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Coprolite palynology from Abrigo do Lagar Velho (Portugal) and a revision of Gravettian vegetation in the Iberian Peninsula

Juan Ochando [a,*], José S. Carrión [a,b], Joan Daura [c,d], Montserrat Sanz [c,d],
Ana Cristina Araújo [d,e,f], Ana Maria Costa [e,f,g]

[a] Department of Plant Biology (Botany Area), Faculty of Biology, University of Murcia, Campus de Espinardo, 30100 Murcia, Spain
[b] Evolutionary Studies Institute, University of Witwatersrand, Johannesburg, South Africa
[c] Grup de Recerca del Quaternari, GRQ-SERP, Department of History and Archaeology, University of Barcelona, 08001 Barcelona, Spain
[d] UNIARQ-Centro de Arqueologia da Universidade de Lisboa, Faculdade de Letras, Universidade de Lisboa, 1600-214 Lisboa, Portugal
[e] Laboratório de Arqueociências (LARC)-DGPC, Calçada do Mirante à Ajuda, n° 10A, 1300-418 Lisboa, Portugal
[f] InBIO | Research Network in Biodiversity and Evolutionary Biology (Associate Laboratory) and CIBIO | Research Centre In Biodiversity and Genetic Resources, University of Porto, Porto, Portugal
[g] IDL | Instituto Dom Luiz, Universidade de Lisboa, Campo Grande, Edifício C6, Piso 3, 1749-016 Lisboa, Portugal

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ABSTRACT

Palynological investigations on Gravettian coprolites of Abrigo do Lagar Velho (Vale do Lapedo, Leiria, Portugal) dated between ca. 30 to ca. 27.3 ka cal BP are presented. The palaeoecological data shows a semi-forested landscape with *Pinus*, Poaceae, *Erica*, *Artemisia*, *Juniperus* and *Quercus* as the dominant taxa. A diversity of trees, shrubs, and herbs is also noticeable, including broad-leaf trees, Mediterranean woody shrubs and trees, conifers, xerothermophytes, indicators of saline substrates and heliophytes such as *Erica*, Asteroideae, Cistaceae, *Ephedra fragilis* and *E. distachya*. The overall reconstruction is a mosaic of different landscapes or types of vegetation around the rock-shelter. Indeed, we provided approach on the Gravettian vegetation of the Iberian Peninsula, connecting the palaeoecosystem with the biogeography of past human populations during the late Pleistocene.

1. Introduction

Coprolite palynology is often associated to cave sedimentary environments, providing a diversity of biogenic materials where pollen, spores and non-pollen palynomorphs (NPPs) can be relatively well preserved (Alcover et al., 1999; Carrión et al., 1995a, 1995b, 2004, 2006, 2007, 2008, 2018; Daura et al., 2017; Gatta et al., 2016; González-Sampériz et al., 2003; Horwitz and Goldberg, 1989; Marais et al., 2015; Ochando et al., 2020a; Scott, 1987, 1994; Yll et al., 2006). Evaluating the palaeoecological potential of coprolites requires more experimental research, especially on the taphonomy of the pollen assemblages as pollen transport, deposition, and preservation (Bottema, 1975; Carrión and Scott, 1999; Carrión et al., 2009; Coles and Gilbertson, 1994; Davis, 1990; Fernández-Jalvo et al., 1999; Hunt and Fiacconi, 2018; Hunt and Rushworth, 2005; Navarro et al., 2000, 2001). Hitherto, studies carried out on this issue suggest that pollen spectra from coprolites complement conventional palynological data by correcting the bias against zoogamous species, which may be abundant in a number of plant communities (Carrión, 2002). Coprolites may also provide palaeoenvironmental information for sites where peatbog and lake pollen sequences are scarce, and for periods where those pollen sequences are interrupted by hiatuses (Carrión et al., 1999). One of the periods with scarce information on palaeovegetation is the Last Glacial Maximum (LGM; ca. 26.5–19 ka cal BP), which embraces Gravettian and Solutrean technocomplexes in western Eurasia. Here we present palynological data of coprolites from Abrigo do Lagar Velho (Portugal), a Gravettian rock-shelter which provided extremely important data for the European Palaeolithic archaeology and for human evolution knowledge (Zilhão and Trinkaus, 2002).

2. Settlement characterization, excavations and chronology

Abrigo do Lagar Velho is a rock-shelter located in the Lapedo Valley (39° 45' 25" N; 8° 43' 58" W, 85 m above sea level), on the municipality of Leiria, about 135 km north of Lisbon, Portugal (Fig. 1). The shelter locates in the Lapedo gorge, on the left bank of the Caranguejeira stream, presenting an elongated shape open to the North (Fig. 1). The site was

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* Corresponding author.
E-mail addresses: juan.ochando@um.es (J. Ochando), carrion@um.es (J.S. Carrión), jdaura_lujan@ub.edu (J. Daura), montsesanzborras@ub.edu (M. Sanz), acaraujo@dgpc.pt (A.C. Araújo), acosta@dgpc.pt (A.M. Costa).

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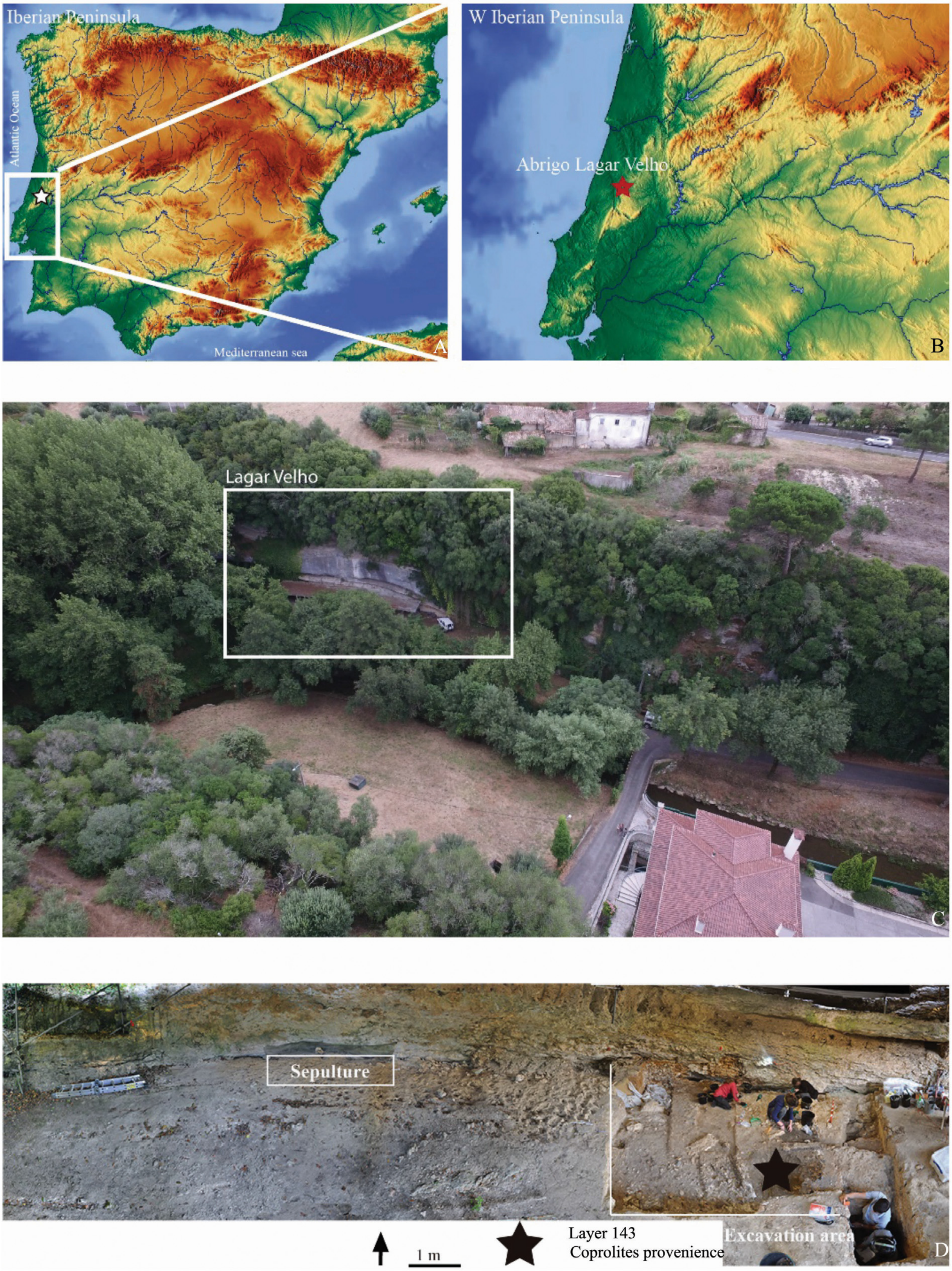


Fig. 1. The Lagar Velho rock-shelter. A and B: Location of the site. C: Aerial view of the shelter, © Pedro Souto D: Excavation area and coprolites provenience. Map extracted from OpenStreetMap © licensed under ODdL 1.0 (https://www.openstreetmap.org/copyright) by the OpenStreetMap Foundation (OSMF). ©OpenStreetMap contributors.

discovered and first excavated in late 1998, soon after the identification of the LV1 infant burial (Duarte et al., 1999; Zilhão et al., 2000). As it was widely reported at the time, LV1 child had skeletal features that indicated an ancestry with Neanderthal input, a hypothesis that stimulated much scientific debate and fostered the development of Palaeolithic archaeological and genetic research.

The bulk of the sedimentary infilling corresponds to a thick vertical sequence up to more than 8 m (detailed description in Angelucci, 2002), with the top ca. 4 m richer in archaeological evidences destroyed by bulldozing activities prior to the discovery of the site. The sedimentary dynamics is spatially variable, according to stratigraphy, pedosedimentary components and features, and human occupation (Zilhão and Almeida, 2002). The uppermost sedimentary units are mostly composed of gravity-driven sediments (Angelucci, 2002) while fluvial deposits are preserved below the gravity-driven sediments at the western part of the shelter containing faunal remains dated to 39–29 ka cal BP. Between the fluvial and gravity-driven sediments, a transitional sedimentary unit was described (Angelucci, 2002) containing carnivore occupancies without human activity dated to ca. 29–27.5 ka cal BP (for additional information see Angelucci, 2002). The upper sedimentological units contain Upper Palaeolithic occupancies dated to the Terminal Gravettian (ca. 27 ka cal BP) and to the Middle Solutrean (24.3 ka cal BP) (Pettitt et al., 2002). The remains associated to these occupations were only preserved in a wall-recess of the shelter known as hanging remnant (from now on referred to as TP).

The coprolites analysed here were collected in layer 143, an organic-rich layer accumulated within a massive brown clay to silty-clay sediment with scarse limestone fragments excavated in the framework of new excavations at the site (previously described as *ls geoarchaeological complex* by Angelucci, 2002) (Figs. 1 and 2). Layer 143 has no direct lateral correlation with the child burial, but the relationships between these two occupations are yet to be defined.

