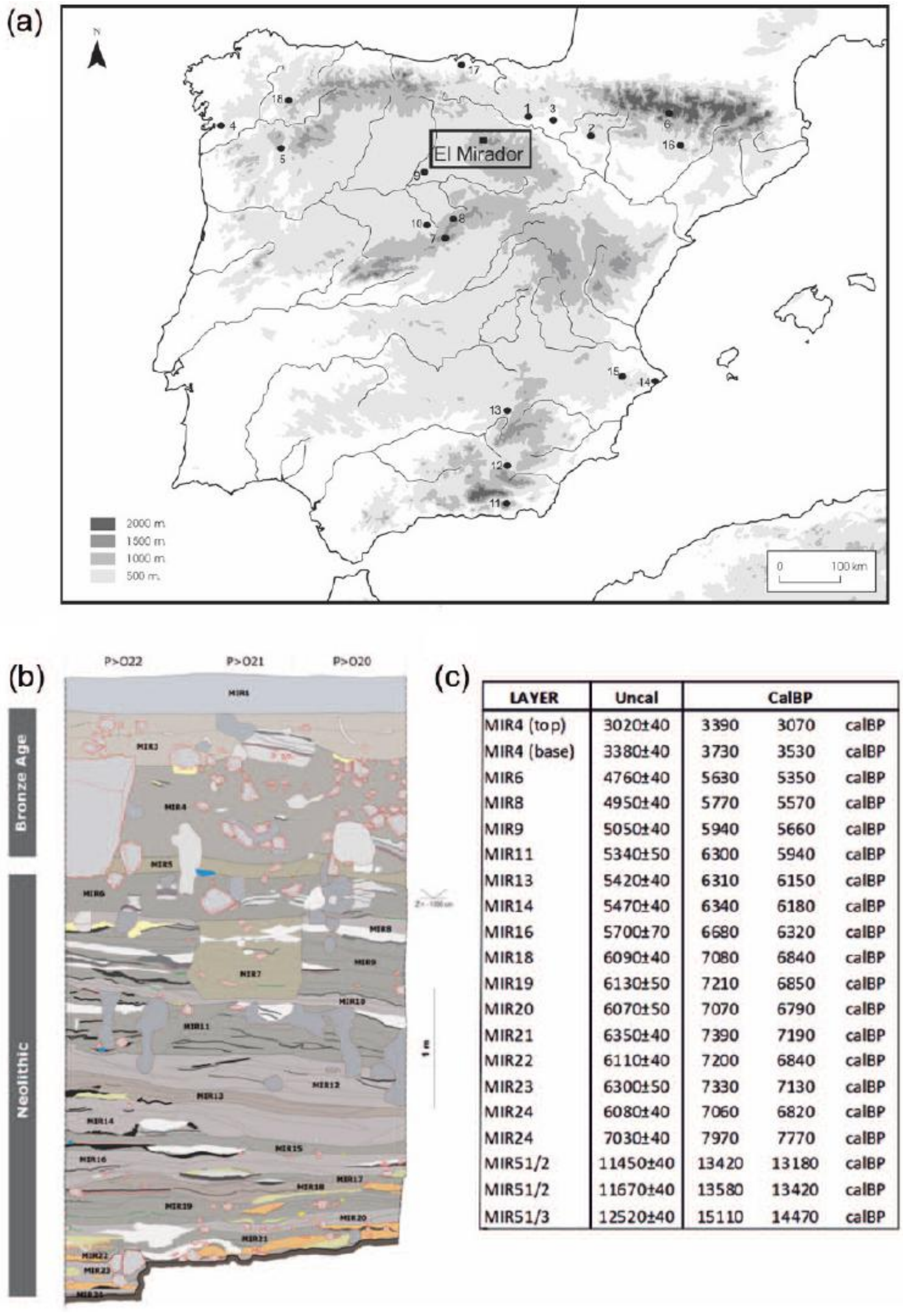

| LAYER | Uncal | CalBP | | |
|---|---|---|---|---|
| MIR4 (top) | 3020±40 | 3390 | 3070 | calBP |
| MIR4 (base) | 3380±40 | 3730 | 3530 | calBP |
| MIR6 | 4760±40 | 5630 | 5350 | calBP |
| MIR8 | 4950±40 | 5770 | 5570 | calBP |
| MIR9 | 5050±40 | 5940 | 5660 | calBP |
| MIR11 | 5340±50 | 6300 | 5940 | calBP |
| MIR13 | 5420±40 | 6310 | 6150 | calBP |
| MIR14 | 5470±40 | 6340 | 6180 | calBP |
| MIR16 | 5700±70 | 6680 | 6320 | calBP |
| MIR18 | 6090±40 | 7080 | 6840 | calBP |
| MIR19 | 6130±50 | 7210 | 6850 | calBP |
| MIR20 | 6070±50 | 7070 | 6790 | calBP |
| MIR21 | 6350±40 | 7390 | 7190 | calBP |
| MIR22 | 6110±40 | 7200 | 6840 | calBP |
| MIR23 | 6300±50 | 7330 | 7130 | calBP |
| MIR24 | 6080±40 | 7060 | 6820 | calBP |
| MIR24 | 7030±40 | 7970 | 7770 | calBP |
| MIR51/2 | 11450±40 | 13420 | 13180 | calBP |
| MIR51/2 | 11670±40 | 13580 | 13420 | calBP |
| MIR51/3 | 12520±40 | 15110 | 14470 | calBP |

**Figure 1.** (a) Geographical location of El Mirador cave and the sites mentioned in the discussion. 1. Peña Larga; 2. Padre Areso; 3. Puy Águila I; 4. Coto da Fenteria; 5. Arcucelos; 6. Basa de la Mora; 7. Tolla Collado de El Berrueco; 8. Rascafría; 9. Espinosa de Cerrato; 10. El Carrizal; 11. Sierra de Gádor; 12. Sierra de Baza; 13. Siles lake; 14. Cova de les Cendres; 15. Cova de l'Or; 16. Cova Colomera; 17. El Mirón; 18. Valdavara. (b) Stratigraphy of El Mirador cave (Angelucci et al., 2009). (c) Radiocarbon datings of studied layers. Uncal: mean of the radiocarbon dates. CalBP: 2σ range of the calibrated dates in cal BP.

