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Silvicolous Neanderthals in the far West: the mid-Pleistocene palaeoecological sequence of Bolomor Cave (Valencia, Spain)

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ABSTRACT

A palynological study of the archaeological layers from the Neanderthal site of Bolomor Cave, located in Eastern Spain, is presented. Vegetational developments for the periods MIS 9 to MIS 5 are described, among which it is worth highlighting the long resilience of mixed oak-pine forests throughout cold phases and the high diversity of woody taxa including deciduous, Mediterranean, and thermophytes. The relative abundance of evergreen *Quercus* and *Castanea*, the continuous occurrences of *Olea*, *Fraxinus*, *Pistacia*, *Myrtus*, *Phillyrea* and Cistaceae, and the presence of *Celtis*, *Ceratonia*, *Pinus pinaster*, and *Rhododendron* are peculiar features of the sequence. The existence of a Mid-Pleistocene glacial refugium is postulated. To our knowledge, there is no similar record of forest landscape that have been described in glacial context for Neanderthals, which at the time bears archaeological and anthropological implications. The records of past vegetation in Bolomor are coherent with palaeontological finds, especially concerning the mammal fauna, which also suggests forested landscapes. The hominids of Bolomor possessed highly adaptative subsistence strategies that match the potential benefits offered by a diverse and rich environment where a broad spectrum of edible plants was available.

1. Introduction

Although the Mediterranean Basin is rich in archaeological sites of the Middle Pleistocene (Carrión and Walker, 2019; Hardy et al., 2018; Margari et al., 2018), there is still a lack of palynological finds from this period (Agustí et al., 2018; Cattani and Renault-Miskovsky, 1989; Cattani et al., 1994; de Beaulieu, 1969; García-Antón, 1989; García-Antón and Sainz-Ollero, 1991; Leroi-Gourhan and Renault-Miskovsky, 1977; Leroy and Arpe, 2007; Leroy et al., 2011; Magri, 2010; Magri and Palombo, 2013; Magri et al., 2017; Postigo-Mijarra et al., 2007, 2008; 2009, 2010; Renault-Miskovsky, 1974; Ruiz-Zapata et al., 2009; van der Hammen et al., 1971), probably due to the difficulties of conducting pollen analysis in caves, rockshelters and open-air sites where either sediments are often non polleniferous, or their taphonomy makes them to lack of pollen-analytical potential for palaeoecological purposes (Carrión and Scott, 1999; Carrión et al., 2009). In the case of the Iberian Peninsula, most palynological records from the Middle Pleistocene are geographically sparse, chronologically short and generally difficult to correlate with reference sequences (Carrión et al., 2013, 2015). A few exceptions are Padul (Camuera et al., 2019; Florschütz et al., 1971; Pons and Reille, 1988), and Atapuerca (Burjachs, 2001; Cattani et al., 1994; García-Antón, 1989; García-Antón and Sainz-Ollero, 1991), Tubilla del Agua (García-Amorena et al., 2011) and Puente Pino (Ruiz-Zapata et al., 2009). However, the combination of geomorphological, paleoclimatic and palaeobotanical characteristics suggest that this peninsula played a fundamental role in the survival of tree taxa during the Quaternary (Carrión and Leroy, 2010; Leroy and Arpe, 2007; Postigo-Mijarra et al., 2008, 2010), acting like a refugium for Arctotertiary taxa, as it similarly occurred during the Tertiary, when it was a reservoir for the Palaeotropical component (Barrón et al., 2010, 2016; Carrión and Fernández, 2009). In the context of human evolution, where palynology has provided relevant data on the habitat (Bonnefille, 2010; Burjachs

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and Julià, 1994; Carrión et al., 2011; González-Sampériz et al., 2010; Sánchez-Goñi, 1993; Sánchez-Goñi et al., 2005), this aspect is worthy of research. The present study aims to reconstruct the paleoenvironment of the Neanderthals of Bolomor Cave during the long period approximately dated between 400 and 100 ka BP.

2. Physical setting, excavations and chronology

Bolomor Cave is located in the Eastern Mediterranean coast of Spain, approximately 100 m above sea level, 2 km southeast of the village of Tavernes de la Valldigna near Valencia, Spain (39° 03′ N/ 0° 15′ W) (Fig. 1). The deposit is located in the Valldigna Valley, a narrow and short basin located between the Iberian Mountain Range (North) and the Pre-Betic Mountain Range (South). East to the site there is an extensive coastal plain next to the Mediterranean Sea. The deposit lies amongst karst rock of the Mondúver mountain range and is embedded in the rocky wall, with an entrance that opened to the outside approximately 500 ka as a result of the continuous erosion of the ravine in which it is located (Fig. 1).

The sedimentary sequence of the Bolomor Cave is mainly formed by allochthonous material of colluvial origin. Next to these deposits there are other autochthonous sediments of gravitational origin that originated from the collapse of the roof as a consequence of tectonic or weathering processes. Fumanal (1995) identified 17 geoarchaeological levels in the stratigraphic sequence, which are listed from the top of the deposit (Fig. 2). The multidisciplinary analysis of Bolomor Cave allowed us to identify a unique stratigraphic sequence that includes the Middle Pleistocene and the early stages of the Upper Pleistocene (Fernández-Peris, 2003; Fernández-Peris and Villaverde, 2001; Fernández-Peris et al., 1994, 1997; 1999; Guillem, 1995; Martínez-Valle, 1995). The use of amino acid racemisation (AAR) and thermoluminescence (TL) allowed us to date the karstic deposit of the deposit between MIS 9 and MIS 5e (Fernández-Peris, 2007). Several dates were obtain through the use of TL: 121 ± 18 ka for level II, 225 ± 34 ka for level XIII and 233 ± 35

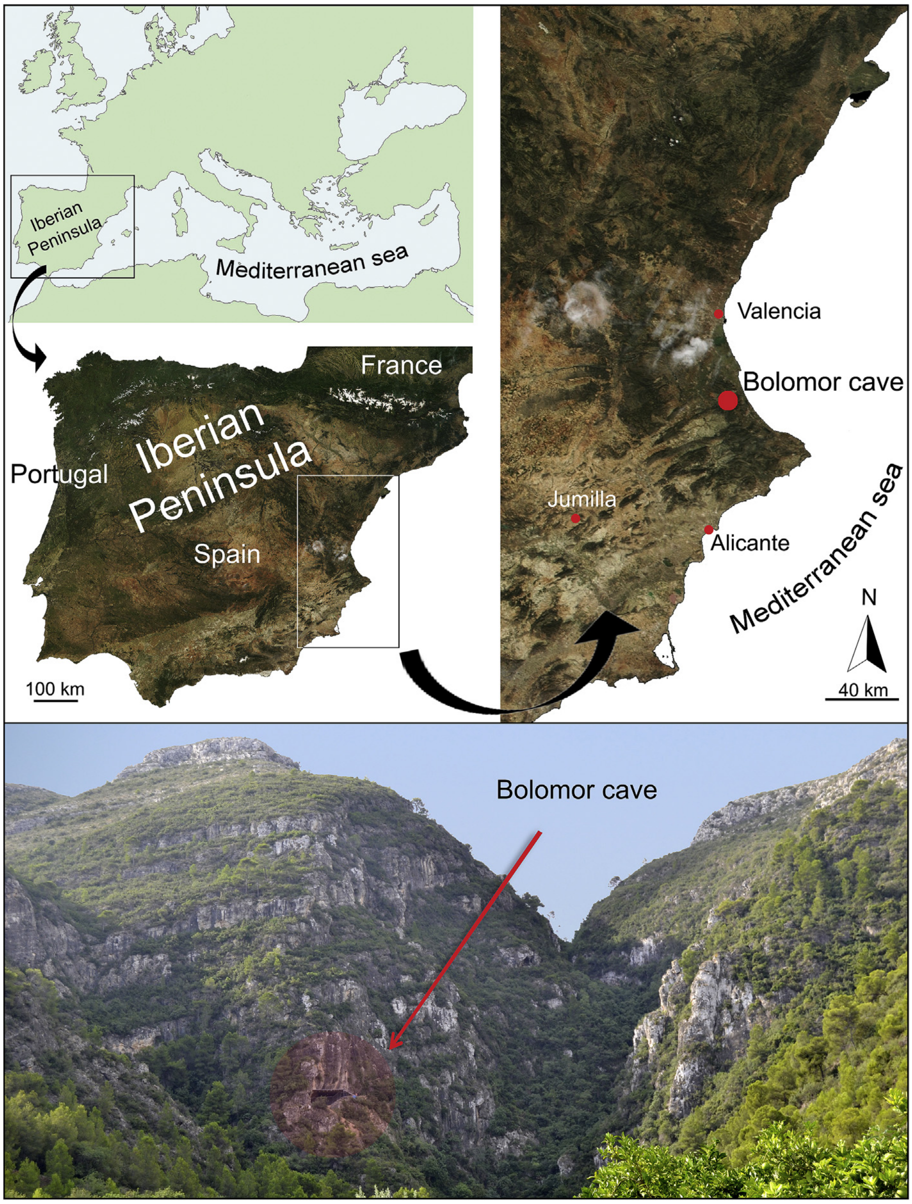


Fig. 1. Location of Bolomor Cave in eastern Iberian Peninsula.

Fig. 2. West sector profile sampled for pollen analysis in Bolomor Cave (after Arsuaga et al., 2012).

ka for level XIV. Similarly, we obtained several other dates through AAR: 228 ± 53 ka for level XIII and 525 ± 125 ka for level XVII. A study of the magnetic susceptibility (EM) of the sediment confirmed the chronological and paleoclimatic data elaborated by the sedimentological analysis and the dates mentioned above. This methodology classifies sediments according to marine isotope stages (MIS) and records time, depth and climate (Ellwood et al., 2004).

The samples for pollen analysis were taken from the inner part of the cave, in the Western sector, which covers a maximum area of 32 m^2 (Figs. 2 and 3). This sector has the particularity of being the only one that perfectly preserves the stratigraphic sequence (levels I to XVII). The excavations of this area began in 1991 and reached 20 m^2 in level I. However, as deeper levels were reached, the excavations were restricted by the presence of a large fallen block. At the end of 2006, the excavation of the western sector at the base of level XIII was temporarily put on hold, with the idea of reactivating it along with the excavation of the northern sector once the study in that area reached the base of level XIII (Sañudo et al., 2016).

3. Climate and vegetation cover

The cave is located in an area of coastal Mediterranean climate (Fig. 1). The annual precipitation amounts surpass 700 mm and the average annual temperature exceeds 16 °C. These conditions derive from the local orography, since the adjacent mountain ranges (Iberian to the NW and Baetic towards the SW) are interposed to the easterly winds favouring the fall of rains mainly in Spring and Autumn, especially in the latter. The site is located in the first mountainous buttresses on a rainy coastal plain. Phytoclimatologically speaking, the area is located in the Upper Thermomediterranean with a sub-humid ombroclimate, although it is also influenced by the proximity of the Infra-Mediterranean belt. Biogeographically, the area belongs to the Catalano-Provenzal-Balearic Province, Sector Setabense (Costa, 1982; Rivas-Martínez, 1987; Rivas-Martínez et al., 1977).

The vegetation of the area where the cave is located is typically Mediterranean, meaning that it is adapted to the summer drought

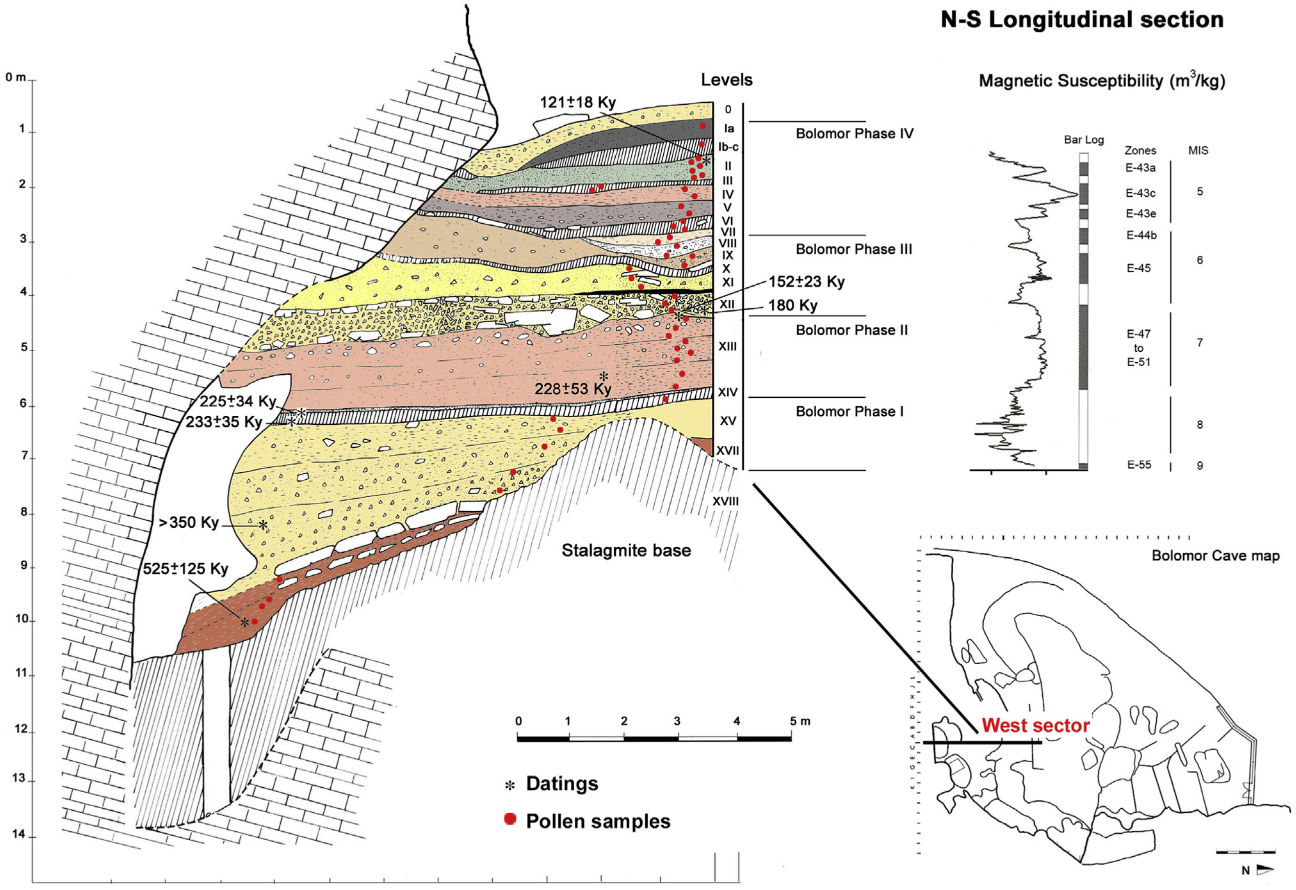


Fig. 3. Stratigrafical profile of Bolomor Cave showing the cronological context and position of pollen samples. Redrawn from Vidal-Matutano et al. (2017).