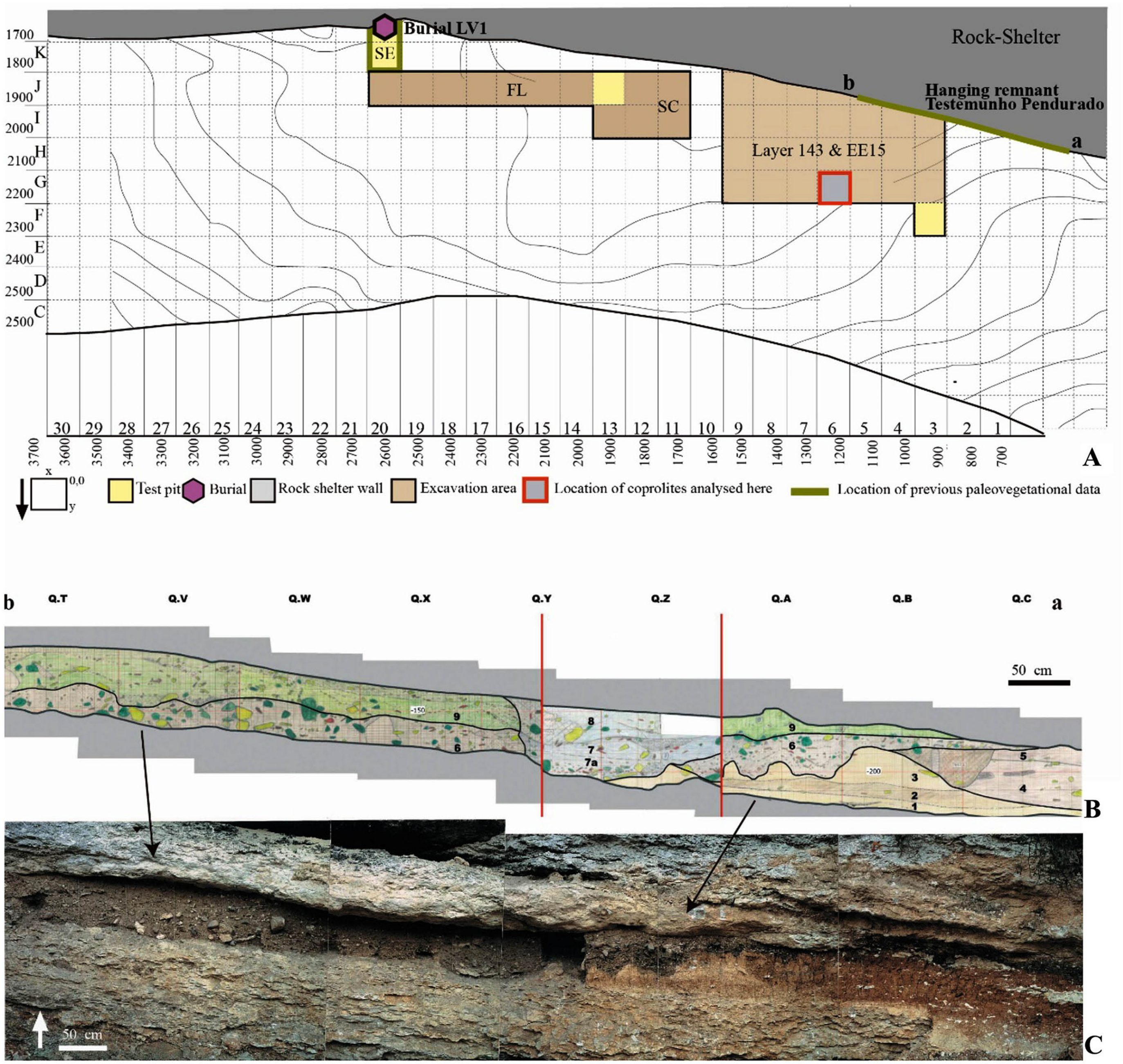


Fig. 2. Lagar Velho paleovegetational data. A: Plan of the Lagar Velho rock-shelter showing the location of coprolites and previous vegetation data (green). For more information concerning SE, FL, SC and EE15 designations please go to Zilhão and Trinkaus, 2002. B-C: The Hanging Remnant (TP) with the position of TP01 to TP09 layers. Drawing by João Zilhão; Photography by J.P. Ruas.

Different units have been distinguished in the *ls* complex with human inputs related to fire activity. The age of this complex could be inferred from the basal age of the overlying sedimentary complex (*ms geoarchaeological complex*) and the child's burial, i.e. ca. 30 to 27.3 ka cal BP (Zilhão and Trinkaus, 2002). The chronological range of layer 143 fits between the boundary of MIS (Marine Isotope Stage) 3 and MIS 2 and could be related to the end of D-O (Dansgaard-Oeschger) 4 and the beginning of HE (Heinrich Event) 3.

3. Modern-day vegetation and climate

Lagar Velho is located in an area with Mediterranean climate, near to the Atlantic coast (ca. 30 km) (Fig. 1). The nearby meteorological station in Leiria shows an annual average temperature of 14.9–16 °C (10.5 °C in the coldest month and 21.5 °C in the warmest month) and annual precipitation of 749–1000 mm. The Lapedo valley is within the Meso-Cenozoic western borderland of the Iberan Peninsula, which constitutes the bulk of the littoral and peri-littoral belt of central Portugal, with an overall NNE-SSW axis, favouring precipitation mainly during Winter and Autumn. Phytoclimatologically speaking, the area is located in the Mesomediterranean with a sub-humid–humid ombroclimate. Biogeographically, the area belongs to the Luso-Extremadurense Province, Sector Beirense litoral (Costa, 1982; Rivas-Martínez, 1987; Rivas-Martínez et al., 1977). In addition, it is worth mentioning that the Leiria depression is characterized by prevalent fog and, in general, by high values of relative moisture of the air, factors which are not recorded by "standard" climatic data (Angelucci, 2002). Thus, the environment of the Lapedo Valley and the Lagar Velho shelter, that faces north, explain their lower temperatures and higher humidity when compared to the nearby territories.

According to Queiroz et al. (2002) the vegetation mosaic that characterizes the area where the rock-shelter is located is conditioned by the ecophysiographical partitioning of the gorge. The Caranguejeira stream flows through a very narrow canyon-like valley where steep slopes developed. Still following these authors, three predominant plant formations prevail in the valley, (i) In the interfluves, characterized by pre-Quaternary coarse substrates where podzols develop, *Erica arborea* dominates. Maritime pine (*Pinus pinaster*) also occurs, associated with heathlands; (ii) Limestone slopes evidence marcescent and evergreen Mediterranean formations with *Quercus faginea* populations and sclerophyllous scrubs developing on the shadier slopes. On the facing south and more xeric slopes, the sclerophyllous vegetation also include *Olea europaea sylvestris* together with *Quercus coccifera*, *Phillyrea latifolia*, *Pistacia lentiscus*, *Rhamnus alaternus*, *Hedera helix*, *Daphne gnidium*, and *Smilax aspera*; (iii) In the bottom of the valley a deciduous riparian forest with *Alnus glutinosa*, *Fraxinus angustifolia*, *Salix atrocinerea*, and *Frangula alnus* crop up.

4. Material and methods

The coprolite assemblage analysed was recovered at Lagar Velho site during the 2018 fieldwork campaign, in Layer 143 (square G6 of the excavation grid) and includes a total of 10 fragments (samples ID ALV-1 to -10) (Figs. 2 and 3). Following Sanz et al. (2016) their general morphology is cylindrical or tube-like with rounded extremities. No bones or tooth inclusions were observed in their external surfaces. The coprolites match that of non-hyena taxa and correspond to other medium to small species.

In the laboratory, the surface layer of each coprolite was cut opened with a steel spatula, and material from inside was scraped out to minimize contamination from external face. After the samples were weighed (ALV-1: 14.9g; ALV-2: 7.3g; ALV-3: 8.5g; ALV-4: 5.8g; ALV-5: 6.3g; ALV-6: 7.8g; ALV-7: 10.3g; ALV-8: 6.1g; ALV-9: 8.8g; ALV-10: 10.0g; Table 1), the "Classic Chemical Method" was followed for the extraction of palynomorphs (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 sample three tablets of *Lycopodium* spores (BATCH No. 177745.500). 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

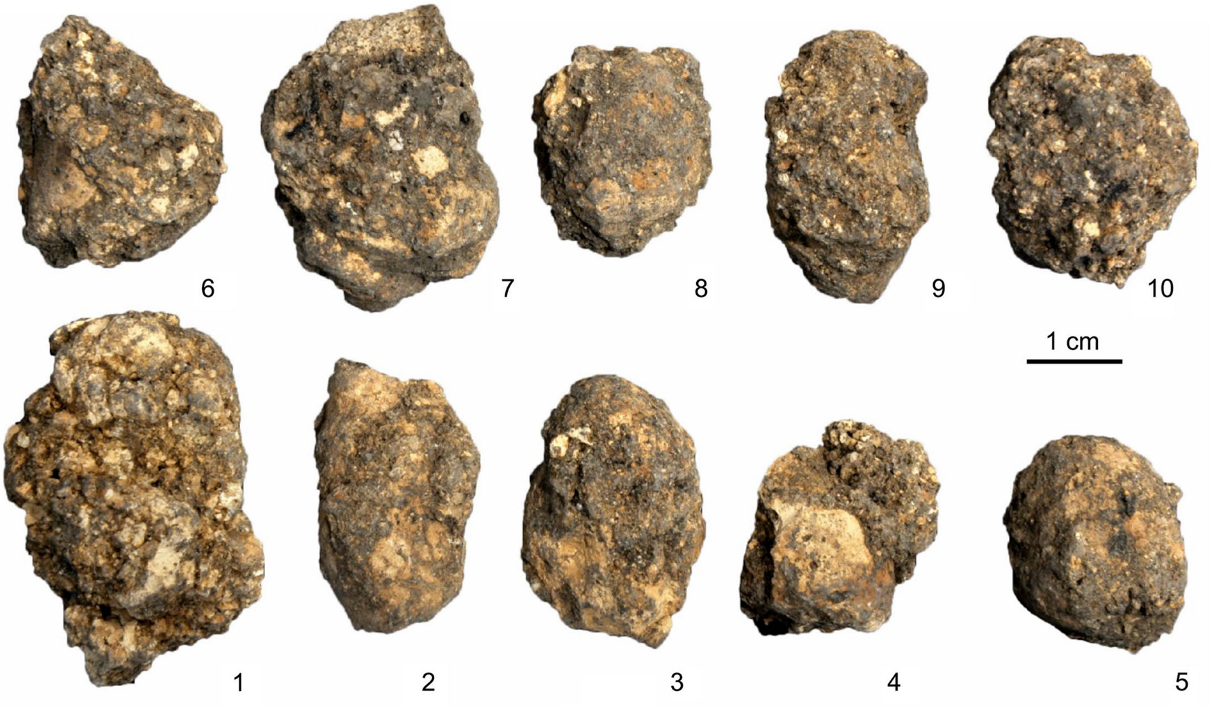


Fig. 3. Coprolite specimens from Lagar Velho rock-shelter (ALV-1 to ALV-10) from layer 143, square G6.

Table 1
Summary of palynological features of the Lagar Velho coprolites.

Sample	Layer	Square	Weight (g)	Concentration (grains/g)	Indeterminable (%)	([a]) Pollen sum	Number of taxa
ALV-1	143	G6	14.9	1444.59	3.27	336	32
ALV-2	143	G6	7.3	2763.17	3.61	221	17
ALV-3	143	G6	8.5	2623.62	2.92	205	15
ALV-4	143	G6	5.8	6442.63	1.68	237	19
ALV-5	143	G6	6.3	2638.95	1.75	229	25
ALV-6	143	G6	7.8	5443.61	4.93	203	20
ALV-7	143	G6	10.3	642.30	3.43	204	20
ALV-8	143	G6	6.1	3517.34	2.83	247	23
ALV-9	143	G6	8.8	15574.65	1.29	231	15
ALV-10	143	G6	10.0	1422.17	3.94	203	17

[a] Asteroideae, Cichorioideae and *Centaurea montana* t. excluded.

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.

Palynological diagrams representing arboreal pollen (AP), non arboreal pollen (NAP) and spores and NPPs were prepared (Figs. 4, 5 and 6) together with a synthetic diagram with the main taxa and ecological groups (Fig. 7). Along with spores and NPPs, we excluded from total pollen sum the counts of Asteroideae, Cichorioideae and *Centaurea montana* assuming they might be overrepresented due to local occurrences. The number of pollen types varies between 15 and 32, with a total of 57 recognized taxa. The percentage of indeterminable types remained, in most cases, in values lower than 5% (Table 1). The number of palynomorphs extracted from the coprolites ranges between 642.30 and 15574.65 grains/g. The pollen grains and spores present a fairly good level of preservation.

5. Palynological results

All (10 out of 10) the analysed coprolite contained pollen grains (Figs. 4, 5 and 7). The pollen sum varied between 203 and 336 pollen grains. AP is predominant across all samples, reaching values >83%, except in coprolite ALV-8, in which the lowest percentage of AP (48%) is reached. *Pinus* sum oscillates between 8 and 58%. *Pinus sylvestris* is highly fluctuating, varying between ca. 57% and <9% as in sample ALV-6. *Juniperus* attains percentages between 2% and 24%. *Quercus* evergreen is represented by 1% to 15%, *Quercus* deciduous reaches 5% and *Quercus* indeterminate does not exceed 2%. Remarkably, *Erica* fluctuates between 9% and 58%. The occurrence of *Salix*, *Castanea*, *Sambucus ebulus*, *Olea*, *Pistacia*, *Myrtus*, Genisteae, and *Cistus* t. is significant, as well as the occurrence of *Pinus pinaster*, *Quercus suber*, *Alnus, Betula, Corylus, Carpinus betulus, Fraxinus, Fagus, Ulmus*, *Ephedra fragilis*, *Ephedra distachya* and *Rhododendron*. Among NAP (Fig. 5), Poaceae (7–43%) and *Artemisia* (3–13%) are remarkable. Asteroideae and Cichorioideae (both counted out of the pollen sum), Brassicaceae, Apiaceae, *Plantago lanceolata*, Liliaceae and Lamiaceae are also frequent. Fungal spores, algae and bryophyta do not abound (Fig. 6) although the occurrences of *Dicellaesporites*, Hyphae, *Microsporonites*, *Monoporisporites*, *Multicellites*, *Pluricellaesporites*, and Zygnemataceae are occasionally noticeable.

