

Paleoenvironmental context of Neanderthal occupations in northeastern Iberia: the small-mammal assemblage from Abric Romaní (Capellades, Barcelona, Spain)

Mónica Fernández-García ^{1*}, Juan Manuel López-García ², Maria Bennàsar ^{2,3}, Maria Joana Gabucio ^{2,3}, Amèlia Bargalló ⁴, M. Gema Chacón ^{2,3,5}, Palmira Saladié ^{2,3,6,7}, Josep Vallverdú ^{2,3,7}, Manuel Vaquero ^{2,3}, Eudald Carbonell ^{2,3}

¹ Sezione di Scienze Preistoriche e Antropologiche, Dipartimento di Studi Umanistici, Università degli Studi di Ferrara, C/so Ercole I d'Este 32, 44121 Ferrara, Italy. E-mail address: monica.fernandez.garcia.90@gmail.com/frnmnc@unife.it

² Institut Català de Paleoecologia Humana i Evolució Social (IPHES). Zona Educacional 4, Campus Sescelades URV (Edifici W3) 43007 Tarragona, Spain

³ Àrea de Prehistòria, Universitat Rovira i Virgili (URV), Av. Catalunya 35, 43002 Tarragona, Spain

⁴ Institute of Archaeology, University College London, Gordon Square 31-34 London WC1H0PY, Great Britain.

⁵ UMR7194 – HNHP (CNRS – MNHN – UPVD – Sorbonne Universités), 1 rue René Panhard 75013 Paris, France

⁶ GQP-CG, Grupo Quaternário e Pré-História do Centro de Geociências (ul&D 73 - FCT), Portugal

⁷ Unit Associated to CSIC, Departamento de Paleobiología, Museo Nacional de Ciencias Naturales (MNCN), Consejo Superior de Investigaciones Científicas (CSIC), Calle José Gutiérrez Abascal 2, 28006 Madrid, Spain

* Corresponding author.

ABSTRACT

The Abric Romaní site (Capellades, Barcelona, Spain) constitutes a key site for understanding the latest Neanderthal occupations in Western Europe. Here we present a comprehensive systematic and taphonomic analysis of a small-mammal assemblage from Level O of the Abric Romaní site, with the aim of reconstructing the paleoecological context in which the Neanderthals lived. The assemblage, which probably dates from a stadial episode between Interstadial 15 and Interstadial 14, contains fifteen small mammal species, including species uncommon for the northeast of Iberia, such as *Sciurus vulgaris*, *Nyctalus lasiopterus* and *Pipistrellus pipistrellus*. Taphonomic studies suggest a predatory origin for the assemblage, probably related to *Strix aluco*, and paleoecological inferences suggest lower temperatures (-

3/-4 °C) and higher rainfall (+70/+170 mm) than at present and a landscape dominated by an open forest with watercourses. The new data improve our knowledge of trends associated with Marine Isotope Stage 3 that affected Neanderthal populations in the Iberian Peninsula, showing that the Neanderthals were well adapted to cooler and wetter conditions across Iberia.

KEYWORDS: Level O; Taphonomy; Climate; Landscape; Middle Paleolithic; Marine Isotope Stage 3

1. Introduction

Given the close relationship between hunter-gatherer societies and the prevailing climate and environment, knowledge of the ecological landscapes in the vicinity of occupations is essential to reach a better understanding of evolutionary processes. The changing paleoenvironmental conditions that occurred during the Middle Paleolithic tend to be related with Neanderthal dynamics and their extinction (Baena et al., 2012; D'Errico and Sánchez Goñi, 2003; Leroy and Leroi-Gourhan, 1983; Mellars, 1998; Sánchez Goñi and D'Errico, 2005; Sepulchre et al., 2007; Zilhão, 2000). Neanderthals inhabited Europe for more than 100,000 years (from Marine Isotope Stages, [MIS] 6/5 to 3/2) and are usually associated with the Mousterian technocomplexes. The end of the Mousterian Phase occurred at ca. 40 ka across Europe. The late survival of Neanderthals in southern Iberia is suggested at sites such as Gorham's Cave (Gibraltar), although this hypothesis has recently been challenged (Finlayson et al., 2006; Higham et al., 2014; Wood et al., 2014). Northern Iberia also contains some late Mousterian sites, such as El Esquilleu, Cova Gran, Abric Romaní and L'Arbreda cave (Martínez-Moreno et al., 2010; Camps and Higham, 2012; Maroto et al., 2012; Vaquero and Carbonell, 2012; Wood et al., 2014). Some authors have connected these relict populations with the favorable environmental conditions associated with peninsulas and

the preservation of larger open woodland areas than in the rest of Europe (Burjachs and Julià, 1994; Zilhão, 2000; Finlayson et al., 2006; Finlayson and Carrión, 2007; Fletcher et al., 2010; López-García et al., 2014b).

The Abric Romaní rock-shelter is a key site for understanding the last Neanderthal populations and their relationships with the paleoenvironment of southwestern Europe. In this paper, we analyze the paleoenvironment of Level O, the richest level for both archaeological and paleontological remains, undertaking the first complete analysis of the small-mammal assemblage, and considering the implications of these environmental conditions for Neanderthal occupations. A combination of paleontological approaches, including the taxonomic identification of small-mammal bone remains and their taphonomic characterization, is used to identify the origin of the assemblage and post-depositional processes. The analysis also takes into account other paleoenvironmental proxies for the Middle Paleolithic Abric Romaní sequence (from B to O; ca. 70-30 ka) and the paleoenvironmental context of the Iberian Peninsula, especially the northeastern part, during MIS 3.

2. Site description

The Abric Romaní archaeological site is a rock-shelter in the Quaternary travertine formation known as “Cinglera del Capelló”, located on the west bank of the Anoia River, near the town of Capellades (Barcelona, Spain). Its coordinates are 41°32'N and 1°41'E and its altitude is 280 m.a.s.l. (Fig. 1A). The deposit was discovered in 1909 by Amador Romaní and the present excavations started in 1983 (Bartolí et al., 1995; Carbonell et al., 1996, 1994). The exposed section is made up of a minimum thickness of 17 m of well-stratified travertine sediments. At present, sixteen levels have been excavated completely (labeled from A to P), most of them belonging to the Middle Paleolithic, with the exception of the uppermost Level A, which has been attributed to the Protoaurignacian (Carbonell et al., 1996; Giralt and Julià,

1996; Vaquero and Carbonell, 2012; Vaquero et al., 2013) (Fig. 1B). The Mousterian lithics, the faunal remains derived from butchering activities and the combustion structures preserved in the succession of layers indicate that Neanderthals occupied this site at different periods during MIS 4 and MIS 3. Dates obtained by U-series and ^{14}C AMS provide calendar ages from ca. 40 ka (Level A) to ca. 70 ka (from the base sediments) (Bischoff et al., 1988). However, new data from Sharp et al. (2016) have suggested that carbonate tufas extend at least 30 m beneath the current base of the excavation, reaching ~ 110 ka at the base of the core, with a possible human occupation as old as ~ 100 ka. The sequence can be considered a natural sequence punctuated by short periods of human occupation using the rock-shelter as a residential camp-site (Vaquero et al., 2013). The sedimentary rate is estimated to be approximately 0.46 mm/yr (Bischoff et al., 1988; Vaquero et al., 2013). Palynological analyses indicate a succession of five different climatic phases, between the final phase of MIS 4 and the Hengelo Interstadial (Burjachs and Julià, 1994). The pollen analysis is complemented by analyses of charcoals, phytoliths, herpetofauna, small mammals and ungulate tooth wear (Allué et al., 2017; Burjachs et al., 2012; Vaquero et al., 2013). The milder conditions documented at the bottom of the sequence progressed towards the interstadial climate in evidence in the topmost levels through cycles of warmer and colder events.

Archaeological Level O comprises poorly stratified sand and fine gravel with a weathered surface (Fig. 1C, 1D). These finer-grained deposits lie above a basal succession composed of gravel, blocks and megablocks originating from the fall of travertine rocks from the cliff above the rock-shelter (Vallverdú et al., 2012). The underlying and overlying travertine layers have been U-series dated to 54.24 ± 0.42 ka and 54.60 ± 0.40 ka, respectively (Bischoff et al., 1988). The excavated surface covers most of the originally occupied surface with an area of 271 m^2 , and more than 40,000 archaeological remains have been reported, including lithic artifacts, faunal remains, charcoal, wood negatives and combustion structures

have been reported. Malacofauna and small-mammal remains have also been recovered (Vallverdú et al., 2012; Chacón et al., 2013). Previous zooarchaeological and taphonomic analyses suggest that Neanderthals were the principal accumulator of large-mammal carcasses, with a small degree of intervention by carnivores and a humid fossilization microenvironment (Gabucio et al., 2018, 2012). Level O exhibits an elaborate technology based on the use of the Levallois flaking method, showing a marked technological difference with respect to the overlying levels, in which discoid knapping is dominant (Chacón et al., 2013; Bargalló, 2014; Bargalló et al., 2016; Picin and Carbonell, 2016). This technological shift is associated with a different use of the space in the settlement and could be related to a modification in the mobility patterns of the Neanderthals (Chacón et al., 2013; Picin and Carbonell, 2016). The paleoenvironmental conditions of Level O fall within the framework of pollen zone 3 (56.8–49.5 ka) (from Level O to J), characterized by short and abrupt oscillations within warmer and wetter episodes at intervals of about 10 kyr (Burjachs and Julià, 1994; Burjachs et al., 2012; López-García et al., 2014b). Previous works have included preliminary small-mammal analyses of Level O when fieldwork on this level was still in progress (Burjachs et al., 2012; Fernández-García et al., 2016; López-García, 2011, 2008; López-García et al., 2009; López-García and Cuenca-Bescós, 2010; López García, 2007).