(in preparation), to analyse the relationship between natural (environmental and climatic) and anthropic influences on the changes in small mammals' diversity. The activities associated with an economy based on agriculture and livestock farming are known to contribute to modifying and homogenizing the landscape, influencing the ethology of small mammals and resulting in the changes in biodiversity (Barnosky et al., 2011; Benton et al., 2003; Torres-Romero and Olalla-Tárraga, 2014). In El Mirador cave (northern Meseta of Iberia), various archaeobotanical and archaeological proxies have been analysed to try to ascertain the difference between the anthropic and the natural origin of the landscape changes that took place during the Holocene (Cabanes et al., 2009; Euba et al., 2016; Expósito and Burjachs, 2016; Martín et al., 2014, 2016a, 2016b; Rodríguez et al., 2016).

## Site

El Mirador cave is situated in the south of the Sierra de Atapuerca (Burgos, Spain). The site is located at an altitude of 1033 m a.s.l. (Figure 1). It was in 1999 that work was started on it, with the excavation of an area of 6 m$^2$ in the central part of the cave, on the basis of which the stratigraphic sequence was established. This is composed of a total of 26 layers displaying high lateral and vertical variability because of the sedimentary characteristics of the cave and the post-depositional processes that took place there, such as the collapse of blocks and anthropic spatial organization, as well as bioturbation (Figure 1). For this reason, it was decided that the naming and excavation of the site should be in assemblages, distinguishing between the characteristic facies of the anthropized units, mainly consisting of burned and unburned

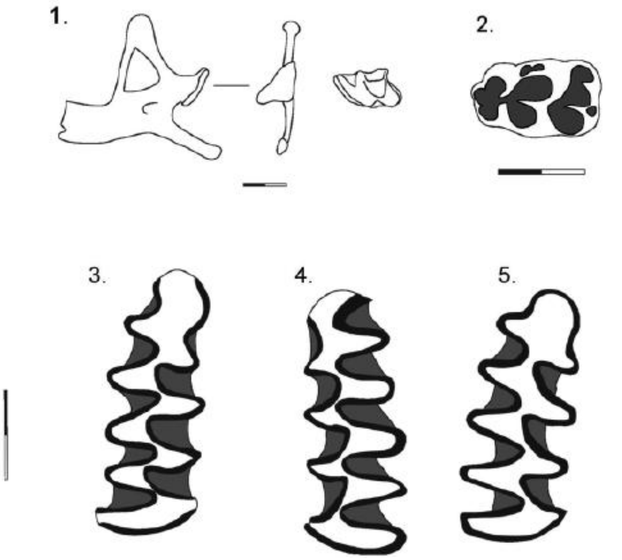

**Figure 2.** Most representative species of El Mirador cave. From left to right: 1. *Crocidura russula*, right mandible (lingual and posterior view) and right m2 (occlusal view); 2. *Apodemus sylvaticus*, right m1 (occlusal view); 3. *Microtus arvalis*, right m1 (occlusal view); 4. *Microtus agrestis*, left m1 (occlusal view); 5. *Microtus (Terricola) duodecimcostatus*, right m1 (occlusal view). Scale bars = 1 mm.

dung (Vergès et al., 2002, 2008). Most of these layers have been dated. There are a total of 17 radiocarbon dates for the sequence of El Mirador cave, which range from the latest Pleistocene to the Bronze Age (Angelucci et al., 2009; Vergès et al., 2002, 2016; Figure 2).

The Pleistocene deposit is composed of 14 m of metric and decimetric limestone blocks with no sedimentary matrix in between. It is the result of the collapsed roof (MIR51/4 and MIR51/1) and contains two intercalated layers: MIR51/3, a shallow, archaeologically sterile layer composed of wind-borne sediment, and MIR51/2, with the same sedimentary characteristics but with evidence of human activity: remains of a hearth, and lithic and faunal materials (Vergès et al., 2016). The 6-m-thick Holocene sedimentary layers rest directly on top of MIR51. Four metres are attributed to Neolithic occupations (layers MIR24–MIR6) occurring between the last third of the sixth millennium and the first half of the fourth millennium cal BC (Vergès et al., 2008), while the remaining 2 m are from the Middle Bronze Age (MIR4 and MIR3A), between the second and fourth quarters of the second millennium cal. BC (Vergès et al., 2002). These Holocene layers were essentially formed as a result of the use of the cave as a livestock pen. The activities related to animal husbandry left sedimentary layers of dung, which was piled together and burned at regular intervals to reduce its volume and to eliminate parasites (Angelucci et al., 2009). These burned layers alternate with partially burned and unburned layers of dung and nodules of ash from burned dung. An artefact record related to domestic occupations is often present in these layers. This kind of deposit is known as a *fumier* (Brochier, 1988; Vergès et al., 2016).

Archaeological remains are abundant in this site, and many specific studies are available in the literature. These include analyses of ceramic and lithic artefacts (Vergès et al., 2002, 2008, 2016), archaeobotanical studies (Cabanes et al., 2009; Euba et al., 2016; Expósito and Burjachs, 2016; Rodríguez et al., 2016), studies of human remains (Cáceres et al., 2007; Ceperuelo et al., 2015; Lozano et al., 2015) and of large mammals (Martín et al., 2009, 2014, 2016a, 2016b), and also preliminary studies of small-mammal remains (Bañuls-Cardona et al., 2013; López-García, 2008).

## Material and methods

### Small mammals

The small mammals analysed in this study belong to 14 Holocene layers (MIR24, MIR23, MIR22, MIR21, MIR19, MIR18, MIR17, MIR16, MIR11, MIR10, MIR9, MIR6, MIR5 and MIR4). These small mammals were identified using the methods of systematic palaeontology from Bañuls-Cardona et al. (in preparation). We used mandibles and isolated teeth to identify insectivores (Cuenca-Bescós et al., 2008; López-García, 2008; Reumer, 1984); for chiropters, mandibles, isolated teeth and humeri (Bruijn and Rumke, 1974; Menu and Popelard, 1987; Sevilla, 1988); for Arvicolinae, the first lower molars (Cuenca-Bescós et al., 2008; López-García, 2008; Van der Meulen, 1973); while the identification of *Apodemus sylvaticus* and *Eliomys quercinus* was based on isolated teeth (Cuenca-Bescós et al., 2008; Damms, 1981; López-García, 2008; Pasquier, 1974).

In this manuscript, we describe the sample of small mammals that is the subject of this study; we start from the premise that all ecosystems are described in terms of the number of individuals of each species represented (Margalef, 1972). The first method that we apply in this basic analysis of biodiversity is Chao-1 (Colwell and Coddington, 1994). This method consists of a simple estimator of the richness in an assemblage.

$$S_{Chao1} = S_{obs} + \frac{F_1^2}{2F_2}$$

$S_{obs}$ is the number of species in the sample, $F_1$ is the number of observed species represented by a single individual and $F_2$ is the number of observed species represented by two individuals.