Coprolite pollen spectra are co-dominated by five or six of the main pollen contributors, namely *Pinus, Quercus, Juniperus*, Poaceae, *Erica*, and *Artemisia* (Figs. 4 and 5). Exceptions include ALV-1 and ALV-9 exclusively dominated by *Pinus* and *Erica*, respectively. Palaeoecologically, the pollen spectra involve the ocurrence of diverse trees, shrubs, and herbs, with broad-leaf trees, Mediterranean component, conifers, xerothermophytes, indicators of saline substrates and heliophytes such as *Erica*, Asteroideae, Cistaceae, *Ephedra fragilis* and *E. distachya* (Figs. 4, 5 and 7). A mosaic landscape can be inferred, with shrubby and heathy grasslands, mixed pine-oak woodlands, pine forests, riverine forest patches, heliophytic matorrals, and rocky scrub with chamaephytes, hemicryptophytes, and *Artemisia* steppes with junipers. The abundance of *Quercus*, and the presence of *Acer*, *Alnus*, *Betula*, *Corylus*, *Carpinus betulus*, *Fraxinus*, *Salix*, *Frangula*, *Castanea*, *Fagus*, *Ulmus*, *Sorbus*, *Olea*, *Pistacia*, *Myrtus*, *Phillyrea*, *Cistus*, *Calluna*, and *Rhododendron* suggest the persistence of angiosperm woodlands during the LGM. Presumably, some enclaves may have been well supplied with atmospheric or edaphic water to support the existence of populations of broad-leaf tree species such as *Fagus sylvatica, Carpinus betulus, Corylus avellana*, and other mesophytes. Certain Atlantic influence is obviously present, regardless those trees that may have been restricted to gullies or depressions with wet conditions. Although we do not know the species and behaviour of the coprolite-producing agent, some pollen grains may have also had its source in the emerged Atlantic coastal shelves (current coast shoreline is ca. 25 km distant from the site and it was ca. 50 km during the LGM, assuming a sea-level drop of ca. 120 m for the Iberian Atlantic coast; Dias et al., 2001).

6. Discussion

6.1. Previous palaeobotanical research

A previous pollen study was carried out at Lagar Velho (Queiroz et al., 2002) on 4 sediment samples collected in the profile underlying the child's burial (Fig. 8). The authors concluded that these sediment pollen spectra were biased and therefore not adequate to perform a palaeoenvironmental reconstruction due to i) the overrepresentation of the more resistant taxa such as *Pinus* and Asteraceae (while the most fragile palynotypes were absent), ii) the concentration of indeterminable pollen and iii) the high proportions of reworked pre-Quaternary pollen grains. In addition, samples were collected in a sedimentary unit composed by an alternation of fine gravel and sand usually with more suitable conditions for vertical particle movements and contamination. Even so, a number of the pollen types refered by Queiroz et al. (2002) has been identified in the coprolites, such as *Betula, Alnus, Salix, Quercus, Erica, Calluna, Juniperus, Cistus, Helianthemum, Phillyrea, Artemisia*, Poaceae, and Chenopodiaceae. We have not found, however, high percentages of indeterminable pollen, or reworked palynomorphs, which could have entered into the coprolite from sediment through the surface cracks. The frequencies of pine pollen are similarly high in the coprolite samples, but not those of Asteraceae.

Queiroz et al. (2002) has also studied five charcoal fragments from the same wood stem collected from the child burial context, right under the foot bones, and dated to ca. 29.1 ka cal BP. All these fragments were identified as Scots pine (*Pinus sylvestris* t.). In addition, a total of 747 charcoal wood fragments were analysed from TP (Queiroz et al., 2002), which includes, as mentioned before, Terminal Gravettian and Middle Solutrean occupations. No major differences were detected between samples regarding charcoal spectra, with 4 taxa dominating the record: *Pinus sylvestris*, *Erica arborea*, *Cytisus scoparius*, and *Ulex*. Other minor taxa include *Betula* cf. *pubescens*, *Medicago/Teline* t., *Ononis* t., *Daphne* cf. *gnidium*, *Erica cinerea*, *Erica umbellata*, *Hedera helix*, *Quercus robur*, Rosaceae, and *Ulmus* (Fig. 9; Table 2).

Due to the poor quality of the data, Queiroz et al. (2002) decided to avoid a direct correlation between the charcoal data and the

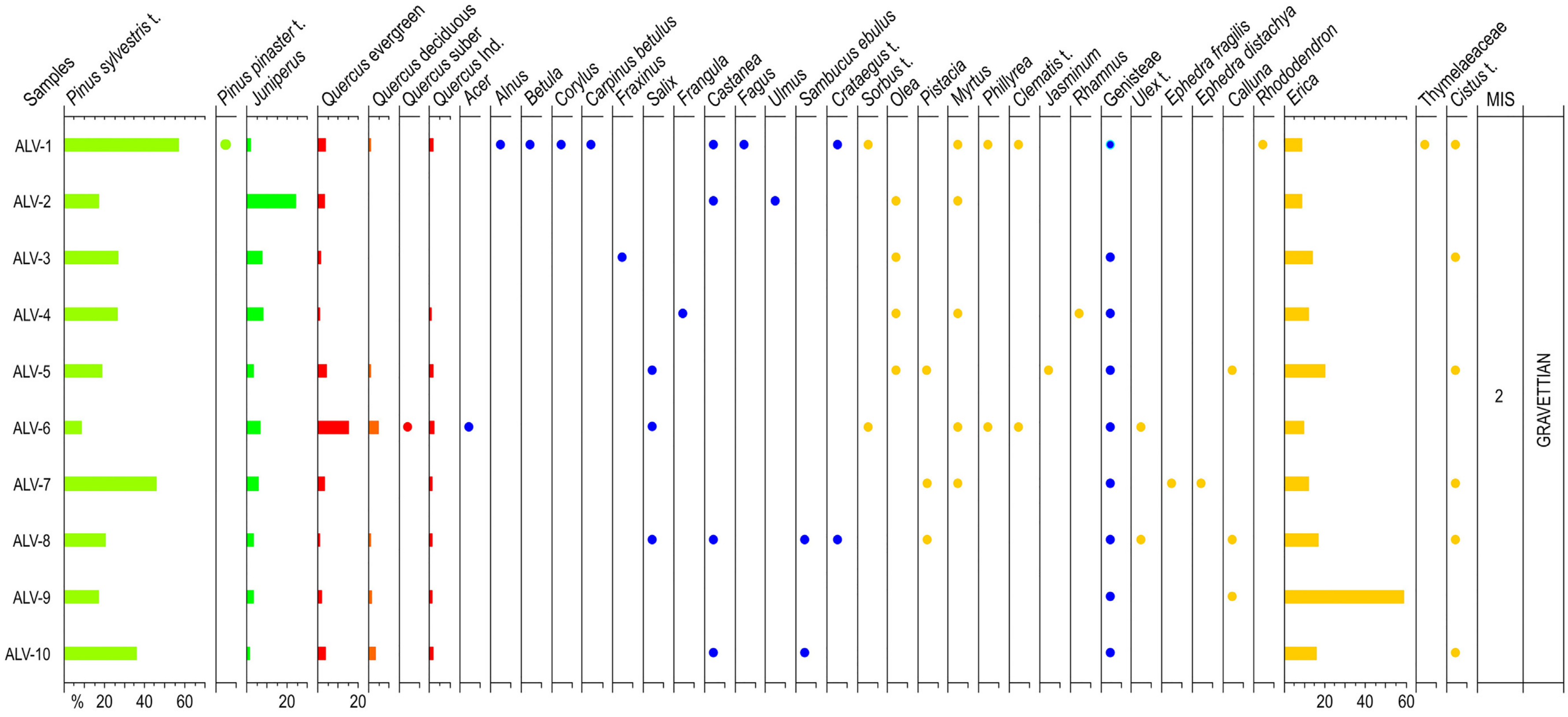


Fig. 4. Pollen diagram of Lagar Velho including the woody component. Asteroideae, Cichorioideae, and *Centaurea montana* type are out from the total pollen sum. Colour dots represent percentages below 3%. Blue dots represent Mesophytic Trees and yellow dots represent Mediterranean forest/scrub (same as in Fig. 7).

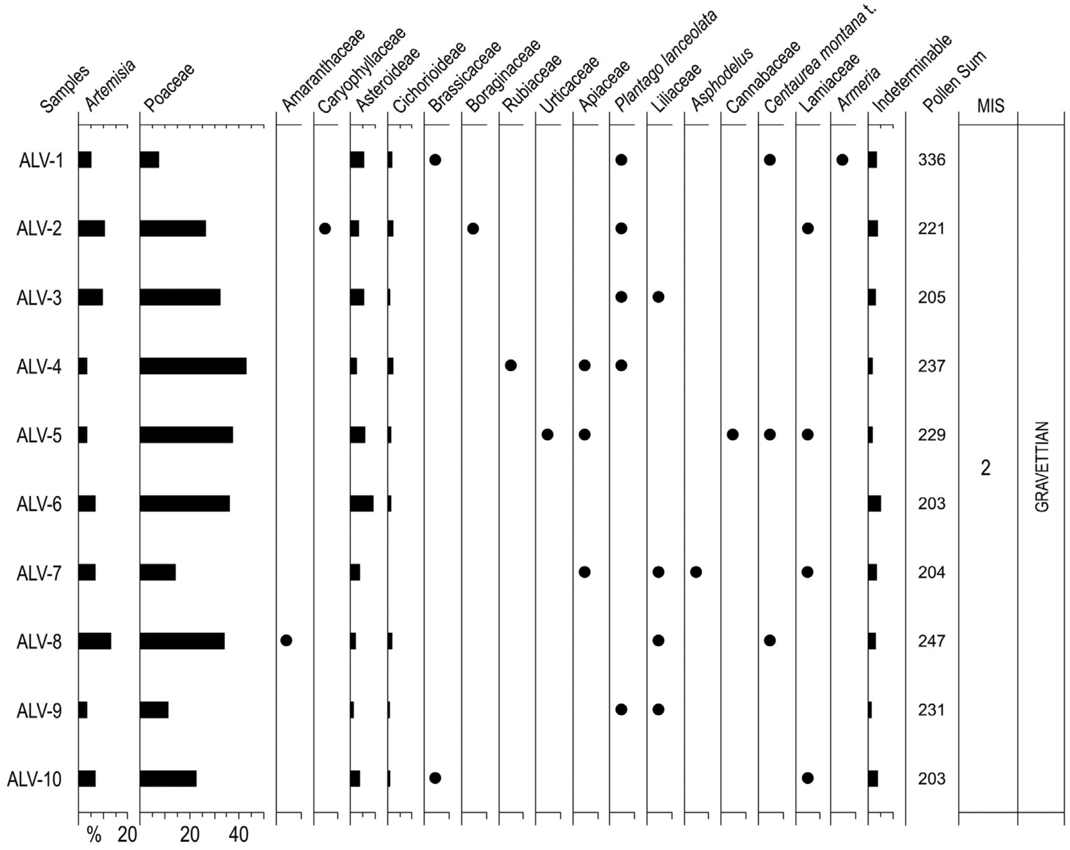


Fig. 5. Pollen diagram of Lagar Velho including non arboreal elements. Asteroideae, Cichorioideae, and *Centaurea montana* type are out from the total pollen sum. Black dots represent percentages below 3%.