and have small, perennial and leathery leaves (Fig. 1). The potential carrascals have disappeared, as a consequence of a long degradation throughout the years due to grazing, fires, agricultural practices, logging and erosion. The area of access to the Bolomor ravine is characterised by the presence of crop fields (*Citrus x sinensis*), shrub vegetation with *Chamaerops humilis*, *Cistus*, *Rosmarinus officinalis*, *Satureja obovata*, *Thymus vulgaris*, and herbaceous elements such as *Ballota hirsuta*, *Bituminaria bituminosa*, *Centaurea aspera*, *Chenopodium murale*, *Cichorium intybus*, *Conyza bonariensis*, *Echium*, *Heliotropium europaeum*, *Lobularia maritima*, *Parietaria*, *Scabiosa atropurpurea* and *Sonchus tenerrimus*. Due to its topography and geographical orientation, the Bolomor ravine is an excellent example of vegetation refugium with growth of *Arbutus unedo*, *Asparagus acutifolius*, *Ceratonia siliqua*, *Erica multiflora*, *Ficus carica*, *Fraxinus ornus*, *Laurus nobilis*, *Myrtus communis*, *Olea europaea*, *Pinus halepensis*, *Pistacia lentiscus*, *Quercus coccifera*, *Quercus ilex* subsp. *ballota*, *Rhamnus alaternus*, *Rhamnus lycioides*, *Rubia peregrina*, *Rubus ulmifolius*, *Ruta*, *Sedum sediforme*, *Smilax aspera* and *Viburnum tinus*, as well as endemisms such as *Antirrhinum valentinum*. Similarly, there is a presence of pteridophytes such as *Asplenium fontanum*, *Selaginella denticulata* and *Polypodium cambricum*.

4. Lithostratigraphy, palaeontology and palaeoenvironmental inferences

The stratigraphic sequence of Bolomor Cave provides paleoclimatic data derived from sedimentology, macrofauna and microfauna records. The 17 stratigraphic levels identified in the site can be divided into 4 paleoclimatic phases (Bolomor I-IV), from the bottom (Bolomor I) to the top (Bolomor IV) of the sequence (Figs. 2 and 3). In addition, a curve of magnetic susceptibility of the whole sequence was elaborated, showing a good correlation with sedimentary cycles and paleoclimatic interpretation (Fernández-Peris, 2003).

Bolomor shows a high faunal diversity (Fig. 4; SI Tables 1 and 2) with more than 30 species belonging to Cercopithecinae, Carnivora and Ungulata, as well as small prey such as Leporidae, Aves, Testudinidae, Amphibia and Salmonidae (Blasco et al., 2013a, 2013b). The stratigraphic sequence is mainly characterised by *Cervus elaphus* and *Equus ferus*, followed by other species such as *Bos primigenius*, *Dama* sp., *Equus hydruntinus*, *Hemitragus bonali*, *Hemitragus cedrensis*, *Hippopotamus amphibius*, *Macaca sylvana*, *Megaloceros giganteus*, *Stephanorhinus hemitoechus*, *Sus scrofa* and *Palaeoloxodon antiquus*. Although the carnivores are documented occasionally, fossils of *Canis lupus*, *Lynx pardina*, *Meles meles*, *Panthera leo fossilis*, *Ursus arctos*, *Ursus tibetanus*, and *Vulpes vulpes* have been retrieved (Blasco, 2008; Rivals and Blasco, 2008; Blasco et al., 2013a, 2013b; Martínez-Valle, 2001; Sañudo et al., 2016; Sarrión and Fernández-Peris, 2006).

The distribution (and relative frequency) of the faunal taxa along the sequence shows slight environmental changes, as well as an evolution of the landscape (SI Tables 1 and 2). The main lithostratigraphic characteristics, and paleoclimatic and paleontological implications in each of the levels are described below (Blasco and Fernández-Peris, 2012b; Blasco et al., 2013a, 2013b; Fernández-Peris, 2007; Guillem, 2001; Martínez-Valle, 2001).

4.1. *Bolomor phase I (levels XVII-XV; MIS 9-8) (Figs. 3 and 4; SI Tables 1 and 2)*

The sedimentary basis is composed of materials showing weathering and interpreted as a mild climatic cycle with a certain level of humidity, at least seasonally. The faunal assemblage is mainly characterised by *C. elaphus*, *H. bonali* and *E. ferus*. The presence of the latter suggests a certain predominance of open

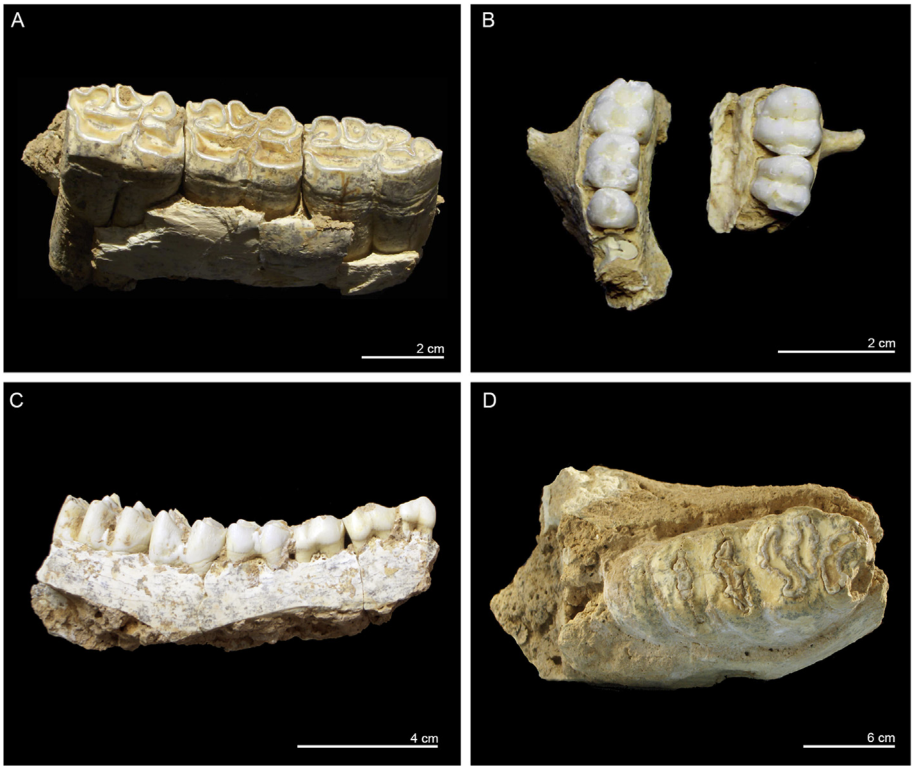


Fig. 4. Some examples of macrovertebrates recovered at Bolomor Cave. A) Horse (*Equus ferus*) mandible from level XII; B) Macaque (*Macaca sylvana*) maxilla from level XII; C) Red deer (*Cervus elaphus*) mandible from level XII; D) Immature elephant (*Palaeoloxodon antiquus*) mandible from level XII.

habitats, while *C. elaphus* is more related to relatively extensive forest formations. The presence of the steppe rhinoceros (*S. hemitoechus*) with the highest values of the sequence, and the megaloceros (*M. giganteus*), would indicate the predominance of fresh and relatively humid climates. The micromammal records reflects the exposure of different ecological niches: the *Allocricetus bursae* occupies open and dry spaces, while the *Talpa europaea* inhabits wet meadows, supporting the domain of fresh climatic conditions with a certain humidity.

4.2. Bolomor phase II (levels XIV and XIII; MIS 7) (Figs. 3 and 4; SI Tables 1 and 2)

This phase is characterised by interstadial parameters, mild-warm and seasonally very wet, which caused periodic flooding of the cave. Environmental characteristics in level XIVa and b show a regression of the cold events of the previous phase, giving rise to soft water flows that filter certain materials. The contact with level XIII seems to indicate the loss of the sedimentary ceiling of level XIV. Levels XIIIc and b, would correspond to warm, and eventually very humid stages. In the same way, the fauna shows that the previous conditions, cold and less humid, oscillate towards more humid and warm environments, with an increase in the dominance of cervids (*Dama* sp., *C. elaphus*), bovids (*H. bonali*) and a significant decline of *E. ferus*. The conditions of high humidity and waterlogging of the cave probably hindered its habitability.

4.3. Bolomor phase III (levels XII, XI, X, IX, VIII and VII; MIS 6) (Figs. 3 and 4; SI Tables 1 and 2)

This phase is initially characterised by the oscillation of cool and wet periods which successively evolve towards more rigorous and dry conditions (level XII). During the most recent stages (level VIII), the climate became extraordinarily warm and very humid, especially when compared to the cold conditions of level VII. The sedimentological analysis shows that the presence of ice particles reaches its maximum peak at level XIIb, while the magnetic susceptibility curve indicates that the maximum values are reached at levels X-IX. The fauna record shows a tendency towards drier and more rigorous climates, as indicated by the disappearance of megaloceros (*M. giganteus*) and the high frequencies of horses (*E. ferus*). The presence of species badly adapted to cold climates such as *B. primigenius*, *M. sylvana* and *Testudo hermanni* suggest a warm phase, while levels X-IX, represent cold periods, with the presence of *Allocricetus bursae*.

4.4. Bolomor phase IV (levels VI, V, IV, III, II and I; MIS 5e) (Figs. 3 and 4; SI Tables 1 and 2)

It is a globally soft interglacial period, in which temperate-humid oscillations are predominant, with few attenuated cool lapses (levels VI-III) that cause the accumulation of small boulders, product of the weathering of the cavity vault due to the ice-thaw. The high humidity caused the occasional and partial flooding of the cave, together with the brecification of sediments. The environmental indicators show a climatic improvement with respect to the cold conditions of the previous levels. On the other hand, a climatic regime of cyclic conditions is established. During this time, there is a predominance of cold periods that lead to deposits of small and subangular detritic material (levels VI, V, IV, III). The upper part of levels VI, III and Ic is formed by the water circulation of continuous and carbonated flows. The faunal assemblage is characterised by species of marked temperate influence, such as the hippopotamus (*H. amphibius*), the wild boar (*S. scrofa*), the auroch (*B. primigenius*) and the wild ass (*E. hydruntinus*), whose presence would indicate an increase of the temperatures and levels of humidity, as well as the gradual expansion of forest areas in the environment of the site. The hippopotamus and the aurochs are associated with lagoon zones of a certain entity. *E. hydruntinus* is typical of temperate and humid climate faunas with interstadial or interglacial characteristics, like the wild boar (*S. scrofa*), which is limited exclusively to this phase.

5. Human remains

Four fossil human remains from Bolomor Cave have been analysed so far (Arsuaga et al., 2012, Fig. 5), namely a fragment of the fibula (HCB-01), two isolated teeth (HCB-02 and HCB-05) and an adult left parietal bone (HCB-07), all of them dating between MIS 7 and 5e. The fossils HCB-01 and HCB-02 were recovered in level IV and dated to MIS 5e. HCB-05 appeared in the sieving work of the sediments from previous mining activities. It is worth noting that the adult left parietal bone (HCB-07) was recovered embedded in a breccia block extracted during the same mining activities. A previous analysis of the specimen suggested certain affinities with *Homo neanderthalensis* (Sarrión and Fernández-Peris, 2006). The sediments where the some specimens were found showed an inverted but coherent stratigraphic succession that helped assign their stratigraphic attribution. Specifically, a small fragment of breccia, which is still attached to HCB-05, made it possible to assign its origin to the Pleistocene levels of the site (Fig. 5). Based on these parallels, HCB-05 possibly comes from level XIII and the MIS 7. Likewise, the lithological properties of the brecciated block adhered to the parietal bone HCB-07 clearly indicate that it was detached from the level VI of the sequence and dated to MIS 5e (Arsuaga et al., 2012).

6. Charcoal analysis

Bolomor Cave offers one of the earliest evidence of controlled use of fire in Southern Europe (Fernández-Peris et al., 2012; Vidal-Matutano et al., 2017). The studies carried out in the site have allowed recovering combustion structures in form of 14 hearths from levels II, IV, XI, XII and XIII (Fig. 5). Their morphology is simple, not overlapping with each other and possessing a flat base. The diameters are between 30 and 120 cm and the thickness between 5 and 10 cm. The hearths are placed directly on the ground without previous preparation, containing pseudomorphs of vegetable ash with different degrees of combustion (Fernández-Peris et al., 2012). Along with hearths, high quantities of archaeological material were documented (SI Figs. 1 and 2). The oldest combustion structures in the stratigraphic sequence come from level XIII, with an age of 228 ± 53 ka, obtained by the use of amino-acid racemisation (AAR).

Vidal-Matutano et al. (2017) carried out a study on charcoals from the combustion structures of levels XIII (MIS 7) and XI (MIS 6), in addition to the dispersed burnt context of level XIII. The identification of the paleobotanical remains allowed the acquisition of paleoecological data about the oldest evidence of *Pinus nigra-sylvestris* in the east of the Iberian Peninsula supported by the collection of woody components by hominids.