Measurement of species diversity is based on the Simpson index, which emphasizes dominance as opposed to richness in assessing the development and evolution of an ecosystem (Magurran, 2004).

$$D = \sum \left( \frac{n_{i[n_i - 1]}}{N[N-1]} \right)$$

$n_i$ is the number of individuals in the *i* species and *N* is the total number of individuals.

We further analyse the percentage of synanthropic species, that is, species that are adapted to conditions created or modified by human activities (Mistrot, 2000). The synanthropization of indigenous small mammals was considered to be a recent phenomenon in European mammals. However, the recent studies show that is readily observable during the late Neolithic in south-eastern Europe, and perhaps before (Cucchi et al., 2011). Within our assemblage, there are four: *Crocidura russula, Microtus arvalis, Microtus* (*Terricola*) *duodecimcostatus* and *E. quercinus* (Table 2). *C. russula* favours human-inhabited areas because its winter survival depends on heat and nutritive resources generated by human activities (Tarjuelo Mostajo et al., 2010). *M. arvalis* prefers landscapes with high percentage of arable land and low habitat diversity (Burel et al., 2004; Fischer et al., 2011). *M.(T) duodecimcostatus* selects open environments, often in human-inhabited areas. It is common in growing areas and pastures and fallow land, as long as there is sufficient grass cover and easy excavability (Campos Marcos et al., 2003). Finally, *E. quercinus* can live in many terrestrial and arboreal habitats and also be found close to rural homes, on roofs or on stone walls between cultures and is a semi-commensal species (Pokines, 1998).

### Chorotypes

This palaeoclimatic reconstruction is completed by classifying the taxa in accordance with the chorotypes established by Sans-Fuentes and Ventura (2000), Real et al. (2003) and López-García

**Table 1.** Distribution of the small-mammal remains of El Mirador cave by layers.

| Taxa | MIR4 | MIR5 | MIR6 | MIR9 | MIR10 | MIR11 | MIR16 | MIR17 | MIR18 | MIR19 | MIR21 | MIR22 | MIR23 | MIR24 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Crocidura russula* | 19 | 6 | 0 | 17 | 0 | 1 | 2 | 16 | 21 | 6 | 0 | 1 | 0 | 8 |
| *Sorex coronatus-araneus* | 6 | 4 | 1 | 5 | 1 | 1 | 0 | 9 | 21 | 4 | 0 | 0 | 0 | 3 |
| *Myotis myotis-blythii* | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 4 |
| *Miniopterus schreibersii* | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 2 | 0 | 2 |
| *Microtus arvalis* | 21 | 20 | 3 | 3 | 1 | 1 | 2 | 18 | 16 | 9 | 1 | 2 | 0 | 22 |
| *Microtus agrestis* | 14 | 37 | 3 | 13 | 2 | 0 | 2 | 34 | 26 | 22 | 1 | 0 | 3 | 15 |
| *Microtus (Terricola) duodecimcostatus* | 17 | 14 | 2 | 1 | 3 | 5 | 2 | 18 | 21 | 11 | 2 | 2 | 4 | 24 |
| *Apodemus sylvaticus* | 18 | 8 | 2 | 9 | 6 | 8 | 4 | 32 | 73 | 58 | 4 | 5 | 2 | 56 |
| *Eliomys quercinus* | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 3 | 6 | 1 | 0 | 1 | 0 |
| Total MNI | 96 | 89 | 11 | 53 | 14 | 17 | 13 | 128 | 185 | 117 | 9 | 12 | 10 | 134 |
| Total NISP | 280 | 193 | 17 | 77 | 19 | 19 | 14 | 230 | 376 | 154 | 17 | 15 | 15 | 240 |

MNI: minimum number of individuals; NISP: number of identified specimens.

**Table 2.** Richness and diversity index and percentage representation of synanthropic species (*Crocidura russula, Microtus arvalis, Microtus* (*Terricola*) *duodecimcostatus* and *Eliomys quercinus*) obtained from small-mammal remains of El Mirador cave by layers.

| Layers | MIR4 | MIR5 | MIR6 | MIR9 | MIR10 | MIR11 | MIR16 | MIR17 | MIR18 | MIR19 | MIR21 | MIR22 | MIR23 | MIR24 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Chao-1 | 7 | 6 | 5 | 9 | 6 | 6 | 6 | 7 | 9 | 8 | 5 | 5 | 4 | 8 |
| Simpson_1-D | 0.82 | 0.74 | 0.78 | 0.79 | 0.73 | 0.68 | 0.80 | 0.81 | 0.78 | 0.70 | 0.72 | 0.74 | 0.70 | 0.75 |
| Synanthropic | 60.42 | 44.94 | 45.45 | 41.51 | 28.57 | 47.06 | 53.85 | 41.41 | 32.97 | 27.35 | 44.44 | 41.67 | 50.00 | 40.30 |

et al. (2010b). A chorotype can be defined as a group of species whose distributions in space overlap more than expected at random. Chorotype 1 (CH-1) refers to species with Euro-Siberian requirements; this implies a mean summer temperature lower than 20°C, a mean annual temperature (MAT) that should be between 10°C and 12°C and a mean annual precipitation (MAP) higher than 800 mm. Chorotype 2 (CH-2) refers to Euro-Siberian species that nonetheless tolerate Mediterranean conditions, with a MAP greater than 600 mm. Chorotype 3 (CH-3) denotes generalist species, and finally Chorotype 4 (CH-4) denotes species with strictly Mediterranean requirements (Table 3).

## Results

### Small mammals

We have identified 1666 remains (number of identified specimens (NISP)), with a minimum number of individuals (MNI) of 888 pertaining to nine small-mammal taxa: two insectivore, two chiropter and five rodent species (Table 1).

The preliminary taphonomic study of the small mammals presents slight signs of digestion on the remains. These slight alterations were examined and it can be surmised that the main animal responsible for the accumulation in the cave was a category 1 predator, a nocturnal bird of prey such as the barn owl (*Tyto alba*) or the long-eared owl (*Asio otus*), both species are present in semi-open forests, with the nearby presence of large clear areas that display an opportunistic trophic pattern and produce slight modifications of the bones it ingests (Andrews, 2006). The small mammals form an assemblage of great taxonomic variety, indicating that it was the work of an opportunistic hunter.

Systematic palaeontology allowed nine different species to be identified: *C. russula, Sorex gr. coronatus-araneus, Myotis myotis-blythii, Miniopterus schreibersii, M. arvalis, Microtus agrestis, M.(T) duodecimcostatus, A. sylvaticus* and *E. quercinus* (Figure 2). The most abundant species in the sequence of El Mirador is *A. sylvaticus* (Table 3).