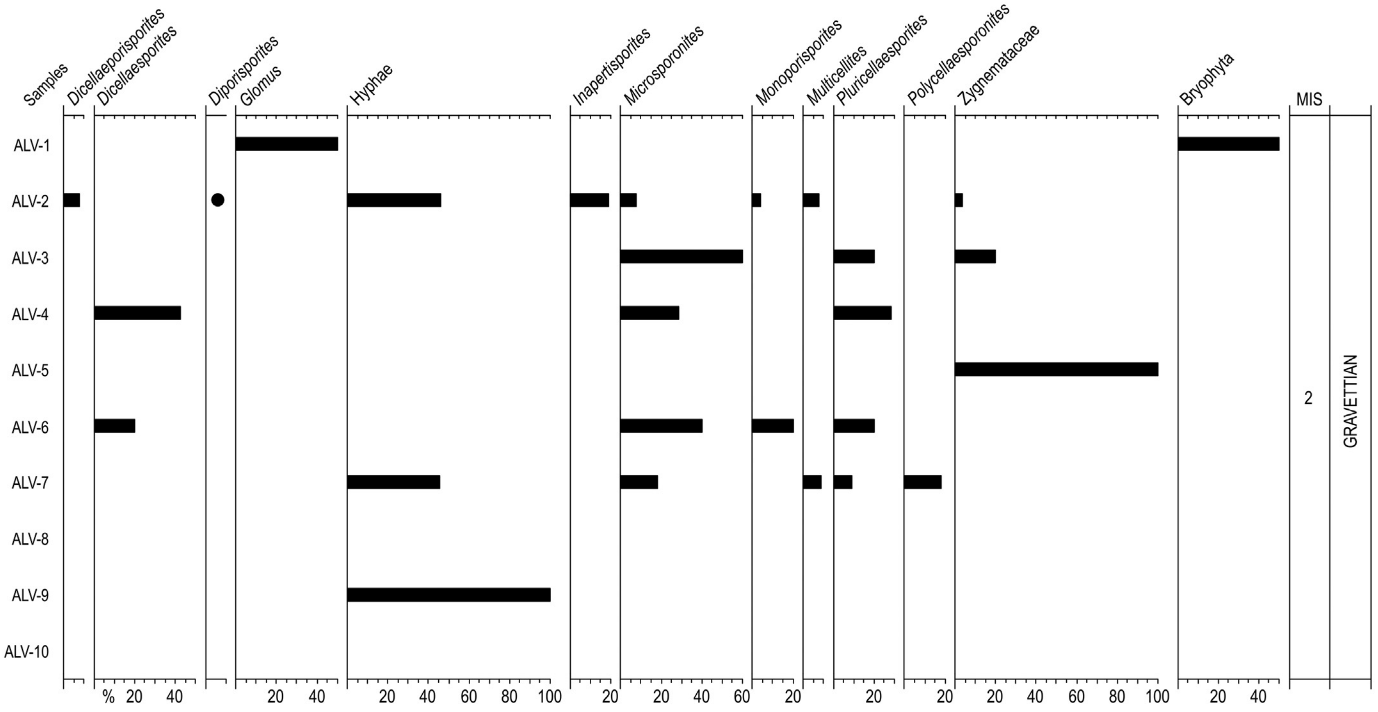


Fig. 6. Palynogram of spore and non-pollen palynomorphs of Lagar Velho. Black dots indicate percentages below 3%. All taxa percentages are calculated out from the total pollen sum.

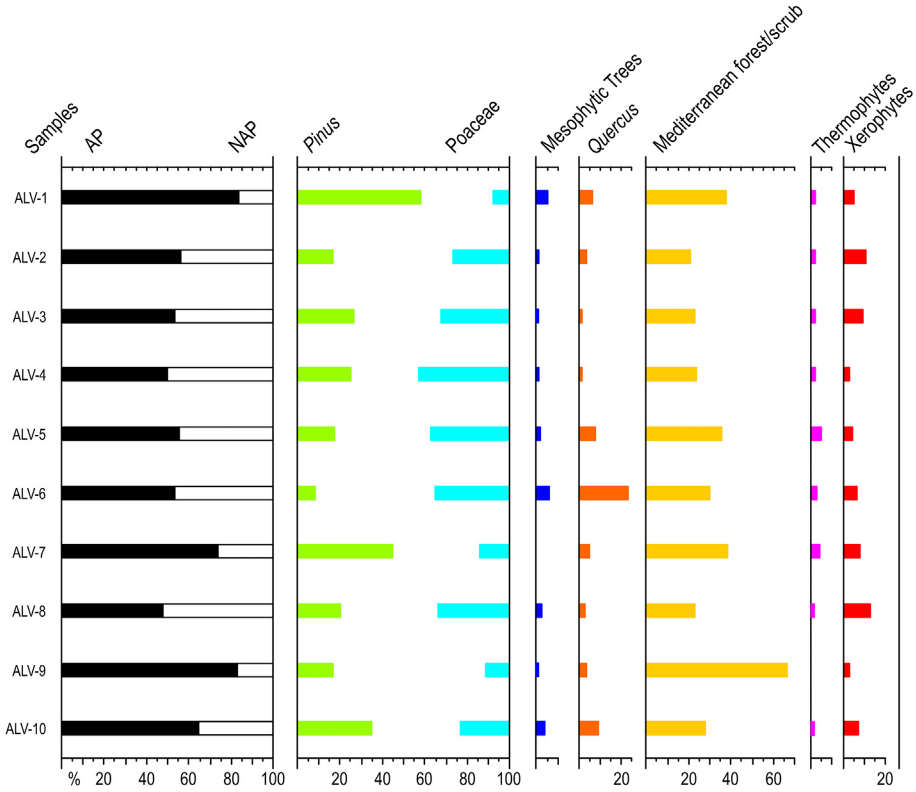


Fig. 7. Synthetic pollen diagram of Lagar Velho including ecological groups and the main pollen contributors. Conifers include *Pinus* and *Juniperus*. Mesophytic Trees include *Quercus* deciduous, *Quercus suber*, *Acer*, *Alnus*, *Betula*, *Corylus*, *Carpinus*, *Fraxinus*, *Salix*, *Frangula*, *Castanea*, *Fagus*, *Ulmus*, *Crataegus* and *Sorbus*. Other Mesophytes comprise mesophytic trees minus *Quercus* deciduous and *Quercus suber*. Mediterranean forest/scrub include *Quercus* evergreen, *Pinus pinaster*, *Sambucus ebulus*, *Olea*, *Pistacia*, *Myrtus*, *Phillyrea*, *Ephedra fragilis*, *Ephedra distachya*, *Erica* and *Cistus*. Other Mediterranean elements comprise Mediterranean forest/scrub minus *Quercus* evergreen and *Pinus pinaster*. Thermophytes include *Olea*, *Pistacia*, *Myrtus*, *Phillyrea*, *Ephedra fragilis*, *Ephedra distachya*, *Cistus* and *Asphodelus*. Xerophytes include *Artemisia*, Amaranthaceae, *Asphodelus*, *Ephedra fragilis*, *Ephedra distachya*, Lamiaceae.

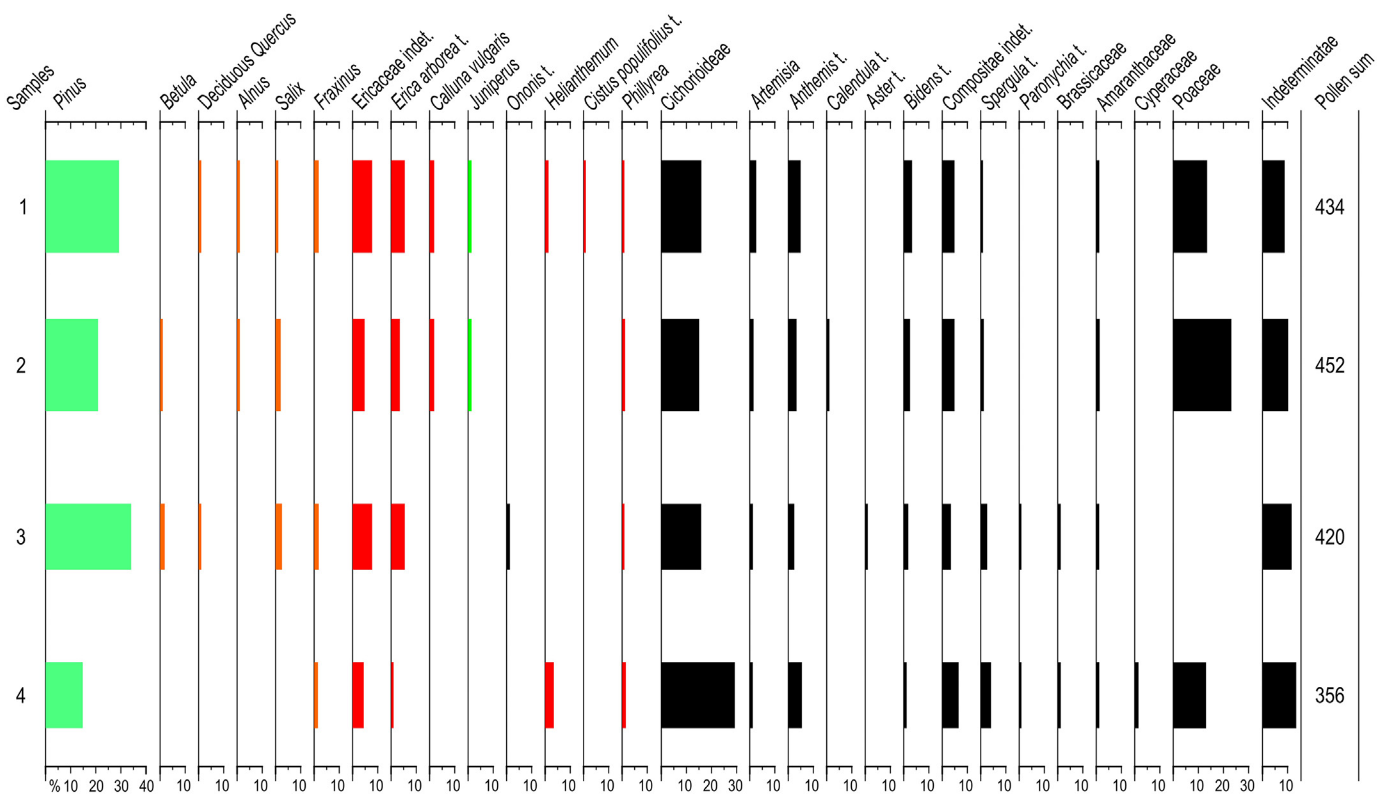


Fig. 8. Pollen diagram from deposits underlying the burial, recovered from the north profile of square L20. Redrawn from Queiroz et al. (2002).