7. Palynological methods

The sampling was conducted on a vertical stratigraphic profile, as it is indicated for archaeological deposits (Girard, 1975). All the samples were taken from the same archaeological profile, in the Western sector (Levels I to XVII). It should be noted that in this site, this is the only complete profile where all the archaeological levels have been preserved, with a power of 7–8 m (Figs. 2, 3 and 5). In an initial sampling, a single sample was taken from each of the levels

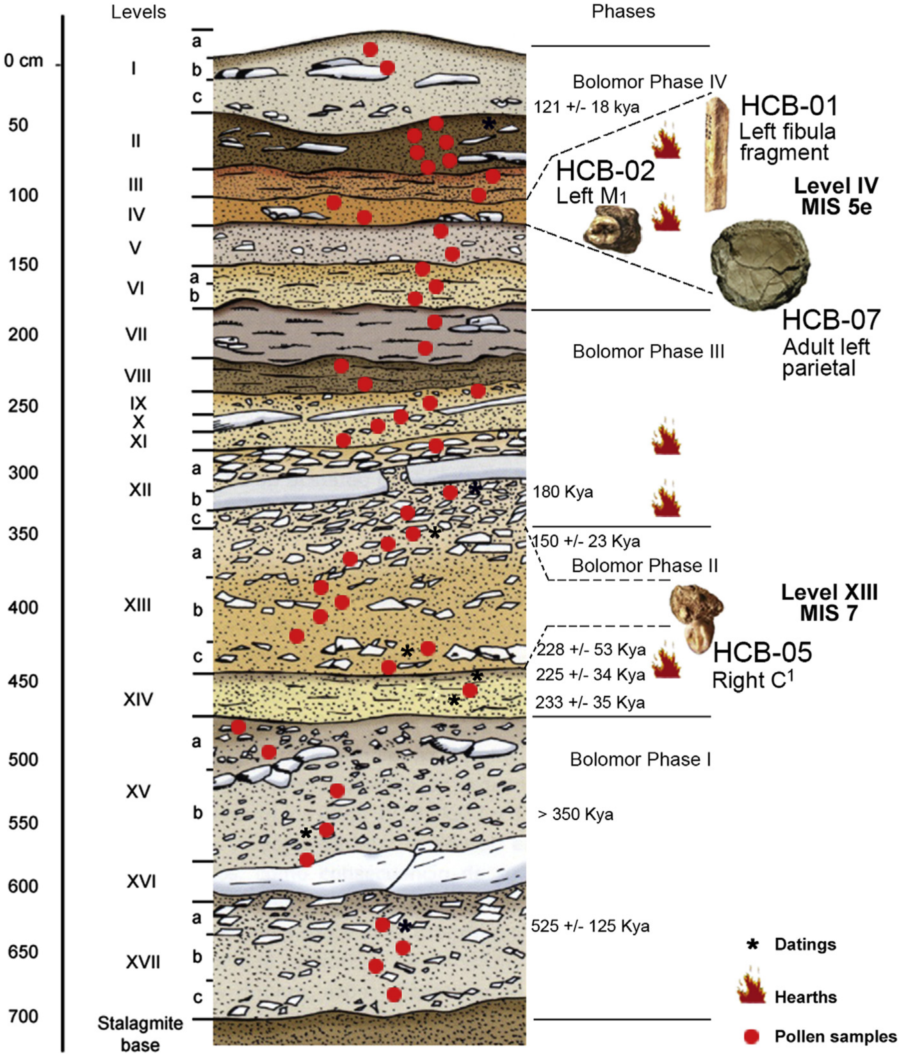


Fig. 5. Location of human fossils, hearths, and pollen samples in the study section. Redrawn from Arsuaga et al. (2012).

to evaluate the potential and presence of palynomorphs. Once we found that the results were positive, a more intensive sampling of each of the levels was carried out, depending on the sedimentological potential of each one of them. Of the 49 samples studied, 48 were polliniferous (SI Table 3) with the sole exception of the sample of level X, a level of collapse which was pollenically sterile. From level XVI, no sample was recovered due to the fact of being a stratum of blocks. Prior to the collection of the samples, the profile was cleaned from the upper to the lower levels.

In addition, a surface layer of sediment about 5–10 cm deep was discarded to avoid potential sources of reworking or contamination by insects and other animals (Fig. 2). For the extraction of palynomorphs, the "Classic Chemical Method" was followed (Dimbleby, 1985; Erdtman, 1969), with the modifications proposed by Girard and Renault-Miskovsky (1969). To evaluate the quality of the laboratory processing, we added to each simple three tablets of Lycopodium spores. After being treated at the laboratory, the samples were mounted on slides with the use of liquid paraffin. The palynological identification was made by conventional microscopy (400x and 1000x) using an optical microscope. We also used the palynomorph reference collection of the Department of Plant Biology of the University of Murcia. The pollen count data was treated with the Tilia Graph 1.7.16 program in order to obtain the pollen diagrams. A palynological diagram divided into several components, arboreal pollen (AP), non arboreal pollen (NAP) and spores was prepared (Figs. 6 and 7; SI Fig. 3) together with a synthetic diagram with the main taxa and ecological groups (Fig. 8). A total of 31,547 palynomorphs were identified, 18,043 pollen grains and 13,504 spores were counted, excluding those not identified. Along with spores and non-pollinic microfossils, we excluded the pollen grains of *Apiaceae, Ceratonia, Helianthemum/Halimium and Lotus* from the total pollen sum because it is assumed that these groups are overrepresented in some of the samples studied, as a consequence of local overdeposition. The number of pollen types varies between 8 and 40, with a total of 79 taxa being recognized. The percentage of undetermined types remained, in most cases, in values lower than 10% (SI Table 3). The pollen grains and spores presented a fairly good level of preservation. The pollinic and non-pollinic palinomorph counts were carried out until reaching a Pollen Base Sum (total of pollen grains, excluding the spores and non-pollen microfossils) of at least 200 pollen grains, except in the two cases in which the reading of all the available material did not allow it (samples III.2 and VII.2) (SI Table 3).

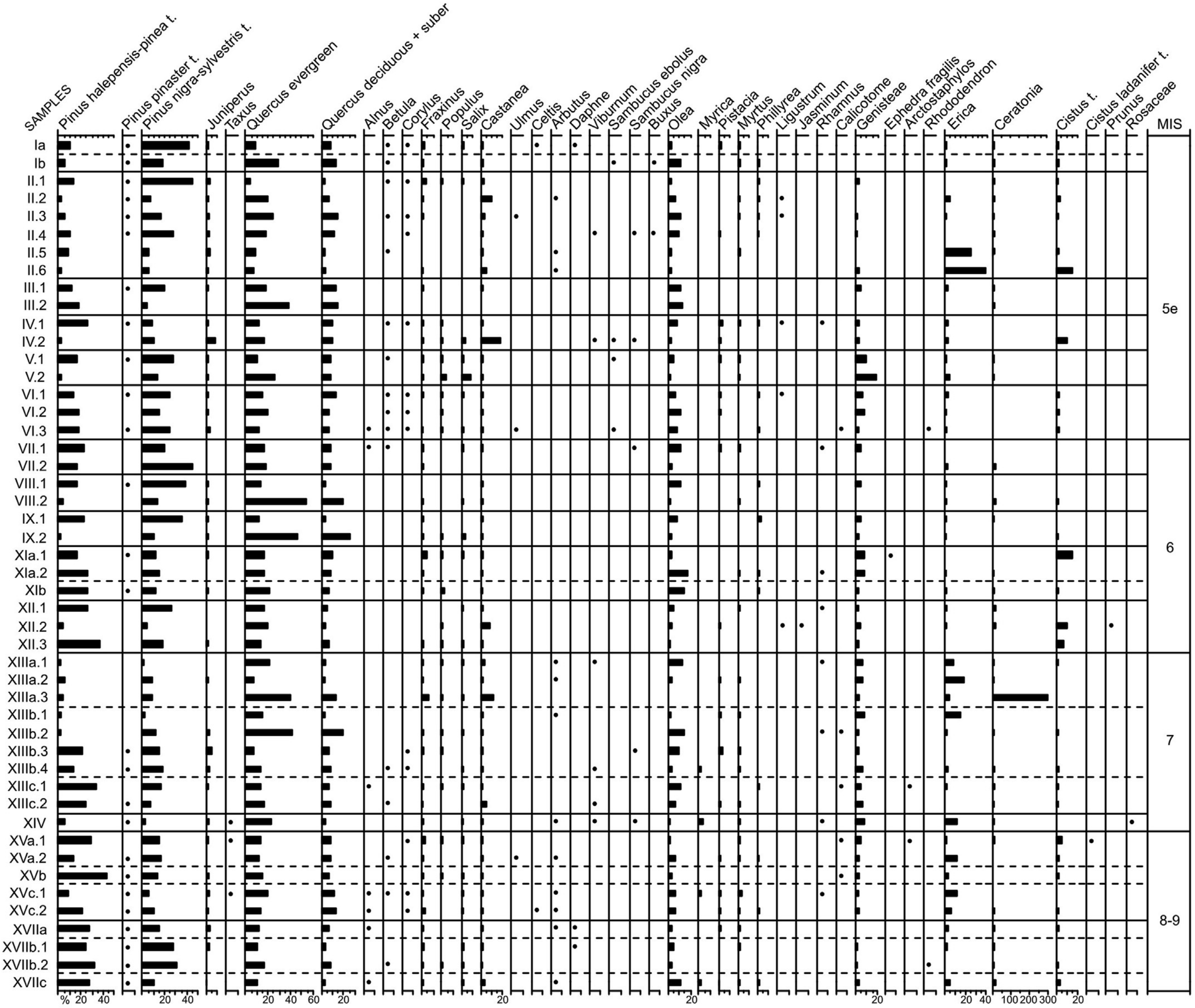


Fig. 6. Pollen diagram of Bolomor Cave including largely arboreal elements. Apiaceae, *Ceratonia*, *Helianthemum*/*Halimium* and *Lotus* are out from the total pollen sum. Black dots for percentages below 3%. The dashed lines indicate subdivisions within a level.

8. Pollen stratigraphy

Thereafter we describe the results of the pollen analysis of 17 stratigraphical levels described for Bolomor (Fernández-Peris, 2003; Fernández-Peris and Villaverde, 2001; Fernández-Peris et al., 1994, 1997; 1999; Fumanal, 1995; Guillem, 1995; Martínez-Valle, 1995) (Figs. 6–8; SI Fig. 3).

8.1. Level XVII

This level includes samples XVIIa, XVIIb.1, XVIIb.2 and XVIIc (Figs. 6–8). It is dominated by AP, which is higher than 98%. *Pinus halepensis-pinea* is above 24%, reaching 31% in sample XVIIb.2. *Pinus nigra-sylvestris* fluctuates (10–31%). *Quercus* deciduous + *suber* attains 2–9%, evergreen *Quercus* reaches 17%. It is worth mentioning the decline of *Olea* from 11 to 4% across this zone. Continued presence of *Castanea* (1–3%). *Erica* varies between 6 and 1%, disappearing in the sample XVIIb.2. Alongside AP appear *Pinus pinaster*, *Juniperus*, *Alnus*, *Betula*, *Fraxinus*, *Populus*, *Salix*, *Myrica*, *Pistacia*, *Myrtus*, *Phillyrea*, *Ceratonia*, *Arbutus* and *Rhododendron*. In NAP it is important to emphasise the presence of *Helianthemum*/*Halimium*, Amaranthaceae, *Lotus*, Apiaceae and *Typha*. Also, Fabaceae, *Daphne*, *Artemisia*, Urticaceae and Cichorioideae are frequent. *Glomus* chlamydospores abound, ranging between 2 and 65% (SI Fig. 3). The continuous presence of *Monoporisporites* (3–29%) stands out. Similarly, *Dicellaesporites*, *Dictyosporites*, *Diporisporites*, *Inapertisporites*, *Pluricellaesporites*, *Quilonia* and *Scleroderma* are present, as well as spores of *Polypodium*, with percentages higher than 10%.

8.2. Level XV

It includes samples XVa.1, XVa.2, XVb, XVc.1 and XVc.2 (Figs. 6–8). The most predominant type of pollen is arboreal, with total values higher than 83%. This is an area characterised by high percentages of *Pinus halepensis-pinea* (8–44%) and *Quercus*

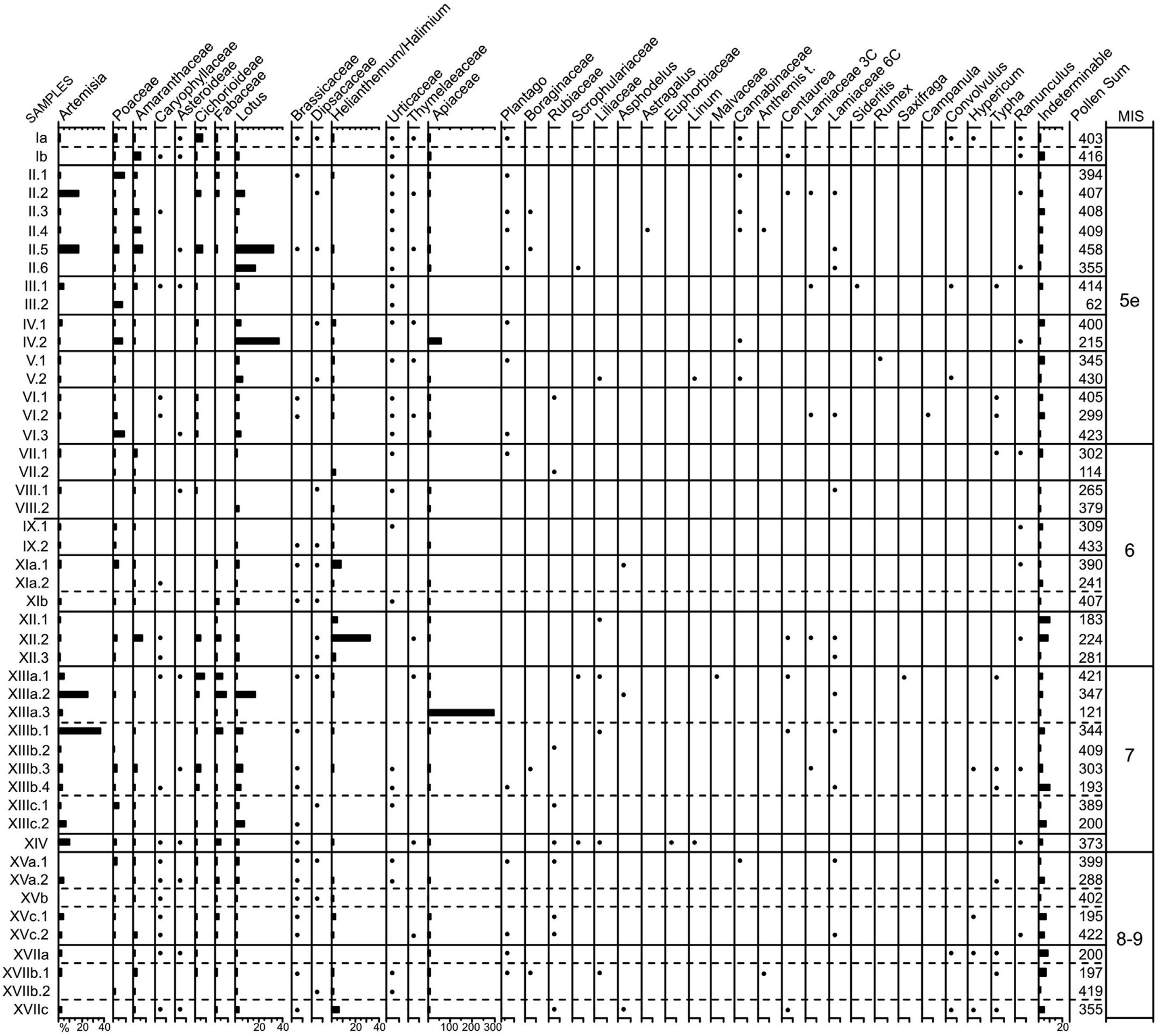


Fig. 7. Pollen diagram of Bolomor Cave including largely non arboreal elements Apiaceae, *Ceratonia*, *Helianthemum/Halimium* and *Lotus* out from the total pollen sum. Black dots for percentages below 3%. The dashed lines indicate subdivisions within a level.

evergreen (13–19%). We found high levels of *Pinus nigra-sylvestris* (6–17%) and *Quercus* deciduous + *suber* (6–14%). *Olea* recovers without reaching the values of level XVII, until it exceeds 7%, but then ends up falling to 2%. *Castanea* (1–3%) remains similar to level XVII. *Fraxinus*, *Salix*, *Erica*, *Myrtus*, *Pistacia*, Genisteae, *Calicotome* and *Cistus* are highly represented throughout the whole level. Similarly, there is a predominance of *Pinus pinaster*, *Alnus*, *Betula*, *Corylus*, *Populus*, *Myrica*, *Ulmus*, *Celtis*, *Phillyrea*, *Arbutus* and *Arctostaphylos*. In NAP, it is worth highlighting the presence of Fabaceae with values ranging from 1 to 5%. *Helianthemum/Halimium*, *Lotus*, Poaceae, *Artemisia*, Amaranthaceae, Cichorioideae, Brassicaceae and Caryophyllaceae appear. *Glomus* and *Inapertisporites* peak up to 76% and 65% respectively (SI Fig. 3). *Hypoxylonites* (6–17%) is present throughout the level. *Diporisporites*, *Monoporisporites*, *Quilonia* and *Reduviasporonites* are also frequent. *Polypodium* attains values of 2–25%.