The Chao-1 analysis of diversity indicates that the highest number of species is in MIR18 and MIR9, with nine species each, whereas the lowest number of species is registered in MIR23, with four species. The Simpson index indicates that the greatest diversity is in MIR11 (0.68), MIR19 (0.70) and MIR23 (0.70), whereas the lowest diversity is recorded in MIR4 (0.82) and MIR17 (0.81). Moreover, the lowest percentage of synanthropic species is detected in MIR19 (27.4%) and MIR10 (28.6%), while the highest percentage is registered in MIR4 (60.4%) and MIR16 (53.8%) (Table 2).

**Table 3.** Percentage of open and woodland areas and chorotypes represented in the studied layers of El Mirador cave.

| Layers | Habitat weighting | | Chorotypes | | | |
|---|---|---|---|---|---|---|
| | Open | Woodland | CH1 | CH2 | CH3 | CH4 |
| MIR4 | 40.6 | 59.4 | 36.5 | 6.3 | 19.8 | 37.5 |
| MIR5 | 45.5 | 54.5 | 64.0 | 4.5 | 9.0 | 22.5 |
| MIR6 | 44.2 | 55.9 | 54.5 | 9.1 | 18.2 | 18.2 |
| MIR9 | 41.6 | 58.5 | 30.2 | 9.4 | 22.6 | 37.7 |
| MIR10 | 28.6 | 71.4 | 21.4 | 7.1 | 50.0 | 21.4 |
| MIR11 | 26.5 | 73.5 | 5.9 | 5.9 | 52.9 | 35.3 |
| MIR16 | 34.6 | 65.4 | 30.8 | 0.0 | 38.5 | 30.8 |
| MIR17 | 37.5 | 62.4 | 40.6 | 7.0 | 25.8 | 26.6 |
| MIR18 | 30.2 | 69.7 | 22.7 | 11.4 | 42.7 | 23.2 |
| MIR19 | 25.2 | 74.8 | 26.5 | 3.4 | 54.7 | 15.4 |
| MIR21 | 27.8 | 72.2 | 22.2 | 0.0 | 55.6 | 22.2 |
| MIR22 | 29.2 | 70.8 | 16.7 | 0.0 | 58.3 | 25.0 |
| MIR23 | 40 | 60.0 | 30.0 | 0.0 | 30.0 | 40.0 |
| MIR24 | 29.1 | 70.9 | 27.6 | 2.2 | 44.8 | 25.4 |

### Climate

From the base to the top, the climatic analysis of the Holocene sequence yields the following results. MIR24 displays mild, humid conditions. By the MER method, we observe that the MAT is 0.1°C lower than nowadays, while the MAP is 252 mm higher than nowadays in the Burgos area (Table 4). The chorotype analysis indicates that 45% of species are generalist (CH-3) (Table 3).

The temperatures recorded in MIR23-22 are the highest in the entire sequence. In these layers, the MAT exceeds the current

**Table 4.** Relation of temperatures and precipitation obtained using the MER (mutual ecogeographic range) method.

| Layers | MAT | | | | | MTC | | | | | MTW | | | | | MAP | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Max. | Min. | Mean | SD | Δ | Max. | Min. | Mean | SD | Δ | Max. | Min. | Mean | SD | Δ | Max. | Min. | Mean | SD | Δ |
| MIR4 | 13 | 5 | 9.94 | 1.52 | 0.16 | 5 | 0 | 2.54 | 1.17 | 0.06 | 22 | 15 | 18.53 | 1.41 | 0.18 | 1500 | 500 | 794 | 221 | −200 |
| MIR5 | 13 | 5 | 10.03 | 1.57 | 0.07 | 7 | 0 | 2.65 | 1.25 | −0.05 | 23 | 15 | 18.60 | 1.44 | 0.10 | 2500 | 500 | 846 | 284 | −252 |
| MIR6 | 13 | 5 | 9.97 | 1.55 | 0.13 | 7 | 0 | 2.64 | 1.20 | −0.04 | 22 | 15 | 18.49 | 1.36 | 0.21 | 2000 | 500 | 867 | 277 | −273 |
| MIR9 | 13 | 5 | 9.94 | 1.52 | 0.16 | 5 | 0 | 2.54 | 1.17 | 0.06 | 22 | 15 | 18.53 | 1.41 | 0.18 | 1500 | 500 | 794 | 221 | −200 |
| MIR10 | 13 | 5 | 9.97 | 1.55 | 0.13 | 7 | 0 | 2.64 | 1.20 | −0.04 | 22 | 15 | 18.49 | 1.36 | 0.21 | 2000 | 500 | 867 | 277 | −273 |
| MIR11 | 13 | 5 | 9.62 | 1.81 | 0.48 | 5 | 0 | 2.46 | 1.24 | 0.14 | 23 | 15 | 18.70 | 1.33 | 0.00 | 2000 | 500 | 792 | 238 | −198 |
| MIR16 | 13 | 5 | 10.17 | 1.47 | −0.07 | 5 | 0 | 2.62 | 1.01 | −0.02 | 23 | 15 | 18.97 | 1.51 | −0.27 | 1500 | 400 | 715 | 230 | −121 |
| MIR17 | 13 | 5 | 9.94 | 1.52 | 0.16 | 5 | 0 | 2.54 | 1.17 | 0.06 | 22 | 15 | 18.53 | 1.41 | 0.18 | 1500 | 500 | 794 | 221 | −200 |
| MIR18 | 13 | 5 | 9.94 | 1.52 | 0.16 | 5 | 0 | 2.54 | 1.17 | 0.06 | 22 | 15 | 18.53 | 1.41 | 0.18 | 1500 | 500 | 794 | 221 | −200 |
| MIR19 | 13 | 5 | 9.94 | 1.52 | 0.16 | 5 | 0 | 2.54 | 1.17 | 0.06 | 22 | 15 | 18.53 | 1.41 | 0.18 | 1500 | 500 | 794 | 221 | −200 |
| MIR21 | 13 | 5 | 10.07 | 1.56 | 0.03 | 5 | 0 | 2.57 | 1.12 | 0.03 | 23 | 15 | 19.05 | 1.44 | −0.35 | 1500 | 400 | 740 | 249 | −146 |
| MIR22 | 15 | 5 | 10.83 | 1.53 | −0.73 | 7 | 0 | 2.96 | 1.14 | −0.36 | 25 | 15 | 20.17 | 1.51 | −1.47 | 2500 | 300 | 608 | 233 | −14 |
| MIR23 | 15 | 5 | 11.02 | 2.07 | −0.92 | 9 | 0 | 3.37 | 1.77 | −0.77 | 25 | 15 | 19.79 | 1.83 | −1.09 | 1500 | 400 | 742 | 233 | −148 |
| MIR24 | 13 | 5 | 10.03 | 1.57 | 0.07 | 7 | 0 | 2.65 | 1.25 | −0.05 | 23 | 15 | 18.60 | 1.44 | 0.10 | 2500 | 500 | 846 | 284 | −252 |