3 Materials and methods

3.1 Recovery and taxonomic study of the material

The small mammal remains included in this analysis consist mainly of isolated teeth and disarticulated bones obtained from a random sediment sampling of the 271 m² surface of Level O, which take place over the course of eight excavation seasons (2004-2011). The remains were collected by washing and sieving the sediment, with two superimposed meshes of 5 mm and 1 mm, and selected by the subsequent sorting. The taxonomic identification is based on various reference criteria (Bab et al., 2007; Chaline, 1972; Cuenca-Bescós et al.,

2014; Gosàlbez, 1987; López-García, 2011; Menu and Popelard, 1987; Nadachowski, 1982; Sevilla, 1988) and on a comparison with the reference collections of the *Institut Català de Paleoecologia Humana i Evolució Social (IPHES)* and the *Università degli Studi di Ferrara (UNIFE)*. Specific identifications are based mainly on the best diagnostic elements: isolated teeth for Murinae, Glirinae and Sciuridae; first lower molars (m1) for Arvicolinae; mandible, maxilla and isolated teeth for Chiroptera and Soricomorpha; and mandible, isolated teeth and postcranial material for Talpidae. The remains were counted (NISP) and grouped using the minimum number of individuals (MNI) method, determined by counting the most highly represented diagnostic element, taking into account laterality, for each species.

3.2 Taphonomic analysis

The taphonomic study is based on the observation and description of the superficial alterations of skeletal elements (Andrews, 1990; Fernández-Jalvo et al., 2016), differentiating between alterations caused by predation (biostratinomic origin) and postdepositional alterations (biostratinomic or fossil diagenetic origin). According to Andrews (1990) and Fernández-Jalvo and Andrews (1992), taphonomic effects of predation can be detected through the skeletal representation, breakages and, particularly, features of digestion. To determine the skeletal representation and the proportions of elements present, all the elements of the sample are considered (Andrews, 1990; Fernández-Jalvo and Andrews, 1992).

To evaluate the patterns of breakage and digestion, only incisors, molars and femora are included. For each skeletal element, the number of complete elements is compared to the number of fractured elements (Andrews, 1990; Fernández-Jalvo and Andrews, 1992). Nevertheless, the most important indicator in determining a predatory origin is the corrosion marks produced by gastric juices during digestion, which is the only type of alteration that cannot be confused with other agents. Digestion is a directional and progressive process (Fernández-Jalvo et al., 2016, 2014). In the present analysis, the proportion of fossil bones

affected together with the degree of alteration is considered, distinguishing between light, moderate, heavy and extreme digestion (Fernández-Jalvo and Andrews, 1992; Fernández-Jalvo et al., 2016). The obtained results are compared with indices obtained for current reference predation collections developed by Andrews (1990). After the accumulation of the small mammal assemblage, post-depositional taphonomic processes occurred, including effects associated with roots, water abrasion, cementation, combustion, manganese oxide pigmentation and weathering (Fernández-López, 2000). To identify and characterize these alterations, we used the criteria published by Shipman et al. (1984), Andrews and Cook (1985), Andrews (1990), Fernández-Jalvo (1992), Lyman (1994), Bennàsar (2010), Fernández-López (2000) and Cáceres (2002), among others. Our analysis evaluates molars, incisors and femora in terms of the absence/presence of these alterations and, in some cases, their degree and location.

3.3 Paleoenvironmental and paleoclimatic reconstruction

To reconstruct the ecological conditions prevalent during the deposition of Level O, several methodologies are used. Firstly, to assess the homogeneity of the environment, the species evenness and diversity is calculated (Margalef, 1974), using Paleontological Statistics (PAST) software (Hammer et al., 2001). Williams et al. (2002) associated a highly even community with complex and heterogeneous vegetation. The evenness of a community can be represented by Simpson's Diversity Index ($1 - \sum((n_i/n)^2)$), where n_i is the number of individuals of taxon i). This, allows us to quantify how equal communities are through numerical representation (between 0 and 1). A larger difference in species within communities results in a higher value for the evenness index (Simpson, 1949).

Climatic conditions prevailing during the formation of the assemblage are inferred by quantitative and qualitative methods. The quantitative method involves the chorotypes previously established for small-mammal faunas in Catalonia by López et al. (2006) and

Sans-Fuentes and Ventura (2000), assigning each taxon to one chorotype according to its current climatic requirements and geographical distribution. The chorotypes differentiated are as follows: *chorotype 1* includes species with mid-European requirements; *chorotype 2* includes mid-European species tolerant of Mediterranean conditions; *chorotype 3* includes Mediterranean species; *chorotype 4* includes generalist species with a broad distribution (*Eliomys quercinus*, *Apodemus sylvaticus* and *Sciurus vulgaris*) or species with a particular habitat (such as *Arvicola sapidus*, *Pipistrellus pipistrellus* and *Nyctalus lasiopterus*), which in general provide little climatic information (Table 1) (Fernández-García and López-García, 2013).

The qualitative Mutual Ecogeographic Range (MER) method is used for a similar purpose. This method determines which present geographical region a given fossil species assemblage would be located through the intersection obtained from the overlap of the current distributions of each species, obtained from Palomo et al. (2007). The current climatic conditions of the intersecting area (Font-Tullot, 2007) are used to infer the past temperatures and precipitation levels, including the mean annual temperature (MAT), the mean temperature of the coldest month (MTC), the mean temperature of the warmest month (MTW), the mean annual precipitation (MAP), the mean precipitation of the winter months (DJF) and the mean precipitation of the summer months (JJA). Careful attention is paid to ensure that the real current distribution of each species corresponds to the potential ecological distribution and has not been strongly affected by other limiting or perturbing parameters (such as human impact or predation). Accordingly, *Iberomys cabreræ* is excluded because its current distribution is conditioned by anthropic factors. The little-known and generally fragmentary distribution of bat species precludes this order of mammals (Palomo et al., 2007). This method has already been applied to assemblages containing extant reptile and amphibian taxa (Blain et al., 2009, 2016) and to Late Pleistocene small-mammal assemblages (López-García,

2011). The results of our analysis were compared to the present climatic conditions for the Capellades region provided by Ninyerola et al. (2003).

Finally, the landscape is reconstructed using the Habitat Weighting Method, employed by Evans et al. (1981) and Andrews (2006). This method is based on the distribution of each taxon in the habitat(s) in which it is currently present on the Iberian Peninsula (Palomo et al., 2007), considering five main habitat types: open dry, open humid, woodland, rocky and water (López-García et al., 2011a). Each species is given a maximum score of 1.00, which is divided among the habitat types according to its habitat preferences (Table 1).

4. Results and discussion

4.1 Origin of the small-mammal assemblage

The taphonomic analysis includes 2,268 elements (MNI: 160). The differential anatomical representation (the relative abundance and the proportional elements representation), the high presence of fragmentation, and especially the detection of digestion marks on the analyzed elements indicate that a considerable portion of the small-mammal accumulation in Level O is associated with predation (Table 2; Fig. 2). The breakage rates and the proportional skeletal representation are not coherent with the expected pattern for any of the predators considered by Andrews (1990) and are probably related with post-depositional agents, as is common in archaeological contexts. Indeed, only 6% of the molars and 2% of the incisors were found *in situ*. These results reinforce the importance of digestion marks, such as the only diagnostic alteration, over other proxies in the determination of predation (Bennàsar, 2010; Bennàsar et al., 2016; Fernández-Jalvo, 1992; Fernández-Jalvo et al., 2016, 2014; López-García et al., 2014a). At least 40% of the elements exhibit digestion marks, demonstrating the predatory origin of the assemblage: 40% of incisors, 32% of molars and 89% of femora. The predominant digestion marks are light in degree (27%), but a

significant presence of moderate (10%) and some heavy digestion marks (2.3%) are also observed.