8.3. Level XIV

This level only includes sample XIV (Figs. 6–8). The pollen of arboreal type represents levels close to 69% and the rest appears formed by non-arboreal pollen type. The descent of *Pinus* stands out, in the case of *Pinus halepensis-pinea* below 5%, and in the case of *Pinus nigra-sylvestris,* it does not reach 2%. It is also worth noting the amount of *Quercus* evergreen, with percentages around 23%. On the other hand, *Quercus* deciduous + *suber* (4%) suffers a notable decline. *Erica* is above 11%, while Genisteae does not exceed 8% and *Olea* falls to values below 1%. AP accompanying include *Pinus pinaster*, *Juniperus*, *Taxus*, *Fraxinus*, *Salix*, *Myrica*, *Myrtus*, *Castanea*, *Rhamnus*, *Arbutus*, *Ceratonia*, *Viburnum*, *Sambucus nigra*, and Rosaceae. In NAP it is worth mentioning the presence of *Artemisia* with values near 10%. Fabaceae increases to almost 5%. Brassicaceae, Euphorbiaceae and Liliaceae maintain frequencies higher than 2%.

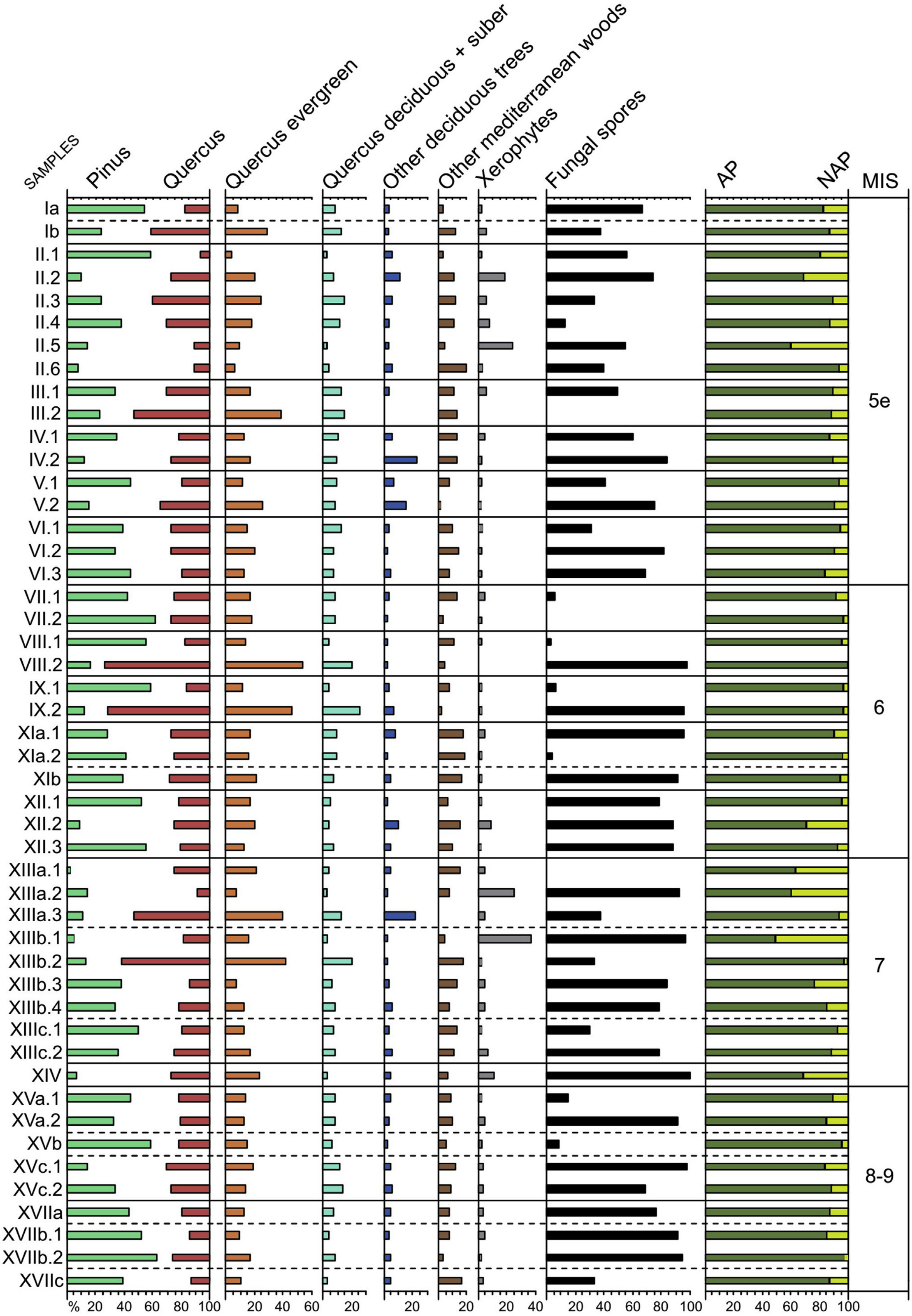


Fig. 8. Synthetic diagram from Bolomor Cave. Other deciduous trees includes *Alnus*, *Betula*, *Castanea*, *Celtis*, *Corylus*, *Fraxinus*, *Populus*, *Salix* and *Ulmus*. Other Mediterranean woods includes *Arbutus*, *Calicotome*, *Cistus* t., *Cistus ladanifer* t., *Ephedra fragilis*, *Ligustrum*, *Myrica*, *Myrtus*, *Olea*, *Pistacia*, *Rhamnus* and *Viburnum*. Xerophytes includes *Artemisia*, *Asphodelus*, Amaranthaceae, *Ephedra fragilis* and *Sideritis*. Fungal Spores excludes *Glomus*. The dashed lines indicate subdivisions within a level.

Similarly, the groups Thymelaeaceae, *Lotus*, Apiaceae, Poaceae, Amaranthaceae, Cichorioideae, Rubiaceae and *Linum* are representative. The presence of *Dicellaesporites* and *Monoporisporites* stands out, both above 26% (SI Fig. 3). *Diporisporites* (15%), *Inapertisporites* (10%) and *Multicellites* (10%) are present. Pteridophyte spores disappear in this level.

8.4. Level XIII

This level includes samples XIIIa.1, XIIIa.2, XIIIa.3, XIIIb.1, XIIIb.2, XIIIb.3, XIIIb.4, XIIIc.1 and XIIIc.2 (Figs. 6–8). The arboreal pollen is predominant, reaching levels higher than 98%, except in sample XIIIb.1, in which the lowest percentage of AP in the sequence is reached with 49%. It is noteworthy the great internal variation of *Pinus*, from values close to 50% at the beginning of the level until falling at the end of it to values below 1%. *Pinus halepensis-pinea* fluctuates between 0.5 and 33%, while *Pinus nigra-sylvestris* varies between 0,5 and 18%. At the same time *Pinus pinaster* (2–3%) appears exclusively in the basal and middle zones of the level. In the same interval, *Quercus* follows an inverse course: from initial percentages around 25% (XIIIc.2), going through peaks over 61% (XIIIb.2) and 52% (XIIIa.3), until being placed again in values of 25% (XIIIa.1). *Quercus* evergreen ranges from 7 to 42% and *Quercus* deciduous + *suber* between 2 and 20%. We found high levels of *Castanea* (1–12%) and Genisteae (1–8%), while *Olea* reaches a maximum of 15% and *Erica* overcame 18%. The occurrence of *Juniperus*, *Fraxinus*, *Populus*, *Salix*, *Pistacia*, *Myrtus* and *Cistus* is significant, as well as the limited presence of *Alnus*, *Betula*, *Myrica*, *Corylus*, *Phillyrea*, *Rhamnus*, *Arbutus*, *Arctostaphylos*, *Viburnum* and *Calicotome*. In NAP, the existence of *Artemisia* (1–36%) and Fabaceae (1–9%) should be emphasised. Additionally, *Helianthemum/Halimium*, Amaranthaceae, Cichorioideae, Brassicaceae, Apiaceae, Urticaceae, Lamiaceae 6C and *Typha* are frequent. The abundance of *Glomus* is outstanding (SI Fig. 3). *Dictyosporites*, *Diporicellaesporites*, *Diporisporites*, *Ctenosporites*, *Hypoxylonites*, *Inapertisporites*, *Microsporonites*, *Monoporisporites* and *Multicellites* are frequent. *Riccia* appears.

8.5. Level XII

This level includes samples XII.1, XII.2 and XII.3 (Figs. 6–8). The most predominant type of pollen is arboreal, with total values higher than 95%. It is an interval characterised by high percentages of *Pinus halepensis-pinea* (4–37%) and *Pinus nigra-sylvestris* (4–26%). We found high levels of *Quercus* evergreen (13–20%). *Olea* does not exceed 5%, as well as *Quercus* deciduous + *suber* does not reach 7%, while *Castanea* overcomes 9% and *Cistus* reaches almost 10%. Accompanying AP, *Fraxinus*, *Populus*, *Salix*, *Erica*, *Ceratonia* and Genisteae are present. It is noteworthy the casual appearances of *Juniperus*, *Pistacia*, *Myrtus*, *Ligustrum*, *Jasminum*, *Rhamnus* and *Prunus*. In NAP, it should be emphasised the existence of Fabaceae (1–5%) and *Artemisia* (1–2%). Species like Dipsacaceae, *Lotus*, Poaceae, Amaranthaceae, Cichorioideae, Apiaceae, Lamiaceae and Caryophyllaceae are also common. The presence of *Diporisporites* (29–73%), *Monoporisporites* (3–59%) and *Glomus* (4–18%) stands out (SI Fig. 3). Similarly, *Hypoxylonites* and *Inapertisporites* are present. Trilete spores attain frequencies of 7%, and *Polypodium* close to 4%.

8.6. Level XI

This level includes samples XIa.1, XIa.2 and XIb (Figs. 6–8). Arboreal pollen consistently presents levels higher than 90%, with maximums above 99%. The rest is formed by pollen of non-arboreal type. The amount of *Pinus halepensis-pinea*, with a percentage that fluctuates between 16 and 27% and *Quercus* evergreen, with percentages ranging between 16 and 21%. We found high levels of *Olea* (1–17%), *Pinus nigra-sylvestris* (12–15%) and *Quercus* deciduous + *suber* (8–9%). Genisteae increases, exceeding 7%. On the other hand, *Cistus* reaches percentages above 15%. *Juniperus*, *Fraxinus*, *Populus*, *Salix*, *Castanea*, *Phillyrea*, *Ephedra fragilis*, *Erica* and *Ceratonia* are very well represented throughout the area. In NAP it worth emphasising the presence of Fabaceae, Poaceae, *Artemisia* and Amaranthaceae. Furthermore, *Helianthemum/Halimium*, Dipsacaceae, Brassicaceae, *Lotus* and Apiaceae are also present. The presence of *Glomus* (4–97%), *Monoporisporites* (1–59%) and *Diporisporites* (1–40%) is significant. *Inapertisporites*, *Scleroderma* and *Uncinulites* appear (SI Fig. 3).

8.7. Level IX

This level includes samples IX.1 and IX.2 (Figs. 6–8). The AP is predominant, reaching levels close to 97%. The most remarkable aspect is the abundance of *Quercus* evergreen (46%) and *Quercus* deciduous + *suber* (26%) in the basal sample (IX.2). This predominance disappears in the surface sample (IX.1), *Quercus* evergreen (12%) and *Quercus* deciduous + *suber* (4%). Conversely, *Pinus halepensis-pinea* (1%) and *Pinus nigra-sylvestris* (11%) continue to decrease at the beginning of the level. There is a notable improvement in the final part of the level, with percentages in *Pinus halepensis-pinea* close to 24% and in *Pinus nigra-sylvestris* greater than 35%. *Olea* ranges between 1 and 8%, while Genisteae vary between 1 and 4%. AP accompanying include *Juniperus*, *Fraxinus*, *Populus*, *Salix*, *Castanea*, *Phillyrea*, *Erica*, *Ceratonia* and *Cistus*. In NAP it is important to emphasise the presence of Poaceae and *Artemisia*. In addition, Dipsacaceae, *Lotus*, Amaranthaceae and *Ranunculus* are also frequent. It is worth highlighting the abundance of fungal spores, with percentages higher than 95% (SI Fig. 3). *Glomus* (5–94%) and *Diporisporites* (4–43%) are common. Similarly, the presence of *Inapertisporites*, *Monoporisporites* and *Trichothyrites* is significant.