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

level by 1°C (Table 4). The principal chorotype in MIR23 is chorotype 4, that is, Mediterranean species (40%), and in MIR22 it is chorotype 3 (58%) (Table 3). In contrast, the MAP of these layers is the lowest in the entire sequence. The MAP in MIR23 is 148 mm higher than nowadays, while in the case of MIR22 the MAP is 608 mm, only 14 mm higher than nowadays (Table 4). In these layers, the end of the African Humid Period can be identified (Bañuls-Cardona et al., in preparation).

The MER method reveals that the MAT in MIR21 is equal to the current levels, but the MAP is 146 mm higher than nowadays. In MIR19, MIR18 and MIR17, the palaeoclimatic analysis shows an increase in precipitation, with the MAP 54 mm higher with respect to MIR21; the temperatures were lower, and we have registered a decrease of 0.5°C in the mean temperature of the coldest months (MTC). The most highly represented chorotype from MIR21 to MIR18 is chorotype 3, whereas in MIR17 species with Euro-Siberian requirements (CH-1) are most abundant. After this slight cooling, in MIR16 temperatures are again similar to nowadays; the MAT is 0.1°C higher than today, and a significant decrease in rainfall of 79 mm is observed with respect to MIR17.

In MIR11, slightly cooler conditions are detected (from ca. 6300 to 5940 cal. BP). The MER shows the MAT (9.6°C) to be the lowest in the Holocene sequence of El Mirador cave, 0.5°C lower than nowadays, mainly because of the low MTC (2.4°C). The climatic data obtained on the basis of the small mammals suggest an increase in MAP in MIR11 (792 mm) with respect to the pluviometric data for MIR16 (715 mm). The chorotype data indicate generalist species to be most abundant in this layer (53%). In MIR10, a significant increase in the rainfall (75 mm) and temperatures (0.4°C) is observed with respect to MIR11, while the principal chorotype is chorotype 3, that is, generalist species (CH-3).

In MIR9, we detect a dry event. This shows a decrease in MAP from 867 mm in MIR10 to 794 mm in MIR9. As regards temperatures, however, we do not observe major changes. The chorotype data indicate that species with Mediterranean requirements (CH-4) are most abundant (38%).

After this dry event, in MIR6 and MIR5 we observe a significant increase in rainfall (73 mm more than in MIR9). The temperature remains similar to MIR9, but chorotype 1 is most abundant (55% and 64% in MIR6 and MIR5, respectively).

Finally, in MIR4 we do not observe changes in temperature with respect to MIR6 and MIR5, but the MAP recorded is 52 mm higher, while chorotype 4 is the most important (Bañuls-Cardona et al., in preparation).

### *Environment*

Woodland is the most representative kind of habitat in El Mirador, but with some changes along the sequence. The highest percentages of woodland are registered in MIR19 (75%) and MIR11 (74%), while the lowest percentages are registered in MIR5 (54%) and MIR6 (56%). The other habitat that is well represented is the 'open humid' habitat, indicating evergreen meadowland with pastures and dense topsoil. It is in MIR23 and MIR6 that the highest percentages of open humid habitat are identified (40% and 32.4%, respectively), whereas MIR24 and MIR22 are the layers with the lowest values (16.8% and 12.5%, respectively). The 'open dry' habitat is the least represented habitat in El Mirador, and in MIR23 it is not registered at all. The maximum value for this type of habitat is recorded in MIR9 and MIR4 (20.8%), while the minimum values are registered in MIR11 (5.9%) and MIR10 (5.4%) (Bañuls-Cardona et al., in preparation).

## Discussion

In the Iberian Peninsula, palaeobotanical studies document the first human landscape modifications around 6000 cal. BP. However, some palaeoenvironmental changes that were probably not the result of the human impact are also recorded; these could have been in response to the arid climate event that occurred at 8200 cal. BP. The clear intensification of farming activities in the landscape started to appear later (Iriarte, 2009; Martínez-Cortizas et al., 2009). We used a range of multiproxy analyses (pollen, charcoal, sedimentology, geochemistry and chironomids) from different parts of the Iberian Peninsula to characterize the main features of the landscape evolution during the Holocene (Badal et al., 1994, 2012; Carrión, 2002; Carrión et al., 2004; Iriarte, 2009; Martínez-Cortizas et al., 2009; Pérez-Sanz et al., 2013).

In the north of Iberia, the first human impact has been registered around 4000–3000 cal. BP. According to this chronology, the lowest values of forest coverage were in Peña Larga (Cripán, Álava) and Padre Areso (Bigüézal, Navarra). A special case was

Puy Aguila I (Bárdenas Reales, Navarra), where the human influence was produced when the site was inhabited (Iriarte, 2009). Among the earliest evidence of significant landscape transformation by humans in northwestern Iberia was the Coto da Fenteira (Redondela, Pontevedra). In this site, two layers have been found (dated to 4690 and 3735 cal. BP) evidencing episodes of forest fire use, a technique that caused serious soil erosion. However, this erosion increases around 3000 cal. BP, with a significant decline in arboreal pollen, as occurs at Arcucelos (Orense) from 3040 cal. BP (Martínez-Cortizas et al., 2009). A multiproxy analysis (pollen, sedimentology, geochemistry, chironomids and charcoal) from the high-mountain glacier-lake of Basa de la Mora (Huesca) in northeastern Iberia reveals probably the first evidence of forest management, indicating negligible anthropogenic pressure until ca 1150 cal. BP (Pérez-Sanz et al., 2013).

Pollen analysis of sites situated on the northern Meseta has revealed an intense human impact on the environment, but only in very recent times (which ones). In the Tolla Collado de El Berrueco (Sierra de Guadarrama, Madrid), dated to 1830 cal. BP, very intense human action was detected by a regression of *Pinus* forest and an increase in anthropophilic species of pollen (Ruiz-Zapata et al., 2009a). In Rascafría (Valle del Lozoya, Madrid), increased soil erosion is detected from 920 ± 50 BP, because of increased grazing throughout the year (Ruiz-Zapata et al., 2009b). Human activity also appears in the Espinosa de Cerrato sequence (Palencia), where a change in the ratio between *Pinus* and *Quercus* pollens from 1400 cal. BP has been detected, and in El Carrizal lake (Cuéllar, Segovia) the presence of weed and *Cerealia* taxa from 2650 cal. BP is a sign of human activity (García-Antón et al., 2011).

