Review of Palaeobotany and Palynology 304 (2022) 104725

Contents lists available at ScienceDirect

Review of Palaeobotany and Palynology

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

Palynological investigations in the Orce Archaeological Zone, Early Pleistocene of Southern Spain

Juan Ochando [a,b,*], José Carrión [a,c], Yul Altolaguirre [d], Manuel Munuera [e], Gabriela Amorós [a], Gonzalo Jiménez-Moreno [f], José Solano-García [g], Deborah Barsky [h,i], Carmen Luzón [j], Christian Sánchez-Bandera [h,i], Alexia Serrano-Ramos [j], Isidro Toro-Moyano [k], Juha Saarinen [l], Hugues-Alexandre Blain [h,i], Hervé Bocherens [m], Oriol Oms [n], Jordi Agustí [o,h,i], Mikael Fortelius [p], Juan M. Jiménez-Arenas [g,q]

[a] *Department of Plant Biology (Botany Area), Faculty of Biology, University of Murcia, Campus de Espinardo, 30100 Murcia, Spain*
[b] *Sapienza University of Rome, Department of Environmental Biology, Rome, Italy*
[c] *Evolutionary Studies Institute, University of Witwatersrand, Johannesburg, South Africa*
[d] *ROCEEH Research Centre 'The role of culture in early expansions of humans' of the Heidelberg Academy of Sciences, Senckenberg Research Institute, 60325 Frankfurt am Main, Germany*
[e] *Department of Agricultural Engineering, Polytechnic University of Cartagena, 30203 Cartagena, Spain*
[f] *Departamento de Estratigrafía y Paleontología, Universidad de Granada, Granada, Spain*
[g] *Departamento de Prehistoria y Arqueología, Universidad de Granada, Museo Primeros Pobladores de Europa 'Josep Gibert', Orce (Granada), Spain*
[h] *IPHES-CERCA, Institut Català de Paleoecologia Humana i Evolució Social, Zona Educacional 4, Campus Sescelades URV (Edifici W3), 43007 Tarragona, Spain*
[i] *Departament d'Història i Història de l'Art, Universitat Rovira i Virili, Avinguda de Catalunya 35, 43002 Tarragona, Spain*
[j] *Programa de Doctorado en Historia y Artes, Universidad de Granada, Granada, Spain*
[k] *Museo Primeros Pobladores de Europa 'Josep Gibert', Orce (Granada), Spain*
[l] *Department of Geosciences and Geography, University of Helsinki, Helsinki, Finland*
[m] *Faculty of Science, University of Tübingen and Senckenberg Centre for Human Evolution and Palaeoenvironment, Tübingen, Germany*
[n] *Departamento de Geologia, Universitat Autònoma de Barcelona, Bellaterra, Spain*
[o] *ICREA, Institución Catala de Recerques Avançades, Barcelona*
[p] *Finnish Museum of Natural History - LUOMUS and Department of Geosciences and Geography, University of Helsinki, Helsinki, Finland*
[q] *Instituto Universitario de Investigación de la Paz y los Conflictos, Universidad de Granada, Granada, Spain*

ARTICLE INFO

Article history:
Received 16 May 2022
Received in revised form 4 July 2022
Accepted 6 July 2022
Available online 11 July 2022

Keywords:
Palaeobotany
Human evolution
Pleistocene
Cenozoic
Orce
Spain

ABSTRACT

Palynological investigations in the Orce Archaeological Zone (OAZ) (Guadix-Baza Basin, Granada, Spain), Venta Micena 1 (VM1), Barranco León (BL) and Fuente Nueva 3 (FN3) are presented. This archaeological region is connected with the first *Homo* populations in Western Eurasia during the Early Pleistocene. The VM1 pollen record is characterized by *Ephedra*, and to a lesser extent, *Pinus*, *Juniperus* and evergreen *Quercus*, occassionally accompanied by *Olea*, Genisteae, *Erica*, deciduous *Quercus*, *Alnus*, *Castanea*, *Fraxinus*, *Salix* and *Phillyrea*. BL is dominated by *Juniperus*, *Olea*, *Pinus*, Poaceae, and evergreen *Quercus*. FN3 is characterized by an open Mediterranean woodland dominated by evergreen *Quercus*, *Pinus*, *Juniperus* and *Olea*, accompanied by deciduous *Quercus*, *Castanea*, *Populus*, *Salix*, *Ulmus*, *Fraxinus*, *Pistacia*, *Phillyrea*, Genisteae, *Erica*, *Cistus*, and *Ephedra fragilis*. Relic Tertiary taxa in OAZ include *Carya*, *Pterocarya*, *Eucommia*, *Zelkova*, and *Juglans*. The Early Pleistocene OAZ vegetation is a mosaic of different landscapes embracing mesophytes, thermophytes, xerophytes, xerothermophytes, and Mediterranean elements. These finds are compared with former pollen analyses in the region and beyond within the Iberian Peninsula.

1. Introduction

This paper provides palynological investigations performed in the Orce Archaeo-paleontological Zone (OAZ) and discusses their implications in palaeoecological and phytogeographical contexts. Except for an attempt carried out by Jiménez-Moreno at the beginning of this century (Jiménez-Moreno, 2003), previous efforts to find pollen in these localities were unsuccessful, such as is often the case with archaeological and continental paleontological sites (Carrión et al., 2009). Notwithstanding the difficulties, attemping new pollen analyses in the OAZ were worth the effort due to the exceptional nature of the OAZ and to the

---

[*] Corresponding author.
E-mail address: juan.ochando@um.es (J. Ochando).

https://doi.org/10.1016/j.revpalbo.2022.104725

scarcity of palaeobotanical data of Early Lower Pleistocene in southwestern Europe (e.g. Leroy, 1997; Postigo-Mijarra et al., 2007; Agustí et al., 2018; Altolaguirre et al., 2019, 2020, 2021). Furthermore, our experience with archaeopalynology points out that sterility is not always ubiquitous within the excavation area of a given site (Carrión et al., 2009).

The OAZ is located at the NE of the Guadix-Baza intramontane basin, found at the SE Iberian Peninsula. This basin was a Mediterranean–Atlantic gateway that at the Messinian-Zanclean interval (Hüsing et al., 2010) was infilled with continental sediments until the Middle Pleistocene (Fig. 1). The current landscape is composed of hills, deep gorges, and ravines, populated by vegetation typical of dry Mediterranean climate, which is often characterized by vast treeless areas. However, this landscape was very different during the Early Pleistocene due to the presence of a lacustrine-palustrine system and plausibly different climatic conditions.

An outstanding feature in the Early Pleistocene Guadix-Baza subbasin was the existence the large saline basin, the Baza lake, whose cyclical retraction provoked the emergence of freshwater springs, ponds and pools, with associated increases in biodiversity (Granados et al., 2021) and known as the Orce wetlands (Martínez-Monzón et al., 2022). Lake sedimentary architecture was also ruled by the different sedimentary accumulation rates, being reduced at the passive basin margins and being expanded at the basin depocenter (tectonic active margin to the east of the Baza fault (Haberland et al., 2017). Such physiographical changes, including subsequent erosive events, are linked to the occurrence of at least 15 Pleistocene sites that have yielded remains of extinct mammals (Maldonado-Garrido et al., 2017). Among these, three OAZ sites are highlighted for their wealth in palaeontological and archaeological remains: Venta Micena (VM), Barranco León (BL) and Fuente Nueva 3 (FN3) (Figs. 1–5). There are no accurate age models for the sedimentary sequences that occur in those sites, nonetheless, according to geo- and biochronological information, the oldest one is VM, followed by BL and the youngest being FN3. VM numerical dates have been obtained using combined U-series/ESR method on ungulate teeth (Duval et al., 2011). The estimated temporal range is 1.37 ± 0.24 Ma. However, the presence of *Allophaiomys ruffoi* (Agustí et al., 2010) and *Soergelia minor* are interpreted as indicative of a *c.* 1.6 Ma age for VM. On the other hand, BL has different numerical dates according to the stratigraphic level dated. In this case, the dating technique applied was ESR on optically bleached quartz grains, giving ages encompasses between 1.2 ± 0.09 Ma in the upper part, and 1.88 ± 0.19 Ma at the base. D1 and D2 yielded an age of 1.46 ± 0.17 Ma (Toro-Moyano et al., 2013). The presence of *A.* aff. *lavocati* and the absence of *S. minor* and the presence of *Equus sussenbornensis* in levels D1 and D2 are indicative of a younger age (Rook and Martínez-Navarro, 2010) for those two levels of BL. Lastly, FN3 was dated, as

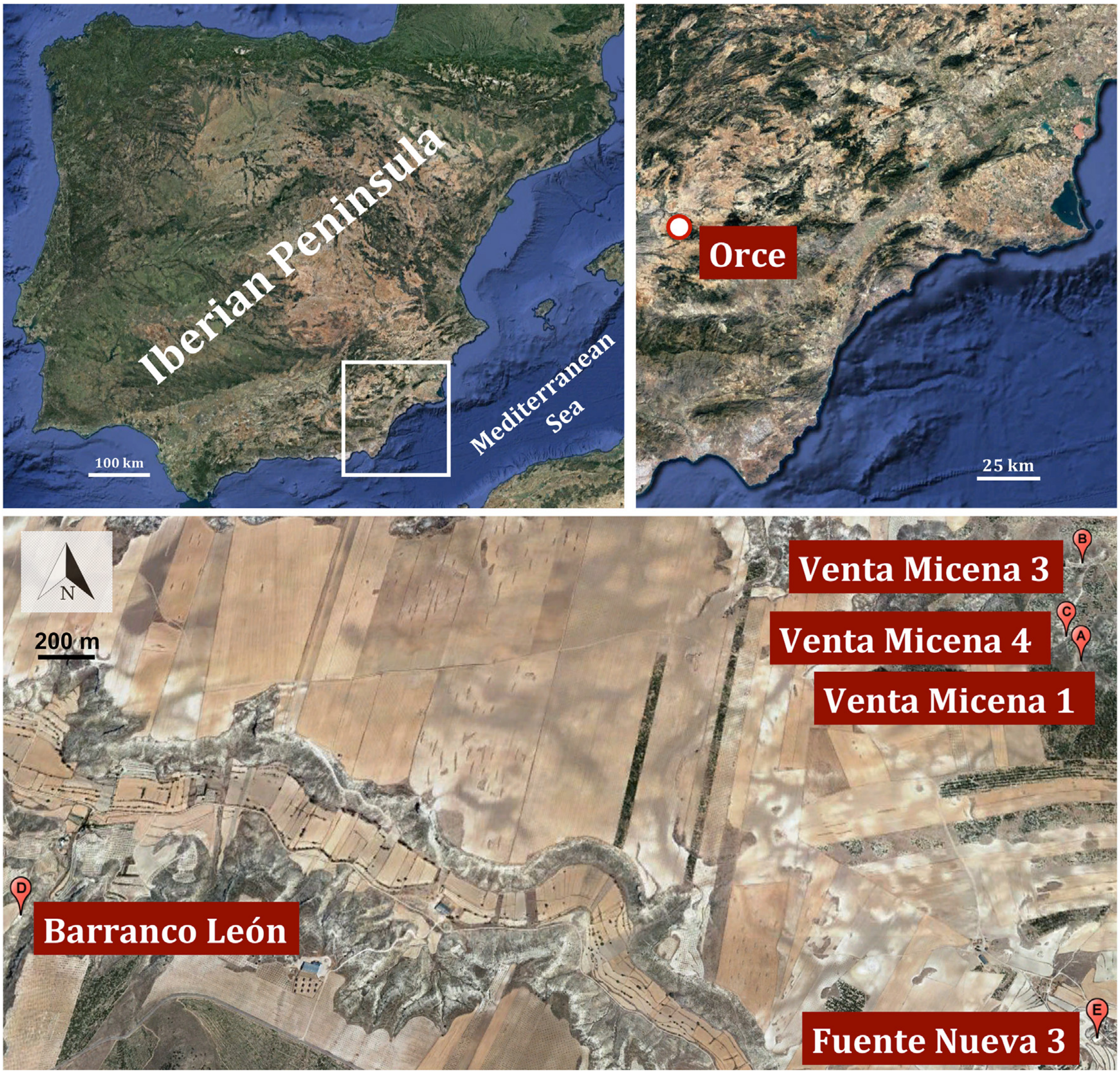


Fig. 1. Location of the Orce Archaeological Zone (OAZ) sites in the Guadix-Baza Basin of southeastern Spain.

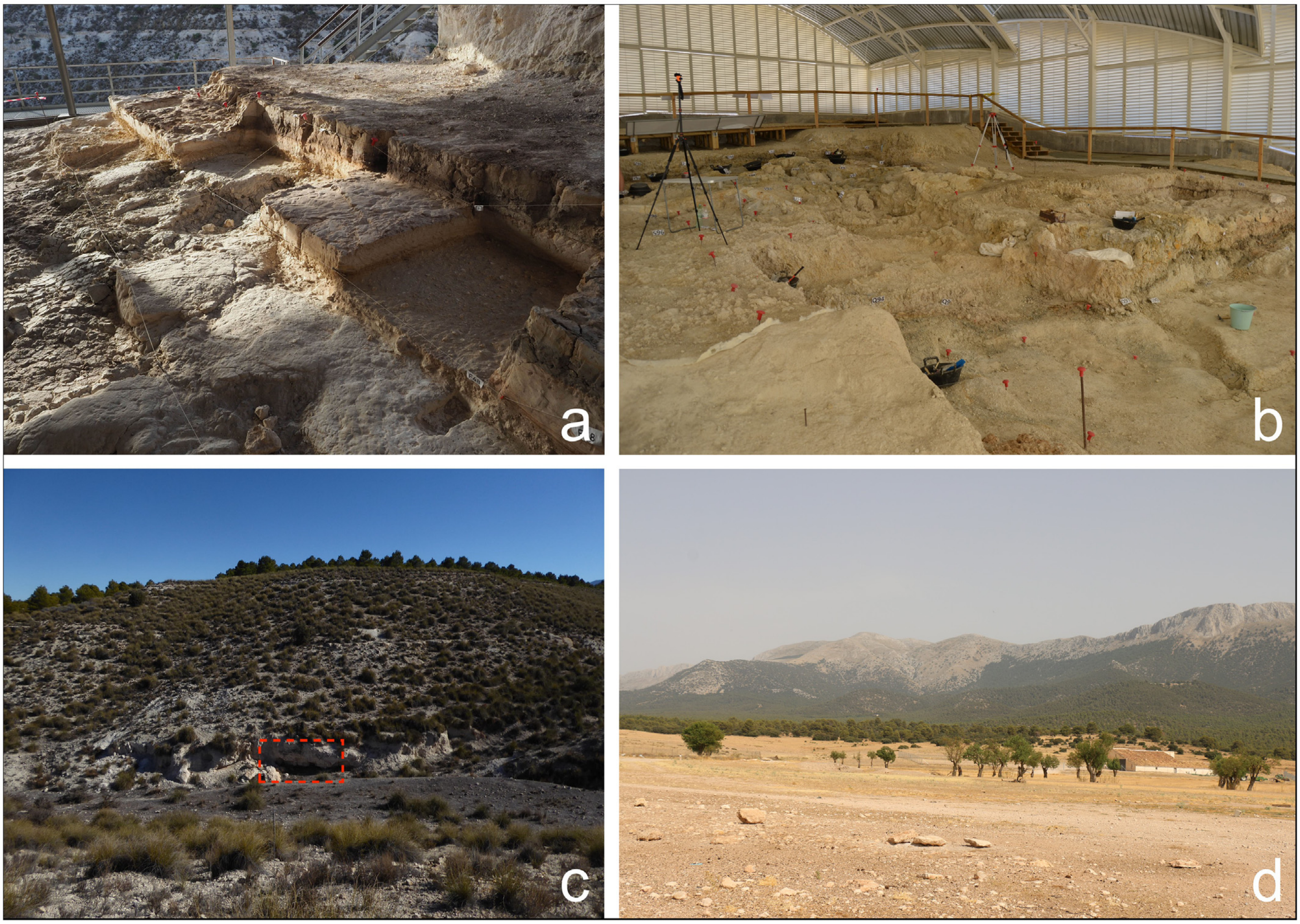


Fig. 2. Excavation sites studied for pollen: (a) Barranco León (BL), (b) Fuente Nueva 3 (FN3), (c)Barranco de los Zagales, Venta Micena 1 (VM1). (d) Sierra de María-Los Vélez mountain range in the southern margin of the Guadix-Baza Basin.

VM, by the means of combined U-series/ESR method (Duval et al., 2012). Results for a horse tooth sample from level 5 yielded a range of 1.19 ± 0.21 Ma. The younger age for FN3 with respect to BL is supported by the evolutionary stage of *Mimomys savini* (Lozano-Fernandez et al., 2015). In addition, paleomagnetism reveals Pre-Jaramillo subchron ages for FN3 and BL (Oms et al., 2000).

VM is a deposit which has yielded several nearby palaeontological sites. Among them, two rich macrovertebate fossiliferous sites stand out, VM3 (e.g. Palmqvist et al., 2022) and VM4 (Luzón et al., 2021). However, none of them have provided abundant microvertebrate remains. On the contrary, VM1 was fertile in such remains, specially in rodents (Agustí et al., 1987). From a stratigraphical point of view, the VM section is composed by 6 units (A to E, see Granados et al., 2021) being Unit C the richest. This unit is subdivided into 3 intervals. Unit C0 is composed of sandy-micritic materials while C1 and C2 are composed of micritic limestone. Unit C is visible along the Barranco de los Zagales, the ravine at the head of which the VM1 section is located (Figs. 2, 3). The VM1 section is rich in microinvertebrates and represents a freshwater pond (Granados et al., 2021). VM3 and VM4 are very similar in terms of geological and sedimentological characteristics (Granados et al., 2021), with fossil remains resting on two different palaeosurfaces in VM4 (Luzón et al., 2021). Nevertheless, they exhibit interesting differences from a taphonomical point of view. While VM3 has been characterized as a hyaena den (vg. Arribas and Palmqvist, 1998), VM4 has been recently interpreted as a marginal area where more biotic agents acted (Luzón et al., 2021, although see Palmqvist et al., 2022).

BL is a succession including 10 litostratigraphical units (A, B, C, D1, D2, F1–F2, E1–E2 and G) (vg. Oms et al., 2011) and two levels with evidences of anthropic activities (vg. Toro-Moyano et al., 2009, 2011, 2013; Espigares et al., 2019; Titton et al., 2018, 2020, 2021) (Fig. 4). D1 and D2 are two distinct levels, although the name may suggest that they are two sublevels. D1, the oldest, provided a deciduous mandibular tooth that represents the oldest hominin fossil evidence from the westernmost part of Eurasia (Toro-Moyano et al., 2013). The D1 level is the result of a combination of a primary and a secondary deposit that includes materials brought by a flash flood event and others materials deposited *in situ* (Titton et al., 2021). Level D2 findings differs from level D1 in that is basically *in situ* sedimentation. Lithic industry is found at level D2 (Titton et al., 2021), and at level D1 and was knapped using two main raw materials: flint and limestone, and the presence of subspheroids is indicative of a late Oldowan (Titton et al., 2020). The use of small-sized flakes to cut meat from the carcasses of large mammals has been attested (Yravedra et al., 2022) in a presumed development of a variability of subsistence strategies within a scenario of interaction with other carnivores, with scavenging activities and possible primary access to carcasses.