8.8. Level VIII

This level includes samples VIII.1 and VIII.2 (Figs. 6–8). The most predominant type pollen is arboreal, with total values higher than 95%. In the lower sample (VIII.2) we found the highest percentages of *Quercus* of the whole sequence, *Quercus* evergreen (54%) and *Quercus* deciduous + *suber* (20%). These values decrease in the upper sample (VIII.1), *Quercus* evergreen (13%) and *Quercus* deciduous + *suber* (5%). Conversely, *Pinus halepensis-pinea* (3%) and *Pinus nigra-sylvestris* (13%) suffer a setback at the beginning of the level. Despite this, both recover at the end of the zone, *Pinus halepensis-pinea* (17%) and *Pinus nigra-sylvestris* (38%). We found low levels of *Olea* (1%) at the beginning of the phase, which recovers at the end of the zone reaching values higher than 11%. *Castanea* is stabilised in percentages of 2%. *Juniperus*, *Erica*, Genisteae, *Fraxinus*, *Salix*, *Myrtus*, *Phillyrea*, *Cistus* and *Ceratonia* are very well represented throughout the area. In NAP it is worth emphasising the presence of Amaranthaceae, Asteraceae, Cichorioideae, Urticaceae, *Helianthemum/Halimium*, *Lotus* and Apiaceae, although only in low percentages. Non-pollen microfossils are only represented by fungal palynomorphs (SI Fig. 3). The presence of *Glomus* (2–98%), *Diporisporites* (1–60%) and *Monoporisporites* (1–39%) stands out. Similarly, *Dictyosporites*, *Hypoxylonites*, *Inapertisporites* and *Microsporonites* are present. Pteridophyte spores are absent from this level.

8.9. Level VII

This level includes samples VII.1 and VII.2 (Figs. 6–8). The arboreal pollen type present levels that oscillate between 92 and 97% and the rest appears formed by non-arboreal pollen. The amount of *Pinus nigra-sylvestris* (20–46%) is noteworthy, reaching its maximum peak of the sequence in this level. *Pinus halepensis-pinea* continues recovering with percentages that fluctuate between 17 and 22%. *Quercus* deciduous + *suber* is closed to 9%, while *Quercus* evergreen ranges from 16 to 18%. *Olea* descends to 4% at the beginning of the level, and in the final part reaches almost 11%. In addition, *Castanea* does not exceed percentages of 1% and *Fraxinus* always has frequencies around 2%. As accompanying of AP appear *Alnus*, *Betula*, *Salix*, *Pistacia*, *Myrtus*, *Rhamnus*, *Sambucus nigra*, Genisteae, *Erica* and *Ceratonia*. In NAP, it is worth mentioning the presence of Amaranthaceae (1–3%) and Poaceae (1–2%). Similarly, *Artemisia*, *Plantago*, Rubiaceae, Urticaceae, *Typha*, *Ranunculus*, *Helianthemum/Halimium* and *Lotus* are representative. The presence of *Glomus* (50–94%) is remarkable, while *Inapertisporites*, *Dictyosporites*, *Diporisporites* and *Dyadosporites* are frequent. The ferns are represented by *Polypodium* (1–50%) (SI Fig. 3).

8.10. Level VI

This level includes samples VI.1, VI.2 and VI.3 (Figs. 6–8). The AP is predominant, reaching levels that vary between 84 and 94%. The most noteworthy aspect is the abundance of *Pinus nigra-sylvestris* (16–25%) and *Pinus halepensis-pinea* (14–18%) throughout the area, while *Quercus* evergreen fluctuates between 13 and 20% and *Quercus* deciduous + *suber* (8–13%) experiences a growth with respect to the previous level. *Juniperus* consistently exceeds 2% and the occurrence of *Olea* (7–11%) is significant. We found high levels of Genisteae (1–7%). AP accompanying include *Pinus pinaster*, *Betula*, *Fraxinus*, *Populus*, *Salix*, *Pistacia*, *Castanea*, *Corylus*, *Phillyrea*, *Cistus* and *Erica*. The specific presence of *Alnus*, *Ulmus*, *Ligustrum*, *Rhododendron*, *Sambucus ebulus* and *Calicotome* is also noteworthy In NAP, the existence of Poaceae (1–9%) and Urticaceae (1–4%) should be emphasised. *Artemisia*, Amaranthaceae, Cichorioideae, Brassicaceae, Caryophyllaceae, *Typha*, *Helianthemum/Halimium*, Apiaceae and *Lotus,* are also common. *Glomus* (17–69%), *Hypoxylonites* (4–15%) and *Diporisporites* (2–3%) are frequent (SI Fig. 3). *Monoporisporites*, *Microsporonites*, *Inapertisporites*, *Multicellites*, *Dicellaesporites* and *Polyadosporites* occur.

8.11. Level V

This level includes samples V.1 and V.2 (Figs. 6–8). The most predominant type of pollen is arboreal, with total values over 90%. The most noteworthy aspect is the dominance of *Quercus* evergreen (26%) and *Pinus nigra-sylvestris* (13%) in the lower sample (V.2). Although *Pinus nigra-sylvestris* decrease in comparison to previous levels, they increase in the upper sample (V.1), reaching almost 28%. *Quercus* evergreen, on the other hand, loses its dominance (11%). *Pinus halepensis-pinea*, as well as *Pinus nigra-sylvestris*, is close to minimum values at the beginning of the level, below 3% (although it manages to recover at the end of the area, exceeding 15%). *Quercus* deciduous + *suber* is preserved throughout the level at values close to 9%. On the other hand, Genisteae (9–21%) and *Salix* (2–9%) reach their highest percentages of the sequence in this level, while *Olea* does not exceed 5%. *Pinus pinaster*, *Juniperus*, *Betula*, *Fraxinus*, *Populus*, *Castanea*, *Myrtus*, *Pistacia*, *Erica* and *Ceratonia* are very well represented throughout the sequence. Of the group NAP, we highlight the presence of Poaceae, *Artemisia*, *Rumex*, *Plantago*, Urticaceae, Liliaceae, *Convolvulus*, *Helianthemum/Halimium*, Apiaceae and *Lotus*. There is a significant presence of *Glomus* (33–57%) and *Monoporisporites* (3–45%) (SI Fig. 3). *Dictyosporites*, *Diporisporites*, *Inapertisporites*, *Microsporonites*, *Reduviasporonites* and *Uncinulites* are frequent.

8.12. Level IV

This level includes samples IV.1 and IV.2 (Figs. 6–8). The arboreal pollen type represents levels close to 90% and the rest appears formed by non-arboreal pollen type. The most remarkable aspect is the abundance of *Quercus* evergreen (17%) at the beginning of the level, although this suffers a slight decline towards the end (12%). On the other hand, *Pinus halepensis-pinea* drops to 3% at the beginning of the level and recovers in the upper part of the area, exceeding 26% and experiencing a significant growth compared to the previous level. *Pinus nigra-sylvestris* and *Quercus* deciduous + *suber* are always around 10%. At this level, the highest frequencies of *Juniperus* (2–7%), *Castanea* (3–18%) and *Pistacia* (2–4%) appear throughout the sequence. *Olea* grows to reach percentages close to 8%, while *Erica* and Genisteae never fall below 2%. AP accompanying include *Pinus pinaster*, *Fraxinus*, *Populus*, *Salix*, *Myrtus*, *Corylus*, *Rhamnus*, *Cistus* t., *Viburnum*, *Sambucus ebulus* and *Sambucus nigra*. In NAP, the presence of Poaceae, *Artemisia*, Amaranthaceae and Cichorioideae stands out. Similarly, Thymelaeaceae, *Plantago*, Cannabinaceae, *Ranunculus*, *Helianthemum/Halimium*, Apiaceae and *Lotus* are representative.

In relation to non-pollen types, it is worth highlighting the abundance of fungal morphotypes (SI Fig. 3). The presence of *Monoporisporites* (3–65%), *Glomus* (16–38%) and *Diporisporites* (4–16%) is especially remarkable. Similarly, *Hypoxylonites*, *Dicellaeporisporites*, *Dictyosporites*, *Microsporonites*, *Inapertisporites* and *Uncinulites* are present.

8.13. Level III

This level includes samples III.1 and III.2 (Figs. 6–8). The arboreal pollen (AP) is predominant, reaching levels close to 90%. The most noteworthy fact is the abundance of *Quercus* evergreen, with percentages around 17–39%. *Pinus halepensis-pinea* is located at frequencies lower than 18%, while *Pinus nigra-sylvestris* declines to the beginning of the level below 5% to reach percentages higher than 20% at the end of the zone. *Quercus* deciduous + *suber* always exceeds 13% and there is a significant presence of *Olea* (10–13%). *Pinus pinaster*, *Juniperus*, *Fraxinus*, *Castanea*, Genisteae, *Erica* and *Ceratonia* appear throughout the area. In NAP, it is important to emphasise the presence of Poaceae (1–8%) and Urticaceae (1–3%). *Artemisia*, Amaranthaceae, Cichorioideae, Caryophyllaceae, *Typha* and *Lotus* are also frequent. The abundance of fungi stands out, with percentages higher than 92%. *Glomus* (43–100%) is quite frequent. In the same way, the presence of *Diporisporites*, *Hypoxylonites*, *Monoporisporites*, *Microsporonites* and *Inapertisporites* is significant (SI Fig. 3). Triletes with percentages of 2% and *Polypodium* with percentages higher than 5% are frequent.

8.14. Level II

This level includes samples II.1, II.2, II.3, II.4, II.5 and II.6 (Figs. 6–8). The level is dominated by AP, with values that oscillate between 60 and 94%. It is worth highlighting the great internal variation of *Pinus*, from values close to 8% at the beginning of the level and an increment towards the end, reaching values above 59%. *Pinus halepensis-pinea* fluctuates between 2 and 13%, while *Pinus nigra-sylvestris* range between 6 and 44%. On the other hand, *Pinus pinaster* (1–2%), only appears in the middle and upper levels. In the same interval, *Quercus* decreases at the beginning of the level (II.5 and II.6), recovers in the middle section of the zone (II.2, II.3 and II.4) and ends up decreasing again in the final part until reaching its lowest values of the whole sequence (II.1). *Quercus* evergreen ranges between 4 and 25% and *Quercus* deciduous + *suber* does it between 2 and 15%. On the other hand, *Olea* (2–11%) follows a pattern similar to *Quercus*, with the minimum values in the lower and upper part, and the maximum values in the middle part of the level. We found high levels of *Castanea* (1–11%), while *Erica* reaches a maximum of 44% at the beginning of the level and *Juniperus* exceeded 2%. *Pinus pinaster*, *Betula*, *Fraxinus*, *Pistacia*, *Myrtus*, *Ulmus*, *Corylus*, *Phillyrea*, *Ligustrum*, *Arbutus*, *Buxus*, *Cistus*, Genisteae and *Ceratonia* are very well represented throughout the level. In NAP, it is worth noting the presence of *Artemisia* (1–18%), Poaceae (1–9%), Amaranthaceae (1–7%) and Urticaceae (1–2%). Fabaceae, Cichorioideae, *Plantago*, Boraginaceae, Cannabinaceae, Lamiaceae, *Lotus* and Apiaceae are also representative. The non-pollen microfossils are represented by a large number of fungal palynomorphs that together reach levels above 95% (SI Fig. 3). *Glomus* (18–86%), *Diporisporites* (1–15%), *Monoporisporites* (1–7%) and *Pluricellaesporites* (1–5%) are frequent. In a similar way, the presence of *Dictyosporites*, *Diporicellaesporites*, *Dyadosporites*, *Hypoxylonites*, *Inapertisporites*, *Microsporonites*, *Scleroderma* and *Uncinulites* is significant. The pteridophytes appear very well represented throughout the sequence. Triletes (1–3%), *Polypodium* (1–2%) and Monoletes (1–2%) particularly stand out.

8.15. Level I

This level includes samples Ia and Ib (Figs. 6–8). The AP represents levels that oscillate between 82 and 87% and the rest appears formed by non-arboreal pollen type (NAP). The most noteworthy aspect is the abundance of *Quercus* evergreen (28%) at the beginning of the level, although this suffers a decrease towards the end (8%). On the other hand, *Pinus nigra-sylvestris* drops to 18% at the beginning of the level and manages to recover at the top, exceeding 41% and obtaining values similar to those found in the final part of the previous level. *Pinus halepensis-pinea* ranges between 5 and 10% and *Quercus* deciduous + *suber* fluctuates between 9 and 13%. *Olea* exceeds 11% at the beginning of the level and decreases in the final part until reaching values lower than 3%. AP accompanying include *Pinus pinaster*, *Betula*, *Fraxinus*, *Pistacia*, *Myrtus*, *Castanea*, *Phillyrea*, *Cistus*, *Erica* and *Ceratonia*. In NAP, the presence of Amaranthaceae (2–6%), Cichorioideae (1–6%) and Poaceae (1–3%) is noteworthy. Similarly, Fabaceae, Brassicaceae, Urticaceae, *Hypericum*, *Ranunculus*, *Lotus* and Apiaceae are representative. The presence of *Glomus* (15–57%), *Dictyosporites* (9–14%), *Hypoxylonites* (3–9%), *Inapertisporites* (4–8%), *Scleroderma* (3–8%), *Monoporisporites* (3–6%), *Microsporonites* (4–5%) and *Multicellites* (4–5%) is remarkable (SI Fig. 3). Similarly, *Diporicellaesporites*, *Diporisporites*, *Dyadosporites*, *Pluricellaesporites* and *Uncinulites* are present.

9. Vegetation history and palaeobotanical remarks

In the Bolomor vegetation sequence, mixed oak-pine forests, strongly inertial throughout the long study period, are a representative feature. Given the well-known under-representation of oak pollen compared to pine, it is likely to find the dominance of one or several species of *Quercus* in the surrounding vegetation. This was once a mixed forest with a high diversity of woody plants, including abundant levels of *Castanea*, *Olea* and *Juniperus*, which were continuously accompanied by broad-leaf trees such as *Alnus*, *Betula*, *Celtis*, *Corylus*, *Fraxinus*, *Populus*, *Salix*, and *Ulmus*, as well as Mediterranean elements such as *Pistacia, Myrtus*, *Arbutus*, *Calicotome*, *Cistus*, *Ephedra fragilis*, *Ligustrum*, *Myrica*, *Rhamnus* and *Viburnum* (Figs. 6 and 8). Interestingly, the xero-heliophytic component with *Artemisia*, Amaranthaceae, *Erica* and Poaceae appears, overall, relatively unimportant with the exception of the samples II.2, II.5, XII.2, XIIIa.1, XIIIa.2, XIIIb.1 and XIV, where there is an increment of xerophytes to the detriment of mainly *Pinus* (Fig. 7). These events were linked to a certain opening of the landscape, probably associated with cold spells. However, it is worth emphasising that the ecosystem structure prevailed and both the forest density and the thermophytic component (e.g. *Olea*, *Pistacia*, *Myrica, Myrtus*, *Fraxinus*, *Populus*, *Salix, Castanea*) were preserved with minor variations. High-diversity forest ecosystems are extremely resilient (Thompson et al., 2009) and this might be the case with Bolomor. It is perhaps worth adding that climatic changes are not the only factor able to modify the vegetation cover to the extent observed in those xerophytic maxima. High densities of wild ungulates may have hampered the regeneration of woody vegetation (Perea et al., 2014). It is also worth noting that the rupicolus vegetation is probably not very accessible for some herbivores species, unlike that located in half-slope or flat areas.