In the southeastern part of the Iberian Peninsula, the intensity and timing of the human impact on vegetation vary from one part to another. In the Sierra de Gádor (Almeria), after 3940 cal. BP a frequent alternation in the dominance of *Pinus* and evergreen *Quercus* at the expense of deciduous *Quercus* is observed. This change is preceded by an increase in microcharcoal particles at 4200 cal. BP, suggesting an increase in fire use. In the Sierra de Baza (Granada), the replacement of mesophytic by more xeric Mediterranean vegetation around 3800 cal. BP is preceded by greater fire activity at 4100 cal. BP. However, deforestation expanded over the next two millennia, with anthropogenic disturbance (agriculture, mining and pastoralism) reaching its maximum after 2560 cal. BP (Carrión et al., 2010). In Siles lake (Jaén), high grazing pressure is registered from 2400 cal. BP; this may well have promoted local increases in the proportion of grasses, because extensive pastures are natural above the tree line (Carrión, 2002).

The debate about anthropogenic versus climatic determinism has been particularly intense with regard to the Mediterranean area (Carrión et al., 2004). During the earliest Neolithic, Mediterranean woodland was dominated by *Quercus* while the presence of secondary plant formations was insignificant in Cova de l'Or (Beniarrés, Alicante) and Cova de les Cendres (Teulada-Moraira, Alicante). However, around 5000 cal. BP, a reduction in *Quercus* is observed in favour of more open formations, and the sedimentology reveals one of the wettest periods in the Neolithic, so these changes may be related to the economic activities of human groups. As has been documented for most of the Iberian Peninsula, this reduction increases at Cova de les Cendres from the Bronze Age on, because of the intensification of farming activities (Badal et al., 1994, 2012).

However, the climatic and the human impact on small-mammal diversity are indiscriminately mentioned as causes of rapid oscillations in the environment during the Holocene, yet efforts to disentangle the specific causes of this process are complicated (Jalut et al., 2009; Jiménez-Moreno et al., 2013; Mercuri et al., 2011). At the beginning of the Holocene, the most frequently cited explanations for patterns of elevational diversity relate to gradients in single factors, such as rainfall, temperature, productivity, competition, resource abundance, habitat complexity or habitat diversity, but the current theory recognizes climatic factors as a principal influence on trends in diversity (Lomolino, 2001; McCain, 2004). In the mid-Neolithic and Bronze Age, in contrast, the richness and diversity of species have been associated with the human impact (Carrión et al., 2010; López-García et al., 2013).

Because of their size, small mammals are more sensitive to minor variations in climate and environment than larger ones, and these changes affect their ethology (López-García et al., 2013). It is for these reasons that we use small mammals in this study. Some small-mammal species have a capacity for adaptation to these new conditions, enabling them to modify their climatic and environmental requirements (McKinney, 1997). This ability allows them to maintain populations in their area of current distribution despite changing environmental conditions, as well as to colonize other areas (Arribas et al., 2012; Bellard et al., 2012), as in the case of synanthropic species, which have adapted to conditions created or modified by human activities (Mistrot, 2000).

### *Climate influence*

The small-mammal studies of levels MIR24–MIR19 of El Mirador establish that the changes in the environment and in the degree of diversity were related to climatic conditions. The palaeoclimatic analysis shows the temperatures to have hovered around 10°C (Table 4). Species belonging to chorotype 3 (species with generalist climatic requirements) are the most abundant (Table 3), and *A. sylvaticus* is the most representative species in these layers. However, MIR23 is an exception to this. In this layer, we have identified the end of the African Humid Period, with higher temperatures than nowadays (Table 4) (Bañuls-Cardona et al., in preparation). Chorotype 4 is the most representative chorotype, and the most abundant species is *M.*(*T*) *duodecimcostatus*, a species with Mediterranean climatic requirements (Table 3).

According to some authors, moreover, the decline in diversity may have been a direct effect of the general transition from a cooler to a warmer climate and the corresponding habitat change (Blois et al., 2010). In contrast, in MIR23 the rise in diversity was related to an increase in temperature (1°C) and an increase in open environment (11%) (Figure 3). The simultaneous availability of water and high temperatures is the best explanation for the variation in species richness (Real et al., 2003). In MIR19, the same Simpson index is recorded (0.70), associated with a minor decrease in temperature (0.3°C) and a decrease in open environment, which is at its lowest level in the sequence of El Mirador (25%).

### *Human impact*

From as early as ca. 6000 cal. BP, some archaeobotanical studies have detected the first evidence of a human impact on the landscape in the Iberian Peninsula (Badal et al., 1994; Fletcher and Sánchez-Goñi, 2008; Iriarte, 2009; Martínez-Cortizas et al., 2009; Zazo et al., 2008). However, this trend increases after ca. 5000 cal. BP, with a drastic reduction in the forest in Europe in general (Carrión et al., 2010; Heinz et al., 2004; Hernández-Beloqui et al., 2015; Kalis et al., 2003; Leira and Santos, 2002; López-Merino et al., 2012; Tarroso et al., 2014).

Farming practices have been documented in El Mirador cave by studies based on pollen, charcoal, seeds and phytoliths (Cabanes et al., 2009; Euba et al., 2016; Expósito and Burjachs, 2016; Rodríguez et al., 2016). These studies have confirmed the forest degradation, which is most likely because of intensified human activity. For example, pollen analyses clearly show higher

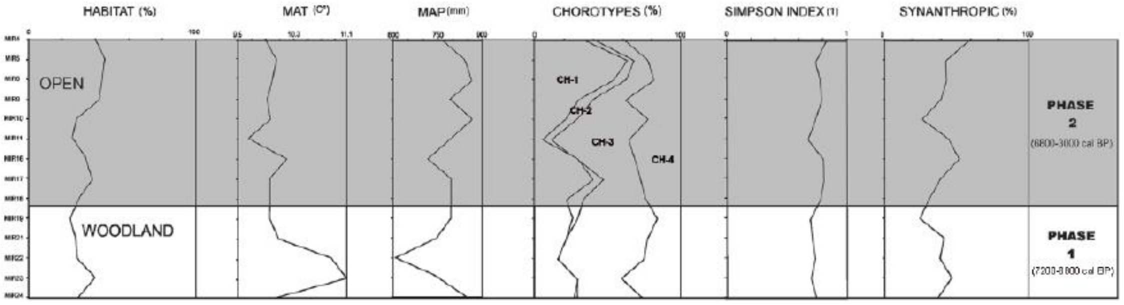

**Figure 3.** Comparisons between various proxies used throughout El Mirador cave sequence. From left to right: habitat interpretation for El Mirador cave based on the habitat weighting method. Mean annual precipitation (MAP) and mean annual temperature (MAT) of the El Mirador cave sequence. Representation of the chorotypes: CH-1 (chorotype 1), CH-2 (chorotype 2), CH-3 (chorotype 3) and CH-4 (chorotype 4). Diversity study with Simpson index. Finally, representation of synanthropic species (*Crocidura russula, Microtus arvalis, Microtus* (*Terricola*) *duodecimcostatus* and *Eliomys quercinus*) for each layer. Phase 1: climatic influence **(**changes associated with climatic influence); Phase 2: human impact (changes associated with human impact).