Digestion is progressive, sequential and dependent on several parameters, such as digestion time, predator age or even the position in the predator's stomach (Andrews, 1990; Duke et al., 1975; Fernández-Jalvo et al., 2014). The homogeneity observed in the assemblage, considering the progressive proportion of degrees of digestion, is indicative of a single predator and rules out mixtures of different predator types (Bennàsar, 2010). The percentage of small-mammal incisors, molars and femora showing digestion marks and the degree of alteration point to the presence of a category 3 predator as defined by Andrews (1990), capable of intermediate modification. Candidates include two different nocturnal raptors: the tawny owl (*Strix aluco*) or the Eurasian eagle-owl (*Bubo bubo*) (Andrews, 1990; Fernández-Jalvo and Andrews, 1992). Both are currently present in the Anoia region (Jiménez, 2003) and have been common in Iberia since the Early Pleistocene (Arribas, 2004). It is difficult to differentiate between the accumulations produced by these two avian predators, although there are small differences. In general terms, *S. aluco* tends to produce concentrations with higher rates of breakage, higher percentages of digested elements and a higher number of strongly digested teeth than *B. bubo*, which rarely produces alterations exceeding the moderate degree (Andrews, 1990; Fernández-Jalvo and Andrews, 1992; López-García et al., 2014a). For these reasons, *S. aluco* is considered the probable accumulator of the small-mammal remains from Level O. Additionally, the general range and size of the species in the fossil assemblage are coherent with the modern tawny owl diet (Olsson, 1979; Andrews, 1990; Kowalski, 1995; Palomo et al., 2007).

The tawny owl is a strongly territorial and sedentary raptor that remains year round in the nesting territory, which is restricted in size (8-75 ha). This owl nests in rocky soil, in rock crevices or in tree holes (Mikkola, 1983; Andrews, 1990; Svensson, 2010). The hunting behavior of this predator involves no preferential criteria in selecting taxa, as it is an

extremely opportunistic feeder. It adjusts its behavior to the environment and its diet to whatever is available in its particular hunting territory. Usually, its hunting range is restricted to less than 1 km from the nest (Andrews, 1990; König et al., 1999; Mikkola, 1983; Svensson, 2010). Consequently, its prey assemblage is extremely diverse (coherent with the high diversity detected in the studied assemblage) and constitutes a good record of the nearby ecosystem inhabited by this predator. The enlarged sample of the present work provides enough remains to undertake a complete taphonomic analysis and rule out preliminary attribution to a Category 1 predator (such as *Asio otus* or *Tyto alba*) (López-García et al., 2014b). Even though the tawny owl inflicts major digestion damage on the remains, it is also an eclectic predator and, like *Asio otus* and *Tyto alba*, is not likely to have produced a significant representation bias in the fossil assemblage. Therefore, the fossil assemblage from Level O is assumed to preserve consistent relative species abundances from the past environment of the Abric Romaní region and can be used to develop paleoecological interpretations.

4.2 Postdepositional processes and taphonomic history

After the deposition of pellets by the predator, postdepositional agents will affect the small-mammal remains (Fernández-López, 2000) (Fig. 3). The most common effects detected in Level O are related to changes in temperature and humidity (striations, 79.6%; fissures, 68.6%; cracks, 25%), the presence of water (manganese oxide, 47.1%; abrasion, 5.5%), plant activity (chemical corrosion, 45.2%) and the use of fire at the site (burned bones, 14.5%) (Table 2). To a lesser degree, cementation is also observed (13.2%). None of the alterations shows a taxonomic or anatomical preference, and the alterations are homogeneously distributed across the surface of the level. All the post-depositional alterations are coherent with a fossiliferous rock-shelter environment (Fernández-Jalvo, 1992) that combines open-

environment agents (such as plant activity) with common karst agents characterized by humidity patterns (for instance, manganese oxide precipitation).

Some of the alterations suggest an important presence of water, related to a wet environment (evidenced by chemical corrosion), abrupt humidity changes (evidenced by cementation and fissures) or flooding (evidenced by manganese oxide). Marín-Arroyo et al. (2014) also associated manganese oxide with a high proportion of abandoned organic matter produced by intensive human occupations. According to Gabucio et al. (2012), this site can be described as a humid fossiliferous microenvironment, characterized by wet conditions and the reactivation of water flows and flooding, which is consistent with the underground streams responsible for the formation of the travertine rock-shelter (Vallverdú et al., 2012). The high rates of breakage, previously noted as incoherent with any of the predation patterns defined by Andrews (1990) (Table 2), are probably related to changes in the humidity level and possibly trampling and sediment compaction. Chemical corrosion, evidence of plant activity, is probably associated with mosses (Gabucio et al., 2012; 2018; Vallverdú et al., 2012; Vaquero et al., 2013). Even though water was present, no transport is detected, due to the low presence of abrasion modifications (with consistently low degrees of polishing and rounding) (Cáceres, 2002). Nevertheless, differential dynamic transport could be related to the low weight and density of small-mammal remains (Korth, 1979; Fernández-Jalvo and Andrews, 2003). In any case, all the taphonomic evidence confirms an *in situ* accumulation of remains, ruling out considerable transport dynamics. Therefore, *S. aluco* likely established its roost in one of the fissures of the rock-shelter, leaving the pellets in the substrate (Olsson, 1979; Svensson, 2010). Moreover, the absence of desquamation and weathering rules out long and continuous exposure to meteorological agents (Fernández-Jalvo et al., 2002), coherent with the site conditions and with the inferred rapid burial dynamics (Bischoff et al., 1988; Vaquero et al., 2013; Sharp et al., 2016).

In comparison with previous zooarchaeological studies (Gabucio et al., 2012; 2018), with the exception of anthropic, carnivore and rodent modifications, all the alterations observed in the large-mammal assemblage are present in the small-mammal assemblage. This confirms the *in situ* nature of the whole deposit. A comparison in spatial terms (Bargalló et al., 2016; Gabucio et al., 2014; 2018) shows homogeneity between small- and large-mammal remains in the spatial distribution of alterations, indicating a unitary taphonomic pattern, with only a few differences probably related to short-distance water transport. In any case, post-depositional alterations have not caused considerable damage to the assemblage as a whole.

4.3 Identified species of small mammals

Level O presents the richest small-mammal assemblage in the whole archaeological sequence (López-García, 2011; Burjachs et al., 2012). From the number of identified specimens (NISP) of 2,666, 990 elements have been identified at the species level, representing 284 individuals (MNI) that belong to 15 different taxa: five insectivores (*Crocidura* cf. *russula*, *Sorex* gr. *araneus-coronatus*, *Sorex minutus*, *Neomys* gr. *fodiens-anomalus* and *Talpa europaea*); two chiropters (*Pipistrellus pipistrellus* and *Nyctalus lasiopterus*) and eight rodents (*Apodemus sylvaticus*, *Arvicola sapidus*, *Iberomys cabrerae*, *Microtus* (*Terricola*) *duodecimcostatus*, *Microtus agrestis*, *Microtus arvalis*, *Eliomys quercinus* and *Sciurus vulgaris*) (Table 1; Fig. 4). With respect to preliminary published works (López-García et al., 2014b), the present study has incorporated 2,451 remains, at least 175 individuals, and found four new taxa not previously identified in Level O: *P. pipistrellus*, *S. vulgaris*, *N. gr. fodiens-anomalus* and *S. minutus*. The latter three are identified for the first time in the Abric Romaní sequence.

The wood mouse (*A. sylvaticus*) is the most abundant taxon in Level O (24%). This species is a generalist but is usually associated with forested environments in a temperate climate without major climatic constraints (Palomo et al., 2007). Consequently, this species is

currently highly widespread on the Iberian Peninsula, and its occurrence in the Late Pleistocene sites of northeastern Iberia is common (Palomo et al., 2007; Fernández-García et al., 2016). The second most frequent species (19%), the southwestern water vole or *A. sapidus*, is an endemic Gallaic-Iberian endemic species that occurs only in freshwater habitats, without specific climatic restrictions (Louarn and Quéré, 2003; Palomo et al., 2007). Cabrera's vole (*I. cabreræ*; 15%) and the Mediterranean pine vole (*M. (T.) duodecimcostatus*; 8%) are endemic Iberian species with typically Mediterranean requirements. Representing lower proportions of the assemblage, both the common vole (*M. arvalis*; 10%) and the field vole (*M. agrestis*; 8%) are associated with open environments, low humidity and cold temperatures. Currently, they are present in the mountainous regions in the north and the center of the Iberian Peninsula (Palomo et al., 2007; Fernández-García et al., 2016).