Oaks are fairly common in the Iberian mid-Pleistocene and they are found conspicuously in Bañolas and Olot (Cataluña), Torralba (Soria), Villaverde (Madrid) and Padul (Granada) (Camuera et al., 2019; Cros et al., 1986; Elhaï, 1966; Florschütz et al., 1971; Menéndez-Amor and Florschütz, 1959; Pons and Reille, 1986, 1988). However, their high occurrences during stadials are an exclusive feature of the Bolomor records. Another issue is concerning those species involved. Nowadays, the only species that grows in the surroundings is a shrubby form of *Quercus coccifera*. *Q. ilex* is restricted to humid intra-mountainous biotopes despite being recurring in the region, generally at higher altitudes and only rarely within the thermomediterranean belt (Blanco-Castro et al., 1997). *Q. ilex* must have been present during the Pleistocene in the Eastern mountains of Spain if due account is taken of anthracoanalysis, although not widespread during the glacial stages (Badal et al., 2012). As for the deciduous oak species, the most common in Bolomor is *Q. faginea* due to the prevailing limestone substrates, while *Q. pyrenaica* could have developed in acidic soils. The cork oak, *Q. suber,* was also present in Pleistocene Bolomor, but not anymore. Overall, this species is nowadays more frequent in Western Iberia. Within the Valencian region, only two relictic populations have been cited, one in Sierra de Espadán (Castellón) and another in Sierra Calderona (Valencia) (Costa, 1982). Carrión and van Geel (1999) found cork oak pollen in the nearby sequence of Navarrés during the late Pleistocene and, based on a revision of the palaeobotanical findings and historical sources, these authors hypothesised that the species must have been more abundant in Eastern Spain from the Pleistocene up to mid Holocene, and perhaps lingering until some centuries ago (Carrión et al., 2000a).

Pollen analysis is not well suited to identify the specific composition of the pine woodlands. However, the anthracological data from Bolomor shows *Pinus nigra-sylvestris* in hearths within the levels XIII and XI (MIS 7- MIS 6: ca. 230-160 ka) (Vidal-Matutano et al., 2017). Nowadays, the main sub-Mediterranean forests of *Pinus nigra* are found in the continental valleys of the Eastern and Central Pyrenees, canyons and karstic valleys of the Iberian System (the Serrania de Cuenca and Alto Tajo, the Sierra de Gúdar and Javalambre) and Sierras de Segura and Cazorla (Blanco-Castro et al., 1997). Given the calcareous nature of the region, *Pinus nigra* is the most abundant species, and it also has a superior eco-climatic amplitude than *Pinus sylvestris*, making this species perfectly adaptable to cold and continental sub-Mediterranean environments, as well as withstanding better the summer drought. Further to the North, in the Tubilla del Agua site (Ebro Basin, Burgos) there are *Pinus nigra* macro remains at different stages of the Middle Pleistocene (García-Amorena et al., 2011).

Although the sites studied for the Middle Pleistocene of Iberia are scarce, pollen evidence is sufficient to confirm *Pinus* as the main tree component of the forests (Cros et al., 1986; Elhaï, 1966; Florschütz et al., 1971; Menéndez-Amor and Florschütz, 1959; Pons and Reille, 1988). Nowadays, the pine forests in the surroundings of the Bolomor site are only formed by *Pinus halepensis*, which is indeed the most extended species in Mediterranean Spain, growing from semi-arid to sub-humid biotopes in the eastern territories, and being well-adapted to summer drought, with annual precipitation tolerances down to 150 mm.

The Bolomor cluster pine, *Pinus pinaster*, is also worth mentioning, although due to its low frequences it could be the result of a medium to long pollen transport, and therefore not necessarily present locally. The palaeoecological significance of this species has been discussed in detail by Carrión et al. (2000b). *Pinus pinaster* woodlands show a Western Mediterranean and Atlantic range, and exhibit a great ecological plasticity, living across different ombrotypes, tolerating both inland winter cold and temperate climates in the vicinity of the coasts. Regionally, cluster pine forests on red sandstones are characteristic of the Iberian system, where they are very widespread on Levantine coastal mountains such as Espadán and Calderona. *Pinus pinaster* is often a component of mixed conifer-angiosperm forests in the Iberian Pleistocene (Carrión and van Geel, 1999; Carrión et al., 2013). Lastly, due to the proximity to the coastal shelves, especially during interglacials and interstadials (Fernández-Peris, 2003; Fernández-Peris and Villaverde, 2001; Fernández-Peris et al., 1994, 1997; 1999; Guillem, 1995; Martínez-Valle, 1995) the existence of *Pinus pinea* in the Middle and Upper Pleistocene of Bolomor seems plausible. During the cold stages of the upper Pleistocene, there are macrobotanical evidences of this pine species in Málaga (Badal et al., 2012) and Gibraltar (Carrión et al., 2008).

It is worth highlighting the presence of *Ceratonia* pollen given the debate on the origin of the modern populations in the Iberian Peninsula (Ruiz de la Torre, 2006). Since *Ceratonia siliqua* often grows in the vicinity of regional caves, a local over-representation in some samples was expected, and therefore its frequency is here presented out of the total pollen sum (Fig. 6). Taking into account that we did not acetolysed the sediment samples of Bolomor and no palynological features of modern or reworked pollen were observed under the microscope, the fossil nature of *Ceratonia* pollen is quite secure, involving its occurrence at least since the MIS 9. The carob tree has been intensively cultivated since ancient times (Battle and Tous, 1997; Zohary, 1973), which often makes difficult to find out whether its origin is autochtonous or allochthonous (Ortiz, 1999; Ramón-Laca and Mabberley, 2004). The current distribution of *Ceratonia siliqua* is restricted to the Iberian Peninsula and western areas of North Africa, both in inhabited areas and in landscapes with low anthropic impact. The carob tree takes a role in thermophilous communities along with woody species like *Chamaerops humilis, Myrtus communis, Olea europaea, Osyris lanceolata, Periploca laevigata, Phillyrea latifolia, Pistacia lentiscus, Quercus coccifera, Rhamnus lycioides* and *Tetraclinis articulata*. In valleys of the South and East of the Iberian Peninsula, the species is considered natural, and some examples are visible in cliffs and rocky outcrops of the Levantine coast (Mascarat and Granadella, both in the Province of Alicante), the Guadalquivir Basin (Hornachuelos Natural Park), and the Sierra de Grazalema, Cádiz (Postigo-Mijarra et al., 2010). The first fossil records of *Ceratonia* in the Iberian Peninsula are from the Middle Miocene, more specifically from the Langhian. Since then, its record is uneven until the Lower Pleistocene (García-Antón, 1992; González-Sampériz et al., 2004; Jiménez-Moreno and Suc, 2007). The pollen sequence from Gran Dolina (Atapuerca) confirms the presence at the TD-6 level of *Ceratonia* pollen, accompanied by other Mediterranean elements such as *Celtis, Olea, Pistacia* and *Phillyrea* (García-Antón, 1989, 1992). In the present study, it is important to highlight the persistence of *Ceratonia* in climatic phases with such severe temperatures, an issue formerly discussed by González-Sampériz et al. (2004). This tolerance to cold could have been key for its survival during the Pleistocene stadials. In any case, its presence in the Southwestern European sequences is very limited, possibly due to the low dispersion of its pollen (Jahns, 2003).

The presence of *Castanea* in Western Europe is well documented during the Pliocene and Early Pleistocene (Huntley and Birks, 1983). However, despite of this evidence, *Ceratonia siliqua* and *Juglans regia*, *Castanea sativa* have not yet been definitively incorporated into the list of native species of the Iberian Peninsula (Galán et al., 1998; Ortiz, 1999; Ruiz de la Torre, 2006). Currently, the healthier *Castanea* populations occupy the contact areas between the Pyrenees and the Cantabrian mountain ranges in Navarra and the Eastern Pyrenees. In our study (Fig. 6), *Castanea* appears almost uninterruptedly along the sequence, which given its usual underrepresentation in the pollen spectra (Huntley and Birks, 1983) suggests a local abundance during the Middle Pleistocene. Since the last century, the native character of sweet chestnut (*Castanea sativa*) has been proposed for the Iberian Peninsula (García-Antón, 1989; García-Antón et al., 1990; Morla-Juaristi, 1996), and the paleobotanical data have been supporting more recently this hypothesis (Carrión et al., 2003; Gómez-Orellana et al., 2007; Muñoz-Sobrino et al., 2004; Postigo-Mijarra et al., 2008, 2010). Molecular studies carried out in populations of the Mediterranean region suggest the recent propagation by humans of the species (Conedera et al., 2004), but certainly, too, the existence during the Quaternary of a significant refuge in the Mediterranean and especially the north of the Iberian Peninsula (García-Antón et al., 1990; Morla-Juaristi, 1996; Postigo-Mijarra et al., 2008, 2010).

The frequencies of *Olea* throughout the Bolomor pollen sequence oscillate between 2 and 18%, which supports the sheltering character of the site, especially if we consider that the olive trees appear together with other sclerophylls like *Pistacia, Myrtus, Phillyrea, Ligustrum, Jasminum, Viburnum, Arbutus, Sambucus, Calicotome, Ceratonia, Ephedra fragilis* and *Cistus*. In this context, the occurrences of *Alnus, Betula, Corylus, Fraxinus, Populus, Salix, Castanea, Ulmus, Celtis, Buxus,* and *Rhododendron*, gather to depict a mesothermal, Mediterranean subhumid, and highly diverse, Bolomor forest. At the Terra Amata (Nice) and the Vallonnet Cave in Cap Martin (Alpes-Maritimes) in the Southeast of France, *Olea* appears as one of the main elements of the Mediterranean forest (Renault-Miskovsky, 1976; Renault-Miskovsky and Girard, 1978). The presence of *Olea* in the Galeria section of Atapuerca can be taken as an indicator of mediterraneity (García-Antón, 1989; García-Antón et al., 1990).

The pollen data presented in this work shows continuous incidences of *Juniperus* as habitual companion of the *Pinus-Quercus* forest. The anthracological study (Vidal-Matutano et al., 2017) confirms the presence of *Juniperus* through the finding of macrocharcoal in the hearths from Level XIII.

The presence of *Rhododendron* is remarkable, although it only appears sporadically in Bolomor and it is generally absent in the fossil record because of its poor pollen dispersion (Gutiérrez, 2008). Nevertheless, it is unknown whether the species involved was *R. ponticum* (today in the Campo de Gibraltar and Sierra del Aljibe, south of Spain), or *R. ferrugineum* (today in the Pyrenees and other mountains of the Eurosiberian region). The genus *Rhododendron* is widely distributed, although its highest diversity takes place in the Southeastern Himalayas. Several of the species also inhabit North America and Europe, the Western Caucasus, Eastern Balkans and Southern Iberia. Several studies show that *Rhododendron ponticum* was widespread in Europe during the Tertiary and Pleistocene (Jessen et al., 1959; Meusel et al., 1978; Mitchell and Watts, 1970), while the origin of present-day populations is still discussed (Erfmeier and Bruelheide, 2004). Using restriction fragment length polymorphisms of chloroplast DNA, Milne and Abbott (2000) confirmed the existence of an origin centre for this species located in the Iberian Peninsula. Their findings support a more extensive past distribution in Western Europe.

The biogeography of *Celtis* has previously been discussed (Ruiz de la Torre, 2006). The appearance of *Celtis* seeds in the Plio-Pleistocene of Eurasia is frequent due to its good conservation through biomineralization processes (Cowan et al., 1997; Green, 1979; Jahren et al., 1998; Matsutani, 1987; Messager et al., 2008; Shillito and Almond, 2010; Simchoni and Kislev, 2011). Several sites of the Lower and Middle Pleistocene stand out, such as Dmanisi, Georgia (Messager et al., 2010), Zhoukoundian, China (Chaney, 1935), Vallonet, France (De Lumley, 1976), Achalkalakai, Georgia (Ljubin and Bosski, 1996), Kärlich, Germany (Bittmann, 1992), L'Arago, Lazaret and Terra Amata (De Lumley, 1976; De Lumley and De Lumley, 1971; De Lumley et al., 1976). Approximately 60 different species of *Celtis* are distributed throughout South America, Africa, Asia and Europe (Demir et al., 2002; Simchoni and Kislev, 2011). *Celtis australis* is the only species that grows in the Iberian Peninsula (Blanco-Castro et al., 1997).

10. Palaeoenvironments of Bolomor

Thereafter are presentend the inferences about the palaeoenvironments of Bolomor based on palaeobotanical, palaeontological and sedimentological characteristics of the archaeological levels (Blasco and Fernández-Peris, 2009, 2012b; Blasco et al., 2013a, 2013b; Fernández-Peris, 2003; Fernández-Peris et al., 1999; Rosell et al., 2015; Vidal-Matutano et al., 2017) (Fig. 9 and Fig. 10; SI Table 4).

10.1. Bolomor phase I (levels XVII-XV; MIS 9-8) (Figs. 9 and 10; SI Table 4)

The beginning of this sequence at level XVII is characterised by the dominance of a pine forest and the presence of *C. elaphus* (Blasco and Fernández-Peris, 2012b; Blasco et al., 2013a, 2013b). Mesothermophytes such as *Quercus* deciduous, *Alnus, Betula, Fraxinus, Populus, Salix* and *Castanea*, as well as Mediterranean elements (*Olea, Myrica, Pistacia, Myrtus, Phyllirea*) indicate humid, not very cold climate, which is supported by faunal remains of *Megaloceros giganteus,* and *Talpa europaea* (Blasco and Fernández-Peris, 2012b; Blasco et al., 2013a, 2013b). MD01-2443 marine pollen sequence (SW Iberia) for MIS 9e suggests a brief forest expansion consisting mainly of pine and juniper to give way to a forest dominated by deciduous oaks (Roucoux et al., 2006; Tzedakis et al., 2004). It seems, however, that the climate in the Southwest was drier and colder than in the peninsular East, since the entrance of sub-polar water masses by the Atlantic Ocean undermined forest developments in favour of Ericaceae during the substages 9c and 9a (Roucoux et al., 2006; Tzedakis et al., 2004). Desprat et al. (2006) suggest that this sudden climatic deterioration detected in the Southwest is not appreciated in the Northwest. In the continental sequence of Praclaux (Massif Central, France) a long warm period is recorded during this stage with some eventual reduction of forests (Tzedakis et al., 2004).