FN3 is the most complex site from a stratigraphical point of view (Fig. 5) comprising 12 levels (Oms et al., 2011) of which level 5 has been the most studied. This level embraces remains of lithic industry (Toro-Moyano et al., 2009, 2011, 2013; Barsky et al., 2015, 2018), extinct fauna (vg. Ros-Montoya et al., 2021) and human activity on faunal remains (Espigares et al., 2019; Yravedra et al., 2022). Level 2 is also rich

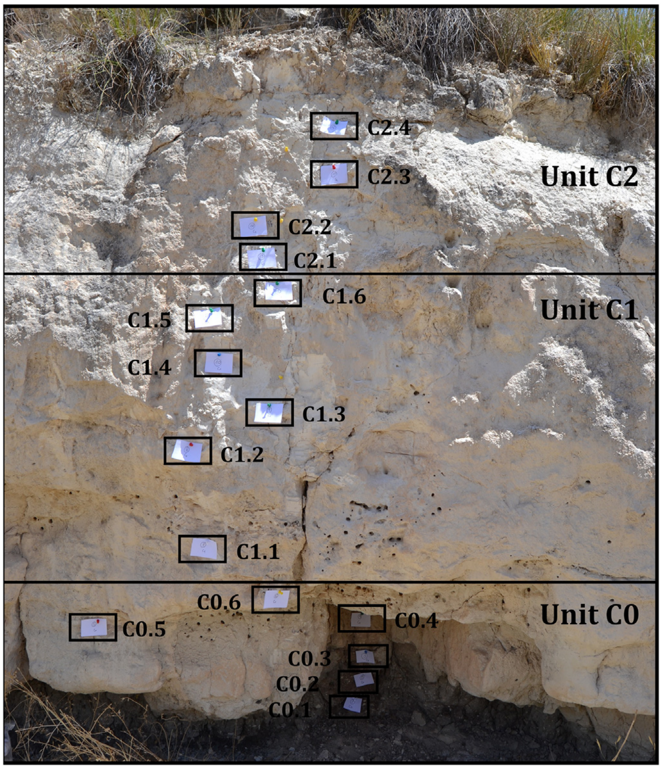


Fig. 3. Lithostratigrafical units and section sampled for pollen analysis in VM1.

in archaeological and palaeontological finds. As in BL, the stone tools were knapped on flint and limestone.

2. Geological setting

2.1. Venta Micena

The stratigraphical succession of Venta Micena (VM) has been defined from five different correlated sections [VM1, VM2, VM3, VM4 and VMX (= Venta Micena – Mushroom Cave)] (Granados et al., 2021). Six units have been described in VM. Unit A is visible at VMX and composed by dolomitic marls and micritic dolostones. The presence pedogenic features such as root bioturbation and the relatively poor content of invertebrates are indicative of important subaerial exposure. Unit B is also present at VMX and consists of bioclastic sands, marls and mudstones. Unit C is divided in 3 parts. C0 is consisted of whitish sandy micritic limestone that is locally greenish and blackish (the last one only visible at VM1). The upper part of Unit C is micritic known as VM limestone contains the macrovertebrate sites and has a thickness of around 1.5 m. Specifically, the lower half of the VM limestone (interval C1) contains fossil bones, with more than 50 elements per m^2, while the upper half (C2) is rather poor in fossil bones. It has been documented that the bones rest on the relief of two paleosurfaces (Luzón et al., 2021), indicating that they accumulated during two phases followed by micritic mud depositions. Generally, no invertebrate fauna is found in unit C, except in some sections such as section VM1, containing ostracods, gastropods and charophyte gyrogonites. Unit D contains muddy limestones interbedded with sandy marls, dolostones and marly dolostones. Some levels in this unit show traces of pedogenic features. Unit E is a sequence of calcareous-dolomitic marls and marly-sandy dolostones alternating with facies of sands and gravels with cross-stratification.

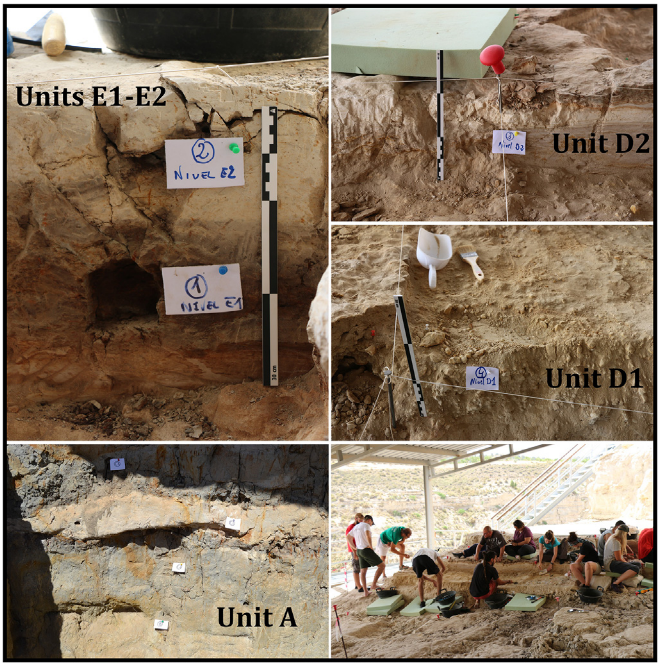


Fig. 4. Lithostratigrafical units and sections sampled for pollen analysis in BL.

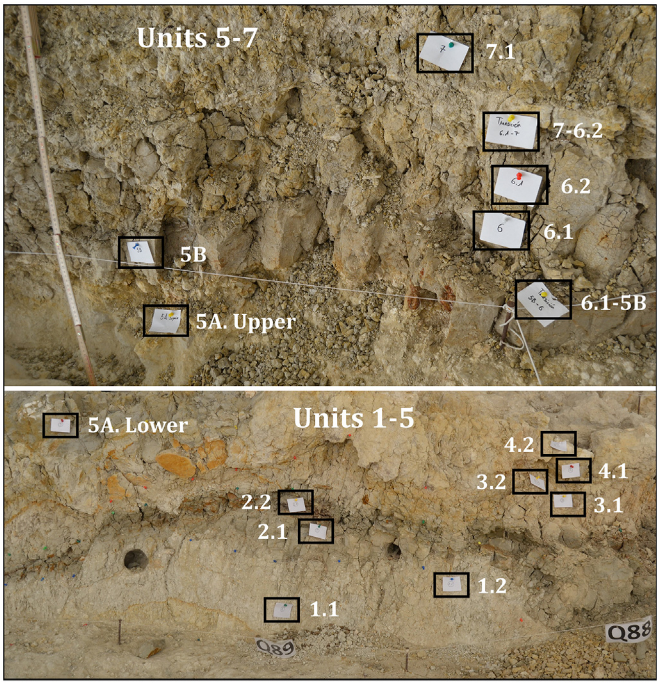


Fig. 5. Lithostratigrafical units and sections sampled for pollen analysis in FN3.

2.2. Barranco León

The stratigraphy sequence of this site is composed by the nine levels (Anadón et al., 2003; Anadón and Gabàs, 2009; Oms et al., 2011). Level A is a sequence of beige calcsiltites to calcarenites. Level B contains black and dark green feldspar quartz muddy sands. Level C is beige calcsiltites to calcarenites. Level D1 is composed by greyish gravels with a sandy matrix deposited during a flashflood episode. This level contains the most of the macrovertebrate fossils and the human knapped lithics. It is worth to note that a part of them, mainly those deposited on the lower part of the layer are in a secondary position. Nevertheless, in situ bones and lithics are also documented (Titton et al., 2021). Level D2 comprises greyish quartz-bioclastic sands, ending in whitish limestones. This level also contains large mammal fossils and lithic tools in primary position. Level E is formed by fine-to-medium-grained quartz and feldspar sands, with reddish, brown and greenish colorations. Sublevel F1 is a layer of black sandy mudstones. Sublevel F2 is a sequence of bioclastic sands of greyish quartz with small chalk nodules in the upper part. Level G is composed by beige-colored sands.

2.3. Fuente Nueva 3

The stratigraphical description of FN3 site was established by Anadón et al. (2003) and Oms et al. (2011). They established 11 different levels. Levels 1, 4, 11 and 12 are whitish limestones of mudstone lumpy texture, common calcrete nodules, and post-depositional hydroplastic depositional structures (the last only presents in levels 1 and 4). Level 2 is a green to greenish clay that towards the southern part of the outcrop becomes more carbonatic and whitish. This level is rich in macrovertebrate fossils and specially in lithic tools. Level 3 is a brown whitish clay with nodular limestones. On the top a transition to level 4 is observable. As a whole, level 5 is very rich in large mammal fossils and human knapped lithics. This unit has been divided in two sublevels. Sublevel 5A is a sequence from coarse sands (massive) to greenish fine-grained sands and locally present evidence of pedogenesis (edaphic nodules of 1 cm in diameter). At the lower part of 5A, fossil bones present evidence of bioturbation (e.g., breakage due to trampling) denoting subaerial exposure. Sublevel 5B becomes brownish finner sands and plenty of lacustrine invertebrates. In this sublevel fossils are more complete and better preserved than in 5A. Level 6 is composed of soft dark brown clays. On the other hand, levels 7 and 9 are greenish-brown dark marly mudstones. Lastly, levels 8 and 10 are pale-brown greenish marly mudstones.

3. Modern climate and vegetation

The climate of the OAZ at the Guadix-Baza Basin is best described as continental Mediterranean with cold winters and hot summers. The nearby meteorological station in Orce shows an annual average temperature of 12.9 °C (3.8 °C in the coldest month, 24.1 °C in the warmest month), which can reach maxima above 40 °C in summer, and annual average precipitation of 366 mm. Mean annual precipitation in the region ranges c. 290–400 mm. The sites VM1, BL, and FN3, studied for pollen, are located in the Mesomediterranean belt of the Guadiciano-Bacense biogeographical Sector of the Betic Province, showing semiarid ombroclimate (Rivas-Martínez et al., 1977), which is characterized by the development of badlands and treeless vegetation zones.

The present-day vegetation in the study basin is dominated by xerophytes with patches of Mediterranean scrub and isolated trees. Halophytes (e.g. *Suaeda vera, Arthrocnemum macrostachyum, Sarcocornia fruticosa, Inula crithmoides, Salsola oppositifolia,* several species of *Plantago, Juncus, Frankenia, Limonium*) and phreatophytes, including some trees (*Ulmus minor* and several species of *Populus, Tamarix* and *Salix*), growing on particular locations (Rivas-Martínez, 1987; Mercado and Tendero, 1988; Rodriguez-Ariza, 1992; Valle et al., 2004; Blanca et al., 2009). The surroundings of Barranco de los Zagales (VM1) are dominated by *Stipa tenacissima*, and other Poaceae (*Dactylis glomerata, Brachypodium retusum, Lygeum spartum*), Apiaceae (*Eryngium campestre*), Asteraceae (*Carduus, Launaea, Centaurea, Santolina*), and Lamiaceae (*Sideritis, Thymus, Lavandula, Rosmarinus*). There is a human reforested small pine forest (*Pinus halepensis*) in the vicinity of the site. The areas of access to the FN3 and BL sites are characterized by the presence of cerealia fields (*Avena*, *Triticum*), and almond tree plantations, accompanied by perennial herbs and shrubs such as *S. tenacissima*, *L. spartum*, *Rhamnus lycioides*, *E. campestre*, *Helichrysum stoechas, Cistus clusii*, *Asparagus* spp., and a diversity of Lamiaceae (especially *Rosmarinus officinalis*), and Fabaceae (*Ulex parviflorus*). In addition, the endemic species (*Vella pseudocytisus* subsp. *pseudocytisus*). Less than 1 km from BL, small formations of *P. halepensis* including *Quercus coccifera, Juniperus oxycedrus, R. lycioides, Pistacia lentiscus,* and *Asparagus acutifolius*, develop on limestones. On gypsum soils, there are characteristic species such as *Jurinea pinnata, Onobrychis stenorhiza, Lepidium subulatum, Gypsophila struthium, Ononis tridentata, Herniaria fruticosa*, and *Helianthemum squamatum*.

Upwards the peribasinal mountains (e.g. Sierras de María, Baza, Castril, El Pozo) the vegetation is increasedly forested with altitude, with species characteristic depending on the bedrock, either calcareous or siliceous. The main tree species are *Quercus rotundifolia, Q. faginea,* and *Pinus nigra,* and less frequently *Q. pyrenaica, Pinus sylvestris, P. pinaster, Acer monspessulanum, A. granatense, Fraxinus angustifolia, Sorbus aria, Taxus baccata, Arbutus unedo, Quercus suber* and dwarf junipers (e.g. *Juniperus sabina*).

4. Materials and methods

As recommended for archaeological sites (Girard, 1975), palynological sampling was conducted on several vertical stratigraphic profiles for each study site (VM1, BL and FN3) (Figs. 2–5). Exposed surface layers of sediment were cleaned back and discarded to a depth of 10–15 cm in every sedimentological unit, to avoid potential sources of contamination and/or recent bioturbation. The quantity of sediment treated for each sample was the net weight (Tables 1–3).

For the extraction of palynomorphs, the "Classic Chemical Method" was followed (Erdtman, 1969; Dimbleby, 1985), with the modifications proposed by Girard and Renault-Miskovsky (1969). In order to calculate the pollen concentrations, we added to each sample three tablets of *Lycopodium* spores. After being treated at the laboratory, the samples were mounted on glycerol jelly and sealed with paraffin. The palynological identification was made by conventional microscopy (400x and 1000x) using an optical microscope, and with help of the pollen collection of the Department of Plant Biology at the University of Murcia as reference. The pollen count data were treated with Tilia Graph 1.7.16 in order to construct pollen diagrams (Figs. 6–12, SI Fig. 1).

5. Results

5.1. Venta Micena 1 (Barranco de los Zagales)

A total of 16 VM1 samples were analysed, with 10 being polleniferous (Table 1, Figs. 6 and 7) and 6 being sterile samples. The later come from Unit C0 (C0.1, C0.2, C0.3, C0.4), and Unit C1 (C1.1, C1.4) (Fig. 3). A total of 2694 palynomorphs were identified, counting 2172 pollen grains and 522 spores, excluding indeterminable grains, which were lower than the 22% total palynomorph count. Spores and non-pollen microfossils were excluded from the pollen sum. The number of pollen taxa was between 11 and 22 per sample, with a total of 32 taxa being recognized.

5.1.1. Unit C0

This unit includes samples C0.5 and C0.6 (Figs. 6 and 7). Arboreal pollen (AP) abundance is between 30 and 42%, with *Pinus* being dominant (23–37%), and *Juniperus* between 3 and 7%. Other lesser contributors to AP include evergreen *Quercus*, *Alnus*, *Salix*, *Olea* and *Rhamnus*. In the non-arboreal pollen (NAP), *Ephedra distachya-nebrodensis* varies between 23 and 40%, *Artemisia* ranges from 6 to 15%, and Poaceae occurs between 1 and 4%. Amaranthaceae, Asteroideae, Cichorioideae, *Centaurea* and *Helianthemum*, are also frequent.

5.1.2. Unit C1

This unit includes pollen samples C1.2, C1.3, C1.5 and C1.6 (Figs. 6 and 7). AP reaches frequencies close to 38%. *Pinus* (6–26%) and *Juniperus*

Table 1
Summary of palynological features of the Venta Micena 1 samples.

Sample	Level	N°	Gross weight (g)	Net weight (g)	Concentration (grains/g)	Indeterminable (%)	Pollen sum	Number of taxa (Pollen)	Spores sum
C2.4	C2	1	59.6	59.6	451.58	8.44	154	11	81
C2.3	C2	2	54.2	54.2	3454.65	11.79	178	14	29
C2.2	C2	3	61.4	61.4	710.19	7.30	219	14	84
C2.1	C2	4	53.4	53.4	416.39	21.32	136	14	50
C1.6	C1	5	68.6	68.6	972.92	5.38	334	22	73
C1.5	C1	6	51.7	51.7	2172.15	7.80	282	15	57
C1.4	C1	–	63.3	63.3	–	–	Sterile	–	Sterile
C1.3	C1	7	55.7	55.7	1724.43	7.25	317	20	40
C1.2	C1	8	64.8	64.8	958.38	5.11	176	16	49
C1.1	C1	–	56.1	56.1	–	–	Sterile	–	Sterile
C0.6	C0	9	63.6	63.6	241.58	5.00	140	12	18
C0.5	C0	10	60.3	60.3	6818.75	5.50	236	15	41
C0.4	C0	–	67.4	67.4	–	–	Sterile	–	Sterile
C0.3	C0	–	60.6	60.6	–	–	Sterile	–	Sterile
C0.2	C0	–	54.5	54.5	–	–	Sterile	–	Sterile
C0.1	C0	–	69.0	69.0	–	–	Sterile	–	Sterile
						TOTAL 2172			522

Table 2
Summary of palynological features of the Barranco León samples.

Sample	Level	N°	Gross weight (g)	Net weight (g)	Concentration (grains/g)	Indeterminable (%)	(**)Pollen sum	Number of taxa (Pollen)	Spores sum
G3	G	–	87.1	53,9	–	–	Sterile	–	Sterile
G2	G	–	55.3	55.3	–	–	Sterile	–	Sterile
G1	G	–	54.4	54.4	–	–	Sterile	–	Sterile
F1	F	–	91.1	80,5	–	–	Sterile	–	Sterile
E2	E	1	87.0	87.0	7602.54	4.83	248	41	9
E2	E	–	93.0	85,3	–	–	Sterile	–	Sterile
E1	E	2	81.3	81.3	2958.16	1.36	220	9	1
E1	E	–	72.6	66.5	–	–	Sterile	–	Sterile
D2	D	3	77.9	46.7	384.81	2.36	211	14	2
D2	D	–	72.1	58,6	–	–	Sterile	–	Sterile
D1	D	4	78.0	13.2	12421.06	2.15	278	28	3
D1	D	–	79.4	75,8	–	–	Sterile	–	Sterile
C1	C	–	56.8	56.8	–	–	Sterile	–	Sterile
B2	B	–	64.2	64.2	–	–	Sterile	–	Sterile
B1	B	–	52.8	52.8	–	–	Sterile	–	Sterile
A6	A	–	56.2	56.2	–	–	Sterile	–	Sterile
A5	A	5	56.1	56.1	667.66	8.49	259	26	34
A4	A	–	83.8	47.6	–	–	Sterile	–	Sterile
A3	A	–	57.6	57.6	–	–	Sterile	–	Sterile
A2	A	–	55.5	55.5	–	–	Sterile	–	Sterile
A1	A	–	107.4	84.7	–	–	Sterile	–	Sterile
						TOTAL 1216			49

[*] Cichorioideae and *Cistus* t. excluded

[*] Pollen sum column without Apiaceae, *Ceratonia*, *Helianthemum*/*Halimium* type and *Lotus*.

(2–7%) are also significant. The occurrence of evergreen *Quercus*, *Olea*, Genisteae, *Fraxinus*, *Phillyrea* and *Erica*, and the minor accounts of *Pinus pinaster*, *Quercus* deciduous, *Castanea* and *Salix*, are significant. The non-arboreous pollen (NAP) is predominant: *Ephedra distachya-nebrodensis* (29–48%), *Artemisia* (7–14%), Poaceae (3–9%) and Amaranthaceae (2–5%). Pollen grains of Asteroideae, Cichorioideae, *Plantago* and Brassicaceae are also common.

5.1.3. Unit C2

This unit includes samples C2.1, C2.2, C2.3 and C2.4 (Figs. 6 and 7). The abundance of the AP ranges between 24 and 33%. The main pollen contributors are *Pinus* (4–18%), *Juniperus* (2–12%) and evergreen *Quercus* (2–5%). Other AP elements include *Alnus*, *Olea*, *Phillyrea*, *Maytenus* and Genisteae. Similarly to the underlying zones, it is worth mentioning the abundance of NAP grains, such as *Ephedra distachya-nebrodensis* (14–40%), and to a lesser extent, *Artemisia* (7–16%), Poaceae (6–12%) and Amaranthaceae (3–5%). Additionally, Asteroideae, Cichorioideae, *Echium*, *Lotus* and Cyperaceae are present.