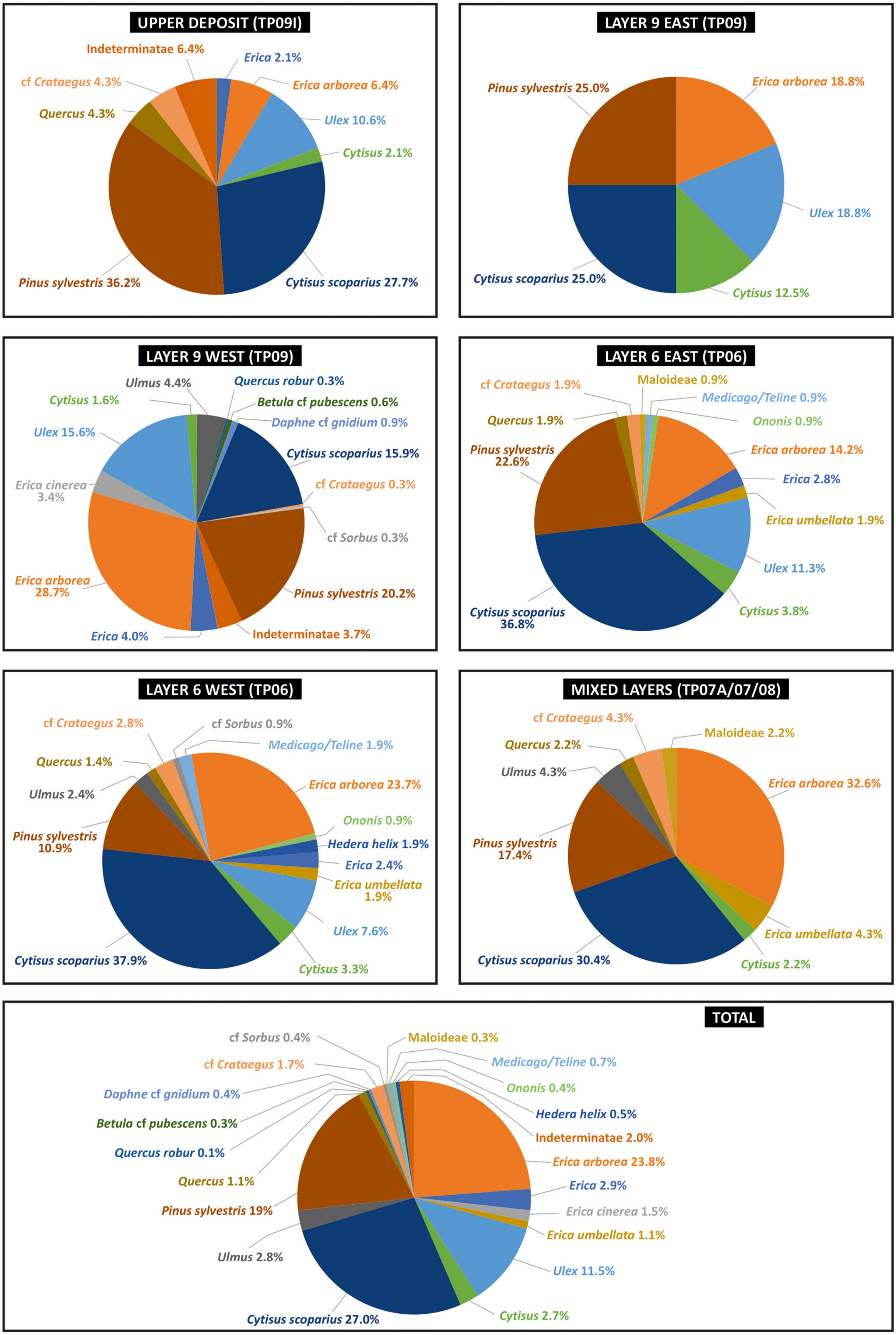
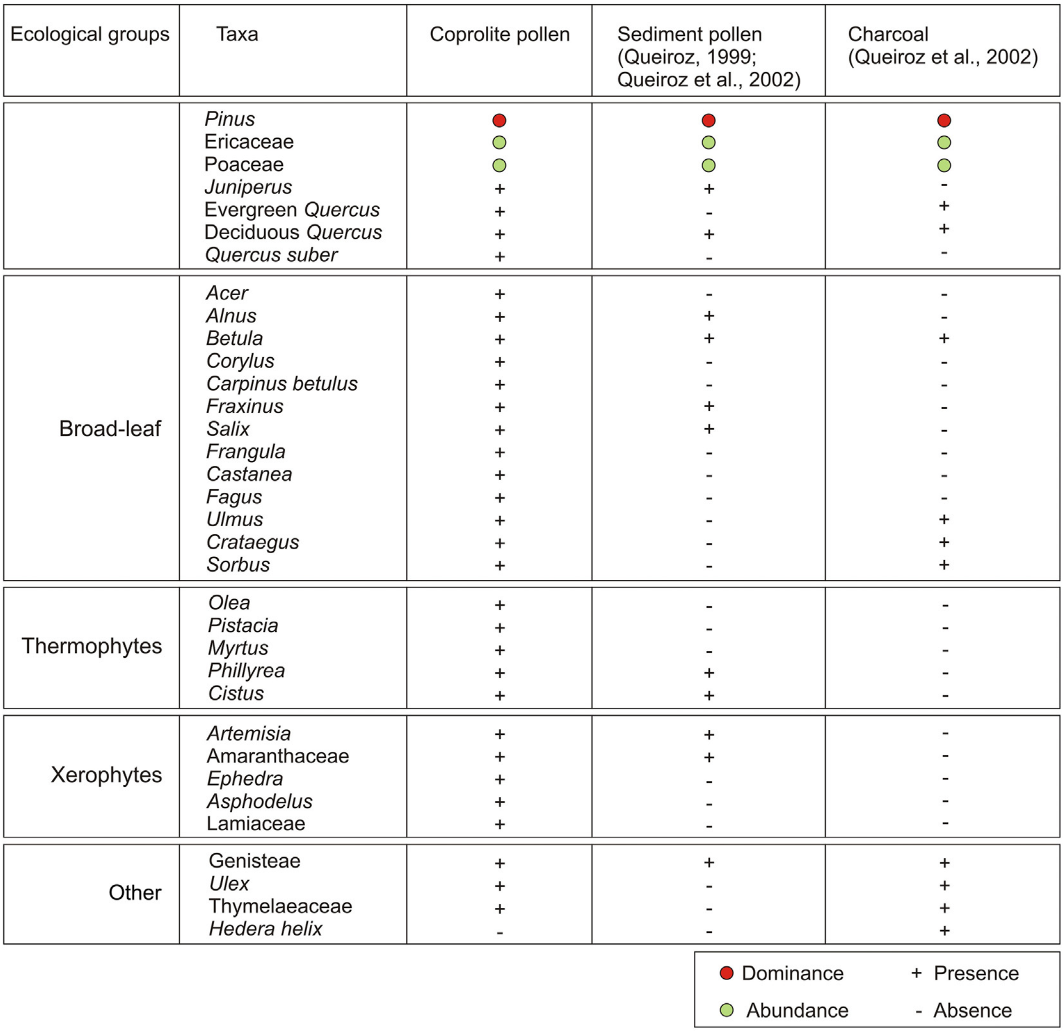


Fig. 9. Anthracological results from the hanging remnant (TP; Fig. 2) representing the Upper Deposit, Layer 9 East and Layer 9 West from TP09, Layer 6 East and Layer 6 West From TP06, Mixed Layers from TP07a, TP07 and TP08 and Total. Redrawn from Queiroz et al. (2002).

Table 2
Charcoal analysis of the hanging remnant (TP), which contains terminal Gravettian and Middle Solutrean lithics and was radiocarbon dated to between ca. 24.3 and 27 ka cal BP. Data from Queiroz et al. (2002).

	Middle Solutrean			Terminal Gravettian		Re-filled channel	
	Upper deposit (TP09l)	Layer 9 East (TP09)	Layer 9 West (TP09)	Layer 6 East (TP06)	Layer 6 West (TP06)	Mixed layers (TP07a/07/08)	Total charcoal fragments
Betula cf. *pubescens*			2				2
Cytisus	1	2	5	4	7	1	20
Cytisus scoparius	13	4	51	39	80	14	201
Ulex	5	3	50	12	16		86
Medicago/Teline				1	4		5
Ononis				1	2		3
Daphne cf. *gnidium*			3				3
Erica arborea	3	3	92	15	50	15	178
Erica cinerea			11				11
Erica umbellata				2	4	2	8
Erica	1		13	3	5		22
Hedera helix					4		4
Pinus sylvestris	17	4	65	24	23	8	141
Quercus	2			2	3	1	8
Quercus robur			1				1
Rosaceae Maloideae cf. *Crataegus*	2		1	2	6	2	13
Rosaceae Maloideae cf. *Sorbus*			1		2		3
Rosaceae Maloideae				1		1	2
Ulmus			14		5	2	21
Indeterminable	3		12				15
Total	47	16	321	106	211	46	747



Ecological groups	Taxa	Coprolite pollen	Sediment pollen (Queiroz, 1999; Queiroz et al., 2002)	Charcoal (Queiroz et al., 2002)
	Pinus	🔴	🔴	🔴
	Ericaceae	🟢	🟢	🟢
	Poaceae	🟢	🟢	🟢
	Juniperus	+	+	-
	Evergreen *Quercus*	+	-	+
	Deciduous *Quercus*	+	+	+
	Quercus suber	+	-	-
Broad-leaf	*Acer*	+	-	-
	Alnus	+	+	-
	Betula	+	+	+
	Corylus	+	-	-
	Carpinus betulus	+	-	-
	Fraxinus	+	+	-
	Salix	+	+	-
	Frangula	+	-	-
	Castanea	+	-	-
	Fagus	+	-	-
	Ulmus	+	-	+
	Crataegus	+	-	+
	Sorbus	+	-	+
Thermophytes	*Olea*	+	-	-
	Pistacia	+	-	-
	Myrtus	+	-	-
	Phillyrea	+	+	-
	Cistus	+	+	-
Xerophytes	*Artemisia*	+	+	-
	Amaranthaceae	+	+	-
	Ephedra	+	-	-
	Asphodelus	+	-	-
	Lamiaceae	+	-	-
Other	Genisteae	+	+	+
	Ulex	+	-	+
	Thymelaeaceae	+	-	+
	Hedera helix	-	-	+

🔴 Dominance
+ Presence
🟢 Abundance
- Absence

Fig. 10. Comparative results between taxa from coprolite pollen (this study), sediment pollen (Queiroz, 1999; Queiroz et al., 2002) and charcoal (Queiroz et al., 2002).

Table 3
Location of Iberian records with palaeobotanical data including archaeological records from caves with Gravettian lithics, and other open-air pollen records synchronous of the Iberian Gravettian. a.s.l - above sea level; m.w.d - mean water depth. Coordinates in the geographic coordinates system (GCS).

	Site	Coordinates and altimetry / bathymetry	Type of site	Age/MIS (only Pleistocene)	Pollen (P) Charcoal (C)	References
Gravettian records						
1	Lagar Velho	39° 45' 25" N, 8° 43' 58" W, 85 m a.s.l.	Rock-shelter	MIS 2	P, C	This study; Queiroz, 2002
2	Marinho	41° 45' 38" N, 08° 02' 50" W, 1150 m a.s.l.	Rock-shelter	MIS 2	C	Figueiral, 1993
3	Buraca Escura	39° 55' N, 08° 33' W, 270 m a.s.l.	Cave	MIS 3-2	C	Aubry et al., 2001
4	Buraca Grande	39° 55' 9" N, 08° 36' 35" W, 350 m a.s.l.	Cave	MIS 2	C	Aubry et al., 1997; Figueiral and Terral, 2002
5	Lapa do Anecrial	39° 35' N, 08° 47' W, 350 m a.s.l.	Cave	MIS 2	C	Figueiral, unpublished data
6	Bajondillo	36° 37' 02" N, 04° 33' 31" W, 0 m a.s.l.	Cave	MIS 3-2	P	López-Sáez et al., 2007; Cortés-Sánchez et al., 2008
7	Nerja	36° 45' 43" N, 03° 50' 26" W, 158 m a.s.l.	Cave	MIS 3-2	C	Badal, 1990
8	Beneito	38° 48' N, 00° 28' W, 680 m a.s.l.	Cave	MIS 3-2	P, C	Carrión, 1991, 1992a; Carrión and Munuera, 1997
9	Cendres	38° 41' 10" N, 00° 09' 09" W, 45 m a.s.l.	Cave	MIS 3-2	C	Badal and Carrión-Marco, 2001; Badal and Martínez-Varea, 2018; Villaverde et al., 2019
10	Malladetes	39° 01' 15" N, 00° 17' 57" W, 500 m a.s.l.	Cave	MIS 3-2	P	Dupré, 1980
11	Arbreda	42° 09' 36" N, 02° 44' 49" E, 200 m a.s.l.	Cave	MIS 5-2	P, C	Burjachs, 1987; Burjachs and Renault-Miskovsky, 1992
12	Sopeña	43° 19' N, 04° 56' W, 450 m a.s.l.	Cave	MIS 3-2	C	Pinto et al., 2006
13	Morín	43° 23' N, 03° 50' W, 57 m a.s.l.	Cave	Upper Pleistocene	P	Leroi-Gourhan, 1971
14	Amalda	43° 14' 06" N, 02° 13' 38" W, 205 m a.s.l.	Cave	MIS 3-2	P	Dupré, 1990
15	Aitzbitarte III	43° 15' 44" N, 01° 53' 43" W, 224 m a.s.l.	Cave	MIS 3-2	P	Iriarte-Chiapusso, 2011a
16	El Mirón	43° 14' 44" N, 03° 27' 10" W, 260 m a.s.l.	Cave	MIS 3-2	P	Straus et al., 2011, 2012
17	Ondaro	43° 19' 51" N, 02° 34' 50" W, 450 m a.s.l.	Cave	MIS 3	P	Iriarte-Chiapusso and Ayerdi, 2016-2017
18	Santimamiñe	43° 20' 47" N, 02° 38' 11" W, 156 m a.s.l.	Cave	MIS 3-2	P	Iriarte-Chiapusso, 2011b
Archaeological records with same chronology of Lagar Velho's coprolites						
19	Gorham's	36° 07' 13" N, 05° 20' 31" W, 5 m a.s.l.	Cave	MIS 3-2	P, C	Carrión et al., 2008; Ward et al., 2012
20	Carihuela	37° 26' 22" N, 03° 26' 12" W, 1020 m a.s.l.	Cave	MIS 5-2	P, C	Carrión, 1990, 1992b; Fernández et al., 2007; Carrión et al., 2019; Ochando et al., 2020a
21	Ventanas	37° 26' 25" N, 03° 26' 00" W, 1056 m a.s.l.	Cave	MIS 3-2	P	Carrión et al., 2001; Ochando et al., 2020a
22	Complejo del Humo (A3)	36° 42' 52" N, 4° 20' 42" W, 5 m a.s.l.	Cave	Upper Pleistocene	P	Ochando et al., 2020b
23	Otero	43° 21' 10" N, 03° 31' 41" W, 60 m a.s.l.	Cave	MIS 2	P	Leroi-Gourhan, 1966