All the species from Level O are common in the Late Pleistocene Iberian sites (Sesé, 1994; Cuenca-Bescós et al., 2010; López-García, 2011; Fernández-García et al., 2016), with the exception of the chiropters and the red squirrel (*S. vulgaris*). Level O of Abric Romaní includes one of the most ancient records of *I. cabreræ* in northeastern Iberia (López-García, 2011). *N. lasiopterus* and *P. pipistrellus* are unusual taxa in Late Pleistocene sites. *N. lasiopterus* has been recorded in Cueva del Agua (Sevilla, 1988) and Cova dels Xaragalls (López-García et al., 2012a), the specimen from Level O being the second oldest in Catalonia (López-García, 2011; López-García et al., 2009). *P. pipistrellus* is only recorded in other levels of Abric Romaní, in Cova Colomera (López-García et al., 2010) and in Cueva del Agua (Sevilla, 1988). The occurrence of *S. vulgaris*, as ascertained in Abric Romaní (Fernández-García et al., 2016), is also rare in the Pleistocene of the Iberian Peninsula. Although nowadays it is common in the north, it is strange to find this species in fossil deposits prior to Holocene (López-García, 2011; Sesé, 2011). Its presence in northern Iberia is only recorded in Cova del Coll Verdaguer (Daura et al., 2017) and in old excavations at Cova del Gegant

(Estévez, 1980). However it has not been detected in the subsequent revisions of the small-mammal assemblage of this site (López-García et al., 2012c, 2008).

4.4 Paleoenvironmental reconstruction

Level O possesses a high species richness and diversity. Fifteen small-mammal taxa are recorded in the assemblage, and the Simpson's Diversity Index is 0.84, indicating that the species are approximately numerically equal and that no one species dominates the assemblage. From a paleoecological perspective, this may be related to stable environmental conditions and heterogeneous vegetation (woodland) capable of sustaining such diversity (Margalef, 1974); evenness is usually coherent with a high presence of forest species (Williams et al., 2002). Comparison of our results with the species currently present in the site area (Gosàlbez, 1987; Jiménez and Tomás, 2009; Palomo et al., 2007) reveals a slight decrease in the diversity and several faunal replacements, as well as the disappearance of mid-European species such as *M. agrestis* and *M. arvalis*.

The small-mammal chorotype distribution in Level O indicates a preponderance of generalist taxa or taxa without particular climatic requirements (chorotype 4: 49.3%) (Fig. 5), as evidenced by the high proportion of *A. sylvaticus* and *A. sapidus*. Nevertheless, the similar proportion of Mediterranean (chorotype 3: 26.4%) and mid-European species (chorotype 1 and 2: 24.3%) is remarkable. Concurrently, the Mutual Ecogeographic Range (MER), connects this assemblage with seven geographical points (10x10 km UTM) located in the northern Iberian region: five in the Cantabrian area (30TVN12; 30TVN33; 30TVN46; 30TVN74; 30TVN85), one in the Ebro Valley (30TVN14), and one in the Catalan Pre-Pyrenees (30TDG38). The present climatic data for these regions, when compared with current climatic information for Capellades (Ninyerola et al., 2003), show lower temperatures (MAT between -3 and -4 °C; MTC between -2 and -3 °C; MTW between -3 and -4 °C). However, the annual precipitation levels are only slightly higher than at present for

Capellades (MAP: between +70 and +170 mm), and the winter precipitation is also slightly higher (DJF: between + 60 and +80 mm) (Table 3). Notable differences are detected between this reconstruction and previous paleotemperature estimations for Level O (Burjachs et al., 2012; López-García, 2011; López-García et al., 2014b), such as an increase of + 2.5°C in the MAT and a decrease of -100mm in the MAP. This is related to new identified species, warning us of the effect that a larger small-mammal sampling can have in drawing paleoenvironmental inferences. For the habitat reconstruction, the Habitat Weighting Method indicated that the area surrounding the site featured an extended open-woodland environment, as confirmed by the presence of forest dwellers (52%) (*A. sylvaticus*, *S. vulgaris* and *N. lasiopterus*) and open-environment taxa (18%) (*M. arvalis*, *M. agrestis* and *T. europaea*). The existence of stable watercourses close to the rock-shelter is confirmed by water-dependent specimens (20%) (*A. sapidus* and *N. gr. fodiens-anomalous*) recovered from Level O (Fig. 5). The presence of water is likely related to the Anoia River, which flows at the foot of the site, and to the hydrologic dynamics (i.e., water streams) directly associated with the formation of the site (Vallverdú et al., 2012). The landscape reconstruction undertaken in the present study differs substantially from previous reconstructions (Burjachs et al., 2012; López-García, 2011), underlining the importance of forest at the expense of open spaces (wet and dry) and the aquatic component. The ecological behavior of the predator responsible for the small-mammal assemblage, *Strix aluco*, coincides with this habitat. In fact, the tawny owl is considered the most common woodland owl in Europe (Mikkola, 1983; Andrews, 1990); it is usually found in deciduous and mixed forests with forest clearings (Jutglar and Masó, 1999; König et al., 1999; Mikkola, 1983; Svensson, 2010). Presently, it is widely distributed on the Iberian Peninsula. It is considered a Palearctic species, and its distribution in the past was likely similar to its present distribution but reaching more southern latitudes during cold periods (Arribas, 2004).

MIS 3 is characterized by large climatic oscillations within a cool general context. After the cold episodes, large and rapid temperature increases occurred, followed by a progressive cooling (Arrizabalaga, 2004; Harrison and Sanchez Goñi, 2010). The lower temperature estimates (MAT: -4/-3 °C; MTC: -2/-3 °C) and the large differences between winter and summer temperatures (a difference of 15 °C between MTC and MTW), which are features more common for Atlantic areas than for the Mediterranean coast (Fletcher et al., 2010), relate Level O with a cool period. Moreover, the presence of some species that currently inhabit high latitudes (*S. gr. araneus-coronatus*, *T. europaea*, *M. arvalis*, *M. agrestis* and *Rana temporaria*) (Burjachs et al., 2012; López-García et al., 2014b; Sans-Fuentes and Ventura, 2000) and the equal proportion of Mediterranean and mid-European taxa are common features in Iberia during cold episodes (Sommer and Nadachowski, 2006). Considering the chronology of Level O (54.24 ± 0.42 ka; 54.60 ± 0.40 ka) (Bischoff et al., 1988; Vaquero et al., 2013), it could be related with a stadial episode, probably between IS15 (55.8 ± 1.2 ka b2k) and IS14 (54.2 ± 1.2 ka b2k) (Svensson et al., 2008; López-García et al., 2014b), enclosing previous correlations based on archaeobotanical analysis (Burjachs et al., 2012). The high levels of precipitation and the forested habitat indicate humid conditions for this cool period. The correlation agrees with the palynological and anthracological studies (Burjachs and Julià, 1994; Burjachs et al., 2012), which characterize this phase as generally cool, interrupted by short, hot, wet episodes. Both proxies reflect equivalent landscapes and humid environments for the level, with the arboreal taxa (*Artemisia*, Poaceae and *Pinus*) representing between 62-81% of the total pollen in the palynological studies. Finally, it is interesting to observe the climatic conditions of Level O within the Abric Romaní sequence (Table 4.) According to previous small-mammal data from the site (Burjachs et al., 2012; López-García et al., 2014), all the levels present lower temperatures than currently (-2.5 °C and -4.7 °C), but not all of them are more humid than at present (between -160 mm and +170 mm). Level O is the most humid level but not the coldest, which is Level E (-3.3 °C to -4.3

°C), correlated with Heinrich Event 5 by López-García et al. (2014b). Regarding the landscape, species associated with woodland are always present. This is also confirmed by the pollen and charcoal analyses, which indicate that arboreal coverage was maintained throughout the sequence, with just brief decreases (Burjachs et al., 2012; Vaquero et al., 2013; Allué et al., 2017). Instead of the differential occupational pattern detected for Level O in relation to the upper levels (Gabucio and Bargallo, 2012; Chacón et al., 2013; Picin and Carbonell, 2016), major changes are not detected in the environment by small-mammal analysis. Even so, it has been shown that when the sample size is increased for a particular level, the estimations of the climatic parameters may well differ; accordingly, paleotemperature reconstructions of these levels should be taken with caution, since the MNI is low throughout the sequence (MNI = 16-39), with the sole exception of Level O.