5.2. Barranco León

A total of 21 BL samples were analysed, of which only 5 were found to be polleniferous (Table 2, Figs. 8 and 9). These successful samples came from Unit A (A5), Unit D (D1 and D2), and Unit E (E1 and E2) (Fig. 4). A total of 1265 palynomorphs were identified, including 1216 pollen grains and 49 spores, excluding indeterminable pollen grains (lower than 9%). Pollen grains of Cichorioideae, and *Cistus* were excluded from the pollen sum due to high percentages in several samples, suggesting over-representation (Carrión, 1992a, 1992b; Carrión et al., 1998) (Figs. 8 and 9). The number of pollen taxa ranges from 9 to 41 per sample, with a total of 53 taxa being recognized (Table 2).

5.2.1. Unit A

This unit only includes sample A5 (Figs. 8 and 9). AP is above 61%. *Olea* reaches 18%, *Pinus* 15%, evergreen *Quercus* 11%, Cupressaceae exceeds 7%, and deciduous *Quercus* 3%. Other AP taxa include *Taxus*, *Pistacia*, *Betula*, *Castanea*, *Corylus*, *Fraxinus*, *Juglans*, *Maytenus*, *Salix* and

Table 3
Summary of palynological features of the Fuente Nueva 3 samples.

Sample	Unit	N°	Gross weight (g)	Net weight (g)	Concentration (grains/g)	Indeterminable (%)	Pollen sum	Number of taxa (Pollen)	Spores sum
7.1	7	–	58.0	58.0	–	–	Sterile	–	Sterile
7–6.2	7–6	1	57.2	57.2	745.56	3.41	205	18	24
6.2	6	2	60.0	60.0	201.27	2.91	206	21	42
6.1	6	3	54.0	54.0	8548.64	1.44	207	23	13
6.1–5B	6–5B	4	58.4	58.4	206.82	1.82	164	17	19
5B	5B	5	62.6	62.6	79.16	3.22	124	18	6
5A.Upper	5A	6	54.7	54.7	410.85	1.92	208	22	55
5A.Lower	5A	7	57.7	57.7	56.57	2.45	204	18	59
4.2	4	8	56.9	56.9	99.11	4.45	202	27	275
4.1	4	9	55.1	55.1	1380.38	4.85	206	32	15
3.2	3	10	51.4	51.4	243.21	4.26	211	18	21
3.1	3	11	56.8	56.8	692.85	2.94	204	21	13
2.2	2	12	57.3	57.3	224.69	2.20	318	19	24
2.1	2	13	58.4	58.4	1304.13	0.98	306	21	24
1.2	1	14	51.1	51.1	293.55	1.30	307	24	40
1.1	1	15	56.8	56.8	30133.56	0.97	307	28	17
						TOTAL 3379			647

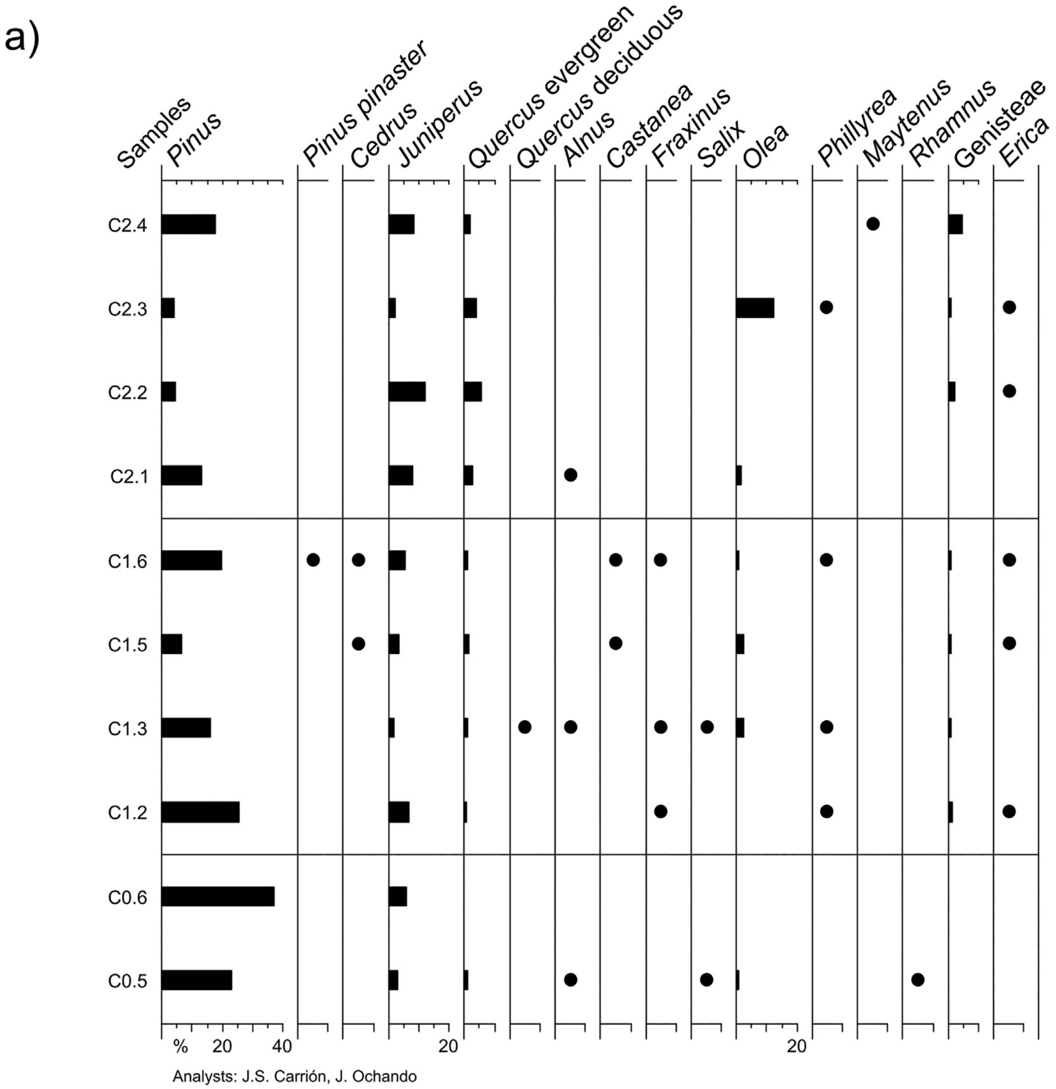


Fig. 6. a) Percentage pollen diagram of VM1 including mainly the woody component. b) Percentage pollen diagram of VM1 including mainly the non-arboreal elements. Black dots for percentages below 3%. Dashed lines for subdivisions within archaeological units.

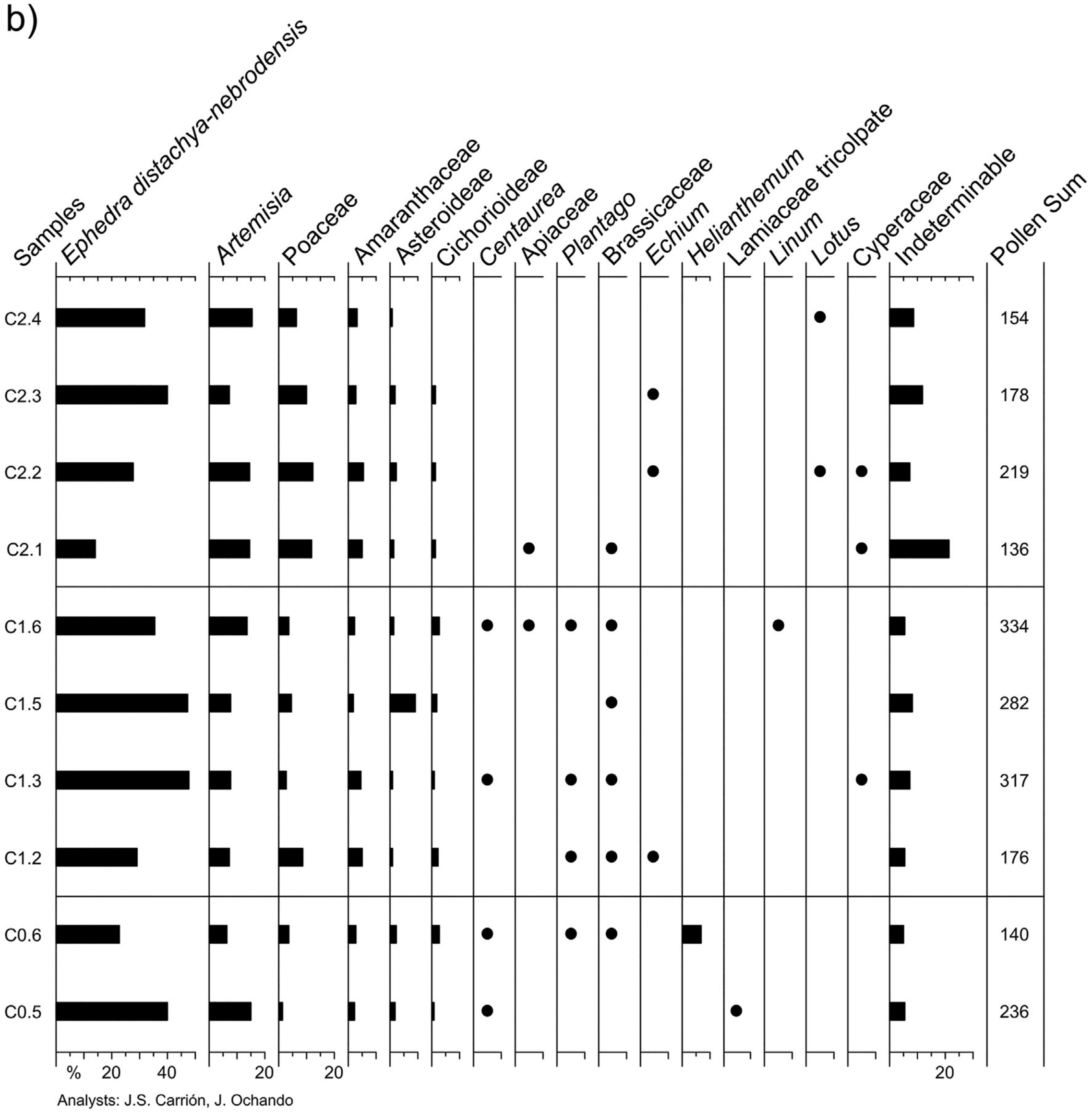


Fig. 6 (*continued*).

Rhamnus. Regarding NAP, *Artemisia* (10%) and Poaceae (9%) are predominant, with occurrences of Amaranthaceae, Fabaceae, Brassicaceae, *Plantago* and Cyperaceae.

5.2.2. Unit D

This unit includes samples D1 and D2 (Figs. 8 and 9). AP occurs with 36 and 40% respectively, with remarkable abundance of Cupressaceae (16-28%). *Olea* does not exceed 7%, evergreen *Quercus* is below 7%, and *Pinus* 7%. Other minor AP contributors include *Cedrus*, deciduous *Quercus*, *Pistacia*, *Alnus*, *Castanea*, *Corylus*, *Fraxinus*, *Sambucus* and *Ephedra fragilis*. In NAP, Poaceae (12–45%) and *Artemisia* (10–12%) are noteworthy. *Lygeum*, Amaranthaceae, Caryophyllaceae, Fabaceae, Gentianaceae, *Plantago* and Urticaceae are also frequent.

5.2.3. Unit E

This unit includes pollen samples E1 and E2 (Figs. 8 and 9), in which the precentages of AP are 27 and 55%, respectively. The most remarkable feature is the abundance of Cupressaceae (22–23%). The occurrences of *Pinus*, evergreen *Quercus*, deciduous *Quercus* and *Eucommia* are noteworthy, as well as the presence of *Taxus*, *Phlomis*, *Pistacia*, *Alnus*, Arecaceae, *Betula*, *Carpinus*, *Carya*, *Castanea*, *Corylus*, *Juglans*, *Maytenus*, *Myrica*, *Populus*, *Pterocarya*, *Rhamnus*, *Sambucus*, Rosaceae, *Ulmus*, *Zelkova* and *Ephedra fragilis*. In NAP, it is worth mentioning the abundance of Poaceae (12–62%) and *Artemisia* (4–10%). Other NAP such as *Lygeum*, Fabaceae, Asparagaceae, *Capparis*, *Hedera*, Iridaceae/Liliaceae, *Plantago*, Zygophyllaceae and Cyperaceae, are present.

5.3. Fuente Nueva 3

In total, from 16 samples that were collected from FN3, 15 were polleniferous (Table 3, Figs. 10–12, SI Fig. 1). The only sterile sample corresponded to Unit 7. A total of 4026 palynomorphs were identified, including 3379 pollen grains and 647 spores, excluding indeterminable which frequencies were lower than 5% (Figs. 10–12). The number of pollen types varies between 17 and 32, with a total of 60 taxa being recognized. Fungal spores are abundant and diverse in this sequence (SI Fig. 1), suggesting decomposing activity, and probably faecal input to the sediment.

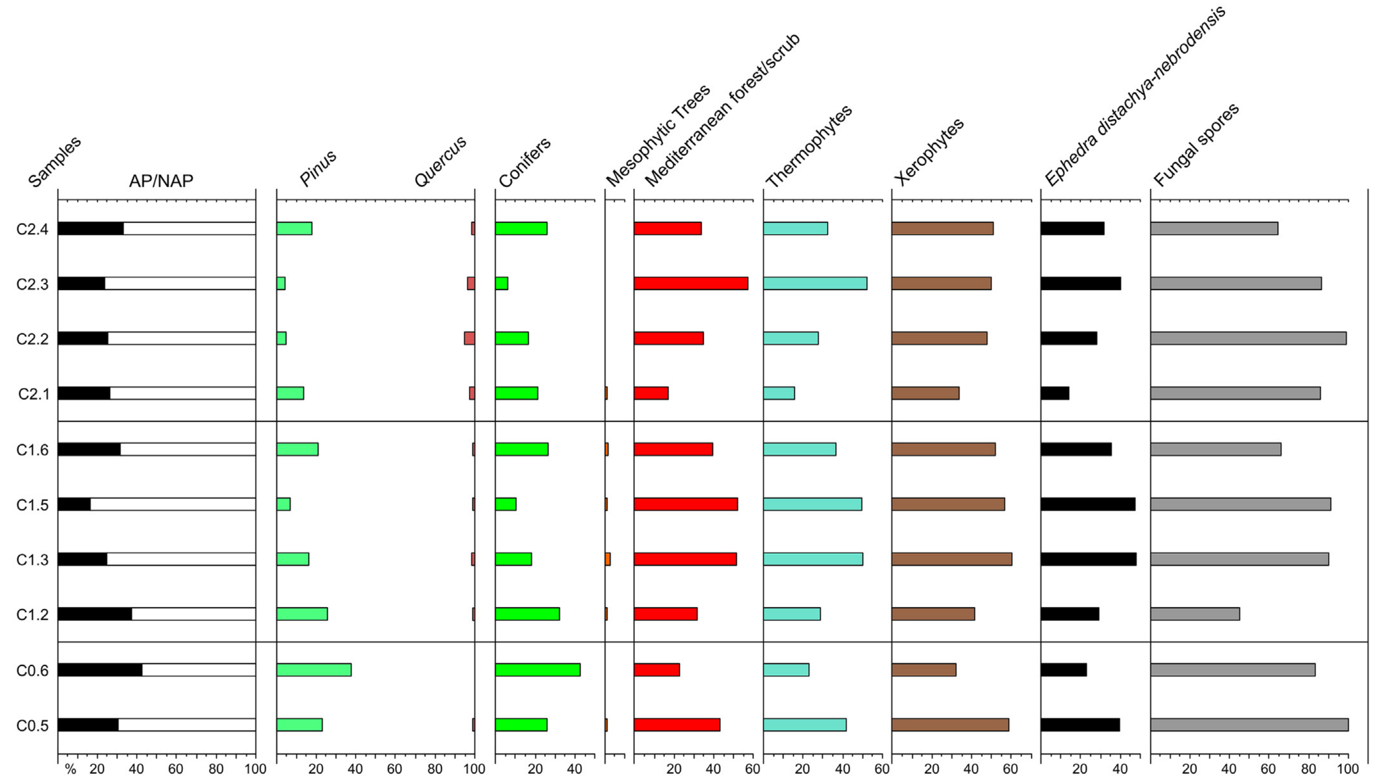


Fig. 7. Synthetic pollen diagram of VM1 including ecological groups and the main pollen contributors.

5.3.1. Unit 1

This unit includes samples 1.1 and 1.2 (Figs. 10–12). AP is predominant, reaching levels higher than 63%. A remarkable feature from this unit is the abundance of *Olea* (15–24%), *Juniperus* (10–24%), and evergreen *Quercus* (12%) and, to a lesser extent, *Pinus halepensis-pinea* (1–5%), and *Pinus nigra-sylvestris* (3–7%). The occurrence of deciduous *Quercus*, *Fraxinus*, Genisteae and *Erica* are also ecologically meaningful, as well as the occurrences of *Carya*, *Castanea*, *Fagus*, *Rhus*, *Salix*, *Ulmus*, *Sambucus nigra*, *Myrica*, *Pistacia*, *Ligustrum*, *Ephedra fragilis*, *Smilax* and *Cistus*. With respect to the NAP, Poaceae (6–21%) and Amaranthaceae (9–23%) prevail, with minor occurrences of *Artemisia*, Asteroideae, Cichorioideae, *Plantago lanceolata* and Liliaceae. Among fungal spores, *Inapertisporites* (SI Fig. 1). *Dicellaesporites*, *Foliopollenites*, *Hypoxylonites*, *Microsporonites* and *Scleroderma* are frequent. The presence of Zygnemataceae spores (water transport) is worth mentioning.

5.3.2. Unit 2

This unit includes pollen samples 2.1 and 2.2 (Figs. 10–12). AP represents between 62 and 71% of the total terrestrial pollen. The amount of *Olea* (25–26%) is noticeable, reaching here a sequence maximum. *Pinus halepensis-pinea* varies between 9 and 11%. *Pinus nigra-sylvestris* is about 9%, while evergreen *Quercus* 10–11%. Additional, ecologically meaningful woody taxa include *Juniperus*, deciduous *Quercus*, Genisteae, *Pinus pinaster*, *Fraxinus*, *Pistacia* and *Erica*. Among NAP, Amaranthaceae (14–21%), Poaceae (2–7%), Asteroideae (4–6%) and *Artemisia* (2–5%) are representative, with lesser frequencies for Cichorioideae, *Centaurea montana*, Fabaceae, Lamiaceae and Urticaceae. The abundance of the fungal type *Microsporonites* (42–50%) is remarkable, while *Diporisporites*, *Inapertisporites* and *Monoporisporites* are frequent (SI Fig. 1).

5.3.3. Unit 3

This unit includes samples 3.1 and 3.2 (Figs. 10–12). The dominant pollen is arboreal, with total values above 77%. This is a phase characterised by the sequence´s highest percentages of *Juniperus* (33–36%) and important contribution of *Olea* (12–14%). Evergreen *Quercus* does not exceed 7%, while *Pinus halepensis-pinea* is about 7–8%. Other woody taxa include deciduous *Quercus*, *Fraxinus*, *Pistacia*, Genisteae, *Pinus pinaster*, *Cedrus*, *Castanea*, *Fagus*, *Populus*, *Sambucus ebulus*, *Phillyrea*, *Erica*, *Cistus* and Rosaceae. Amaranthaceae (14%) and Poaceae (2–8%) dominate the herbaceous contingent. *Artemisia*, Asteroideae, Cichorioideae and Urticaceae are also common. The presence of *Microsporonites* (15–48%) and *Monoporisporites* (46%) stands out (SI Fig. 1). Similarly, *Diporisporites*, *Inapertisporites*, *Dictyosporites*, Zygnemataceae and Bryophyta spores, are present.