(continued on next page)

Table 3 (*continued*)

	Site	Coordinates and altimetry / bathymetry	Type of site	Age/MIS (only Pleistocene)	Pollen (P) Charcoal (C)	References
24	Chufín	43° 17' 33” N, 04° 27' 36” W, 130 m a.s.l.	Cave	MIS 2	P	Boyer-Klein, 1984
25	Oia	42° 00' N, 08° 52' W, 0 m a.s.l.	Cave	MIS 2	P	Ramil-Rego and Gómez-Orellana, 2002; Iriarte et al., 2005
26	Pardo	38° 48' 57” N, 00° 17' 53” W, 650 m a.s.l.	Cave	MIS 2	P	Soler et al., 2008
27	Calaveres	38° 47' 40” N, 00° 00' 59” W, 70 m a.s.l.	Cave	MIS 2	P	Dupré, 1988
Other records with same chronology of Lagar Velho's coprolites						
28	Padul	37° 00' 21” N, 03° 36' 43” W, 723 m a.s.l.	Peat bog	MIS 7-2	P	Pons and Reille, 1988; Camuera et al., 2019
29	Estanya	42° 02' N, 00° 32' E, 670 m a.s.l.	Lake	MIS 2	P	González-Sampériz et al., 2017
30	Tramacastilla	42° 43' 27” N, 00° 22' 07” W, 1668 m a.s.l.	Lake	MIS 3-2	P	Montserrat Martí, 1992
31	Portalet	42° 48' N, 00° 23' W, 1802 m a.s.l.	Peat bog	MIS 2	P, C	González-Sampériz et al., 2006; Gil-Romera et al., 2014
32	Villarquemado	40° 30' N, 01° 18' W, 1000 m a.s.l.	Lake	MIS 6-2	P	González-Sampériz et al., 2013, 2020; Aranbarri et al., 2014
33	Fuentillejo	42° 07' 21” N, 06° 43' 09” W, 635 m a.s.l.	Lagoon	MIS 2	P	Ruiz-Zapata et al., 2008
34	San Gregorio	39° 18' N, 03° 01' W, 640 m a.s.l.	Dune	MIS 2	P	Ruiz-Zapata et al., 2000b
35	Salines	38° 30' 02” N, 00° 53' 18” W, 470 m a.s.l.	Lagoon	MIS 6-2	P	Burjachs et al., 2007; Burjachs, 2009, 2012
36	Banyoles	42° 08' 07” N, 02° 45' 23” E, 173 m a.s.l.	Lake	MIS 2	P	Pérez-Obiol and Julià, 1994
37	KEB 25	40° 48' 12” N, 00° 59' 30” E, 88 m m.w.d	Delta	MIS 2	P	Yll, 1995
38	Caamaño	42° 39' N, 09° 02' W, 0 m a.s.l.	Cliff	MIS 3-2	P	Ramil-Rego et al., 1996; Carrión et al., 2005
39	Tarna	43° 07' N, 05° 15' W, 1415 m a.s.l.	Lagoon	MIS 2	P	Ruiz-Zapata et al., 2000a, 2002
40	Asperillo	37° 05' 13” N, 06° 41' 51” W, 20 to 2 m a.s.l.	Dune	MIS 2	P	Stevenson, 1984; Fernández et al., 2021
41	MD95-2043 (Alborán sea)	36° 08' N, 02° 37' W, 1841 m m.w.d.	Marine record	MIS 3-2	P	Sánchez-Goñi et al., 2002; Fletcher and Sánchez-Goñi, 2008
42	ODP-976 (Alborán sea)	36° 09' N, 04° 08' W, 1107 m m.w.d.	Marine record	MIS 54-2	P	Combourieu-Nebout et al., 1999, 2002, 2009; Bout-Roumazeilles et al., 2007
43	MD99-2331 (Galicia)	42° 09' N, 09° 40' W, 2110 m m.w.d	Marine record	MIS 5-2	P	Sánchez-Goñi et al., 2005; Naughton et al., 2007
44	MD95-2039 (Portugal)	40° 34' N, 10° 20' W, 3381 m m.w.d.	Marine record	MIS 4-2	P	Roucoux et al., 2001, 2005
45	SU81-18 (Portugal)	37° 46' N, 10° 11' W, 3135 m m.w.d.	Marine record	MIS 2	P	Lézine and Denèfle, 1997; Turon et al., 2003

palaeovegetation of the site. It is nevertheless clear that *Pinus sylvestris* was frequently collected by the Lagar Velho groups while other woody species should occur nearby regardless their abundance. Indeed, several of these woody taxa have been found as well in coprolite pollen assemblages (*Quercus*, *Erica*, *Hedera*, Genisteae, *Sorbus*, *Crataegus*, *Ulmus*, *Betula*). It is worth mentioning that heaths and legumes often include pyrophytic species, especially *Ulex*, *Cytisus* and *Erica* (Daibes et al., 2019; Ojeda et al., 2016, 2019; Pausas, 2015; Pausas and Keeley, 2014), so humans may well have made selection of these to promote ignition.

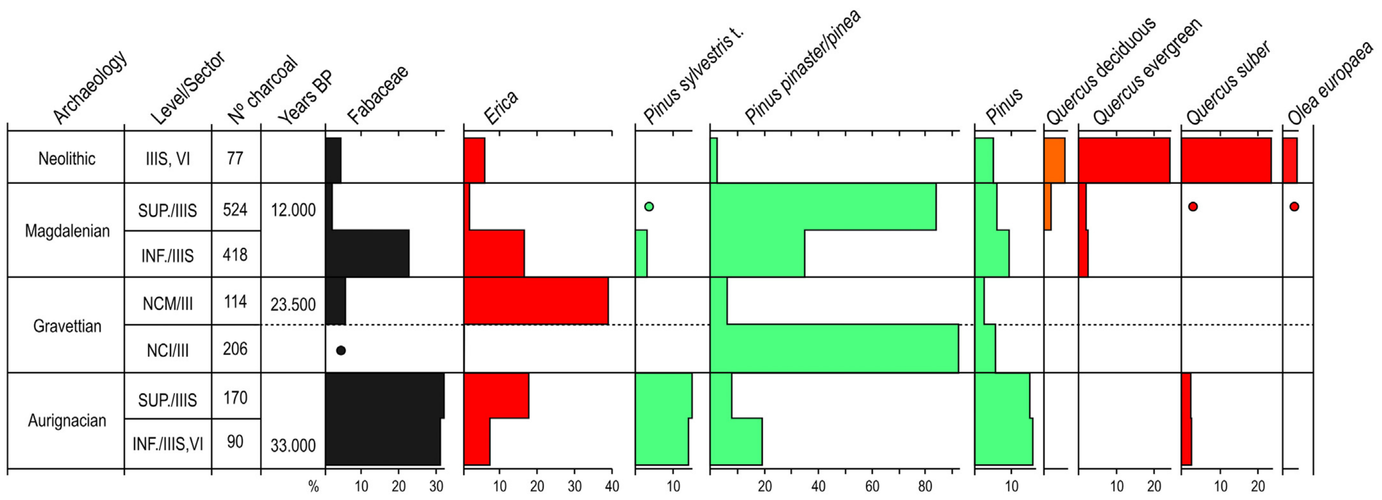


Fig. 11. Anthracological diagram from Cabeço de Porto Marinho. Redrawn from Figueiral (1993).

In general, the pollen spectra of coprolites and sediment, and the charcoal record, seem compatible with a last glacial picture of patchy, forested to semi-forested landscape, with abundance of shrubs and high plant diversity including warm-loving species and riparian, gallery forests (Fig. 10). The occurrences of *Artemisia, Ephedra distachya*, chenopods (Amaranthaceae) and grasses (Poaceae) is in concordance with the existence of regional steppes in western Iberia and the generally cold climate that characterizes MIS2 (Aubry et al., 1997, 2001; Figueiral, 1993; Figueiral and Terral, 2002; Figueiral, unpublished data; Lézine and Denèfle, 1997; Naughton et al., 2007; Roucoux et al., 2001, 2005; Sánchez-Goñi et al., 2005; Turon et al., 2003).

Coprolite, sediment, and charcoal may complement to reconstruct past environments. Studies in Gorham´s and Vanguard Caves, Gibraltar, are a good example of the complementary use of them in palaeoecological reconstructions of the last glacial stages (Carrión et al., 2008, 2018). Coprolites should be expected to reflect different environments coexisting within a patchy landscape rather than a temporal record concerning vegetation stages. In addition, we should take into account that the animal that produced the coprolite has certainly exerted a role in the pollen content (Scott, 1987; Scott and Brink, 1992; Scott et al., 2003). Furthermore, the differences in the pollen composition of the coprolites may have diverse explanations, as coprolites being accumulated at different seasons or reflecting diversity of the regional landscape, or even both situations. Charcoal might reflect the woody component and mostly represent the anthropic choices, and sediment pollen the local environment including the herbaceous types.

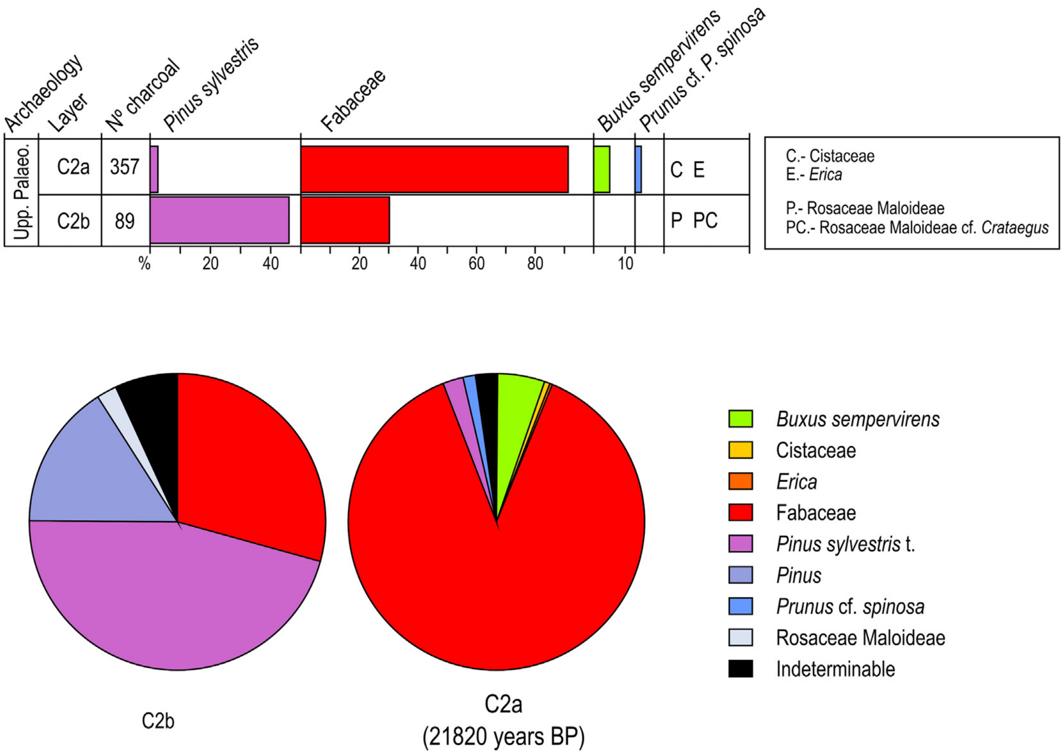


Fig. 12. Anthracological results from Buraca Escura, Portugal. Redrawn from Aubry et al. (2001) and Carrión et al. (2015).