4.5 Environmental aspects of the Neanderthal occupations in Iberia during MIS 3

Middle Paleolithic sites with a significant human presence are scarce in Iberia almost until the arrival of MIS 3. This period is related to globally warm conditions characterized by extended forest cover and interrupted by semiarid and cool phases (Burjachs and Julià, 1994; D'Errico and Sánchez Goñi, 2003; Sánchez Goñi and D'Errico, 2005; Sánchez Goñi et al., 2008; Fletcher et al., 2010). There are many Middle Paleolithic sites located in the northeast of Iberia during MIS3. In some cases, complete climatic reconstructions have been based on small mammals, such as level III (45,870 – 44,840 cal yr B.P.) and II (44,210 – 33,060 cal yr B.P.) of Teixoneres cave, level IV of Cova del Gegant (60,000 \pm 3800 cal yr B.P.) and level I of Arbreda cave (45,840-41,410 cal yr B.P.) (López-García, 2011; López-García et al., 2015, 2014b, 2012b, 2012c; Talamo et al., 2016) (Fig. 1A; Fig. 6). Irrespective of whether they shown a stadial or an interstadial correlation, all these assemblages indicate a cold (6-10 °C) and humid climate (1500-870 mm precipitation) related to major presence of forest (always greater than 60%). The temperatures are lower than at present (between -9.1 and -5.3 °C) and

the precipitation levels are higher (between +692 and +349 mm). Level O fits within this general climatic context.

This is in accordance with the climatic pattern that López-García et al. (2014b) associated with Neanderthals in northeastern Iberia during MIS 3, based on lower temperatures and higher precipitations than at present and a major presence of an open woodland habitat. In all these Middle Paleolithic sites, temperatures oscillated but the precipitation levels and woodland estimates were always high. This is evidenced by assemblages with oscillations in the balance of Mediterranean and mid-European taxa but the continuous presence of woodland dwellers. This scheme seems to become a little more complex when other MIS 3 archaeological sites with small-vertebrate studies from throughout Iberia are considered. The considerable environmental differences among the different regions of the Iberian Peninsula, with a mix of Atlantic, Mediterranean and continental influences, have to be taken into account. Some archaeological sites exhibit diverse dynamics, such as El Mirón cave, Zafarraya and Ibex cave (Barroso et al., 2014; Finlayson et al., 2016), but the overall trend seems to fit well with the northeastern pattern of lower temperatures than at present and the major presence of the forest biotope integrated within mosaic environments with high levels of humidity. This pattern is recorded at Lezetxiki II, Askondo, Cueva del Conde, Vanguard cave and Gorham's cave (López-García et al., 2011b, 2011c; Murelaga et al., 2012; Blain et al., 2013; Garcia-Ibaibarriaga, 2015; Finlayson et al., 2016). Similar environmental characteristics are also in evidence in level 3 of Cova Eirós (Rey-Rodríguez et al., 2016), subunit Xb of El Salt (Fagoaga et al., 2017) and Cova del Coll Verdaguer (Daura et al., 2017), three sites with chronologies close to Level O but geographically and climatically different.

This general situation is coherent with palynological studies that have suggested that southern Europe (below 40°N) never experienced a complete loss of woodland, even in stadials or Heinrich Events (Fletcher et al., 2010; Harrison and Sanchez Gofí, 2010), making

Iberia an optimal region for human occupation. The maintenance of woodland cover or at least mosaic landscapes preserves the ecological quality of the surrounding area. Indeed, the Neanderthal occupations at Abric Romaní are probably more closely related to the conditions of ecological and faunal diversity that an open woodland landscape allows, than to any specific climatic condition. Also, it is well-known that fuel wood for fire production played an important role in Neanderthal settlements, as occurs in Abric Romaní (Vallverdú et al., 2012; Allué et al., 2017). Bearing in mind other Iberian Middle Paleolithic sites, our results suggest that the climate instability of MIS 3 within the cool global context had no real impact on the Neanderthal populations that occupied the northeastern part of the Iberian Peninsula at the time, remaining unclear what effects this instability could have exerted on their shifts in adaptive behavior that are evidenced in the Abric Romaní sequence. In environmental terms and in accordance with previous studies of the Late Pleistocene in the northeastern Iberia, a general preference for woodland landscapes is confirmed, probably in relation with Neanderthal habits of adaptation.

5. Conclusions

Level O represents the richest level in small-mammal remains from the Abric Romaní rock-shelter, a fundamental archaeological site for the understanding of the last Neanderthals occupations in Iberia. A detailed study of this assemblage reveals that:

- The origin of the assemblage is related to the activity of the tawny owl (*Strix aluco*), and post-depositional alterations indicate a fossiliferous microenvironment of relative environmental humidity and occasional water flows. Both taphonomic analyses confirm the reliability of the assemblage for paleoecological reconstructions.
- During the deposition of this level, the region of Capellades was colder (MAT: -3-4 °C) and slightly wetter (MAP: +70/+170 mm; DJF: +60/+80 mm) than at present and featured semi-open woodland with a watercourse in the vicinity of the site. Further, the

equal proportion of Mediterranean and mid-European species and the chronology of the level suggest a correlation with a cool climatic phase, probably between interstadials IS15 and IS14.

- Considering the Abric Romaní sequence and other Iberian MIS3 sites, it is suggested that these hominid groups were well adapted to the instability of this period. It is not clear what direct impact the climate had on their adaptive shifts on a local scale, as occurred in Abric Romaní. However, a general preference for occupying forest biotopes is detected.

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Figures

Figure 1. (A) Location of the Abric Romaní site in Iberia and the locations of other Middle Paleolithic sites: 1, Teixoneres cave; 2, Arbreda cave; 3, Cova del Gegant; 4, Cova del Coll Verdager; 5, El Salt; 6, Zafarraya cave; 7, Vanguard cave; 8, Gorham's cave; 9, Ibex cave; 10, Askondo; 11, Lezetxiki II; 12, El Mirón; 13, Cueva del Conde; 14, Cova Eiros (Barroso et al., 2014; Daura et al., 2017; Fagoaga et al., 2017; Finlayson et al., 2016; García-Ibaibarriaga, 2015; López-García, 2011; López-García et al., 2011b, 2011c, 2012b, 2012c, 2014b, 2015; Murelaga et al., 2012; Rey-Rodríguez et al., 2016; Talamo et al., 2016)(B) Stratigraphy of Abric Romaní with U/Th dates (Bischoff et al., 1988); (C) Level O surface in the excavation campaign of 2010; (D) Level O surface. Lines indicate areas with combustion structures; brick pattern corresponds to rock-shelter wall; in gray, areas included in the small-mammal taphonomic sample of this study.

Figure 2. Taphonomic features associated with the small-mammal remains from Level O. (A) right m1 *Arvicola sapidus* with light digestion; (B) left m1 *Iberomys cabreræ* with moderate digestion; (C) upper molar Arvicolinae with heavy digestion; (D) right M2 *Apodemus sylvaticus* with moderate digestion; (E) proximal epiphysis of a rodent left femur with light digestion; (F) proximal epiphysis of a rodent right femur with moderate digestion; (G) proximal epiphysis of *Talpa europaea* left femur with light digestion; (H) distal epiphysis of *Talpa europaea* left femur with light digestion; (I) rodent upper incisor with light digestion; (J) rodent upper incisor with moderate digestion; (K) rodent lower incisor with heavy digestion; (L) rodent upper incisor with dispersed manganese oxide pigmentation; (M) detail of manganese oxide pigmentation; (N) rodent upper incisor with dispersed manganese oxide pigmentation; (O) rodent upper incisor with chemical corrosion associated with roots; (P) detail of chemical corrosion; (Q) rodent left femur with generalized root corrosion; (R) left

m1 *Arvicola sapidus* with cracking due to changes in humidity; (S) left m1 *Iberomys cabrerae*, burned (Grade 2); (T) Arvicolinae molar, burned (Grade 3); (U) rodent right femur with rounded breaking edge; (V) left mandible *Arvicola sapidus* with cement concretion.

Figure 3. Simplified taphonomic sequence to explain the formation of the Level O small mammal assemblage.

Figure 4. Small-mammal species identified in Level O of Abric Romaní. (A) left m1 *Arvicola sapidus* (occlusal view); (B) left m1 *Microtus arvalis* (occlusal view); (C) left m1 *Microtus agrestis* (occlusal view); (D) left m1 *Microtus (Terricola) duodecimcostatus* (occlusal view); (E) right m1 *Iberomys cabrerae* (occlusal view); (F) left m1 *Apodemus sylvaticus* (occlusal view); (G) right m2 *Apodemus sylvaticus* (occlusal view); (H) left M1 *Apodemus sylvaticus* (occlusal view); (I) left m1-m2 *Eliomys quercinus* (occlusal view); (J) right M1-M2 *Eliomys quercinus* (occlusal view); (K) right m1 *Sciurus vulgaris* (occlusal view); (L) right M1 *Sciurus vulgaris* (occlusal view); (M) right mandible *Crocidura russula* (buccal view); (N) right mandible *Sorex minutus* (buccal view); (O) right mandible *Sorex* gr. *araneus-coronatus* (lingual view); (P) right mandible *Sorex* gr. *araneus-coronatus* (posterior view); (Q) left mandible *Neomys* gr. *fodiens-anomalous* (posterior view); (R) left mandible *Neomys* gr. *fodiens-anomalous* (lingual view); (S) left humerus *Talpa europaea*; (T) right mandible *Nyctalus lasiopterus* (buccal view); (U) left Ci *Nyctalus lasiopterus* (buccal view); (V) left mandible *Pipistrellus pipistrellus* (buccal view).