values of anthropogenic signatures related to human activities, especially during the Bronze Age period (MIR4) (Expósito et al., in preparation). Zooarchaeological studies confirm the development of herding practices throughout the sequence. These were based on goat and sheep breeding. Moreover, the 'fumier' sequence and an abundance of ovicaprine foetal and neonatal remain suggest the use of the cave for livestock penning and, especially, as a breeding cave (Angelucci et al., 2009; Martín et al., 2016b; Vergès et al., 2016).

*MIR18–MIR16 (7000–6300 cal. BP).* The small-mammal studies of El Mirador cave provide the first, minor evidence of a human impact on diversity in MIR18 (ca. 7000–6800 cal. BP). From MIR19 to MIR17, the MER analysis indicates the same temperatures and the same level of precipitation, but we have registered a progressive increase in an open environment type (Figure 3). Nevertheless, we observe a higher level of richness (nine species) and a significant decrease in diversity in MIR18 (Table 2), probably related to the increased volume of herds and/or the higher intensity of the occupation of the cave because of its use as a sheepfold (a large number of remains, large number of perinatal individuals) (Table 5) (Martín et al., 2016b).

However, in MIR17, although no climatic variations are observed with respect to MIR19 (Table 4), we see a change in the predominant chorotype (Table 3). In MIR17, *M. agrestis*, a Euro-Siberian species (with 26% of the total of the assemblage), was more abundant than *A. sylvaticus*, a generalist species that was predominant from MIR24 to MIR18 (Table 1). The increase in the open environment (from 30% in MIR18 to 38% in MIR17) (Figure 3) and the abundance of *M. agrestis* and microtines in general (54%) could indicate an increase in cultivated lands to the detriment of herding practices, as indicated by the low percentage of large mammals (Table 5) (Martín, 2015). However, it remained a minor increase at this point, because agricultural intensification would have favoured the dominance of other species such as *M. arvalis* or *C. russula* (Burel et al., 2004).

In MIR16 (ca. 6600–6300 cal. BP), an increased number of synanthropic small mammals is registered (53.8%) (Table 2), as well as the highest percentage of large-mammal remains (8.43% of MNI), especially perinatal remains (11.43% MNI; Table 5; Martín et al., 2016b). These data could indicate a more intense occupation of the cave in this period. The intense occupation had effects on the diversity and richness of small mammals (Cam et al., 2000). In this layer, the diversity continued to be low (0.80; Table 2). The data from El Mirón cave (Cantabria) reveal a higher diversity than in El Mirador for the same period (López-García et al., 2013). In El Mirón, *M. schreibersii* has been found, indicating that the cave was probably not occupied, because in general these bats do not cohabit with humans (Cuenca-Bescós et al., 2008).

**Table 5.** General composition of the faunal assemblage in the studied layers of El Mirador cave and ovicaprine perinatal data, considering NR (number of remains) and MNI (minimum number of individuals). Percentages were calculated taking into account the sum of NR and MNI for all El Mirador layers.

| Layers | NR | %NR | MNI | %MNI | Perinatals | | | |
|---|---|---|---|---|---|---|---|---|
| | | | | | NR | %NR | MNI | %MNI |
| MIR4 | 560 | 6.10 | 24 | 6.74 | 18 | 2.09 | 5 | 4.76 |
| MIR5 | 19 | 0.21 | 8 | 2.25 | 2 | 0.23 | 2 | 1.90 |
| MIR6 | 62 | 0.68 | 9 | 2.53 | 4 | 0.47 | 3 | 2.86 |
| MIR9 | 161 | 1.75 | 10 | 2.81 | 24 | 2.79 | 4 | 3.81 |
| MIR10 | 107 | 1.16 | 10 | 2.81 | 17 | 1.98 | 3 | 2.86 |
| MIR11 | 1364 | 14.85 | 24 | 6.74 | 23 | 2.67 | 4 | 3.81 |
| MIR16 | 1386 | 15.09 | 30 | 8.43 | 183 | 21.28 | 12 | 11.43 |
| MIR17 | 79 | 0.86 | 8 | 2.25 | 18 | 2.09 | 2 | 1.90 |
| MIR18 | 762 | 8.30 | 28 | 7.87 | 138 | 16.05 | 13 | 12.38 |
| MIR19 | 740 | 0.81 | 27 | 7.58 | 44 | 5.12 | 6 | 5.71 |
| MIR21 | 630 | 6.86 | 24 | 6.74 | 61 | 7.09 | 8 | 7.62 |
| MIR22 | 110 | 1.20 | 7 | 1.97 | 10 | 1.16 | 2 | 1.90 |
| MIR23 | 130 | 0.14 | 10 | 2.81 | 13 | 1.51 | 3 | 2.86 |
| MIR24 | 80 | 0.87 | 7 | 1.97 | 21 | 2.44 | 3 | 2.86 |

Moreover, the MER indicates a small increase in temperature (0.3°C) with respect to the previous layers (MIR19–MIR17), and the most abundant species is once again *A. sylvaticus*. This increase in temperature (Table 4) produces a reduction in the species that eat herbaceous plants throughout the year, such as species belonging to the genus *Microtus*. In contrast, omnivorous species such as *A. sylvaticus* and *E. quercinus* remain practically constant (Soriguer et al., 2003).