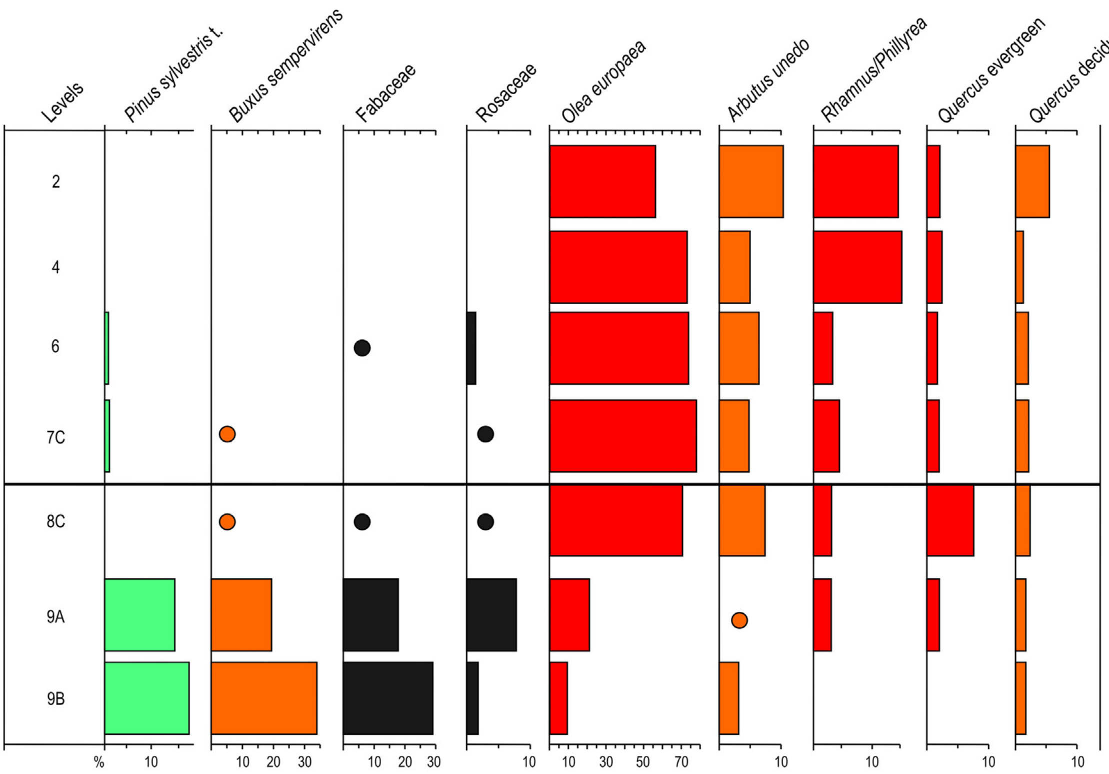


Fig. 13. Anthracological results from Buraca Grande, Portugal. Redrawn from Figueiral and Terral (2002), and Carrión et al. (2015).

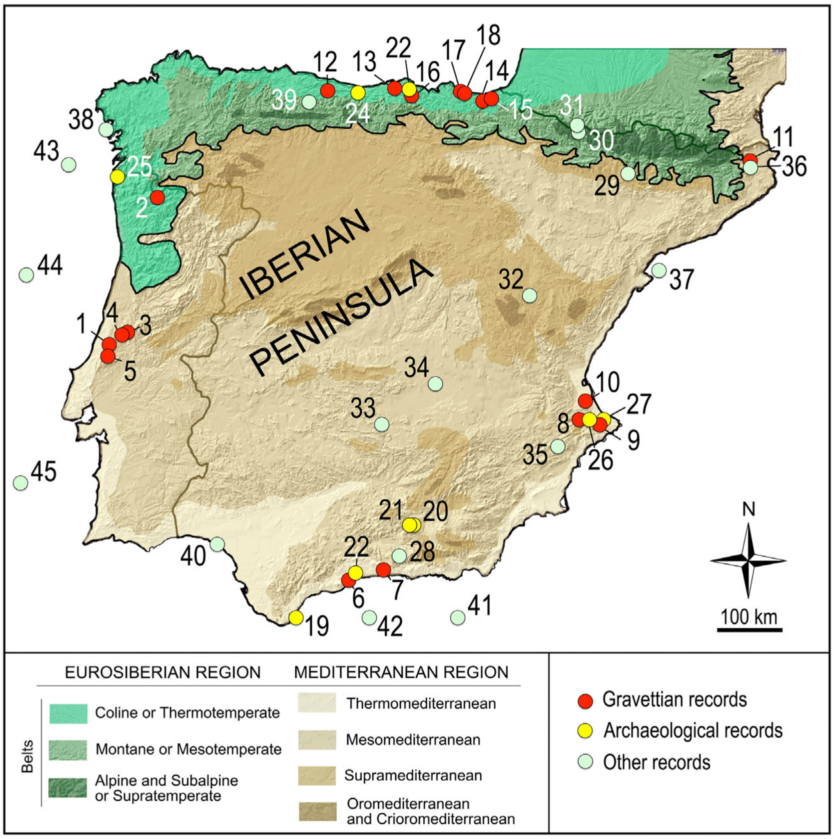


Fig. 14. Location of Iberian records with palaeobotanical data including archaeological caves with Gravettian lithics, and other records synchronous of the Iberian Gravettian.

6.2. Other sources of palaeoecological information

Archaeological data (including lithics and ecofactual elements) from de basal secuence of the Lagar Velho rock-shelter are rather small, due to the limited area of excavation. The faunal remains recovered and the lack of other environmental evidences recovered from the basal sedimentary sequence of Lagar Velho could be a bias of the excavation and is a challenging issue concerning the palaeoevironmental reconstruction of the studied area. Preliminary studies have provided some palaeoecological information on Lagar Velho palaeoecology through the analyses of palaeontological and sedimentological data (Angelucci, 2002; Figueiral and Carcaillet, 2005; Moreno-García and Pimenta, 2002; Pettitt et al., 2002; Queiroz et al., 2002; Zilhão and Almeida, 2002; Zilhão and Trinkaus, 2002). A first observation of the top of the lowest slope deposit identified in the rock-shelter, characterized by cryoclastic breccias and dated to ca. 31.4 ka cal BP, comprises a faunal assemblage dominated by red deer, followed by horse and aurochs, an association that could reflect a relatively open forest. These deposits have been interpreted as the result of a cold event related to HE3, which is consistent with the cryoclastic nature of the deposit (Zilhão and Almeida, 2002). Major climatic impact of HE3 on the Iberian Atlantic seaboard is apparent in the pollen profile of the deep-sea core MD95-2042 (Sánchez-Goñi and d'Errico, 2001; Sánchez-Goñi et al., 2002), as we shall see later. The erosional event identified at the top of the cryoclastic accumulation is consistent with patterns of accumulation and erosion previously reported for the open air sites of the earliest Upper Paleolithic of Portugal (Aubry et al., 2011, 2012; Zilhão, 1995, 1997).

The decrease in the representation of red deer and horse together with the presence of squirrels in the overlying sedimentary unit dated to 29.2 ka cal BP, point to a more wooded environment (Moreno-García and Pimenta, 2002). The presence of *Cervus elaphus*, *Sus scrofa*, Gliridae and *Sciurus vulgaris* and the high sedimentation rate that was determined for this unit suggest a more temperate environment than previously.

Above, the sedimentary unit that comprehends layer 143 (ca. 30 and 27.4 ka cal BP) shows evidences of human occupation taking place on the top of the stabilized surface with soil development. The faunal record and the coprolite pollen from this layer suggest an opening of the forested areas with the establishment of a mosaic of different landscapes around the site. Although zooarchaeological studies are in progress, the large mammals recovered from layer 143 are clearly dominated by red deer, a mixed feeder that can browse in open forests and graze in grasslands. The presence of species related to more closed forests, such as wild boar and roe deer are also relevant in this layer. By contrast, open environmental taxa are less frequent, such as equids. In this sense, and despite the fact that the floristic assemblage of coprolites is dominated in most cases by trees and shrubs pollen (*Pinus*, *Quercus*, *Juniperus* and *Erica* mainly, together with other mesophytic trees and other Mediterranean elements), it can be observed a remarkable representation of xerophytes such as *Artemisia* and Amaranthaceae, but especially Poaceae. In this way, the increase in steppe components allowed the establishment of a more open environment than in the preceding times, as well as the configuration of other landscape formations that could dominate during this period.

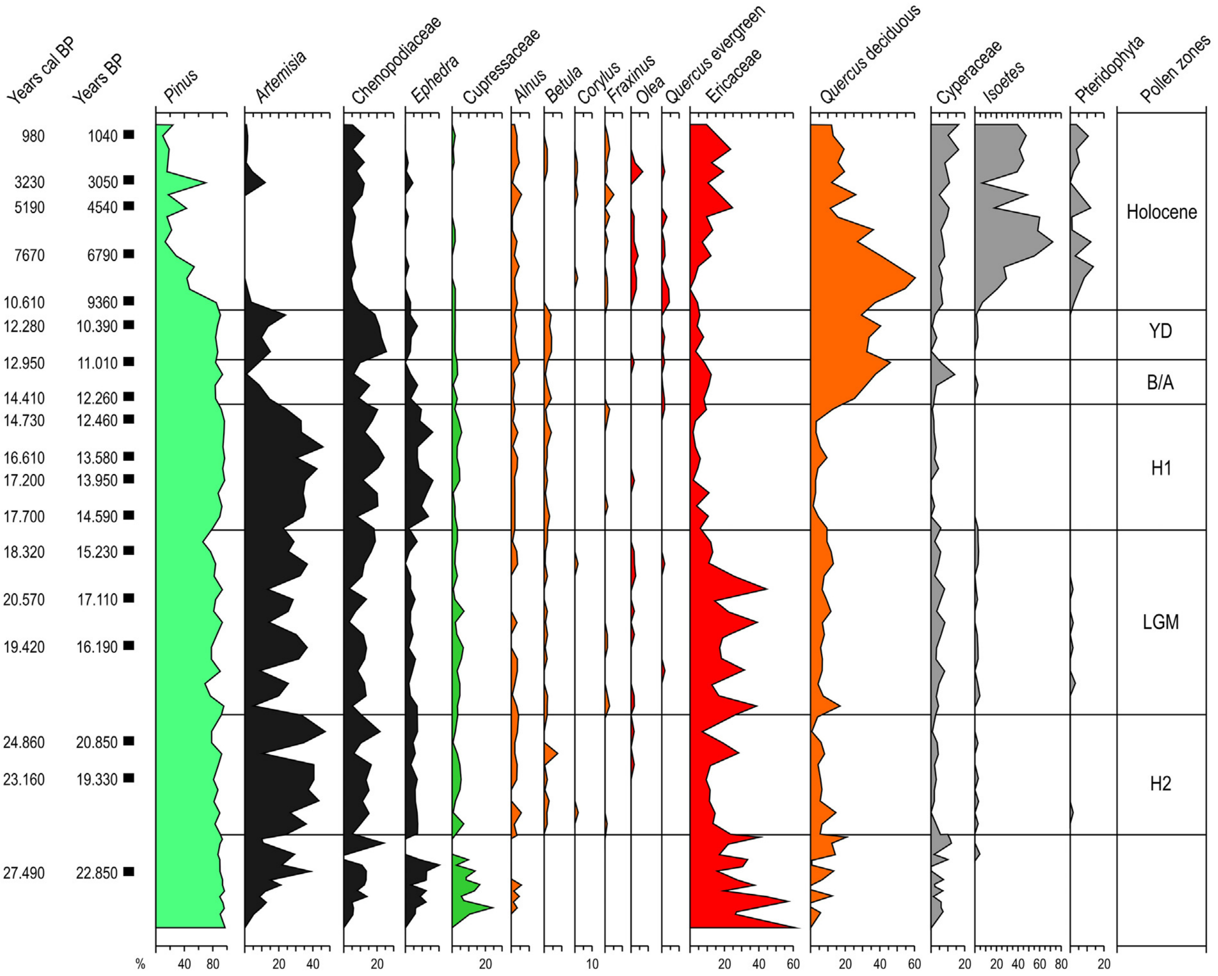


Fig. 15. Pollen diagram of the SU81-18 core. Redrawn from Lézine and Denèfle (1997), Turon et al. (2003), and Carrión et al. (2015).