Figure 5. Distribution by chorotype and landscape preferences of the small mammals from Level O of Abric Romaní. C1, chorotype 1 (mid-European species); C2, chorotype 2 (mid-European species tolerant of Mediterranean conditions); C3, chorotype 3 (Mediterranean species); C4, chorotype 4 (generalist species or species with a particular habitat, which

provide little climatic information); OD, open dry (meadows with seasonal change); OH, open humid (evergreen meadows with dense pastures and suitable topsoils); WO, woodland (mature forest including woodland margins and forest patches, with moderate ground cover); R, rocky (areas with suitable rocky or stony substratum); WA, water (areas along streams, lakes and ponds).

Figure 6. Mean annual temperature (MAT) and mean annual precipitation (MAP) estimates and woodland (WO) vs. open landscape (OL) proportions from five northeastern Iberian sites, provided by previous small vertebrate studies (López-García, 2011; López-García et al., 2015, 2014b, 2012b, 2012c; Talamo et al., 2016). The assemblages are correlated with the NorthGRIP $\delta^{18}\text{O}$ curve, published by Svensson et al. (2008).

Tables

Table 1. Number of identified specimens (NISP), minimum number of individuals (MNI) and the MNI as a percentage of the total for the small-mammal assemblage of Level O of Abric Romani. C1, chorotype 1; C2, chorotype 2; C3, chorotype 3; C4, chorotype 4; OD, open dry; OH, open humid; WO, woodland; R, rocky; WA, water.

Table 2. Synthesis of taphonomic analysis, including number of items (number of identified specimens; minimum number of individuals), alterations caused by predation (skeletal representation, proportional representation indexes, breakage and digestion) and post-depositional alterations. The Relative Abundance Index compare the number of skeletal elements recovered with the expected number of each element multiplied by MNI; the proportion postcranial/cranial ratio relates the number of postcranial elements (humerus, radius, ulna, femur and tibia) to cranial ones (mandible, maxillae and isolated molars). Digestion and post-depositional analysis are performed on incisors, molars and femurs (NISP: 1327).

Table 3. Reconstruction of the temperature and precipitation of Level O of Abric Romani, using the Mutual Ecogeographic Range based on 10 x10 km UTM squares with equivalent species presence, and modern climatic data of the site. The 10 x10 km UTM square names (e.g., 30TDG38) are taken from <http://www.aitorgaston.com/utm10.php>. Mean, average values obtained; Max, maximum values obtained; Min, minimum values obtained; SD, standard deviation; MAT, mean annual temperature; MTC, mean temperature of coldest month; MTW, mean temperature of warmest month; MAP, mean annual precipitation; DJF, mean precipitation of winter months; JJA, mean precipitation of summer months. Temperature data in degrees centigrade (°C) and precipitation data in millimeters (mm).

Table 4. Mean annual temperature (MAT) and mean annual precipitation (MAP) estimates corrected for Abric Romaní levels with high MNI content (López-García et al., 2014b). Level O data belong to the estimates in this study. (*) López-García et al., 2014b; (**) Burjachs et al., 2012. To allow comparison with previous small-mammal studies (López-García, 2011; López-García et al., 2014b), some corrections are applied to the temperature and precipitation estimates related to the climatic source (this work uses Ninyerola et al. (2003) rather than Font-Tullot (2000) employed in previous works).

Table 1. Number of identified specimens (NISP), minimum number of individuals (MNI) and the percentage of MNI through the assemblage of small mammals of level O from Abric Romaní.

Taxon	Recount			Chorotypes					Habitat			
	NISP (n)	MNI (n)	MNI (%)	C 1	C 2	C 3	C 4	O D	OH	WO	R	WA
<i>Microtus agrestis</i>	47	25	8.8		x				0.5	0.5		
<i>Microtus arvalis</i>	54	30	10.56	x				0.5		0.5		
<i>Iberomys cabreræ</i> <i>M. (Terricola)</i>	87	45	15.85			x			0.5	0.5		
<i>duodecimcostatus</i>	46	25	8.8			x			0.25	0.5	0.25	
<i>Arvicola sapidus</i>	284	55	19.37				x					1
<i>Apodemus sylvaticus</i>	327	69	24.3				x			1		
<i>Eliomys quercinus</i>	55	8	2.82				x			0.5	0.5	
<i>Sciurus vulgaris</i>	10	2	0.7				x			1		
Rodentia indet.	1195											
<i>Crociodura russula</i>	17	3	1.06			x		0.5		0.5		
<i>Sorex</i> gr. <i>araneus-coronatus</i>	3	2	0.7	x					0.5	0.5		
<i>Sorex minutus</i>	1	1	0.35		x				0.5	0.5		
<i>Neomys</i> gr. <i>fodiens-anomalous</i>	10	2	0.7	x					0.25			0.75
<i>Talpa europaea</i>	31	7	2.46		x				0.75	0.25		
Soricidae indet.	10	7	2.46									
<i>Pipistrellus pipistrellus</i>	1	1	0.35				x			0.5	0.5	
<i>Nyctalus lasiopterus</i>	6	1	0.35				x			1		
Chiroptera indet.	1	1	0.35									
Indet.	481											
Total	2666	284	100									

Table 2. Taphonomic analysis synthesis, including recount (number of identified specimens; minimum number of individuals), predation alterations (skeletal representation, proportion representation indexes, breakage and digestion) and postdepositional alterations.

Recount		
NISP (n)	2268	
MNI (n)	160	
Skeletal representation		
Relative Abundance Index (%)	29.1	
SD of Relative Abundance Index	24.9	
Proportional representation indexes		
Postcranial/Cranial Index	0.69	
Humerus+Femur/Maxilla+Mandible Index	0.03	
Radius+Tibia/Humerus+Femur Index	0.78	
Isolated molars/ Empty Alveolus Index	1.47	
Breakage		
Incisors fracture (%)	67.3	
Molars fracture (%)	41	
Femora fracture (%)	96.5	
Digestion	(n)	(%)
Total of digested elements	401	39.3
Light degree	277	27
Moderate degree	101	10
Heavy degree	23	2.3
Extreme degree	0	0
Digested incisors	151	40.5
Light degree	115	31
Moderate degree	30	8
Heavy degree	6	1.5
Extreme degree	0	0
Digested molars	191	33
Light degree	119	20.5
Moderate degree	55	9.5
Heavy degree	17	3
Extreme degree	0	0
Digested femora	59	89.4
Light degree	43	65.2
Moderate degree	16	24.2
Heavy degree	0	0
Extreme degree	0	0
Post-depositional agents	(n)	(%)
Cracking for humidity and temperature changes	332	79.6-25
Desquamation	92	6.9
Manganese oxide pigmentation	625	47.1
Plant Activity	600	45.2
Cementation	175	13.2

Burned	192	14.5
Water abrasion	73	5.5
Weathering	3	0.2

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Table 3. Temperature and precipitation estimates for level O of Abrie Romani.

	30TDG38	30TXN14	30TVN74	30TVN85	30TVN33	30TVN46	30TVN12	Mean	Max	Min	SD	Current data
MAT	11	11	11	11	12	12	12	11.4	12	11	± 0.53	14-15
MTC	4	4	3	3	3	2	5	3.4	5	2	± 0.97	5-6
MTW	19	21	18	18	18	17	17	18.3	21	17	± 1.38	21-22
MAP	1000	1000	1000	1000	700	700	700	871	1000	700	± 160	700-800
DJF	129	204	204	204	136	256	136	181	256	129	± 48	100-120
JJA	138	131	131	131	71	102	71	111	138	71	± 29	100-120

Table 4. Mean annual temperature (MAT) and mean annual precipitation (MAP) estimates corrected for Abrić Romani levels with high MNI content.