5.3.4. Unit 4

This unit includes pollen samples 4.1 and 4.2 (Figs. 10–12). AP is above 50%, with *Juniperus* (13–16%), *Olea* (8–13%), and evergreen *Quercus* (7–8%) as the main taxa, accompanied by *Pinus halepensis-pinea*, *Pinus nigra-sylvestris*, deciduous *Quercus*, *Fraxinus*, *Populus*, *Salix*, *Juglans*, *Pistacia* and Genisteae. Amaranthaceae (24–26%) and Poaceae (7–8%) are NAP dominant. In addition, *Artemisia*, Asteroideae, Cichorioideae, Fabaceae, *Plantago lanceolata*, Scrophulariaceae and Urticaceae are also frequent. It is worth highlighting the abundance of fungal spores, with *Hypoxylonites* (2–53%), *Inapertisporites* (27%), *Microsporonites* (13–17%) and *Monoporisporites* (7–15%) being very common (SI Fig. 1). Zygnemataceae is also noticeable.

5.3.5. Unit 5

This unit includes samples 5A.Lower, 5A.Upper and 5B (Figs. 10–12). AP is predominant, reaching between 54 and 69%. The most noteworthy characteristics of this zone are the abundance of *Olea* (12–22%), evergreen *Quercus* (5–18%) and *Juniperus* (4–14%), while *Pinus nigra-sylvestris* fluctuates between 2 and 13%, and *Pinus halepensis-pinea* (4–8%) increases with respect to the previous zone. Other AP include deciduous *Quercus*, *Fraxinus*, *Ulmus*, *Pistacia*, *Phillyrea*, *Salix*, *Sambucus ebulus*, *Pistacia*, *Ephedra fragilis*, *Erica* and *Cistus*. NAP is characterized

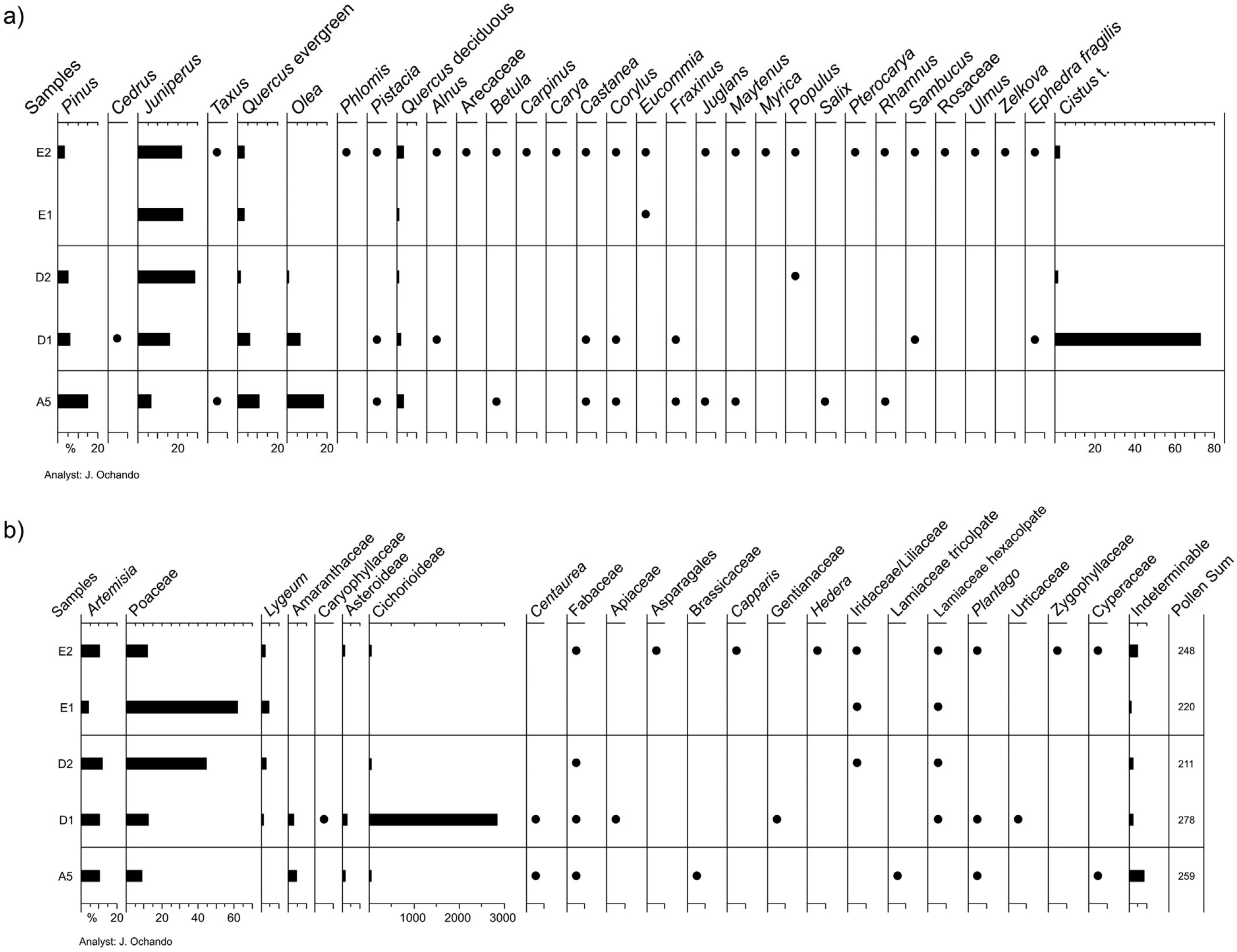


Fig. 8. a) Percentage pollen diagram of BL including mainly the woody component. b) Percentage pollen diagram of BL including mainly non-arboreal elements. Cichorioideae and *Cistus* t. out from the total pollen sum. Black dots for percentages below 3%. Dashed lines for subdivisions within archaeological units.

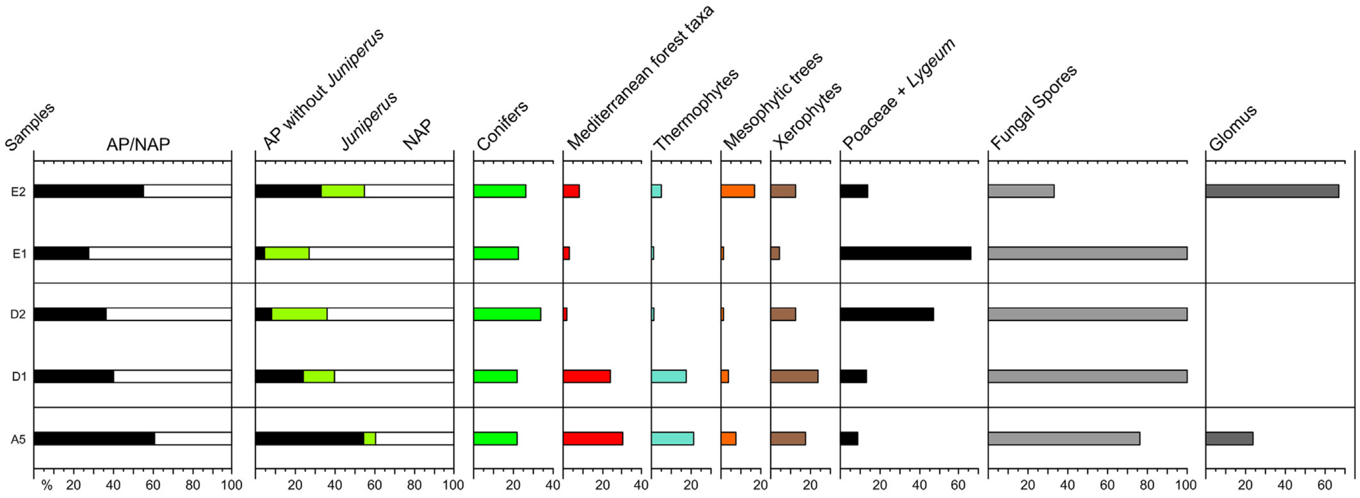


Fig. 9. Synthetic pollen diagram from BL including ecological groups and the main pollen contributors.

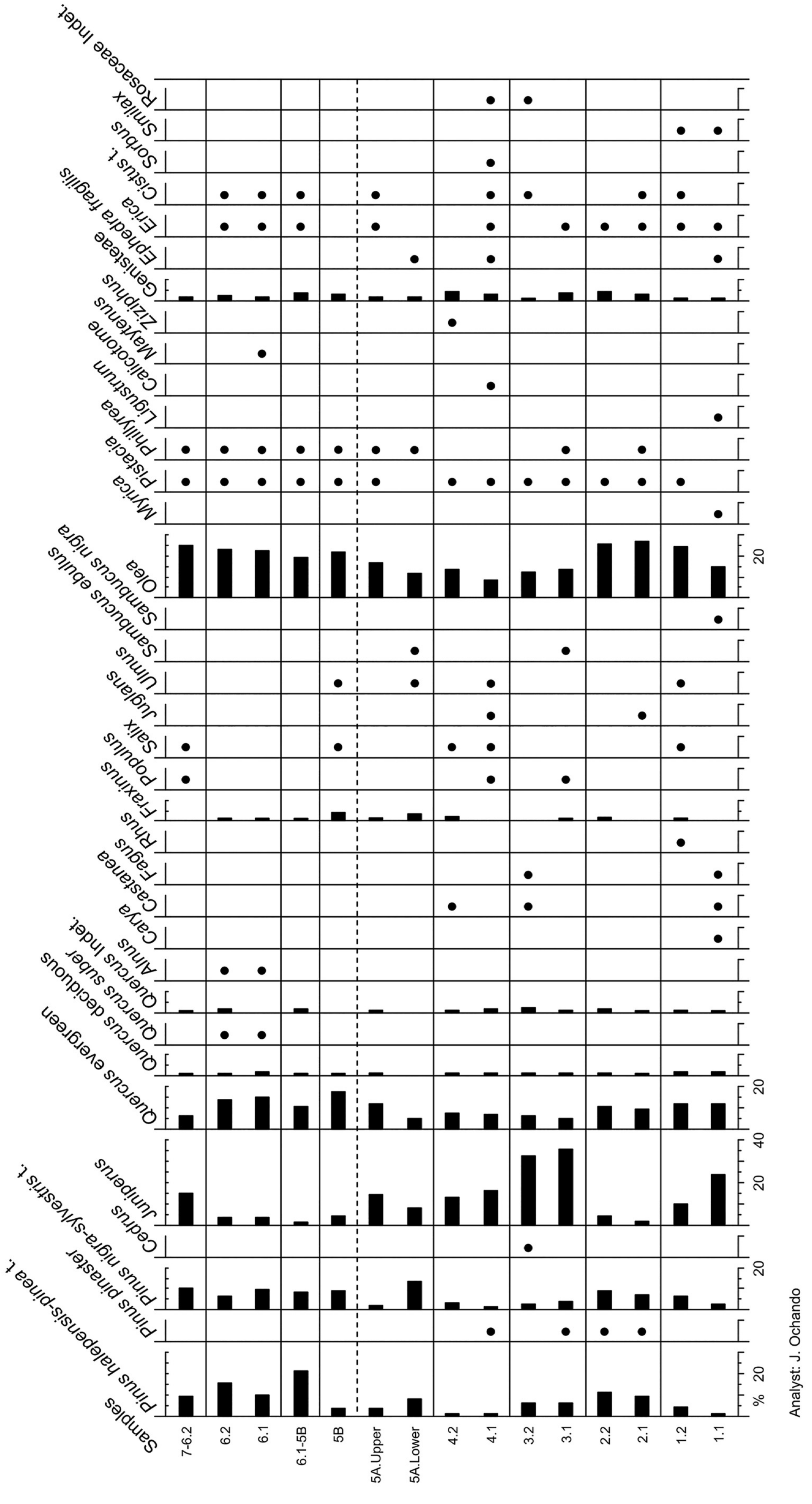


Fig. 10. Percentage pollen diagram of FN3 including mainly the woody component. Black dots for percentages below 3%. Dashed lines for subdivisions within archaeological units.

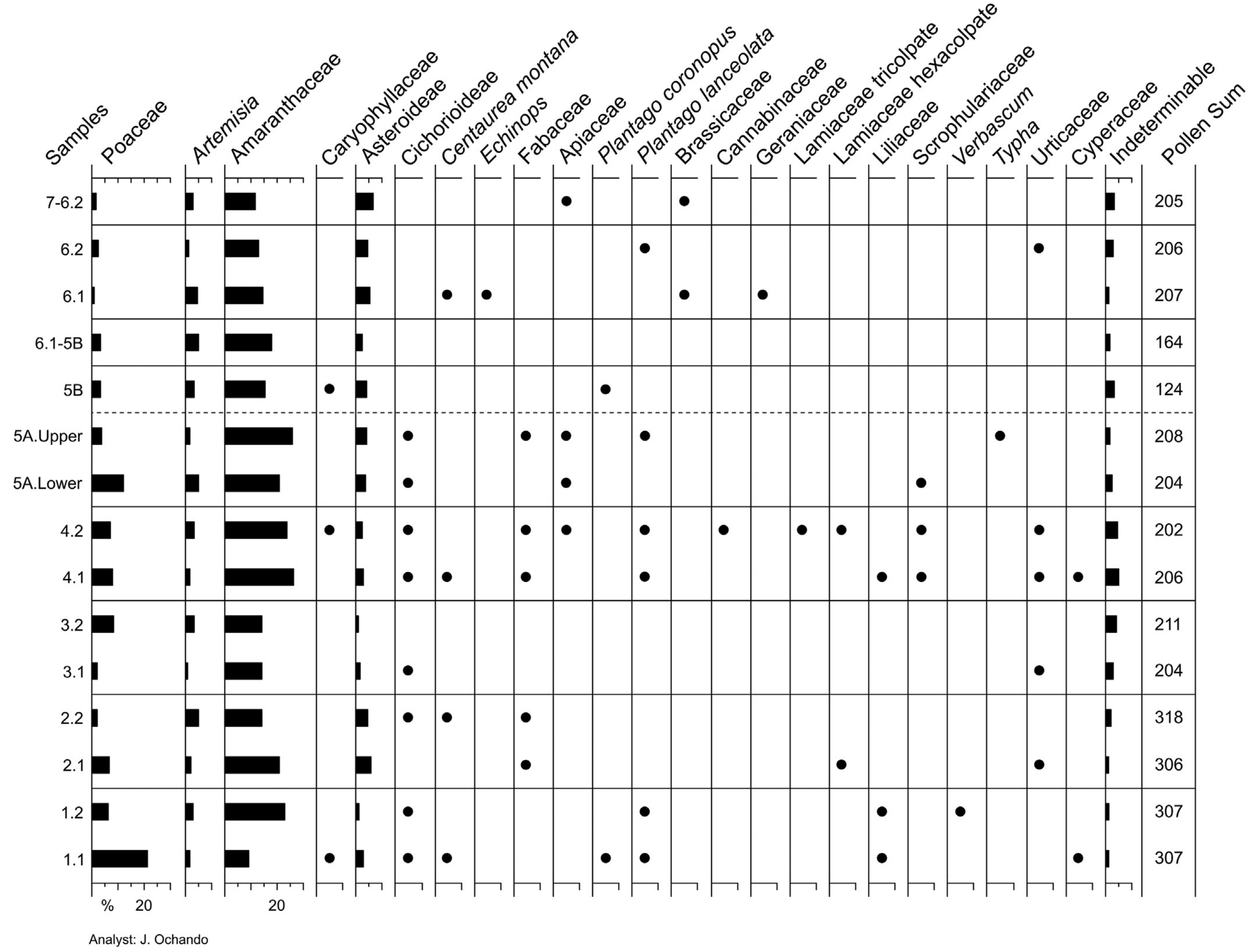


Fig. 11. Percentage pollen diagram of FN3 including mainly non-arboreal elements. Black dots for percentages below 3%. Dashed lines for subdivisions within archaeological units.

by Amaranthaceae (15–26%), Poaceae (3–12%) and to a lesser extent, *Artemisia*, Asteroideae, Cichorioideae and Apiaceae. Chlamydospores of the mycorrhizogenous fungus *Glomus* (17–20%), and *Inapertisporites* (7–33%) and *Polycellaesporonites* (16–17%) are frequent (SI Fig. 1). *Monoporisporites*, *Microsporonites*, *Pluricellaesporites* and *Reduviasporonites* occur. Zygnemataceae reach values higher than 42% (out of the total pollen sum).

5.3.6. Unit 6-5B

This unit includes sample 6.1-5B (Figs. 10–12). AP accounts for c. 71%, with mainly *Pinus halepensis-pinea* (21%), *Olea* (19%), evergreen *Quercus* (12%), *Pinus nigra-sylvestris* (9–10%), and Genisteae (4%). Other minor taxa include *Juniperus*, deciduous *Quercus*, *Fraxinus*, *Pistacia*, *Phillyrea*, *Erica* and *Cistus*. With respect to NAP, it is worth mentioning the abundance of Amaranthaceae (18%). The presence of conidia Type 200 (79%) is significant, together with the occurrences of *Glomus*, and *Gelasinospora* (SI Fig. 1).

5.3.7. Unit 6

This unit embraces pollen samples 6.1 and 6.2 (Figs. 10–12). AP reaches 74%, including relatively high percentages of *Olea* (22–23%), evergreen *Quercus* (14–15%) and *Pinus halepensis-pinea* (10–16%). *Pinus nigra-sylvestris* is about 7–10%, while *Juniperus* does not exceed 4%. Accompanying AP are deciduous *Quercus*, *Quercus suber*, *Alnus*, *Fraxinus*, *Pistacia*, *Phillyrea*, *Maytenus*, *Erica* and *Cistus*. In NAP, Amaranthaceae (13–14%) and Asteroideae (4–5%), Poaceae, *Artemisia*, *Plantago lanceolata*, Brassicaceae and Geraniaceae are common. The presence of *Microsporonites* (12–38%), *Inapertisporites* (7–23%) and *Glomus* (2–31%) stands out (SI Fig. 1). Similarly, *Monoporisporites*, and *Multicellites*, are present.

5.3.8. Unit 7-6

This unit is represented by sample 7-6.2 (Figs. 10–12). AP is about 74%, including *Olea* (25%), *Juniperus* (15%), *Pinus nigra-sylvestris* (11%), *Pinus halepensis-pinea* (10%), and evergreen *Quercus* (7%), among others (deciduous *Quercus*, *Populus*, *Salix*, *Pistacia*, *Phillyrea*, Genisteae). The herbaceous component is characterized by Amaranthaceae (12%), Asteroideae (7%), and to a lesser extent, Poaceae, *Artemisia*, Apiaceae and Brassicaceae. The presence of *Dicellaesporiporites* (63%) and *Monoporisporites* (17%) is significant (SI Fig. 1). *Dictyosporites*, *Hyphae*, *Microsporonites*, *Multicellites* and *Reduviasporonites*, appear.