The sandy loam deposit overlying layer 143 recorded a period of large and repeated human use of the rock-shelter. This move in the human use of the site coincides with a return to cold conditions in the area. Thus, the charcoal fragments analysed in Cabeço de Porto Marinho III show 98.5% of *Pinus* among the 206 identified pieces of charcoal from the lower cultural level, among which are *Pinus sylvestris* and *Pinus pinaster*/*pinea* (Figueiral, 1993; Figueiral and Carcaillet, 2005; Zilhão et al., 1995). Moreover, a charcoal of *Pinus sylvestris* trees from Cortegaça also was dated to ca. 22.6 ka cal BP (Granja and Soares de Carvalho, 1995).

6.3. Gravettian landscapes in western Portugal and the Iberian Peninsula

The vegetation picture inferred from pollen in Lagar Velho suggests the local existence of forest refugia of mesothermophilous trees, including Atlantic and Mediterranean elements. Indeed, these full-glacial times were undoubtedly stressful for tree populations in western Eurasia (Aubry et al., 1997, 2001; Badal, 1990; Badal and Martínez-Varea, 2018; Carrión, 1991, 1992a; Carrión and Munuera, 1997; Figueiral, 1993; Figueiral and Terral, 2002; Figueiral, unpublished data; Iriarte-Chiapusso, 2011a, 2011b; Iriarte-Chiapusso and Ayerdi, 2016-2017; Pinto et al., 2006; Villaverde et al., 2019). Palaeobotanical data of the Iberian Peninsula suggests that the Gravettian inhabitants had to adapt to an unequal distribution of resources (Straus et al., 2000, 2011, 2012; Villaverde et al., 2019; Zilhão, 2005, 2017).

Palaeovegetation data for the Iberian Peninsula are scarce for the Gravettian period (Carrión et al., 2013, 2015; Fig. 14 and Table 3). Considering the Portuguese palaeorecord, the charcoal analysis of Cabeço de Porto Marinho suggests populational absence of *Pinus sylvestris* with decreased Fabaceae and dominance of heather during the Late Gravettian (Figueiral, 1993) (Fig. 11). Similarly, in a hearth at Lapa do Anecrial associated to the Terminal Gravettian or Proto-Solutrean, Scots pine, Fabaceae and Ericaceae are the main types identified (Zilhão, 1997). At the Cortegaça beach (Esmoriz), near to the northern limit of the west-central sandy littoral fringe, fossil tree trunks are evidence for *Pinus sylvestris* formation, dated from ca. 28–22 ka cal BP (Granja, 1993).

The trend towards an opening of the landscape in Lagar Velho during the formation of layer 143 is in concert with the floristic component of the archaeological site of Buraca Escura (Fig. 12), which allows inferring the existence of relatively open vegetation, with sporadic presence of Scots pine, *Erica*, *Buxus sempervirens*, Cistaceae and Rosaceae (Aubry et al., 2001). (See Fig. 13.)

In the Spanish record (Fig. 4 and Table 3), the Gravettian occupation of Bajondillo cave coincides with the expansion of heliophytes, the retraction of trees and the disappearance of the xerothermophilic maquia (López-Sáez et al., 2007). Anthracological studies in Cueva de Nerja show a similar composition for all samples of the Gravettian levels, with the presence of *Pinus nigra* and a higher abundance of *Pinus pinea*, accompanied by woody legumes, junipers and rockrose (Badal, 1990). Pollen in Cova Beneito (Carrión, 1991, 1992a; Carrión and Munuera, 1997) shows for the Gravettian increased Poaceae, *Artemisia* and *Ephedra distachya*, and decreased *Pinus*. The Gravettian charcoal record of Cova de les Cendres (Badal and Carrión-Marco, 2001; Badal and Martínez-Varea, 2018; Villaverde et al., 2019), show a predominance of *Pinus* t. *nigra* and *Pinus sylvestris* accompanied by oaks, junipers, Fabaceae and Lamiaceae. However, there is a main trend along the sequence indicating an opening of the landscape towards the end of the Gravettian and the beginning of the Solutrean, between ca. 23 and 19 ka cal BP. In the case of the Malladetes cave, the Gravettian period is characterised by oscillations in the concentration of *Pinus* pollen, the dominant taxon, and accompanied by abundant *Phillyrea* and small proportions of *Alnus*, deciduous *Quercus*, *Ulmus*, *Fraxinus*, *Pinus pinaster*, Cupressaceae and Ericaceae (Dupré, 1980). The palynological record of Cova de l'Arbreda shows the dominance of Poaceae, Asteraceae, *Artemisia* and *Ephedra*, with low percentages of arboreal pollen, in the coldest moments of the Gravettian (Burjachs, 1987; Burjachs and Renault-Miskovsky, 1992).

The Abrigo de Sopeña (Asturias) allowed for the study of the Gravettian period based on anthracological analyses (Pinto et al., 2006). The floristic information obtained is revealing, since it differs from the results obtained in other Cantabrian sites. *Juniperus* is the dominant taxon alternating with the presence of *Erica*, *Ulex* and *Cytisus*, among others, with a striking absence of *Pinus sylvestris*. The greater representation of *Juniperus* is clear in the ALV-2 sample, as well as the appearance of *Ulex* in the ALV-6 and ALV-8 samples. In this sense, a similar pattern occurs in Morín Cave (Cantabria), where the pollen analyses show relatively important concentrations of *Juniperus* during the Gravettian occupation (Leroi-Gourhan, 1971). A succession of cold and temperate conditions is observed in a climate whose general trend is cooling. Thus, the changes in the concentrations of taxa such as *Alnus*, *Juniperus*, *Quercus*, *Ulmus* and Cichorioideae are interpreted in terms of climatic pulses.

In Amalda Cave, Basque Country, the Gravettian levels show a predominance of pine, sometimes accompanied by hazelnuts, oaks, birches and Cupressaceae, and with a marked proliferation of grasses and Asteraceae, which indicate a trend towards a decrease in tree pollen and an opening of the landscape at the end of the period (Dupré, 1990). Additionally, pollen remains had been studied in several Gravettian sites located along the Basque Country (Arrizabalaga et al., 2021; Iriarte-Chiapusso and Murelaga, 2013), among which stand out Aitzbitarte III (Iriarte-Chiapusso, 2011a), El Mirón (Straus et al., 2011, 2012), Ondaro (Iriarte-Chiapusso and Ayerdi, 2016-2017), and Santimamiñe (Iriarte-Chiapusso, 2011b), showing in most cases a predominance of cold climate events within this region (Arrizabalaga et al., 2021; Iriarte-Chiapusso et al., 2016).

The alternation of cold and temperate phases in the north and northwest of the Iberian Peninsula for the Gravettian period, although with a tendency towards the loss of certain vegetal tree cover, can be observed in the percentages and in the diversity of taxa showed by Lagar Velho coprolites. In open environmental contexts depleted in arboreal formations, bones have provided an alternative as a fuel as it was suggested in e.g. Coímbre Cave (northern Iberian Peninsula) (Yravedra et al., 2017). However, this behaviour has not yet been documented at Lagar Velho.

The establishment of more steppe landscapes, as well as the increase in the xerophytic component, is confirmed by other sequences from lakes, peat bogs, deltas, lagoons, dunes and cliffs (Fig. 14 and Table 3). Among them, the following stand out for the studied period: Padul (Camuera et al., 2019; Pons and Reille, 1988), El Portalet (Gil-Romera et al., 2014; González-Sampériz et al., 2006), Estanya (González-Sampériz et al., 2017), Tramacastilla (Montserrat Martí, 1992), Villarquemado (Aranbarri et al., 2014; González-Sampériz et al., 2013, 2020), KEB 25 (Yll, 1995), Caamaño (Carrión et al., 2005; Ramil-Rego et al., 1996), Tarna (Ruiz-Zapata et al., 2000a, 2002), Fuentillejo (Ruiz-Zapata et al., 2008), San Gregorio (Ruiz-Zapata et al., 2000b), Salines (Burjachs, 2009, 2012; Burjachs et al., 2007), Banyoles (Pérez-Obiol and Julià, 1994), and to a lesser extent, El Asperillo (Fernández et al., 2021; Stevenson, 1984).

Marine records available for the Atlantic coast allowed to the reconstruction of the vegetation for the period in which the Lagar Velho coprolite samples were abandoned (Fig. 14 and Table 3). MD95-2039, focused on the 65–10 ka cal BP interval, shows a dominance of Poaceae and other herbaceous plants, as well as fluctuations in *Pinus* concentration and the continuous presence of Ericaceae and *Juniperus* between 27 and 15 ka cal BP (Roucoux et al., 2001, 2005). Similarly, SU81-18 (Fig. 15) comprising the last 27 ka, reflects high percentages of *Pinus*, accompanied by notable concentrations of *Artemisia* and Ericaceae between 27.5 and 23.2 ka cal BP, corresponding to a dry and cold climate (Lézine and Denèfle, 1997; Turon et al., 2003). In addition, MD99-2331 recovered approximately 65 km the coast of Galicia involving the last 130 ka shows a decline in *Pinus*, accompanied by the noticeable presence of Ericaceae, as well as a trend towards an increase in Poaceae and other herbaceous plants during the MIS 2 (Naughton et al., 2007; Sánchez-Goñi et al., 2005). This marked trend towards the dominance of semi-desert vegetation accompanied by arboreal species (mainly *Pinus*) and by shrub species such as Ericaceae can also be observed in other marine records from the Alboran Sea ODP-976 (Bout-Roumazeilles et al., 2007; Combourieu-Nebout et al., 1999, 2002, 2009) and MD95-2043 (Fletcher and Sánchez-Goñi, 2008; Sánchez-Goñi et al., 2002).

Overall, based on our results and previous studies carried out for the Gravettian period in Portugal and in other sequences of the Iberian Peninsula, the vegetation cover is generally characterized by open woodlands with a ground layer rich in ericaceous, several Leguminosae species, and to a lesser extent thermophytes, Mediterranean and deciduous elements, which would be restricted to more protected areas from the cold (e.g. valleys) and environments with higher moisture and exposed to sun. In the same way, xerophytes taxa present a trend to increase as a consequence of a drop in temperatures and the subsequent establishment of the LGM.

7. Final remarks

The Gravettian palyno-record of Lagar Velho depicts a diverse vegetation landscape, which may well represent a general trend in western Iberian coastlines for this period. Thus, the pollen results presented here provide new insights into the biogeography of the Gravettian populations in SW Iberia that used the present-day thermo- and mesomediterranean belts as corridors.

It is likely that the temperature increase that took place during the period established between ca. 30 and 27.3 ka cal BP (period in which the coprolites that have been studied appear) favored the growth of a wider and dense vegetation at low altitude in karst systems. This climatic improvement could favor the growth of some species of the Mediterranean forest such as evergreen *Quercus ilex*, *Quercus suber*, *Pinus halepensis*, *Pinus pinaster*, *Sambucus ebulus*, *Olea*, *Pistacia*, *Myrtus*, *Phillyrea*, *Ephedra fragilis*, *Ephedra distachya*, *Erica arborea* and *Cistus* in environments with milder conditions, as well as the growth of riparian taxa including species of *Alnus*, *Frangula*, *Fraxinus*, *Salix*, and *Ulmus*. Indeed, the presence of riparian species near the site is in itself a proof of fresh water availibility both for humans and hunted animals that frequented the region. Other Iberian Gravettian sites studied for pollen provide also evidences of riparian environments such as: Bajondillo (Cortés-Sánchez et al., 2008; López-Sáez et al., 2007), Beneito (Carrión, 1991, 1992a, 1994; Carrión and Munuera, 1997), Cendres (Badal and Carrión-Marco, 2001; Badal and Martínez-Varea, 2018; Villaverde et al., 2019), Malladetes (Dupré, 1980), Morín (Leroi-Gourhan, 1971) and Amalda (Dupré, 1990).

In sum, the prolonged persistence of human populations in the study region could be associated to the persistence of mild climatic conditions in specific periods and habitats of the Upper Pleistocene (Finlayson, 2008; Finlayson et al., 2006; Sepulchre et al., 2007), even despite the occurrence of colder phases. The coastal shelves are also important for the preceding Neanderthals and early Upper Palaeolithic people (Finlayson, 2004; Finlayson et al., 2000), Bajondillo (Cortés-Sánchez et al., 2004), Abrigo 3 and 4 del Complejo del Humo (Ferre et al., 2004) and Carihuela (Carrión et al., 2019), among others. Carrión et al. (2008, 2018) maintain that the late Pleistocene coasts of the south of the Iberian Peninsula are outstanding in showing the coexistence of thermo-, meso-, and supramediterranean plant and animal including dry and humid, wooded and treeless biotopes.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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