Level	Chronology (ka BP)	Climatic Event	MAT (°C)	MAP (mm)
D	49 - 44.9	Interstadial 12**	-3.3/-4.3	-160/-60
E	49	Heinrich Event 5*	-3.7/-4.7	-48/+48
J	51-49		-3.4/-4.4	-160/-60
N	54.6	Interstadial 16**	-2.5/-3.5	-130/-30
O	54.2	Stadial 17-15	-3/4	+70/+170

Highlights

- MIS 3 is characterized by large climatic oscillations within a global warm context
- Environmental reconstruction and taphonomic analysis of small mammals
- The results enable to identify a stadial climatic episode between IS15 and IS14
- Landscape dominated by open woodland and climate cooler and wetter than nowadays
- Data in accordance with environmental pattern of MIS3 in Iberia Peninsula

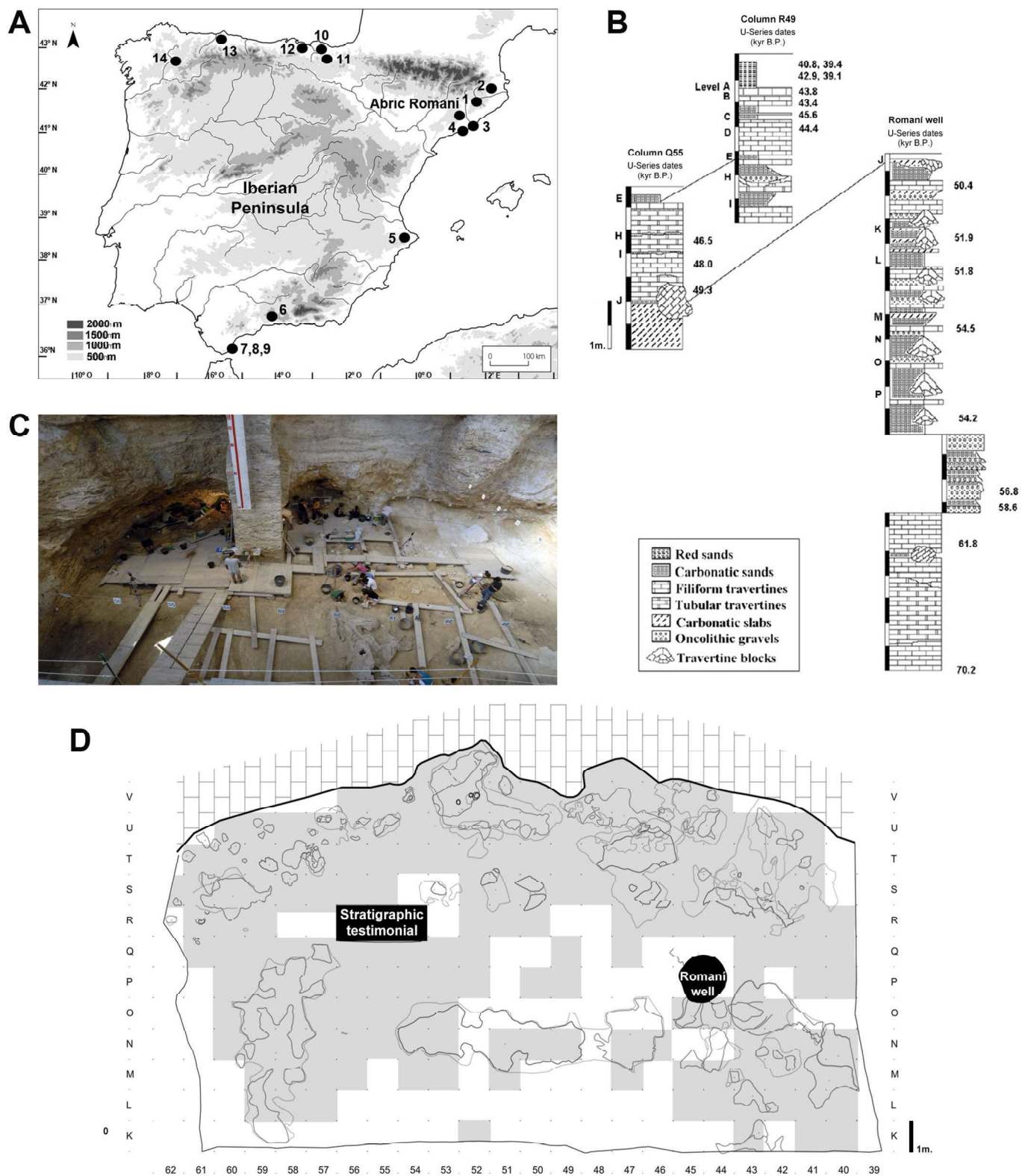


Figure 1

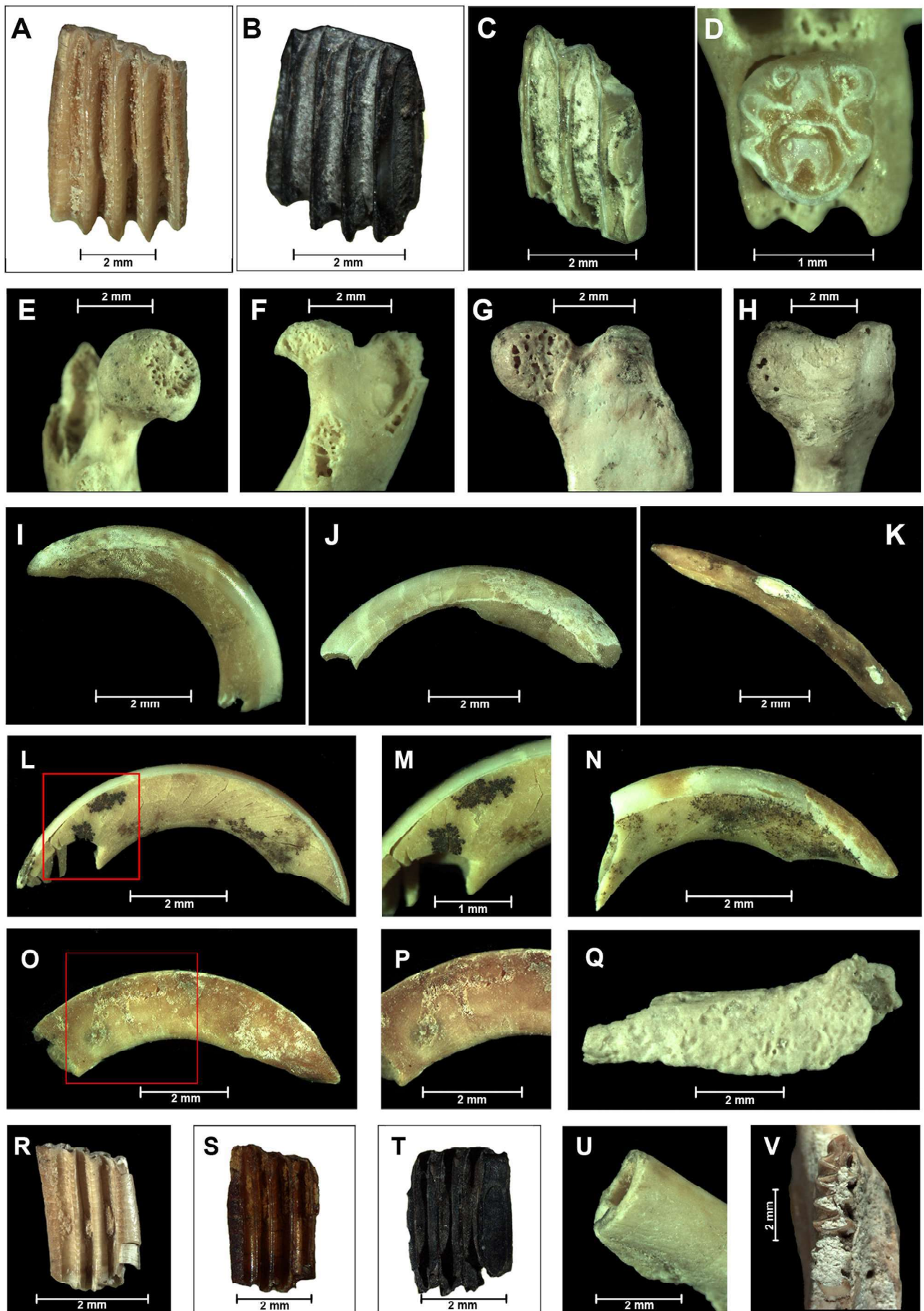


Figure 2

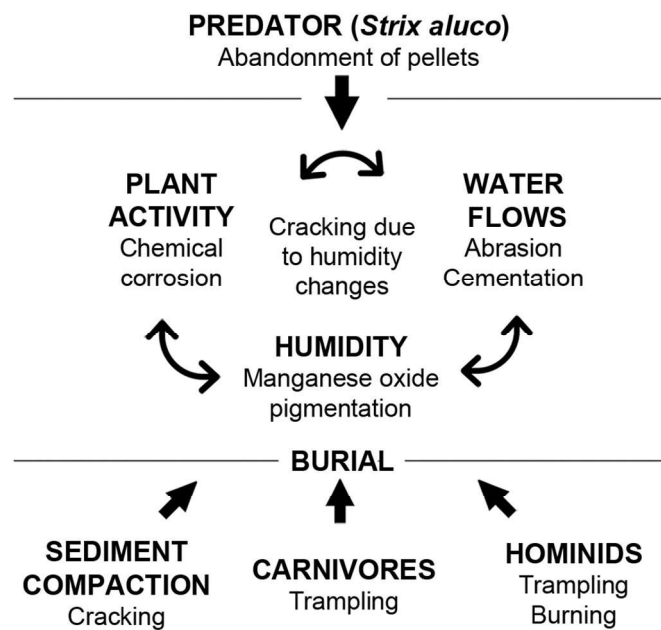


Figure 3

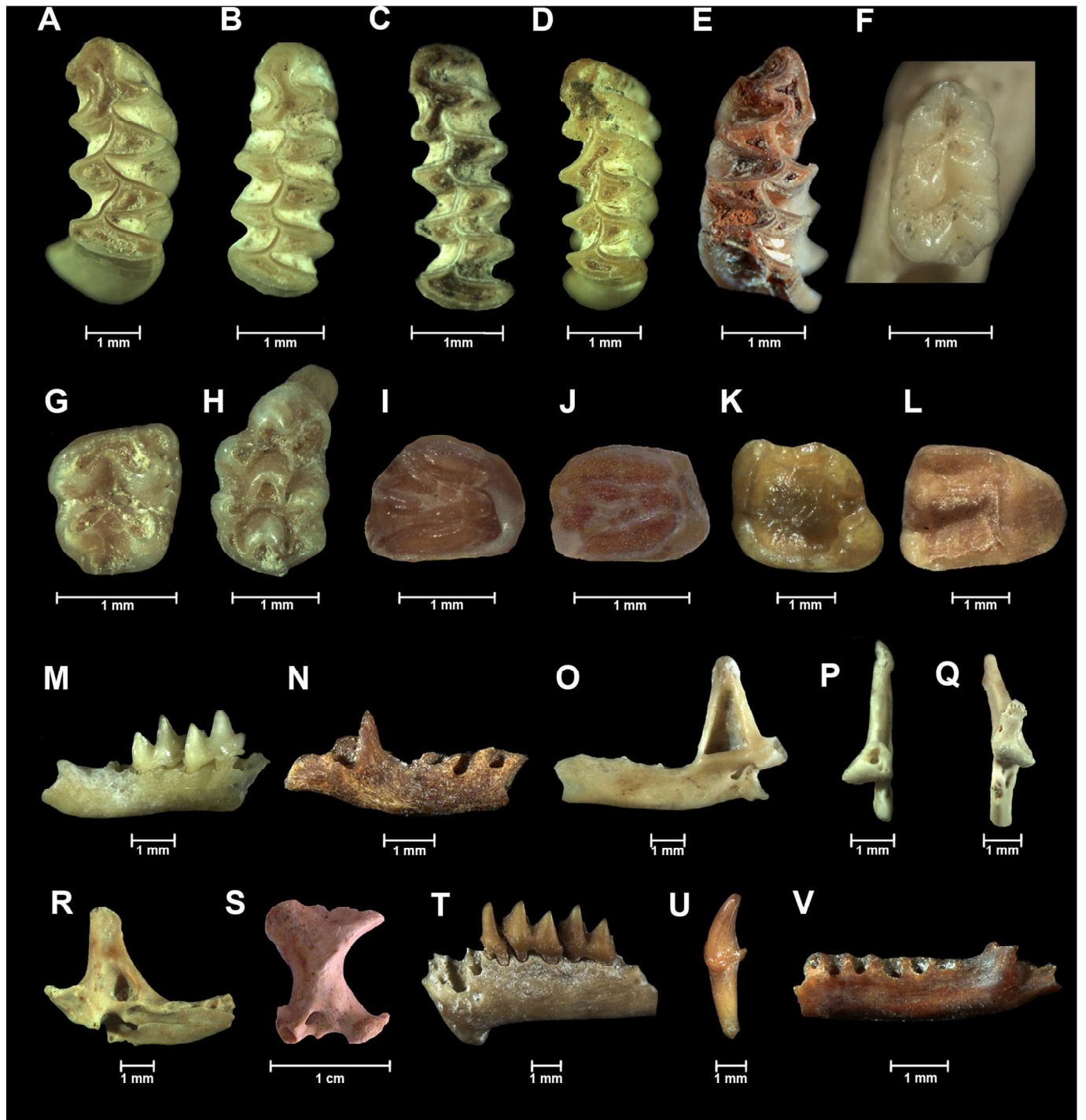


Figure 4

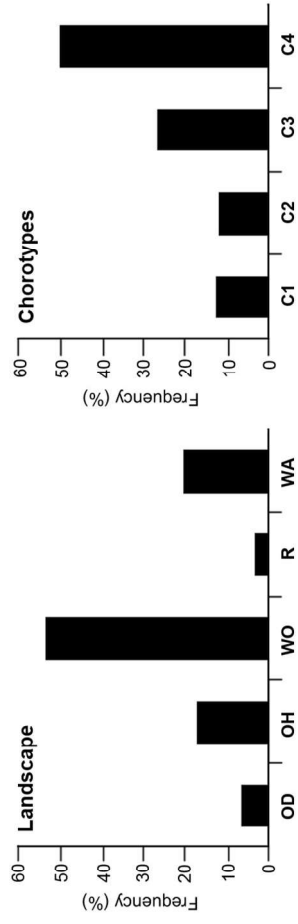


Figure 5

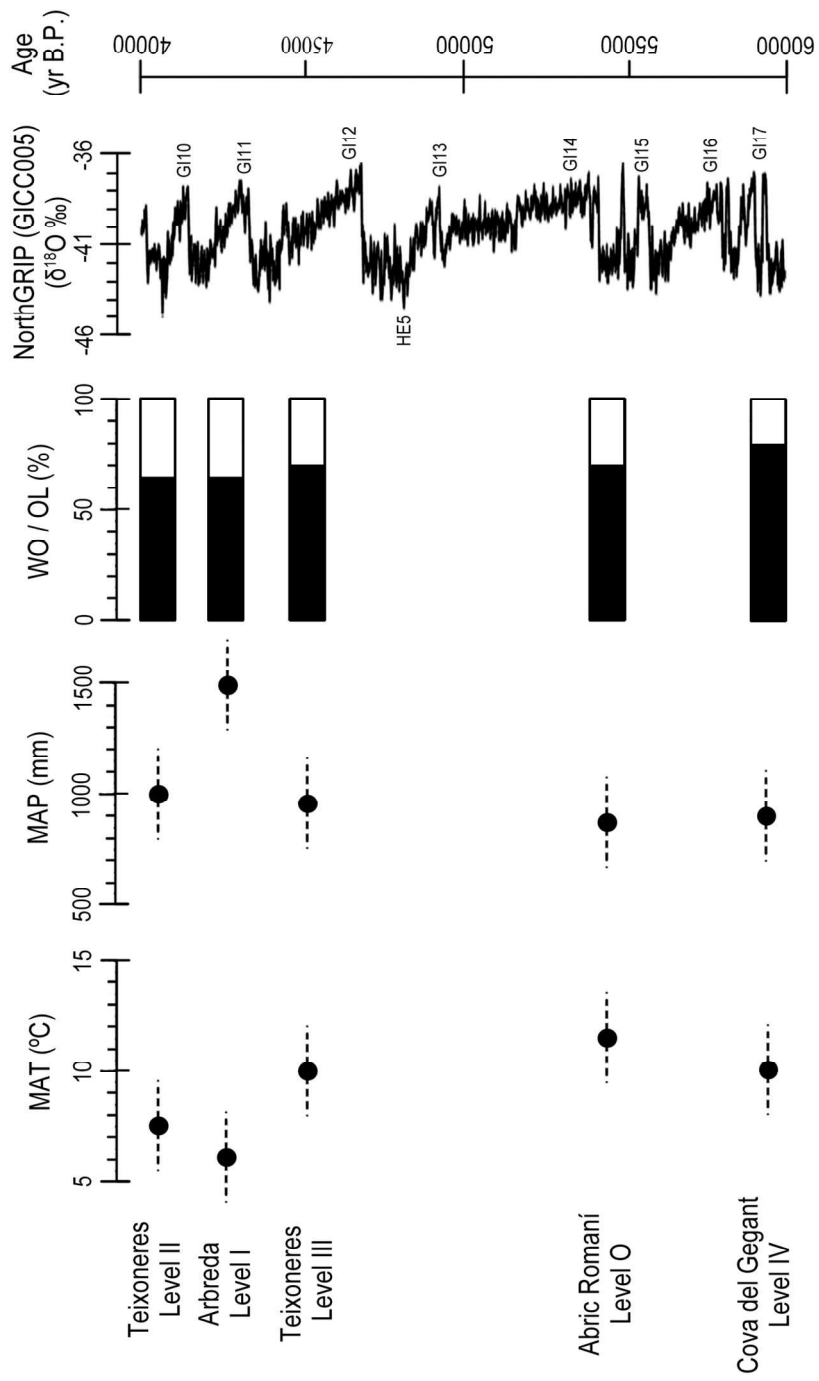


Figure 6