6. Discussion

6.1. Previous palynological research and pitfalls with palaeoecological interpretation

Previous studies for pollen on 18 samples from BL were performed by Jiménez-Moreno (2003). A total of 9 of those samples contained pollen, being dominated by *Pinus*, *Olea*, Cupressaceae and *Quercus*,

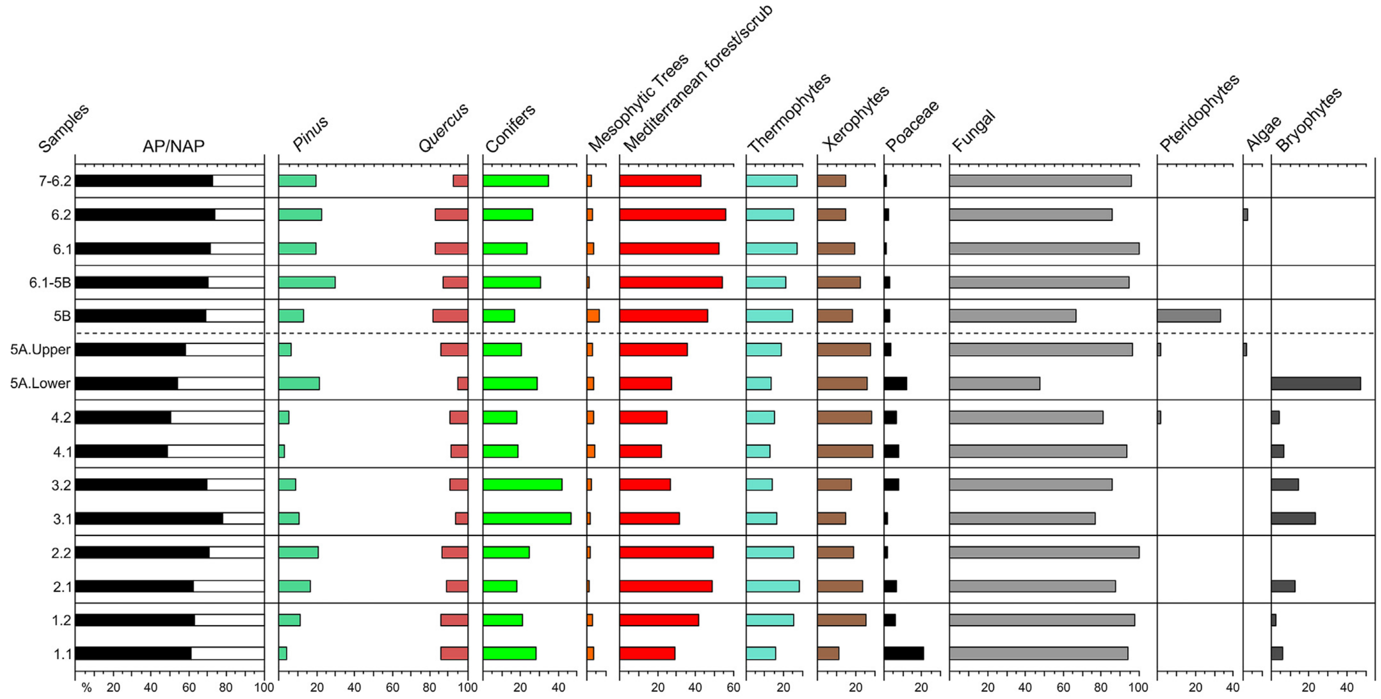


Fig. 12. Synthetic pollen diagram from FN3 including ecological groups and the main pollen contributors.

accompanied by *Betula*, *Corylus*, *Ilex*, *Ligustrum*, *Fraxinus*, *Ulmus, Cedrus, Picea,* and *Salix*. Among the herbaceous elements, *Artemisia*, *Plantago*, Poaceae, Amaranthaceae, Asteraceae, Brassicaceae, *Ephedra* and *Centaurea* were recorded. The abundance of *Glomus* was suggested to indicate hydric transport into the sediment, which was fluvio-marsh in origin.

Jiménez-Moreno (2003) warned about the uncertainties associated with the taphonomy of these pollen spectra. It must be taken into account that, when dealing with archaeological sediments, we can never categorically discard the possibility of alteration of the pollen assemblages by differential preservation, bioturbation, and/or vertical movement, or reworking, leading to contamination of sediments by younger or modern pollen (Bryant and Holloway, 1983; Burney and Burney, 1993; Coles and Gilbertson, 1994; Carrión et al., 1999). It is also clear that palynology at these environments still needs much experimentally-based work before we can make the best inferences concerning past environments (Carrión and Scott, 1999; Carrión, 2002b; Carrión et al., 2009; Hunt and Fiacconi, 2018). However, there have been advances over the last decades providing taphonomical studies and sequences with good palynomorph preservation and concentration, ecological coherence of the pollen assemblages, and acceptable correlation with reference to lacustrine sequences (e.g. Navarro et al., 2000, 2001, 2002; López-Sáez et al., 2003, 2007; Carrión et al., 2008, 2013, 2018, 2019a; González-Sampériz et al., 2010; Burjachs et al., 2012; Revelles et al., 2016; Ochando et al., 2019, 2020a, 2020b, 2020c, 2020d).

In addition, archaeological sites such as those in OAZ may lie in physiographically different scenarios from lake and mire sites, thus potentially adding useful information on montane palaeovegetation and on the location of glacial reservoirs of particular plant species. In support of the reliability and usefulness of the pollen assemblages described here is that they: (i) point to the existence of vegetation with higher plant diversity, and indication of more forested, and more humid conditions than today; (ii) include taxa which became extinct during the Middle Pleistocene, (iii) correlate acceptably with lacustrine pollen record. We shall discuss these points below.

6.2. Past vegetation features inferred from VM1, BL and FN3 pollen

It is important to keep in mind that archaeological pollen records, which are often discontinuous and/or altered by humans, should not be used to assess vegetational and climatic fluctuations with the same confidence as when they are interpreted from continuous and pristine lacustrine or marshy pollen records (Carrión et al., 1999). In this way, in VM1, BL and FN3, the changes in the frequencies of the major taxa must be taken with many reservations, especially considering that they are not very striking variations.

The VM1 pollen record is characterized by the prevalence and extraordinary abundance of *Ephedra distachya-nebrodensis*, while *Pinus* and *Juniperus* are also continuously relatively abundant, with only few exceptions. Often, pines and junipers are accompanied by *Olea,* evergreen *Quercus* (especially in unit C), Genisteae, *Erica*, and to a lesser extent, deciduous *Quercus*, *Alnus*, *Castanea*, *Fraxinus*, *Salix* and *Phillyrea* (Figs. 6 and 7). The woody component shows a moderate to low cover, but includes a combination of mesophytes (deciduous *Quercus*, *Alnus*, *Castanea*, *Fraxinus*, *Salix*), and Mediterranean taxa. The xeroheliophytic component (Poaceae, *Artemisia*, Amaranthaceae, *Ephedra,* Lamiaceae) is remarkable. The VM1 pollen record shows the higher indication of xericity, especially due to the high frequencies of *Ephedra*. The thermophilic character of the vegetation in the area can be deduced by the pollen occurrences of *Maytenus* and *Olea*.

In contrast, FN3 can be characteristically connected with forest ecosystems. This richer pollen record suggests the prevalence of a thermo-Mediterranean woodland dominated by evergreen *Quercus, Pinus, Juniperus* and *Olea* (Fig. 12) with a high diversity of woody plants, including deciduous *Quercus*, *Castanea*, *Populus*, *Salix*, *Ulmus, Fraxinus*, *Pistacia*, *Phillyrea*, Genisteae, *Erica*, *Cistus*, and *Ephedra fragilis* (Fig. 10). It is worth emphasizing that the pollen record contains mesophytes, thermophytes, xerophytes, xerothermophytes, and Mediterranean elements, all indicative of summer drought, together with deciduous trees indicative of humid biotopes. FN3 is therefore reflecting the biotic mosaicity inherent to a highly geodiverse landscape, including highelevation areas, intramontane valleys, lacustrine and riverine basins, highplains and depressions conditioned edaphically by gypsum and clay.

Plausibly, deciduous trees species within mixed forests developed on the deeper soils at higher altitudes, ravines, or plain enclaves associated to edaphic water such as lake, wetland and river margins. In these biotopes, the most likely species involved would be *Quercus faginea* (calcareous soils on limestones and dolomites), *Q. pyrenaica* (acidic soils), *Pinus nigra, P. sylvestris, P. pinaster, Castanea sativa,* and several species of *Sorbus* (e.g. *S. domestica, S. aucuparia*). Relictic stands of *Juglans regia, Fagus sylvatica* and *Carya* would probably form part of these communities at higher altitudes. Mediterranean open forests would have occurred not far from the FN3 site, possibly in highplains and mountain slopes.

Downwards, xerothermic scrub would have been growing in depressed lands under water stress, with taxa such as *Ziziphus lotus, Calicotome intermedia, Ephedra fragilis, Pistacia lentiscus, Phillyrea angustifolia, Maytenus europaeus* and Genisteae varia (e.g. *Ulex, Genista, Cytisus*). The moderate abundance of chenopods (Amaranthaceae) in FN3 is probably related with the existence of saline soils in the surroundings, which would have extended during dry phases.

The record of BL, although not as palynologically productive as FN3, is still palaeoecologically meaningful. This sequence is characterized by the prevalence of *Juniperus*, *Olea*, *Pinus*, Poaceae, and evergreen *Quercus* (Fig. 9), which is accompanied in several samples by other taxa such as *Cistus*, *Artemisia* and Cichorioideae with relatively high values (Fig. 8). A diversity of trees, shrubs and herbs can also be observed. Poaceae is particularly abundant in D2 and E1; Cichorioideae dominant in D1. The woody component also shows diversity, combining mesophytes, thermophytes and Tertiary relics such as *Carya, Eucommia, Pterocarya* and *Zelkova*. The later may well represent transport from the mid-elevation montane refugia previously described. The presence of *Pistacia, Maytenus, Olea* and Arecaceae suggests that the local climate was relatively warm. The occurrences of *Lygeum* in Units D, and E, and both Zygophyllaceae and *Capparis* in Unit E suggest local xericity.

6.3. Palaeobiogeographical remarks

Several fossil pollen taxa need to be discussed. A first consideration concerns the incidence of cedar pollen. Doubts persist about whether pollen records of *Cedrus* in the Iberian Quaternary are due to long-distance transport from North Africa (Sánchez-Goñi et al., 1999; Magri and Parra, 2002; Jiménez-Moreno et al., 2020), or if the species indeed survived naturally until a few millennia ago (Postigo-Mijarra et al., 2009, 2010; González-Sampériz et al., 2010). It is generally accepted that cedars, although never forest dominants, were naturally present across Iberia at least since the Eocene (Postigo-Mijarra et al., 2009; Barrón et al., 2010; Casas-Gallego et al., 2015; Verdú et al., 2020), spreading during the Miocene and Pliocene (Gaussen, 1964). The available Early-Middle Pleistocene palaeobotanical records from the Iberian Peninsula also suggest that *Cedrus* formed part of the Mediterranean flora (Julià and Suc, 1980; Suc and Cravatte, 1982; Antunes et al., 1986; Leroy, 1997, 2008; Postigo-Mijarra et al., 2007). At first, the minor pollen occurrences of *Cedrus* in the Palominas sequence (Altolaguirre et al., 2020) might suffice to support its presence in Guadix-Baza Basin during the Early Pleistocene. Alghough not excluding the former possibility, it cannot be ruled out, however, the influence of north African pollen-source populations, with the intra-montane condition of the Baza Basin serving as physiographical pollen trap (Altolaguirre et al., 2020). Postigo-Mijarra et al. (2010) contend that part of the cedar pollen obtained in the fossil records may well have its origin in the Betic mountain ranges, where optimum conditions are given for *Cedrus* forests (Cheddadi et al., 2009). Clearly, macrofossil remains are needed to solve this issue.

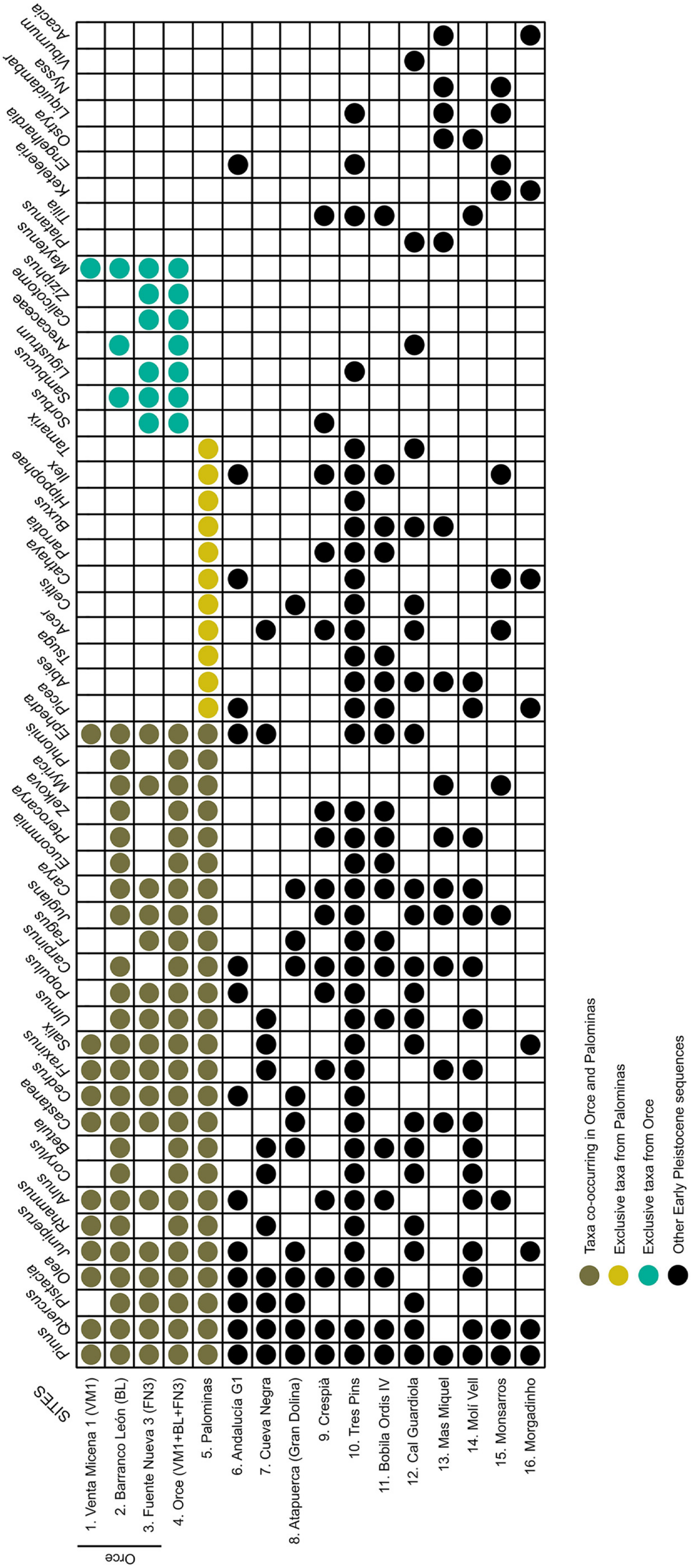
The past geography of *Carpinus betulus* is another bone of contention. The presence of *Carpinus* is documented in Iberia since the Oligocene (Postigo-Mijarra et al., 2008, 2009, 2010; Barrón et al., 2010; Verdú et al., 2020), and there are frequent palynological evidences during the Pleistocene (García-Antón and Sainz-Ollero, 1991; Desprat et al., 2005, 2007; Postigo-Mijarra et al., 2008, 2009, 2010; Carrión et al., 2013; González-Sampériz et al., 2013; Camuera et al., 2019; Altolaguirre et al., 2020; Ochando et al., 2020a, 2020b, 2020c, 2020d), now reinforced by the occurrences at BL in the Early Pleistocene. Similarly, the presence of *Carpinus* in the Palominas core has been associated to warm-temperate humid periods, and reinforced by our findings, supports the naturalness of the current populations in southwestern Europe (Altolaguirre et al., 2020). According to Magri et al. (2017) the increased vulnerability of *Carpinus* communities through glacial-interglacial cycles during the Pleistocene, together with diverse ecological factors, may have caused the disappearance of this taxon during the Late Pleistocene and Holocene (Camuera et al., 2019).

The genus *Carya* was widely distributed throughout Central Europe during the Miocene and Pliocene (Pontini and Bertini, 2000; Kovar-Eder et al., 2006; Jiménez-Moreno et al., 2008, 2010). Similarly, *Carya* had a significant representation during the Pliocene-Pleistocene transition in southern European palaeobotanical records (Magri et al., 2017). In Banyoles, northeastern Spain, the records of *Carya*, together with *Ostrya* and Mimosaceae, are quite imprecise, although they were still well represented at the Early to Middle Pleistocene transition (Geurts, 1979). The last occurrences of *Carya* in southern Europe are recorded during the Middle Pleistocene (Magri et al., 2017). Its presence in the OAZ, along with other Arctotertiary taxa, suggests the existence of ecological refugia in the Betics ranges during cold stages of the Early Pleistocene (Orain et al., 2013; Altolaguirre et al., 2020), being probably more abundant in the interglacial warm-temperate forest (Leroy, 1997; González-Sampériz et al., 2010), as suggested in BL Unit E2 (Fig. 8), where palaeoclimatic reconstruction postulate a temperate stage (Sánchez-Bandera et al., 2020; Saarinen et al., 2021).

Eucommia was present in Central Europe during the Pliocene (Hably and Kvacek, 1998), and until the late Early Pleistocene in northeastern Spain and southern France (Ber, 2005; Barrón et al., 2010; Magri et al., 2017; Verdú et al., 2020). Altolaguirre et al. (2020) find the latest evidence of *Eucommia* in the Palominas pollen record at a depth of 40 m, which could place its disappearance in this area around 1.2 Ma. However, as the authors point out, these associations between palynological results and age models should be taken with caution given the scarcity of regional pollen records. *Eucommia* is more tolerant of dry climate than other similarly extinct genera (Svenning, 2003), which could indicate its presence in both E2 and E1 within BL, the latter corresponding to a more severe phase based on previous palaeoclimatic reconstructions (Sánchez-Bandera et al., 2020; Saarinen et al., 2021).

During the Miocene and Pliocene, *Pterocarya* was a regular part of evergreen and deciduous mixed forest in Europe, together with other riverine taxa (Jiménez-Moreno et al., 2008, 2010; Barrón et al., 2010; Popescu et al., 2010; Verdú et al., 2020). This genus was associated in northwestern and central Europe to interglacial phases during the Pleistocene (Binka et al., 2003). In the Cañizar de Villarquemado long pollen record (González-Sampériz et al., 2013; García-Prieto, 2015), evidences of *Pterocarya* were identified in the lowest part of the sequence (MIS 5). Magri et al. (2017) point out that *Pterocarya* had a fairly wide distribution range in Europe with variations in density depending on the location up to at least 400 ka. From this moment on, *Pterocarya* populations suffered severe fragmentation causing the general disappearance of the genus towards the end of the Middle Pleistocene and the beginning of the Upper Pleistocene. Our records may well represent one of the latest refugia in western Europe.