*MIR11–MIR10 (6.200–6.000 cal. BP).* In MIR11, the MER method allows a minor cold event to be identified (Bañuls-Cardona et al., in preparation), and these climatic conditions would be expected to be associated with a lower percentage of diversity (Figure 3). However, we register the greatest level of diversity (0.68; Table 2), and there is also an increase in thermo-Mediterranean species such as *C. russula* and *M.*(*T*) *duodecimcostatus*, especially the latter, which increased 14% with respect to MIR16, in which the climatic conditions were milder. These results could be related to a change in herding strategies at this point in El Mirador. The importance of goats and sheeps decreases while the presence of equids, whose origin is likely to be wild, is more important in this layer (Martín et al., 2016a). This change in livestock management may, in part, be influenced by the low temperatures shown by the small-mammal study (Bañuls-Cardona et al., in preparation). Furthermore, archaeobotanical studies of El Mirador indicate that there are no cereals in this layer (Rodríguez et al., 2016). All these factors could have caused the increased presence of *M.*(*T*) *duodecimcostatus*. This species requires areas free from rapid and frequent changes to build the underground galleries that provide it with refuge and food storage, which explains its scarcity in fields (Tarjuelo Mostajo et al., 2010).

In contrast to MIR11, the changes seen in MIR10 could be associated with a lower intensity of herding activities, as indicated by the large mammals' remains (2.8% MNI). The index of synanthropic species is lower and the diversity decreases 18.5% with respect to MIR11 (Table 2). Moreover, the presence of synanthropic species such as *M.*(*T*) *duodecimcostatus* has decreased, and *C. russula* has disappeared, in spite of the thermal recovery (from 9.6°C to 10°C) (Figure 3).

*MIR9–MIR4 (5.900–3.000 cal. BP).* From MIR9 to MIR4, the small-mammal analysis reveals an increase in open environments. In this period, the MER results indicate a minor decrease in precipitation (Table 4), but this cannot justify the strong reduction in forest cover. This reduction is more likely to be related to the human impact on the landscape, as multidisciplinary studies have shown this amplified aridity to be because of the significant human impact and the resulting soil disturbance (Domínguez-Villar et al., 2012; Frigola et al., 2007; Pérez-Lambán et al., 2014).

Moreover, the palaeoclimatic analysis of the small mammals of El Mirador shows that the temperature remains stable from MIR9 to MIR4, although the chorotype analysis indicates important changes. Thermo-Mediterranean species are more abundant in MIR9 and MIR4, whereas in MIR6 and MIR5 species with Euro-Siberian requirements are more important (Table 3). However, the amount of large-mammals is lower, as in MIR10, and there is a decrease in the intensity of the occupation as a sheepfold 'sensu stricto', with a reduced herd or a limited number of shepherds (Martín, 2015). At the same time, however, the pollen remains indicate a significant increase in crops around the cave (Expósito et al., in preparation). The agricultural intensification causes a deterioration in habitat quality and a reduction in availability, leading to a homogenization of the landscape. This phenomenon affects diversity, favouring the dominance of a few species, in particular more generalist species as opposed to others whose needs are more stringent (Benton et al., 2003; Dunning et al., 1992).

The Simpson diversity index in MIR9 undergoes a decline with respect to MIR10, while we see an increase in the percentage of synanthropic species (13%), and these tendencies persist through to MIR4 (Table 2). In general, the most abundant species in the entire sequence had been *A. sylvaticus* but from MIR9 this trend changes. In MIR9, the most abundant species is *C. russula*, a generalist species in terms of habitat and food requirements (Table 1). Such a species would benefit from a reduction in landscape heterogeneity that reduces the presence of other species such as *A. sylvaticus* (Blanco, 1998; Tarjuelo Mostajo et al., 2010). In MIR6 and MIR5, the most abundant species is *M. agrestis*, whose presence has been shown to increase when grazing levels decrease (Wheeler, 2008). A comparison of the small-mammal diversity of MIR6 with that of a layer from El Mirón with the same chronology (layer 8.1) shows them to be equal (0.78) (López-García et al., 2013). This would indicate that, as observed in the palaeobotanical analysis, landscape anthropization was quite widespread throughout the Iberian Peninsula around 6000–5000 cal. BP (López-Merino et al., 2012; Morales-Molino et al., 2011). In the case of MIR5, small-mammal diversity can be compared with that of three different sites: Colomera cave (Lleida), El Mirón cave (Cantabria) and Valdavara-1 cave (Lugo). The diversity in El Mirón cave (Cantabria) and Valdavara-1 cave (Lugo) can be seen to be higher and in Colomera cave (Lleida) lower than in El Mirador. This analysis confirms the theory of low human occupation intensity in the northern Meseta (García-Antón et al., 2011; Ruiz-Zapata et al., 2009a) and in high mountainous areas, as proposed by various authors (Carrión et al., 2010; Tarroso et al., 2014). Finally, during the Bronze Age, cereal-growing and livestock farming are widely documented throughout Europe (Broothaerts et al., 2014; López-Sáez et al., 2001; Pérez-Díaz et al., 2015). In MIR4 of El Mirador, bovid remains with pathologies related to traction force have been detected (Martín, 2015), and the palaeobotanical records and small-mammal analysis indicate that cultivated fields were gaining ground over forest (Allué and Euba, 2008; Bañuls-Cardona et al., in preparation; Expósito et al., in preparation). As we have seen in MIR9, this intense agricultural system favours the dominance of the most generalist species, compared with other species with more stringent requirements (Arribas et al., 2012; Dunning et al., 1992). In MIR4, we see the greatest values in diversity in El Mirador (0.82) and also the highest index of synanthropic species (60.4%). The most representative species was *M. arvalis*, a synanthropic species that occurred in landscapes with a high percentage of arable land. Also, this species can cause significant economic losses during population outbreaks (Jacob and Tkadlec, 2010; Luque-Larena et al., 2013).

## Conclusion

The small-mammal study of El Mirador has proved to be a useful tool to identifying the changes in diversity related to human activities during the middle- to late-Holocene of the northwest of the Iberian Peninsula. El Mirador is particularly valuable in this context because it has a sequence with a well-documented human occupation from 7200 to 3000 cal. BP. Two phases are identified by our studies of diversity and synanthropic species. In the first phase (7200–7000 cal. BP), small changes in diversity related to climatic oscillations have been established; while in the second phase (7000–3000 cal. BP), changes in diversity associated with the human impact have been detected. Moreover, from 5900 to 3700 cal. BP, the dominance of microtines and the evidence from other remains studied (large mammals, seeds, charcoal, pollen, phytoliths) indicate changes probably caused by intensive agricultural practices. In general, the most significant decline in biological richness in El Mirador cave was caused in the layers with the greatest human pressure derived from both agriculture and livestock. Further comparison with other proxies has allowed us to corroborate generalized human pressure on the landscape throughout the Iberian Peninsula from 6000 cal. BP on. Moreover, it has confirmed the theory of low human occupation intensity in the northern Meseta and in high mountainous areas.

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