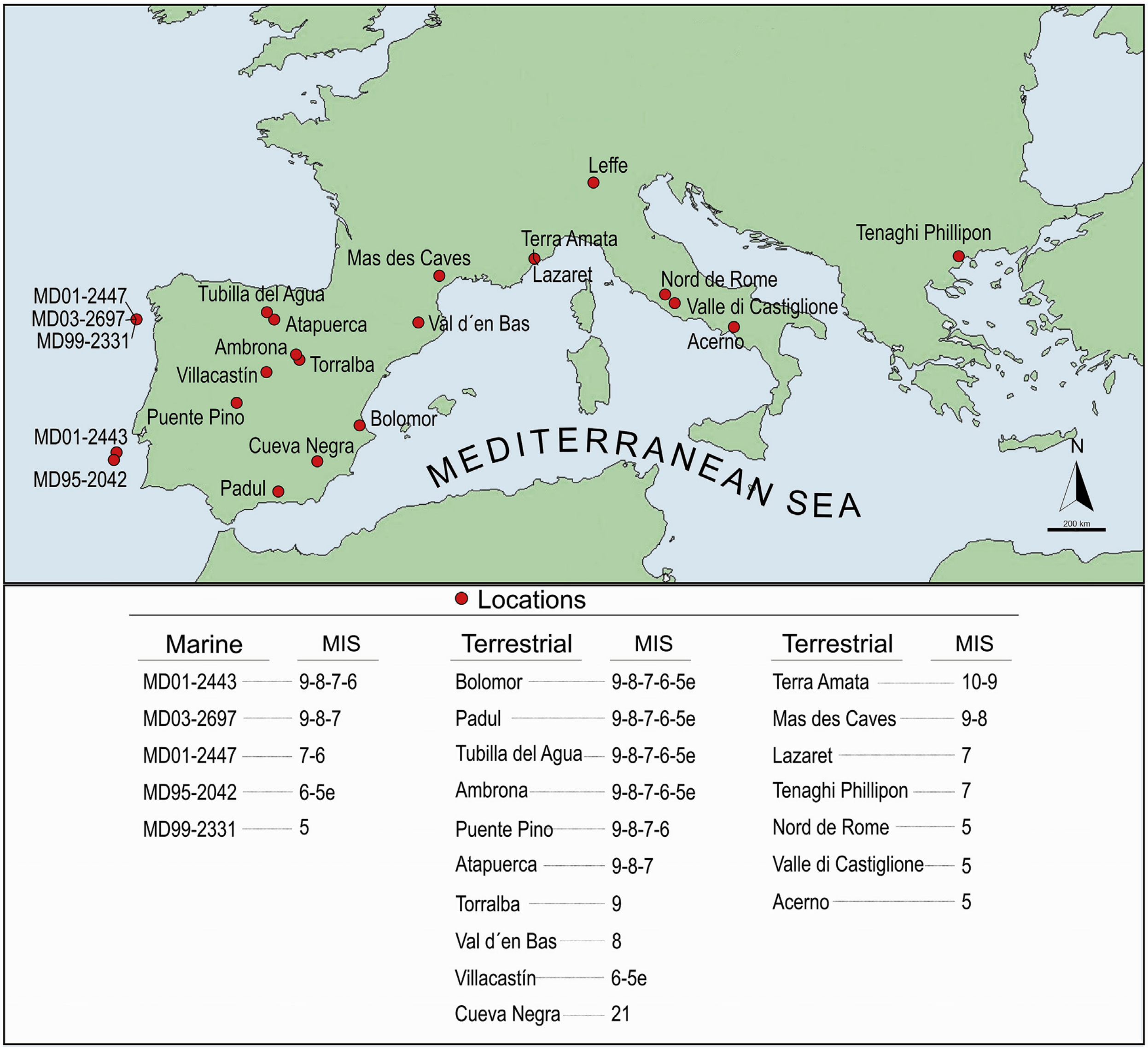
In level XV the forest becomes codominated by *Pinus* and *Quercus*, with *Pinus* still the main arboreal component. However, the increase in *Erica* and *Juniperus* suggests a certain replacement of the pine forest and a slight opening of the landscape, which could benefit the establishment of species such as *E. ferus* and *A. bursae*, both adapted to open vegetational spaces, and in the case of *Allocricetus*, to dry environments (Guillem, 2001; Blasco and Fernández-Peris, 2012b; Blasco et al., 2013a, 2013b). In any case, mesothermophilous taxa (*Alnus, Betula, Corylus, Fraxinus, Populus, Salix, Castanea, Ulmus, Celtis*) are still abundant, and so the permanence of flooded areas or small rivers in the environment of the deposit is present during phase I, enhancing the presence of *M. giganteus* and *T. europaea* (Guillem, 2001; Blasco and Fernández-Peris, 2012b). During the onset of MIS 8, the MD01-2443 record shows a high volume of ice (McManus et al., 1999). Similarly, the planktonic record shows low temperatures in the first part of this phase, with warmer conditions in the second half (Shackleton, 2000). The terrestrial sequences show open landscapes with small forests at the beginning of MIS 8 and the expansion of these in the second part. This development of the forests appears in all the studied sequences, characterised in MD01-2443 by *Quercus* deciduous, in Lac du Bouchet by *Pinus* (Reille et al., 2000), in Valle di Castiglione by *Betula, Quercus, Corylus* and *Pinus* (Follieri et al., 1988) and in Tenaghi Philippon by *Quercus* and *Pinus* (Wijmstra and Smit, 1976). Whereas in places further North (such as France), only an expansion of *Pinus* can be seen, it is possible that in more southerly areas like Bolomor, warm and humid conditions allowed an expansion of temperate trees (Roucoux et al., 2006).

10.2. Bolomor phase II (levels XIV and XIII; MIS 7) (Figs. 9 and 10; SI Table 4)

The beginning of Phase II (level XIV) shows a gradual but marked change in climatic conditions (Fernández-Peris, 2003), while there is an opening of the pine forest and a predominance of evergreen *Quercus* among the trees, with the expansion of *Erica* and *Artemisia* and the predominance of *E. ferus* among mammals, even when it declines in favour to previous levels (Blasco and Fernández-Peris, 2009, 2012b; Blasco et al., 2013a, 2013b). From level XIV, a dating by TL of 233 ± 35 ka was calculated (Fernández-Peris, 2007). Level XIII is fluctuating in vegetation with a tendency to reduce the *Pinus* forest and an increase in evergreen and deciduous *Quercus*. The presence of *Pinus nigra-sylvestris* charcoal in level XIII reinforces the importance of this taxon in Bolomor during MIS 7 (Vidal-Matutano et al., 2017). The phases dominated by *Quercus* alternate with others in which *Artemisia* and *Erica* rise, and with wet periods with *Fraxinus, Castanea, Salix, Populus, Alnus, Betula* and *Corylus*. At the base of level XIII two dates, one with AAR of 228 ± 53 ka, and another with TL of 225 ± 34 ka, are provided (Fernández-Peris, 2007). The sequence MD01-2443, in the Southwest of the Iberian Peninsula, also shows these changes in the landscape (Roucoux et al., 2006). The fauna indicates more humid and warm environments, with an increase of cervids (*Dama* sp., *Cervus*) and bovids (*H. bonali*) (Blasco et al., 2013a, 2013b). The sequences MD01-2447, MD03-2697 and MD99-2331 in the Northwest of Iberia, show parallels in the paleoclimatic inference (Desprat et al., 2006).

10.3. Bolomor phase III (levels XII, XI, X, IX, VIII and VII; MIS 6) (Figs. 9 and 10; SI Table 4)

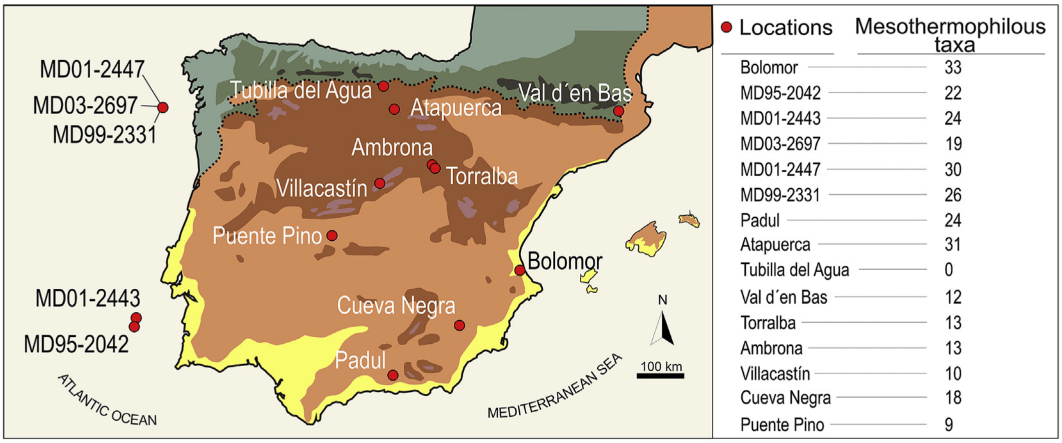
The vegetation is dominated by a mixed forest of *Pinus-Quercus*, in which there seem to be episodic competitive displacements. *Pinus nigra-sylvestris* is present in the anthracoflora (Vidal-Matutano et al., 2017). There is a certain regression of mesothermophilic taxa, but *Fraxinus, Populus, Salix* and *Castanea* survived. The fauna indicates drier and more rigorous climates, with disappearance of *M. giganteus* and abundance of *E. ferus* and *A. bursae* (level IX-VIII) (Guillem, 2001; Blasco et al., 2013a, 2013b). The presence in level XII of *B. primigenius, M. sylvanus* and *T. hermanni* suggests less rigorous conditions (Blasco and Fernández-Peris, 2009; Blasco et al., 2010). For MIS 6, marine and terrestrial sequences from southern Europe show cold and dry conditions, especially at the beginning of the period as a consequence of the entrance of polar water masses (Carrión et al., 2013; Follieri et al., 1988; Reille et al., 2000; Roucoux et al., 2006;



● Locations

Marine	MIS	Terrestrial	MIS	Terrestrial	MIS
MD01-2443	9-8-7-6	Bolomor	9-8-7-6-5e	Terra Amata	10-9
MD03-2697	9-8-7	Padul	9-8-7-6-5e	Mas des Caves	9-8
MD01-2447	7-6	Tubilla del Agua	9-8-7-6-5e	Lazaret	7
MD95-2042	6-5e	Ambrona	9-8-7-6-5e	Tenaghi Phillipon	7
MD99-2331	5	Puente Pino	9-8-7-6	Nord de Rome	5
		Atapuerca	9-8-7	Valle di Castiglione	5
		Torralba	9	Acerno	5
		Val d´en Bas	8		
		Villacastín	6-5e		
		Cueva Negra	21		

Fig. 9. Refugial pollen sites in western Europe during MIS 9 to MIS 5e.



● Locations	Mesothermophilous taxa
Bolomor	33
MD95-2042	22
MD01-2443	24
MD03-2697	19
MD01-2447	30
MD99-2331	26
Padul	24
Atapuerca	31
Tubilla del Agua	0
Val d´en Bas	12
Torralba	13
Ambrona	13
Villacastín	10
Cueva Negra	18
Puente Pino	9

Fig. 10. Refugial pollen sites in the Iberian Peninsula during MIS 9 to MIS 5e.

Sánchez-Goñi et al., 1999; Wijmstra and Smit, 1976), although these conditions were more variable in the peninsular East due to their proximity to the Mediterranean Sea (Schulte et al., 2008). In spite of the aforementioned fluctuations, the permanence of Mediterranean forest-scrub indicators (*Olea, Pistacia, Myrtus, Phillyrea, Ligustrum, Rhamnus, Calicotome, Genisteae, Ephedra fragilis, Cistus, Prunus*) is confirmed.

10.4. Bolomor phase IV (levels VI, V, IV, III, II and I; MIS 5e) (Figs. 9 and 10; SI Table 4)

There is a clear climatic improvement in this forest phase with respect to the former, adding a notable increase in meso-thermophilous flora (*Alnus, Betula, Corylus, Fraxinus, Populus, Salix, Castanea, Ulmus and Celtis, Olea, Pistacia, Myrtus, Arbutus, Viburnum, Sambucus ebolus, Sambucus nigra, Buxus, Phillyrea, Ligustrum, Rhamnus, Calicotome,* Genisteae, *Cistus*). The fauna is characterised by taxa with humid temperate affinities such as *H. amphibious*, *S. scrofa*, *B. primigenius* and *E. hydruntinus* (Blasco and Fernández-Peris, 2009, 2012b; Blasco et al., 2013a, 2013b). The abundance of *C. elaphus* is consistent with the silvicolous character of this phase. From the upper part of level II a TL dating of 121 ± 18 ka was obtained (Fernández-Peris, 2007). Marine pollen sequences establish a warming at the beginning of MIS 5e and the tendency towards an increase in rainfall, accompanied by a slight cooling (Sánchez-Goñi et al., 1999). In the East of the peninsula, climatic conditions were probably milder (Schulte et al., 2008).