In the case of the fossil records of *Zelkova*, it is difficult to reconstruct its history in the Iberian Peninsula due to the scarcity of biogeographic and genetic data (Barrón et al., 2010; Magri et al., 2017; Verdú et al., 2020). Most Pleistocene palynological records from the Iberian Peninsula fail to show any separation between pollen from *Zelkova* and



SITES	Pinus	Quercus	Pistacia	Olea	Juniperus	Rhamnus	Alnus	Corylus	Betula	Castanea	Cedrus	Fraxinus	Salix
1. Venta Micena 1 (VM1)	🟤	🟤		🟤	🟤	🟤	🟤			🟤	🟤	🟤	🟤
2. Barranco León (BL)	🟤	🟤	🟤	🟤	🟤	🟤	🟤	🟤	🟤	🟤	🟤	🟤	🟤
3. Fuente Nueva 3 (FN3)	🟤	🟤	🟤	🟤	🟤		🟤			🟤	🟤	🟤	🟤
4. Orce (VM1+BL+FN3)	🟤	🟤	🟤	🟤	🟤	🟤	🟤	🟤	🟤	🟤	🟤	🟤	🟤
5. Palominas	🟤	🟤	🟤	🟤	🟤	🟤	🟤	🟤	🟤	🟤	🟤	🟤	🟤
6. Andalucía G1	⚫	⚫	⚫	⚫	⚫		⚫				⚫		
7. Cueva Negra	⚫	⚫	⚫	⚫		⚫		⚫	⚫			⚫	⚫
8. Atapuerca (Gran Dolina)	⚫	⚫	⚫	⚫	⚫				⚫	⚫	⚫		
9. Crespià	⚫	⚫		⚫			⚫					⚫	
10. Tres Pins	⚫	⚫		⚫	⚫	⚫	⚫	⚫	⚫	⚫	⚫	⚫	⚫
11. Bobila Ordis IV	⚫	⚫		⚫			⚫		⚫				
12. Cal Guardiola	⚫	⚫	⚫		⚫	⚫		⚫	⚫	⚫			⚫
13. Mas Miquel	⚫									⚫		⚫	
14. Molí Vell	⚫	⚫		⚫	⚫		⚫	⚫	⚫	⚫		⚫	
15. Monsarros	⚫	⚫					⚫						
16. Morgadinho	⚫	⚫			⚫								⚫

SITES	Ulmus	Populus	Carpinus	Fagus	Juglans	Carya	Eucommia	Pterocarya	Zelkova	Myrica	Phlomis	Ephedra	Picea
1. Venta Micena 1 (VM1)												🟤	
2. Barranco León (BL)	🟤	🟤	🟤		🟤	🟤	🟤	🟤	🟤	🟤	🟤	🟤	
3. Fuente Nueva 3 (FN3)	🟤	🟤		🟤	🟤	🟤				🟤		🟤	
4. Orce (VM1+BL+FN3)	🟤	🟤	🟤	🟤	🟤	🟤	🟤	🟤	🟤	🟤	🟤	🟤	
5. Palominas	🟤	🟤	🟤	🟤	🟤	🟤	🟤	🟤	🟤	🟤	🟤	🟤	🟡
6. Andalucía G1		⚫	⚫									⚫	⚫
7. Cueva Negra	⚫											⚫	
8. Atapuerca (Gran Dolina)			⚫	⚫		⚫							
9. Crespià		⚫	⚫		⚫	⚫		⚫	⚫				
10. Tres Pins	⚫	⚫	⚫	⚫	⚫	⚫	⚫	⚫	⚫			⚫	⚫
11. Bobila Ordis IV	⚫		⚫	⚫		⚫	⚫	⚫	⚫			⚫	⚫
12. Cal Guardiola	⚫	⚫	⚫		⚫	⚫						⚫	
13. Mas Miquel			⚫		⚫	⚫		⚫		⚫			
14. Molí Vell	⚫		⚫		⚫	⚫		⚫					⚫
15. Monsarros					⚫					⚫			
16. Morgadinho													⚫

SITES	Abies	Tsuga	Acer	Celtis	Cathaya	Parrotia	Buxus	Hippophae	Ilex	Tamarix	Sorbus	Sambucus	Ligustrum
1. Venta Micena 1 (VM1)													
2. Barranco León (BL)												🟢	
3. Fuente Nueva 3 (FN3)											🟢	🟢	🟢
4. Orce (VM1+BL+FN3)											🟢	🟢	🟢
5. Palominas	🟡	🟡	🟡	🟡	🟡	🟡	🟡	🟡	🟡	🟡			
6. Andalucía G1					⚫				⚫				
7. Cueva Negra			⚫										
8. Atapuerca (Gran Dolina)				⚫									
9. Crespià			⚫			⚫			⚫		⚫		
10. Tres Pins	⚫	⚫	⚫	⚫	⚫	⚫	⚫	⚫	⚫	⚫			⚫
11. Bobila Ordis IV	⚫	⚫				⚫	⚫		⚫				
12. Cal Guardiola	⚫		⚫	⚫			⚫			⚫			
13. Mas Miquel	⚫						⚫						
14. Molí Vell	⚫												
15. Monsarros			⚫		⚫				⚫				
16. Morgadinho					⚫								

SITES	Arecaceae	Calicotome	Ziziphus	Maytenus	Platanus	Tilia	Keteleeria	Engelhardia	Ostrya	Liquidambar	Nyssa	Viburnum	Acacia
1. Venta Micena 1 (VM1)				🟢									
2. Barranco León (BL)	🟢			🟢									
3. Fuente Nueva 3 (FN3)		🟢	🟢	🟢									
4. Orce (VM1+BL+FN3)	🟢	🟢	🟢	🟢									
5. Palominas													
6. Andalucía G1								⚫					
7. Cueva Negra													
8. Atapuerca (Gran Dolina)													
9. Crespià						⚫							
10. Tres Pins						⚫		⚫		⚫			
11. Bobila Ordis IV						⚫							
12. Cal Guardiola	⚫				⚫							⚫	
13. Mas Miquel					⚫				⚫	⚫	⚫		⚫
14. Molí Vell						⚫			⚫				
15. Monsarros							⚫	⚫		⚫	⚫		
16. Morgadinho							⚫						⚫

🟤 Taxa co-occurring in Orce and Palominas

🟡 Exclusive taxa from Palominas

🟢 Exclusive taxa from Orce

⚫ Other Early Pleistocene sequences

Fig. 13. Presence/absence of ecologically significant pollen taxa in the pollen sequences of OAZ, Palominas (Altolaguirre et al., 2020), and other early Pleistocene sites of the Iberian Peninsula: Andalucía G1 (Feddi et al., 2011), Cueva Negra (Carrión et al., 2003a), Atapuerca Gran Dolina (García-Antón, 1995; Rodríguez et al., 2011), Crespià (Villalta and Vicente, 1972; Geurts, 1977; Suc, 1980; Suc and Cravatte, 1982; Roiron, 1983), Tres Pins (Leroy, 1987, 1990, 1997), Bobila Ordis IV (Leroy, 2008), Cal Guardiola (Postigo-Mijarra et al., 2007, 2008), Mas Miquel (Geurts, 1979; Leroy, 1990), Molí Vell (Geurts, 1977, 1979), Monsarros (Vieira, 2009), Morgadinho (Antunes et al., 1986).

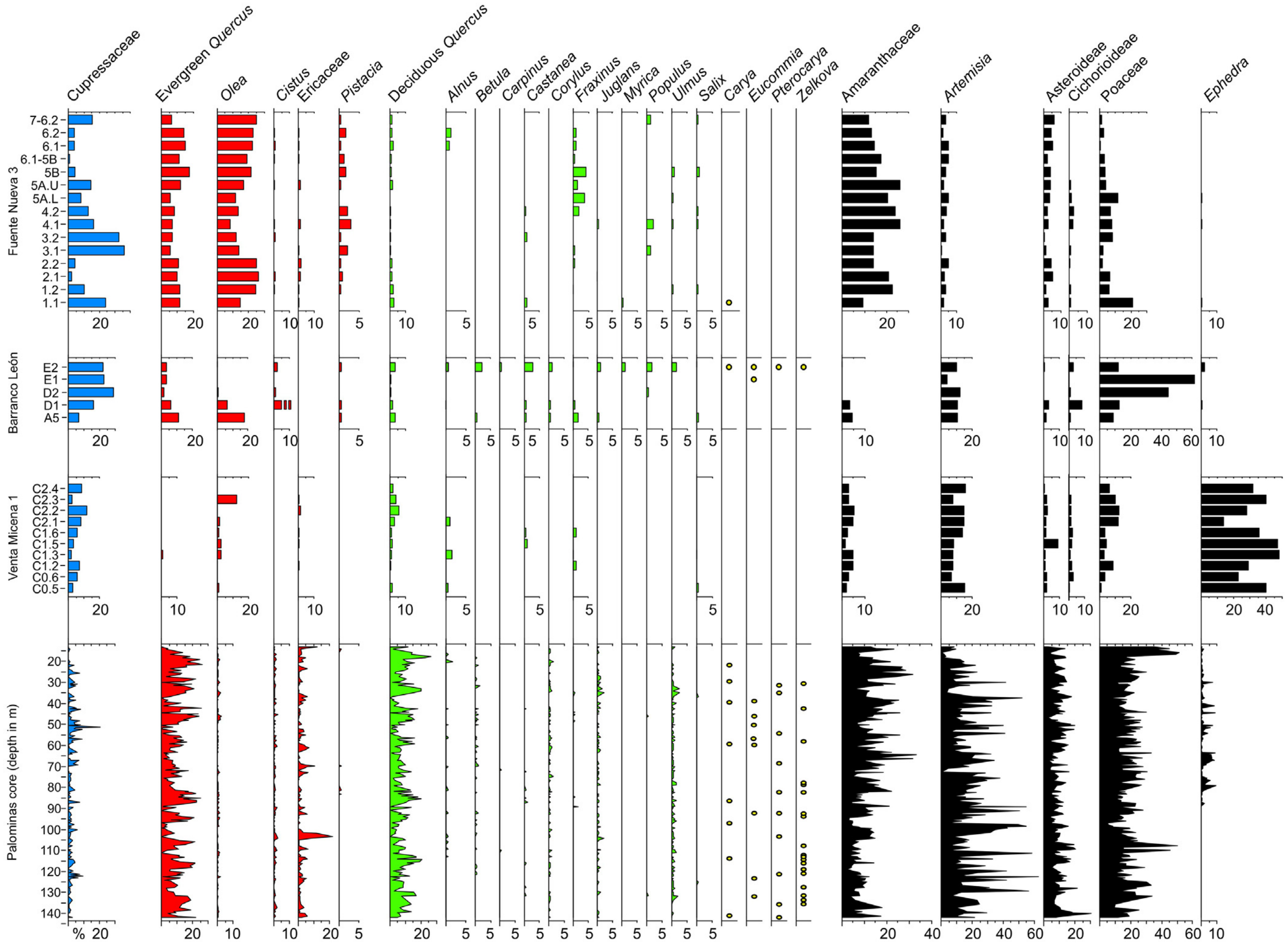


Fig. 14. Comparative diagram of selected pollen taxa from the three sites of the OAZ (present study) and the Palominas core record (Altolaguirre et al., 2020). Cupressaceae/*Juniperus* pollen in blue, Mediterranean forest/scrub taxa in red, mesic taxa in green and xerophytes/herbs in black. The diagram compares pollen abundances of the same taxa between the four pollen records using the same scale.

Ulmus, which makes their reconstruction difficult. Nevertheless, the peninsular presence of *Zelkova* is documented in the 1.6–2.6 Ma Crespià outcrop (De Villalta and Vicente, 1972; Suc, 1980; Roiron, 1983, 1992), the 1.2–2.6 Ma Tres Pins site (Leroy, 1988, 1997), and the Caranceja site (Alonso et al., 1999; Alcalde Olivares et al., 2004). Hitherto, there are no evidence of *Zelkova* during the Middle and Upper Pleistocene. Our data, together with that of Altolaguirre et al. (2020), suggest the existence of southern peninsular refugia for *Zelkova* during the Early Pleistocene.

6.4. Comparison with the Palominas pollen record and other Iberian sites

The fine-resolution palynological results of the palaeolake site of Palominas (Altolaguirre et al., 2019, 2020, 2021), show the well-known glacial-interglacial fluctuations of Quaternary vegetation types. In this sequence, covering approximatedly 400 kyr, at least 10 vegetation cycles driven by obliquity forcing, are recorded (c. 1.6–1.1 Ma). Cold dry periods, with reconstructed temperatures similar to those contemporary, would be characterized by steppes (*Artemisia*, chenopods, grasses, composites) and open woodlands, while interglacial periods, under warmer and humid conditions, would be dominated by Mediterranean woodlands, still with relative abundance of herbs. As expected for a lacustrine record, the pollen diversity and stratigraphical resolution is higher in Palominas than any of the OAZ records, since it records anemophilous taxa transported from a greater area and different altitude belts. Nonetheless, the OAZ records are still a useful palaeoecological complement by bringing into scene local zoogamous taxa difficult to find in conventional pollen records, dominated by the airborne component (Carrión, 2002b; Fiacconi and Hunt, 2017). This is the case, for instance, with *Maytenus, Capparis, Calicotome, Ziziphus, Sambucus,* and *Smilax*, which are absent in Palominas (Fig. 13).

The floristic assemblages in Palominas show similarities with those in OAZ. Leaving apart *Pinus*, which is considered over-represented in Palominas, evergreen *Quercus* is the commonly dominant arboreal taxon, which is accompanied by *Olea*, *Cistus,* Ericaceae, and *Pistacia* (Altolaguirre et al., 2020). The mesic vegetation is dominated by deciduous *Quercus*, with smaller amounts of *Alnus*, *Betula*, *Carpinus*, *Castanea*, *Corylus, Celtis*, *Fraxinus*, *Juglans*, *Myrica*, *Populus*, *Salix* and *Ulmus*, among others (Figs. 13 and 14). The xerophytic component in OAZ and Palominas is equally represented mainly by *Artemisia*, Amaranthaceae, Poaceae, Asteraceae, and *Ephedra* (Altolaguirre et al., 2020). In the case of Poaceae, its presence should not necessarily be associated with dry conditions, leaving open the possibility of localized humid grasslands, such as suggested by dental mesowear analysis in OAZ (Saarinen et al., 2021). As for Amaranthaceae, its almost uninterrupted occurrence in all the sites, and especially the high frequencies of FN3, could be linked to the development of saline environments (Gibert et al., 2007; Altolaguirre et al., 2020). Similarly to Palominas, Cupressaceae/*Juniperus* pollen is relatively frequent in OAZ, mainly in FN3, probably reflecting a pollen signal from continental dry biotopes/ stages (Carrión, 1992a, 1992b). Both in Palominas and OAZ are

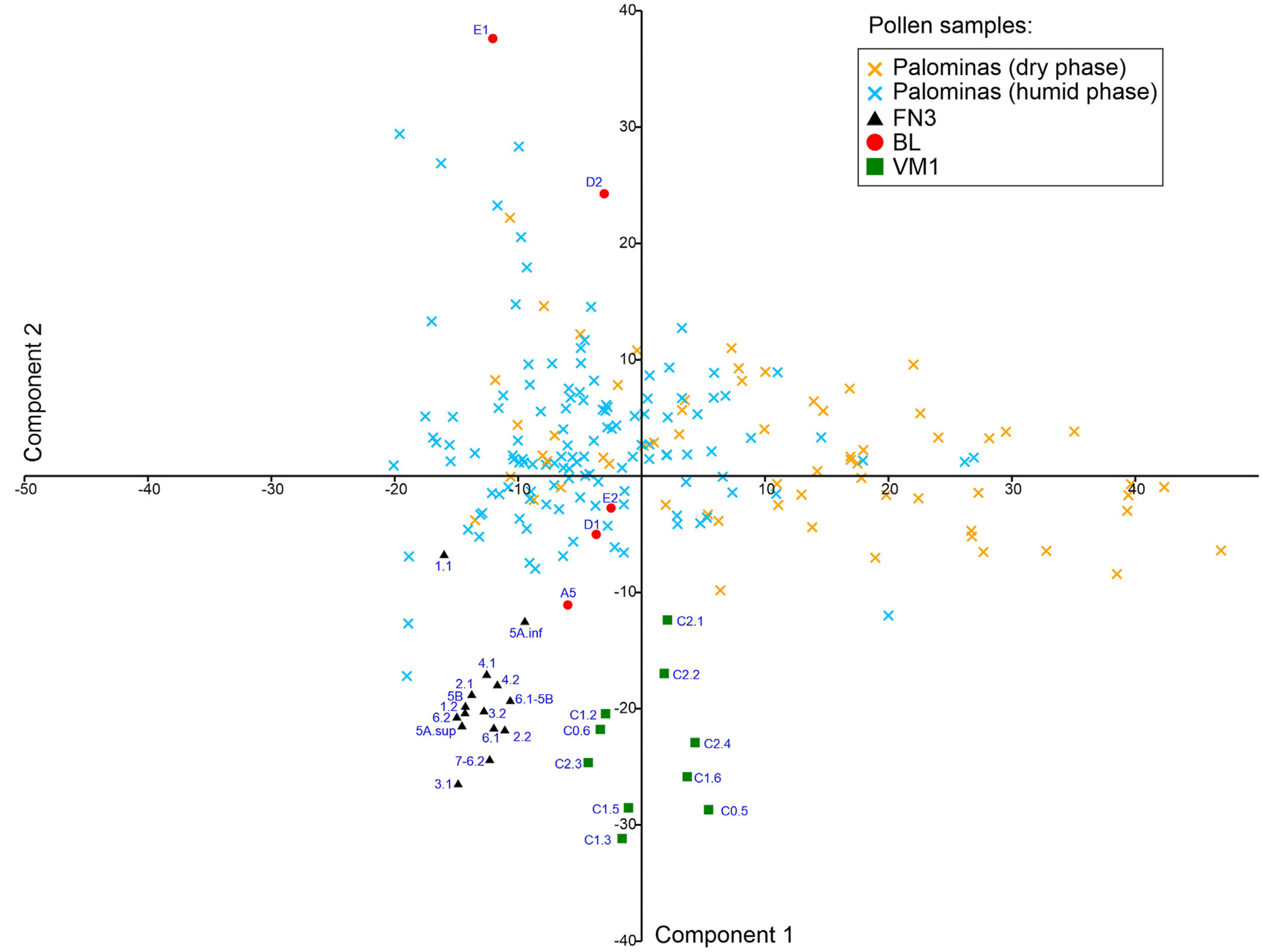


Fig. 15. Principal component analysis of the pollen proportional data of the OAZ together with the pollen samples from the Palominas pollen record. Note that the first component (horizontal axis) discriminates between glacial and interglacial samples in the Palominas record. The OAZ samples cluster around the Palominas samples from interglacial phases.

palaeoecological indicators of wetlands, which might have developed around the Baza palaeolake and nearby riverine ecosystems, and dominated by communities with *Alnus*, *Fraxinus*, *Populus*, *Salix*, *Ulmus* and Cyperaceae, among others (Figs. 13 and 14). Plausibly, this marshland vegetation would amplify its cover during humid periods when the lake was at its greatest extent (Altolaguirre et al., 2021). Although in the particular case of the Orce sites, it could have developed in association with the wetlands generated during the periods of regression of the saline lake (Granados et al., 2021). In these phases, the presence of fresh groundwater would have generated local conditions compatible with such communities (Figs. 13 and 14).

Although providing lesser diversity than Palominas, the OAZ sites also show the occurrence of Arctotertiary taxa (e.g. *Carya*, *Pterocarya*, *Eucommia*, *Zelkova*), which probably disappeared from the Iberian Peninsula during the Middle Pleistocene (Postigo-Mijarra et al., 2010; Casas-Gallego et al., 2015, 2021; Magri et al., 2017; Postigo-Mijarra and Barrón, 2017). The joint pollen data from Palominas and OAZ, show that *Zelkova*, *Carya*, *Ostrya*, *Eucommia*, *Parthenocissus*, *Symplocos*, *Parrotia*, *Cathaya*, *Pterocarya* and *Tsuga*, could have been a common taxa in the Eastern Betics forests during the Early Pleistocene, expanding downwards from mountains during humid phases (Figs. 13 and 14).

A principal component analysis of the pollen data of the OAZ samples shows the positive correlation with samples of the Palominas core interpreted as belonging to interglacial periods (Altolaguirre et al., 2020; Fig. 15). This suggests that an interglacial climate (warm and humid) occurred during the sedimentation of the studied sites. Nonetheless, such direct comparison between a lacustrine record (Palominas) and an archeological record may be flawed, due to differences in pollen catchment and deposition (Fig. 15).

Several comprehensive works have been published on the Early Pleistocene Iberian floras (Postigo-Mijarra, 2003; Suc and Popescu, 2005; Postigo-Mijarra et al., 2009; Carrión et al., 2013; Altolaguirre et al., 2019, 2021; González-Sampériz et al., 2020). While the autoecology of the taxa involved may not have changed substantially (Suc, 1980), there are no analogs regarding modern-day plant communities both at the species composition and assembling levels (Leroy, 1990) (Fig. 13). This lack of equivalence must be connected with survival and extinction patterns. The Iberian Peninsula is peculiar in the context of the European continental extinctions. Here, major biotic crises occurred at the end of the Oligocene (c. 28–23 Ma), at the Middle Miocene (c. 14 Ma), at the Piacenzian (3.6–2.5 Ma) and during the Early-Mid Pleistocene transition (1.4–0.7 Ma) (Carrión and Fernández, 2009; Postigo-Mijarra et al., 2009; Jiménez-Moreno et al., 2010).

Pliocene floras appear therefore contingent on Early Pleistocene vegetation dynamics in a context where temperature and precipitation would be higher than currently during the interglacials and similar to the present during the glacial stages (Fauquette et al., 1998a, 1998b; Altolaguirre et al., 2019). The Garraf 1 pollen record (Catalonia, NE

Spain) extends from Late Miocene to Early Pleistocene (Suc and Cravatte, 1982) and is a good example of this influence. In comparison with southern Spain, including OAZ and Palominas (Altolaguirre et al., 2020), the high arboreal cover of Early Pleistocene forests in northeastern Iberian sites during the interglacials is remarkable, as well as the scarcely marked heliophytization during the glacial stages (De Villalta and Vicente, 1972; Geurts, 1977, 1979; de Deckker et al., 1979; Julià and Suc, 1980; Roiron, 1983, 1992; Antunes et al., 1986; Leroy, 1987, 1988, 1997, 2008; Postigo-Mijarra et al., 2007; Vieira, 2009). We know now that eccentricity was not the principal astronomic control on climate variability during the Early Pleistocene in the region. Instead, obliquity was the main force, and this seems to be the reason why glacial periods were relatively short (Ehlers and Gibbard, 2008; Altolaguirre et al., 2020).

6.5. Comparison of the pollen records with other OAZ proxies

Previous studies on excavation sediments from OAZ shed light into the past environments of the Guadix-Baza region, deserving comparison with pollen data. Palaeoclimatic inferences from the analysis on small mammals (mainly rodents) (Agustí et al., 2009, 2010, 2015a) and amphibia and reptilian assemblages (Blain et al., 2011, 2016), suggest that Early Pleistocene structural climatic conditions in the Guadix-Baza Basin were not very different from the current ones (Sánchez-Bandera et al., submitted). Nevertheless, the rainfall may have been generally higher and temperatures in winter milder (Blain et al., 2011, 2016; Saarinen et al., 2021; Sánchez-Bandera et al., 2022). In particular, the occurrence in BL and FN3 of fully aquatic herpetofauna species, such as *Pelophylax* cf. *perezi*, *Discoglossus* sp. and *Natrix maura*, together with species with preference for habitats with tree cover, such as *Bufo* gr. *B. bufo*, *Zamenis scalaris*, and above all *Ophisaurus*, to a lesser extent *Chalcides* cf. *bedriagai*, *Coronella girondica*, *Hyla* sp. and *Natrix* gr. *N. natrix*, suggests the establishment of permanent humid areas with a wide plant diversity (Sánchez-Bandera et al., 2020). Pollen data are consistent with this picture. Doubtless, the Early Pleistocene landscapes do show more arboreal component than today, which could have only been maintained through higher rainfalls. Otherwise, the composition of the thermophytic component (Figs. 7, 9, 12) resembles that seen in local modern ecosystems (Rivas-Martínez, 1987; Blanca et al., 2009; Carrión et al., 2013).

Using large mammal dental ecometrics, Saarinen et al. (2021) showed that the climatic and productivity estimates for the earliest human occupation sites in FN3 and BL were climatically within the range of modern Mediterranean evergreen oak (*Quercus ilex-coccifera*) and pine forest environments (mean annual precipitation about 600–800 mm/yr). The relatively high NPP (net primary production) in both sites suggests a landscape similar to African dry woodlands/shrublands. Similarly, the identification of large mammals such as *Praemegaceros* cf. *verticornis*, *Metacervocerus rhenanus*, *Mammuthus meridionalis*, *Stephanorhinus etruscus*, *Hippopotamus antiquus*, as well as the prevalence of *Equus altidens* support the presence of humid woodlands and open meadows in the vicinity of both sites (Martínez-Navarro et al., 2003; Abbazzi, 2010). This parallels the common occurrence of certain pollen taxa in BL and FN3, such as *Alnus*, *Castanea*, *Fraxinus*, *Populus*, *Salix*, *Ulmus*, and Cyperaceae.

The broad interpretations of vegetation type in the paleoenvironments of VM, BL an FN3 based on dental ecometric analyses of the fossil large herbivorous mammal communties from these sites (Saarinen et al., 2021) correspond with the observed pollen-based reconstructions of vegetation, with VM being more dominated by open and grassy vegetation ("steppe-forest") and BL and FN3 being dominated by Mediterranean forest or woodland/shrubland vegetation. Dietary interpretations of the large herbivorous mammal communities based on dental mesowear analysis reflect these differences in vegetation. VM is the only site where the abundant, small-sized horse *Equus altidens* had a mesowear signal indicating purely grazing diet similar to extant zebras and prairie bison for example (Saarinen et al., 2021). Nonetheless, even in VM the rest of the herbivorous mammal community are characterized by browsers and mixed-feeders (Saarinen et al., 2021). In BL and FN3 the ungulate communities were clearly dominated by browsers, even with the larger species of horse (*E.* cf. *suessenbornensis*) having a strongly browse-dominated mesowear signal. Bison and large deer have somewhat more browsing dietary signals in FN3 and more mixed dietary signals in BL, which could reflect a somewhat more forested paleoenvironment in FN3. The smaller horse *E. altidens* had a more grass-dominated mesowear signal in BL and FN3 than the rest of the ungulate communities in those sites, but even for that species the mesowear signal indicates a less purely grazing diet than in VM. The relatively high percentage of low cusp relief associated with sharp cusps in *E. altidens* from BL and FN3 (see Saarinen et al., 2021 supplement) probably reflects diets that included a high proportion of tough and dry but not abrasive vegetation, such as dry shrubs.

Herpetofaunal assemblages provide palaeoclimatic insights to BL. An increased aridity trend from D1 to E has been inferred (Sánchez-Bandera et al., 2020). Pollen data for BL show an increase in the grass component from D1 to E1 (Fig. 8) with retraction of sylvicolous and thermophilous taxa (Fig. 9). This suggests more severe climatic conditions, perhaps associated to glacial stages. The ecosystem inference described by Sánchez-Bandera et al. (2020) fits well into the palaeoclimatic reconstruction from microvertebrates (Agustí et al., 2015b) and isotopes of biogenic lacustrine carbonates (Anadón et al., 2015).

Unit D1 in BL, with evidences of human presence, is palaeozoologically interpreted as relatively wooded (Sánchez-Bandera et al., 2020; Saarinen et al., 2021), which is not easy to confirm by palynology since D1's pollen spectrum appears statistically altered by *Cistus* and Cichorioideae. Even so, *Quercus, Juniperus, Pinus*, and *Olea* are frequent in D1, and the presence of *Alnus, Castanea, Corylus, Fraxinus* and *Sambucus,* are indicative of forest patches. The establishment of a more arid period in the Unit D2 according to Sánchez-Bandera et al. (2020), coincides with lesser arboreal pollen, and the absence of *Alnus*, *Betula*, *Castanea*, *Corylus*, *Fraxinus*, and *Sambucus* (Fig. 8). The increase in aridity and openness of the landscape at Unit E through the herpetofauna data (Sánchez-Bandera et al., 2020), can be assessed by pollen in E1 (decrease in tree abundance and diversity, but not in E2 where a BL's maximum diversity of arboreal taxa is recorded (Figs. 8 and 9).

Regarding to FN3, the appearance of *Manchenomys orcensis* and *Allophaiomys lavocati* have been taken as indication of the establishment of a more open habitat and with lower humidity than in BL (Agustí et al., 2019, 2022). In general, this agrees with the amphibian and reptile fauna (Sánchez-Bandera et al., 2020, 2022). This interpretation is not supported by the pollen records presented here. Nonetheless it cannot be categorically discarded as the pollen record of BL is poor. *Quercus* and *Pinus* are more abundant in FN3 than in BL, and *Juniperus* equally abundant.

An open question remains regarding the growth habit of *Olea*, which is the most prominent feature of FN3. Pollen analysis alone cannot conclude about the variety of wild olive and/or it was rather arboreal or shrubby. The same could be applied to *Juniperus*, and even for evergreen *Quercus*. Present-day habits for species such as *Olea europea var. sylvestris, Juniperus phoenicea, J. oxycedrus, J. communis, J. thurifera, Q. ilex*, and *Q. coccifera*, are strongly conditioned by human action (Blanca et al., 2009; Carrión et al., 2013).

The palaeoclimate inference from herpetofauna in FN3 suggests a trend towards aridity from Unit 2 to Unit 5, then a return to humid conditions during Unit 7. Although, this is not clearly seen in the FN3 pollen sequence (Figs. 10–12), there is a certain reduction of the arboreal component accompanied by xerophytization from the end of Unit 2 to the basal part of Unit 5. Then, from Unit 5 to 7 there is a trend of increase of AP which could be related to an increase of humid conditions, although only minor changes are perceived in the mesophytic group.

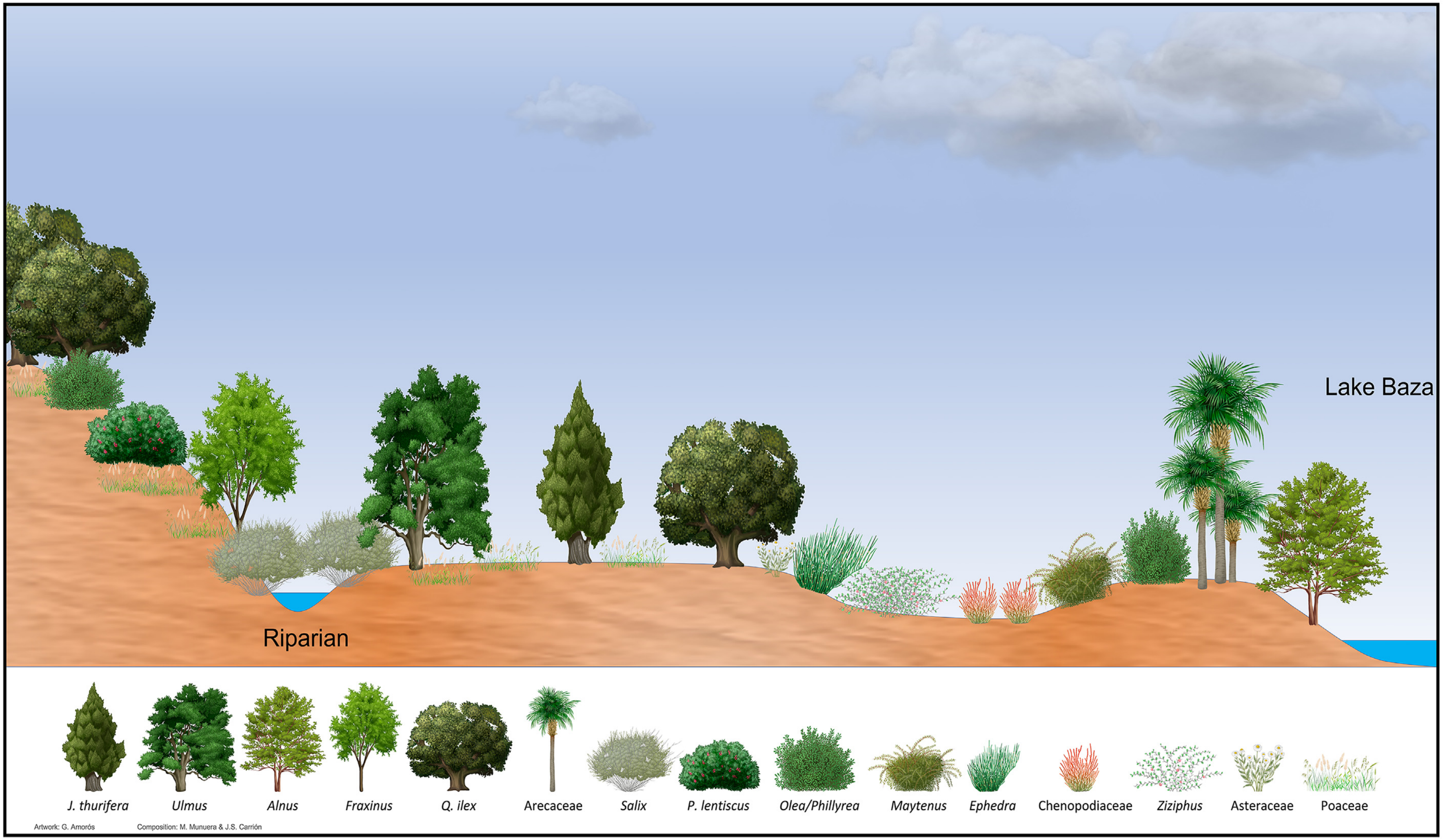


Fig. 16. Artistic interpretation of a catena of vegetation in the mountains adjoining the depression where OAZ is located. Artwork: Gabriela Amorós.

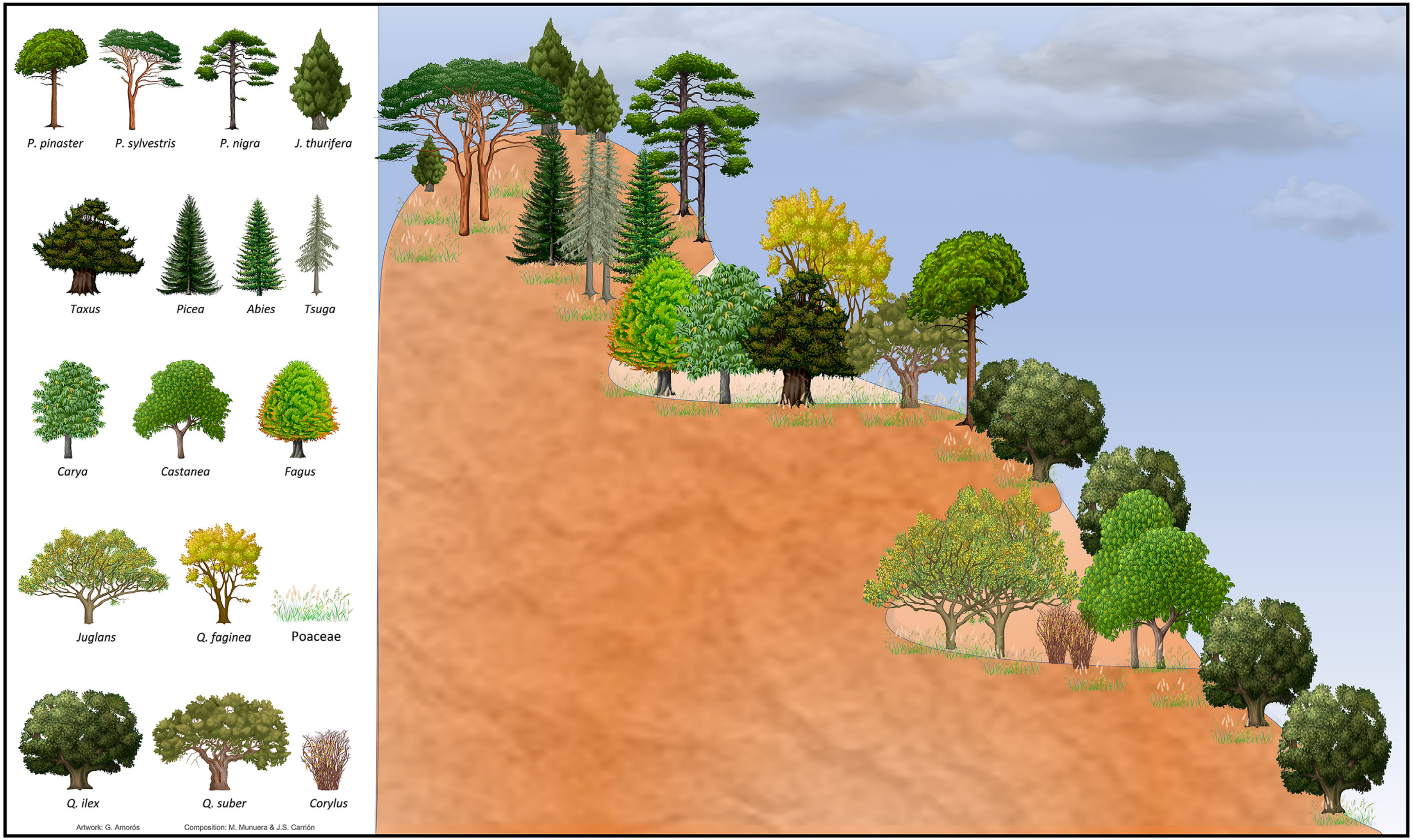


Fig. 17. Artistic interpretation of a catena of vegetation in the flat areas around OAZ, including the margin of the Baza paleolake. Artwork: Gabriela Amorós.

Amphibian and reptile assemblages in FN3 suggest that Unit 5 could correspond to a 'glacial' stage (Sánchez-Bandera et al., 2020, 2022). The associated record of *Mammuthus meridionalis* and *Equus altidens* is linked with the existence of open territories within the regional landscape (Martínez-Navarro et al., 1997; Toro-Moyano et al., 2010; Espigares et al., 2013). In agreement with these conclusions, the less forested landscapes correspond, according the pollen sequence, to Units 4 and 5. In any case, palynology indicates that local conditions were not truly cold: the record of thermophilous taxa such as *Pistacia, Olea*, *Calicotome, Ziziphus,* and *Ephedra fragilis* suggest that there were no frequent frosts. Furthermore, climate would have not been too arid if we take into account the presence of deciduous *Quercus*, *Quercus suber, Pinus pinaster, Castanea, Fraxinus, Populus, Salix, Juglans,* and *Ulmus*. Admittedly, some of these trees may well have behaved as phreatophytes. Palaeozoological data are still not free from discrepancies in their interpretation about the past landscapes of Unit 5. Agustí et al. (2019) regard the presence of *Apodemus* aff. *sylvaticus* as indicative of a more wooded habitat than in Units 4, 6 and 7.

7. Final remarks

Saarinen et al. (2021) postulated the predominance of browser diets for most of the mammal species in OAZ, except for *Equus altidens* in VM which is the only notable grazer. In coincidence, grasses would have not been frequent in FN3 and only relatively frequent in BL Units D2 and E1, probably corresponding to glacial conditions (Sánchez-Bandera et al., 2020). According to palynology, open grasslands may have had a limited presence in the region during the study period (Figs. 16 and 17). They were perhaps more a fluctuating part of more complex heliophytic communities with *Artemisia, Ephedra, Plantago*, Amaranthaceae, Cistaceae, Asteraceae, Lamiaceae, Fabaceae, and Caryophyllaceae, among others (Figs. 16 and 17). Mediterranean climates, often with only one rainy season, are not particularly favourable for grass-dominated biomes (Dallman, 1998; Nogueira et al., 2017).

These findings disagree with the over-generalist viewpoint that savannas and grasslands are essential to the earliest human expansions out of Africa, the so-called "savannahstan hypothesis" (Dennell and Roebroeks, 2005; Dennell, 2009). This is not to deny that physiognomically savanna-like environments may have been important for early human evolution and dispersal in some regions of Eurasia (Carrión et al., 2011; Domínguez-Rodrigo, 2014; Zhu et al., 2018; Messager et al., 2011; Owen-Smith, 2021), but Mediterranean vegetation, modulated long before the Quaternary (Carrión, 2003), and rich in summer-drought adapted understory, is not prone to grass-dominated communities. In that sense, paleoherpetofaunal analyses at Dmanisi suggested the occurrence of a warm and semi-arid climate during hominin presence, similar to the present-day Mediterranean climate, together with a slightly higher but much more irregular amount of rainfall (Blain et al., 2014, 2022). The reconstructed aridity indexes suggest a six months dry period, from May to October, and associated regional paleoenvironment is mainly characterized by Mediterranean forests, woodlands, and scrub, and the potential tree coverage is around 25%, that is, much less forested than today. The stronger links between Poaceae and early *Homo*, regardless the continent, can be rather placed at the evolutionary scale. As pointed out by Carrión et al. (2019b), the evolution of the grass family after the Cretaceous and its ecological success during the Neogene must be interpreted as historical contingencies (ss. Gould, 1989, 2002) for human evolution.