11. Glacial refugia of the Middle Pleistocene

There are certain correspondences of Bolomor with other sites relevant in the discussion about glacial refugia of temperate trees during the Middle Pleistocene in the Mediterranean basin (Figs. 9 and 10, SI Table 5). In Mas des Caves, Hérault, SE France, dated c. 300 ka BP, the mid-Pleistocene vegetation consists mainly of pines, accompanied by temperate and Mediterranean elements (Leroi-Gourhan and Renault-Miskovsky, 1977), in correlation with levels XVII and XV of Bolomor. The site of Terra Amata (De Lumley et al., 1976; Renault-Miskovsky, 1976), dated around 380 ka BP, has certain similarities with level XVII of Bolomor. In addition to coprolites (de Beaulieu, 1967), a palynological analysis was carried out (Renault-Miskovsky, 1976) and there are high percentages (40–90%) of arboreal taxa including *Picea, Abies, Pinus sylvestris, Betula, Alnus, Salix, Pinus halepensis, Pinus pinaster, Quercus ilex, Olea, Phillyrea, Pistacia, Rhamnus* and Cupressaceae, as well as broad-leaf trees (*Quercus, Tilia, Acer, Fraxinus, Castanea, Ulmus*). In Lazaret Cave, dated approximately between 186 and 127 ka BP (MIS 6), de Beaulieu (1969) studied pollen samples of sediments and coprolites, finding high percentages of *Pinus sylvestris* type. The presence of *Phillyrea* and *Buxus sempervirens* charcoal (Vernet, 1969) suggests the existence of a microrefugium in the coastal area of Nice. Subsequently, Guyomarch (1979) observes, as in Bolomor for MIS 6, that the site acted as a refuge for the meso-thermophilic component. The importance of pines and firs in Middle Pleistocene forests is confirmed here also through anthracology (Vernet, 1975).

The survival of Tertiary relics during the Middle Pleistocene is a defining feature of the Italic peninsula (Di Rita and Sottili, 2019; Di Rita et al., 2013, 2015; Follieri, 1964; Follieri et al., 1988; Lona, 1950; Lona and Follieri, 1957; Magri and Parra, 2002; Magri et al., 2006, 2010; Martinetto, 2001, 2015; Russo-Ermolli et al., 2010, 2015; Sadori et al., 2010, 2016) (Fig. 9). At the site of Leffe (Bergamo) and in the vicinity of Rome (Riano Romano, Via Flaminia, Capena and Torre in Pietra), the end of the Middle Pleistocene is characterised by a rapid transition of steppe landscapes inherited from MIS 6, by forest formations dominated by *Quercus*, *Corylus*, Oleaceae, Ericaceae, *Carpinus, Zelkova, Ulmus* and in the warmer phases by *Quercus ilex* (Follieri et al., 1986). These data coincide with the dynamics of MIS 5 in Bolomor (Fig. 6; SI Table 4). In the south of Italy, the site of Acerno (Follieri, 1962) shows a mixed forest of *Quercus, Ulmus, Fraxinus, Corylus, Betula, Carpinus* and *Abies*.

The Tenaghi Philippon sequence has provided one of the most complete climatic and vegetation records of the European Quaternary (Tzedakis et al., 2003; van der Hammen et al., 1971; Wijmstra and Smit, 1976), together with Padul, in Spain (Camuera et al., 2019). In MIS 7, the forests of *Quercus* alternate with mixed forests of *Pinus* and *Quercus*. These forest phases are interspersed with episodes of *Artemisia* and Amaranthaceae. The results obtained for the same period at Bolomor (levels XIV and XIII, MIS 7) show similar alternating phenomena. Similarly, the permanence of Mediterranean elements in Tenaghi Philippon, such as *Pistacia, Nerium, Cistus* and *Myrtus*, is also observed throughout the MIS 7 of Bolomor, with the continued presence of *Olea, Myrica, Pistacia, Myrtus, Rhamnus* and *Calicotome*.

The sequences studied in the Iberian Peninsula for the Middle Pleistocene (Fig. 10) are scarce and generally discontinuous (García-Antón, 1989). In Val d'en Bas (Olot, Gerona) several samples from the volcanic zone were studied (Cros et al., 1986), where the oldest ones were dated at approximately 250 ka BP. As in Bolomor, the pine is abundant and, in Olot is accompanied by *Abies* and *Betula*. Evergreen *Quercus, Carpinus, Corylus, Juglans, Tilia* and *Corylus*, are present. In the central Peninsula, the paleontological site of Torralba (Soria), has provided along with the site of Villaverde (Madrid), the first results on Middle Pleistocene vegetation of the Iberian Peninsula (Menéndez-Amor and Florschütz, 1959). The curve of paleotemperatures places the most recent levels of the Torralba deposit in MIS 9, although the fauna seems to indicate more recent dates (Menéndez-Amor and Florschütz, 1959). The arboreal taxa vary between 30 and 50%, with pine being the main element. In addition, it should be noted the minor appearances of genera such as *Betula, Salix, Picea, Fagus, Alnus, Quercus, Corylus, Juglans, Castanea* and *Taxodium*. Here we find parallels with Bolomor level XVII, where *Pinus* is the main taxon, with percentages ranging between 40 and 64%, along with the presences of *Quercus, Alnus, Betula, Salix* and *Castanea*. Another site in the central Peninsula is Ambrona (Soria), which covers a similar period of Bolomor during the Middle Pleistocene (Ruiz-Zapata et al., 2005; Stika, 1999, 2005). *Pinus* is the main component and, to a lesser extent, mesophilous taxa (*Corylus*, *Castanea*, *Juglans*), as well as riparian trees (*Alnus*, *Salix*, *Ulmus)*. The palynology of hyaena coprolites from Villacastín in Segovia (Carrión et al., 2007) shows some coincidences with the MIS 6-5e phase at Bolomor, but there is less forest cover, and rather a mosaic vegetation with grasslands and woodlands in patchy pattern. At the Acheulean site of Puente Pino in Toledo (Ruiz-Zapata et al., 2009), there is a pollen record with three sequences, one of which (SPe-I) was associated with the PNA archaeological level and dated to the second half of the Pleistocene Medium (350-150 ka), confirming a clear predominance of the arboreal landscape, formed mainly by *Pinus*, *Quercus* and Oleaceae, accompanied by deciduous trees such as *Alnus, Fraxinus, Salix* and *Ulmus*. At the "Galería" site in Atapuerca, the palynology of the levels corresponding to the isotopic stages 7, 8 and 9 was studied (Burjachs, 2001; García-Antón, 1989; García-Antón and Sainz-Ollero, 1991). The values of the arboreal elements usually have percentages close to 50%. Here the landscape ranges from phases with predominance of temperate taxa (*Quercus, Picea, Fagus, Fraxinus, Betula, Castanea, Salix, Populus, Ulmus*) to phases with mixed forests in which *Pinus* and the Mediterranean elements (*Olea, Pistacia, Myrtus, Rhamnus, Ceratonia, Phillyrea*) reach a greater importance. Although it is difficult to establish correlations between Atapuerca and Bolomor, in both cases there is little variation in the floristic structure of the Middle Pleistocene during MIS 7, 8 and 9. However, the more forested landscape of Bolomor is noteworthy.

12. The silvicolous Neanderthals of Bolomor

There are very few paleobotanical studies in hominid sites of the Middle Pleistocene of the Iberian Peninsula and this affects sites with remains of Neanderthals (Carrión et al., 2013, 2015; García-Antón, 1989) (Figs. 9 and 10). With the presence of Neanderthals or Heidelbergs, in addition to Bolomor, Atapuerca (Burjachs, 2001; Cattani et al., 1994; García-Antón, 1989; García-Antón and Sainz-Ollero, 1991), Cova Negra (Richard et al., 2019), Cueva Negra (Carrión et al., 2003, 2005; Yll and Carrión, 2003) and Sima de las Palomas (Carrión et al., 2003, 2005; Yll and Carrión, 2003) must be mentioned. In the case of Cueva Negra (Murcia, Spain), the chronology probably places it about MIS 21, which makes it much older than Bolomor, while in Sima de las Palomas the interval MIS 6-5 may be represented (Walker et al., 2004, 2008), although the pollen data correspond to MIS 4 or MIS 3. In any case, there are remarkable similarities: in Bolomor, Sima de las Palomas and Cueva Negra, there is a common dominance of mixed oak-pine forests, deciduous trees in the frame of a high diversity of Mediterranean elements (Carrión et al., 2003, 2005). However, the tree cover of Cueva Negra and Sima de las Palomas never reaches the high values recorded in Bolomor, being the steppic component more abundant.

From a biogeographical perspective, the Bolomor site appears as a unique paleofloristic record in the Middle European Pleistocene and in relation to Neanderthal palaeoecology, highlighted by the existence of a more forested habitat than what has been found in other sites, with a high plant diversity, typical of the southern tip of the Iberian Peninsula in the context of glacial refugia (Carrión et al., 2003, 2008; 2018; González-Sampériz et al., 2010). This closed forest environment could have favored Neanderthal hunting strategies, as pointed out by Finlayson and Carrión (2007) and later by other authors (Rosas, 2016); and now strongly suggested by the recent work of Stewart et al. (2019). Using an analysis of the frequency distribution of power-associated alleles in Neanderthal genomes, these authors postulate that North European Neanderthals were particularly adapted to the conditions of temperate episodes such as Marine Isotope Stage 5e or the warmer interstadials of MIS 3 such as GI12, during which a wooded landscape and a rich faunal diversity existed. Stewart et al. (2019) contend that their hunting strategy is more likely to be encounter or ambush in style than pursuit hunting, which involves a power mode of locomotion such as sprinting rather than an endurance-based long distance running pursuit mode.

The human groups that inhabited in Bolomor processed and consumed a wide diversity of animal species, among which ungulates and small preys (lagomorphs, tortoises and birds) are included. Through the analysis of cut marks, bone breakage to access to marrow, human tooth marks and burning patterns, it was possible to identify the anthropogenic use of the animals composing the assemblage, and demonstrate a broad spectrum diet in the site (Blasco, 2008; Blasco and Fernández-Peris, 2009, 2012a; 2012b; Blasco et al., 2010, 2013b; Sanchis-Serra and Fernández-Peris, 2008). This breadth of species in the diet also reflects the diversity of environments that hominids are capable of exploiting: the steep forest environment with wooded ravines, and spaces that combine the middle mountain and the plain towards the valley. However, there are significant differences along the Bolomor stratigraphy that seem to be closely related to the climate and the coastline. During the end of MIS 9 and especially during MIS 8, a phase of general regression and retreat of the coastline occurs, which is related to level XVII where the predominant animals are somewhat associated with open environments. However the maximum regression of the Middle Pleistocene in the littoral is located in MIS 6 with a surface emerged between 15 and 20 km higher than the current one and related to level XII, where the animals of the plain, especially horses, are predominant. The interglacial periods would show the opposite phenomenon. The maximum marine advance would be located around 120 ka and linked to level IV, which yields the highest representation and diversity of taxa related to forest environments and steep environments typical of the ravine.

The lithic industry recovered at Bolomor Cave is included within the early Middle Palaeolithic techno-complex. According to Fernández-Peris (2007), although these techniques are not related to the Acheulean industries, it is a techno-complex older than the period in which the classic Mousterian is found, whose beginning is at some stage of the Middle Pleistocene. More than 35,000 pieces of lithic industry have been recovered in the site. These tools were made using flint, limestone and quartzite as raw materials. All of them come from marine, colluvial and fluvial stones near the site. The artifacts are formed mostly by scrapers and lateral denticulates. In addition, intensive reuse and recycling of lithic artifacts are routinely observed (Fernández-Peris et al., 2008). Several bone retouchers have been recovered at levels XVII, XIII y XII (Blasco et al., 2013a; Rosell et al., 2015).

Clearly, the Neanderthals of Bolomor were great experts of their environment. For instance, the acquiring of fast-running (mostly lagomorphs) and quick flying small prey requires a sophisticated technology and involves obtaining and processing ways different from those used for large and medium-sized animals (Blasco, 2008; Blasco and Fernández-Peris, 2009, 2012a, 2012b; Blasco et al., 2010, 2013a, 2013b). These hominids possessed highly adaptive subsistence strategies, which are coherent with the potential benefits offered by a diverse and rich environment (Blasco et al., 2011; Carbonell et al., 2010; Saladié et al., 2011). It is in this context where the palaeobotanical findings become more relevant, because we could add now to the Neanderthal diet the possibility of a broad spectrum of edible plants which grew in the vicinity, such as hazelnut (*Corylus avellana*), chestnut (*Castanea sativa*), Mediterranean hackberry (*Celtis australis*), strawberry tree (*Arbutus unedo*), carob tree (*Ceratonia siliqua*), holly oak (*Quercus ilex*), olive (*Olea europaea*), elderberry (*Sambucus nigra*), and probably wild Rosaceae such as several species of *Prunus, Rubus, Rosa*, and *Sorbus*. Given the altitudinal position of Bolomor, it is also likely, as commented above, that the Stone pine (*Pinus pinea*) developed on the coastal shelves.

The case of *Celtis* is particularly interesting. Several authors (Bittmann, 1992; Chaney, 1935; De Lumley, 1976; De Lumley et al., 1976; Ljubin and Bosski, 1996; Messager et al., 2008) consider that *Celtis* may well have been part of the diet of hominids. As we have previously commented, the presence of *Celtis* seeds is not exceptional in Pleistocene archaeological sites and is probably related to human consumption given their nutritional properties (Demir et al., 2002). According to Allué et al. (2015), the presence of biomineralised seeds of *Celtis* in TD6 (Atapuerca) provides evidence of the harvesting of plants by hominins, as in the case of *Homo antecessor*.

In Bolomor there is human activity in almost all the archaeological levels (Arsuaga et al., 2012; Blasco et al., 2013a, 2013b; Rosell et al., 2015; Sañudo et al., 2016; Vidal-Matutano et al., 2017). We speak of more than 300,000 years of survival in a relatively stable ecological scenario, with that well-known forest resilience capable of cushioning the numerous climatic oscillations of such a long period of time and keeping a remarkable biological diversity. But the ecological resilience is also to be considered in this case, given by the animal and plant biodiversity of the mountainous chains of the Alicante coast. Carrión et al. (2011) argued that the regions of maximum evolutionary innovation in hominids coincide with biodiversity hotspots; and the lowermost altitudinal belt of the Mediterranean Region is one of them. The position at low altitude in an intra mountainous valley and its proximity to marine resources and what should have been large coastal platforms, as well as the availability of fresh water, make of Bolomor a glacial refugium with floristic and structural features similar to the large phytodiversity reservoirs of the Balkans (Bennet et al., 1991; Magri, 2010; Magri et al., 2017; Okuda et al., 2001; Pross et al., 2015; Sadori et al., 2016; Tzedakis, 1994, 1999; Willis, 1994). In a series of works of paramount importance for ecology, several authors (Bascompte, 2010; Jordano et al., 2003; Rezende et al., 2007) showed that in a scenario of climatic stress due to global change, the ecological structures in which there are more interactive networks (outcome of biodiversity) will be those in which a lower rate of extinction eventually would take place. Indeed, a though-provoking corollary, because before taxonomic extinction is population extinction. And Bolomor is an extraordinary case of biological tenacity to the avatars of the physical environment during the rigors of the Quaternary.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.quascirev.2019.03.015.

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