In connection with this debate, and through ecometrics-based distribution modelling to analyse environmental conditions for Early and Middle Pleistocene human sites in Europe, Saarinen et al. (2021) have concluded that humans tended to occupy a broad diversity of habitats including woodlands and savannoid biotopes (Figs. 16 and 17), while avoiding very open environments, which might have been inhospitable. Other authors, such as Finlayson and Carrión et al. (2007), Leroy et al. (2011), and Kahlke et al. (2011), indicated that the tendency of human fossil and archaeological sites to occur preferentially in areas with a high diversity of habitats and resources, including large river systems, especially between 1.7 and 1.3 Ma, when humans spread through the Mediterranean region (Carrión et al., 2011, 2019b). Thereafter during the Pleistocene, the situation is not generally different. Thus, the first inhabitants of Cueva Negra del Estrecho del Río Quípar and Sima de las Palomas sites, in Murcia, are also associated with high phytodiversity (Carrión et al., 2003b; Walker et al., 2008), and during the Mid-Pleistocene of Bolomor, Alicante, early Neanderthals lived in biodiversity reservoirs (Ochando et al., 2019).

The difficulties described above to correlate palaeoecological inferences from different palaeobiological assemblages must be the consequence of disparities in the sources and spatial scales of data. Concerning palynology, the problem with pollen sources is paramount and well-known (Birks and Birks, 1980). However, palaeobotanical studies may help interpret fossil assemblages when applied out from the conventional perspective and using complementary proxies and a network of sites in the same region. A recent work by Barboni et al. (2019) has shown the connections between hominin evolution and environmental changes, beyond the conventional wisdom that the principal control should be obtained from the combination of high-latitude influences (glacial-interglacial cycles) and low-latitude insolation forcing (e.g. monsoonal rainfall changes) (e.g. Trauth et al., 2007; Potts and Faith, 2015). Barboni et al. (2019) paid due attention to environmental changes at basinal and local scales to show deviations from regional trends and document the relevance of groundwater to the first hominin record in the Awash Valley, Ethiopia, and Lake Eyasi-Lake Manyara region, Tanzania.

This could be the case with Early Pleistocene OAZ. A mosaic landscape has been depicted with groundwater-fed springs, Mediterranean forests and scrub, mountain mixed forests with Eurosiberian and Arctotertiary trees, and more arid biotopes including saline depressions and xerophytic scrub on marls and gypsic soils (Figs. 16 and 17). Geophysical complexity in OAZ would come to shape ecosystems, biodiversity, and in the long term, plant geography and evolution.

Little is known about the rest of the Pleistocene in the region (Carrión, 2002a; Carrión et al., 2003b, 2013, 2019a; Camuera et al., 2019), but detailed Holocene pollen sequences (Carrión et al., 2003a, 2004, 2007; Ramos-Román et al., 2018; Jiménez-Moreno et al., 2019) suggest that mid-elevation intramontane valleys may have been the last hydro-refugia facilitating the development of mixed forests with deciduous trees and a diversity of woody species superior to that observed in modern ecosystems (Blanco-Castro et al., 2005). These forests would have remained in mountains until the last millennia, or even centuries (Carrión et al., 2003a, 2007; Gil-Romera et al., 2009, 2010; Connor et al., 2019). This allows us a conservationist corollary that can be expressed almost metaphorically. It seems that the levels of tree diversity and disparity of forest communities exhibited by the Iberian Tertiary ecosystems (Postigo-Mijarra et al., 2009, 2010; Barrón et al., 2010; González-Sampériz et al., 2010; Magri et al., 2017) have not been reached since. Thus, considering that most European regions, especially at higher latitudes, suffer climatically-induced regional extinctions of tree species earlier than in the Iberian Peninsula (Carrión and Fernández, 2009; Carrión et al., 2010; Verdú et al., 2020), the Early Pleistocene would be here the continent's last moment of forest grandeur. The Iberian southeast would have been in turn, and essentially, a scenario of survival, with delayed and less dramatic extinctions, but finally disrupted by the action of humans, exceeding the macroclimatic forces of taxonomic and ecological amputation.

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.

Acknowledgements

This research has been carried out thanks to the permissions and financial support of the General Research Project “Primeras ocupaciones humanas y contexto paleoecológico a partir de los depósitos Pliopleistocenos de la cuenca Guadix-Baza. Zona Arqueológica de la cuenca de Orce” (BC.03.032/17) funded by the General Direction of Historical and Documental Heritage (Junta de Andalucía, Spain). The development of this work was supported by the projects: i) PID2019-1049449GB-I00, funded by FEDER/Ministry of Science and Innovation – Agencia Estatal de Investigación, Fundación Séneca (grant no. 20788/PI/18); ii) Proyecto LifeWatch ERIC-SUMHAL, LIFEWATCH-2019-09-CSIC-13; (iii) MICINN through European Regional Development Fund (SUMHAL, LIFEWATCH-2019-09-CSIC-13, POPE 2014-2020). We acknowledge the funding of the project “Environment of early hominins outside Africa: the Guadix-Baza Basin” by the Leakey Foundation to H. Bocherens. Ariadna Amorós was of great help with artwork. C.S.B is supported by a FPI Predoctoral Scholarship (PRE2020-094482) associated to project CEX2019-000945-M-20-1 with the financial sponsorship of the Spanish Ministry of Science and Innovation.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.revpalbo.2022.104725.

References

Abbazzi, L., 2010. La fauna de cérvidos de Barranco León y Fuente Nueva-3. In: Toro, I., Martínez-Navarro, B., Agustí, J. (Eds.), Ocupaciones humanas en el Pleistoceno inferior y medio en la Cuenca de Guadix-Baza. Arqueología Monografías, Sevilla, pp. 273–290.

Agustí, J., Arbiol, S., Martín-Suárez, E., 1987. Roedores y lagomorfos (Mammalia) del Pleistoceno inferior de la region de Orce (Granada, España). Paleontol. Evol. Memoria especial 1, 95–107.

Agustí, J., Blain, H.-A., Cuenca-Bescós, G., Bailon, S., 2009. Climate forcing of first hominid dispersal in Western Europe. J. Hum. Evol. 57, 815–821.

Agustí, J., Blain, H.-A., Furió, M., de Marfá, R., Santos-Cubedo, A., 2010. The early Pleistocene small vertebrate succession from the Orce region (Guadix-Baza Basin, SE Spain) and its bearing on the first human occupation of Europe. Quat. Int. 223-224, 162–169.

Agustí, J., Blain, H.-A., Lozano-Fernández, I., Piñero, P., Oms, O., Furió, M., Blanco, A., López-García, J.M., Sala, R., 2015a. Chronological and environmental context of the first hominin dispersal into Western Europe: the case of Barranco León (Guadix-Baza Basin, SE Spain). J. Hum. Evol. 87, 87–94.

Agustí, J., Lozano-Fernández, I., Oms, O., Piñero, P., Furió, M., Blain, H.-A., López-García, J.M., Martínez-Navarro, B., 2015b. Early to Middle Pleistocene rodent biostratigraphy of the Guadix-Baza Basin (SE Spain). Quat. Int. 389, 139–147.

Agustí, J., Leroy, S., Julià, R., 2018. Joint vegetation and mammalian records at the early Pleistocene sequence of Bòvila Ordis (Banyoles-Besalú Basin, NE Spain) and their bearing on early hominin occupation in Europe. Palaeobiodiv. Palaeoenviron. 98, 653–662.

Agustí, J., Blain, H.-A., Sánchez-Bandera, C., Lozano-Fernández, I., Piñero, P., Furió, M., Oms, O., Barsky, D., Jiménez Arenas, J.M., 2019. Small vertebrates from Fuente Nueva 3 (Guadix-Baza Basin, SE Spain) and their bearing on the early Pleistocene hominin occupation of western Europe. 20th Congress of the International Union for Quaternary Research (INQUA), Dublin, Ireland, 25-31th July, 2019 (Poster).

Agustí, J., Piñero, P., Lozano-Fernández, I., Jiménez-Arenas, J.J., 2022. A new genus and species of arvicolid rodent (Mammalia) from the Early Pleistocene of Spain. Comptes Rendues Palevol in press.

Alcalde Olivares, C., García Antón, M., Gómez Manzaneque, F., Morla Juaristi, C., 2004. Palaeoenvironmental interpretation of the Neogene locality Caranceja (Reocín, Cantabria, N Spain) from comparative studies of wood, charcoal, and pollen. Rev. Palaeobot. Palynol. 132, 133–157.

Alonso, A., García-Amorena, I., Garzón, G., Gómez Manzaneque, F., González Díez, A., Morla Juaristi, C., Remondo, J., Roig, S., 1999. Estudio preliminar del yacimiento de macrorrestos vegetales del Caranceja (Reocín, Cantabria, España). Boletín de la Real Sociedad Española de Historia Natural (Sección Geológica) 94, 23–40.

Altolaguirre, Y., Postigo-Mijarra, J.M., Barrón, E., Carrión, J.S., Leroy, S.A.G., Bruch, A.A., 2019. An environmental scenario for the earliest hominins in the Iberian Peninsula: early Pleistocene palaeovegetation and palaeoclimate. Rev. Palaeobot. Palynol. 260, 51–64.

Altolaguirre, Y., Bruch, A., Gibert, L., 2020. A long early Pleistocene pollen record from Baza Basin (SE Spain): major contributions to the palaeoclimate and palaeovegetation of Southern Europe. Quat. Sci. Rev. 231, 106199.

Altolaguirre, Y., Schulz, M., Gibert, L., Bruch, A.A., 2021. Mapping Early Pleistocene environments and the availability of plant food as a potential driver of early *Homo* presence in the Guadix-Baza Basin (Spain). J. Hum. Evol. 155, 102986.

Anadón, P., Gabàs, M., 2009. Paleoenvironmental evolution of the early Pleistocene lacustrine sequence at Barranco León archaeological site (Orce, Baza basin, southern Spain) from stable isotopes and Sr and Mg chemistry of ostracod shells. J. Paleo. 42, 261–279.

Anadón, P., Julià, R., Oms, O., 2003. Estratigrafía y estudio sedimentológico preliminar de diversos afloramientos en Barranco León y Fuente Nueva (Orce, Granada). In: Toro, I., Agustí, J., Martínez, B. (Eds.), El Pleistoceno inferior de Barranco León y Fuente Nueva 3, Orce (Granada). Memoria científica Campañas 1999–2002. Monografías de Arqueología. Junta de Andalucía. Consejería de Cultura. 17, pp. 47–72.

Anadón, P., Oms, O., Riera, V., Julià, R., 2015. The geochemistry of biogenic carbonates as a paleoenvironmental tool for the Lower Pleistocene Barranco León sequence (BL-5D, Baza Basin, Spain). Quat. Int. 389, 70–83.

Antunes, M.T., Mein, P., Nascimento, A., Pais, J., 1986. Le gisement pleistocène de Morgadinho, en Algarve. Ciênc. Terra (UNL) 8, 9–22.

Arribas, A., Palmqvist, P., 1998. Taphonomy and palaeoecology of an assemblage of large mammals: hyaenid activity in a Lower Pleistocene site at Spain. Geobios 31, 3–47.

Barboni, D., Ashley, G.M., Bourel, B., Arráiz, H., Mazur, J.-C., 2019. Springs, palm groves, and the record of early hominins in Africa. Rev. Palaeobot. Palynol. 266, 23–41.

Barrón, E., Rivas-Carballo, R., Postigo-Mijarra, J.M., Alcalde-Olivares, C., Vieira, M., Castro, L., Pais, J., Valle-Hernández, M., 2010. The Cenozoic vegetation of the Iberian Peninsula: a synthesis. Rev. Palaeobot. Palynol. 162, 382–402.

Barsky, D., Sala, R., Menéndez, L., Toro-Moyano, I., 2015. Use and re-use: Re-knapped flakes from the Mode 1 site of Fuente Nueva 3 (Orce, Andalucía, Spain). Quat. Int. 361, 21–33.

Barsky, D., Vergès, J.M., Titton, S., Guardiola, M., Sala, R., Toro-Moyano, I., 2018. The emergence and significance of heavy-duty scrapers in ancient stone toolkits. Comptes Rendus Palevol 17, 201–219.

Ber, A., 2005. Polish Pleistocene stratigraphy-A review of interglacial stratotypes. Neth. J. Geosci. Geologie en Mijnbouw 84, 61–76.

Binka, K., Nitychoruk, J., Dzierzek, J., 2003. Parrotia persica C.A.M. (Persian witch hazel, Persian ironwood) in the Mazovian (Holsteinian) interglacial of Poland. Grana 42, 227–233.

Birks, J.B., Birks, H.H., 1980. Quaternary Palaeoecology. Edward Arnold, p. 289.

Blain, H.-A., Bailon, S., Agusti, J., Martínez-Navarro, B., Toro, I., 2011. Palaeoenvironmental and palaeoclimatic proxies to the Early Pleistocene hominids of Barranco León D and Fuente Nueva 3 (Granada, Spain) by means of their amphibian and reptile assemblages. Quat. Int. 243, 44–53.

Blain, H.-A., Agustí, J., Lordkipanidze, D., Rook, L., Delfino, M., 2014. Paleoclimatic and paleoenvironmental context of the Early Pleistocene hominins from Dmanisi (Georgia, Lesser Caucasus) inferred from the herpetofaunal assemblage. Quat. Sci. Rev. 105, 136–150.

Blain, H.-A., Lozano-Fernández, I., Agustí, J., Bailon, S., Menéndez, L., Patrocinio, M., Ros-Montoya, S., Manuel, J., Toro-Moyano, I., Martínez-Navarro, B., Sala, R., 2016. Refining upon the climatic background of the early Pleistocene hominid set- tlement in western Europe: Barranco León and Fuente nueva-3 (Guadix-Baza Basin, SE Spain). Quat. Sci. Rev. 144, 132–144.

Blain, H.-A., Fagoaga, A., Sánchez-Bandera, C., Ruiz-Sánchez, F.J., Sindaco, R., Delfino, M., 2022. New paleoecological inferences based on the Early Pleistocene amphibian and reptile assemblage from Dmanisi (Georgia, Lesser Caucasus). J. Hum. Evol. 162, 103117.

Blanca, G., Cabezudo, B., Cueto, M., Fernández López, C., Morales Torres, C., 2009. Flora Vascular de Andalucía Oriental, 4 vols. Consejería de Medio Ambiente, Junta de Andalucía, Sevilla.

Blanco-Castro, E., Casado Gonzalez, M.A., Costa Tenorio, M., 2005. Los bosques ibéricos. Una interpretación geobotánica. Planeta, Barcelona.

Bryant, V.M., Holloway, R., 1983. The role of palynology in archaeology. Adv. Archeol. Method Theory 6, 191–224.

Burjachs, F., López-García, J.M., Allué, E., Blain, H.-A., Rivals, F., Bennàsar, M., Expósito, I., 2012. Palaeoecology of Neanderthals during Dansgaard-Oeschger cycles in northeastern Iberia (Abric Romaní): from regional to global scale. Quat. Int. 247, 26–37.

Burney, D.A., Burney, L.P., 1993. Modern pollen deposition in cave sites, experimental results from New York State. New Phytol. 124, 523–535.

Camuera, J., Jiménez-Moreno, G., Ramos-Román, M.J., García-Alix, A., Toney, J.L., Scott-Anderson, R., Jiménez-Espejo, F., Bright, J., Webster, C., Yanes, Y., Carrión, J.S., 2019. Vegetation and climate changes during the last two glacial-interglacial cycles in the western Mediterranean: a new long pollen record from Padul (southern Iberian Peninsula). Quat. Sci. Rev. 205, 86–105.

Carrión, J.S., 1992a. Late quaternary pollen sequence from Carihuela cave, southern Spain. Rev. Palaeobot. Palynol. 71, 37–77.

Carrión, J.S., 1992b. A palaeoecological study in the western Mediterranean area. The Upper Pleistocene pollen record from Cova Beneito (Alicante, Spain). Palaeogeogr., Palaeoclimatol. Palaeoecol. 92, 1–14.

Carrión, J.S., 2002a. Patterns and processes of Late Quaternary environmental change in a montane region of Southwestern Europe. Quat. Sci. Rev. 21, 2047–2066.

Carrión, J.S., 2002b. A taphonomic study of modern pollen assemblages from dung and surface sediments in arid environments of Spain. Rev. Palaeobot. Palynol. 120, 217–232.

Carrión, J.S., 2003. Evolución Vegetal. Diego Marín, Murcia.

Carrión, J.S., Fernández, S., 2009. Taxonomic depletions and ecological disruption of the Iberian flora over 65 million years. J. Biogeogr. 36, 2023–2024.

Carrión, J.S., Scott, L., 1999. The challenge of pollen analysis in palaeoenvironment studies of hominid beds, the record from Sterkfontein caves. J. Hum. Evol. 36, 401–408.

Carrión, J.S., Munuera, M., Navarro, C., 1998. The palaeoenvironment of Carihuela Cave (Granada, Spain): a reconstruction on the basis of palynological investigations of cave sediments. Rev. Palaeobot. Palynol. 99, 117–144.

Carrión, J.S., Munuera, M., Navarro, C., Burjachs, F., Dupré, M., Walker, M.J., 1999. The palaeoecological potential of pollen records in caves, the case of Mediterranean Spain. Quat. Sci. Rev. 18, 1061–1073.

Carrión, J.S., Sánchez-Gómez, P., Mota, J.F., Yll, El, Chaín, C., 2003a. Holocene vegetation dynamics, fire and grazing in the Sierra de Gádor, Southern Spain. The Holocene 13, 839–849.

Carrión, J.S., Yll, E., Walker, M., Legaz, A., Chaíns, C., López, A., 2003b. Glacial refugia of temperate, Mediterranean and Ibero-North African flora in south-eastern Spain: new evidence from cave pollen at two Neandertal man sites. Glob. Ecol. Biogeogr. 12, 119–129.

Carrión, J.S., Yll, E.I., Willis, K.J., Sánchez-Gómez, P., 2004. Holocene forest history of the eastern plateaux in the Segura Mountains (Murcia, southeastern Spain). Rev. Palaeobot. Palynol. 132, 219–236.

Carrión, J.S., Fuentes, N., González-Sampériz, P., Sánchez-Quirante, L.S., Finlayson, J.C., Fernández, S., Andrade, A., 2007. Holocene environmental change in a montane region of southern Europe with a long history of human settlement. Quat. Sci. Rev. 26, 1455–1475.

Carrión, J.S., Finlayson, C., Fernández, S., Finlayson, G., Allué, E., López-Sáez, A., López-García, P., Fuentes, N., Gil, G., González-Sampériz, P., 2008. A coastal reservoir of biodiversity for Upper Pleistocene human populations: palaeoecological investigations in Gorham`s Cave (Gibraltar) in the context of the Iberian Peninsula. Quat. Sci. Rev. 27, 2118–2135.

Carrión, J.S., Fernández, S., González-Sampériz, P., Leroy, S.A.G., López-Sáez, J.A., Burjachs, F., Gil-Romera, G., Rodríguez-Sánchez, E., García-Antón, M., Gil-García, M.J., Parra, I., Santos, L., López-García, P., Yll, E.I., Dupré, M., 2009. Sterility cases and causes in Quaternary pollen analysis in the Iberian Peninsula: the advantages of reporting bad luck. Internet Archaeology 25, 1–54.. http://intarch.ac.uk/journal/issue25/5/toc.html.

Carrión, J.S., Fernández, S., González-Sampériz, P., Gil-Romera, G., Badal, E., Carrión-Marco, Y., López-Merino, L., López-Sáez, J.A., Fierro, E., Burjachs, F., 2010. Expected trends and surprises in the Lateglacial and Holocene vegetation history of the Iberian Peninsula and Balearic Islands. Review of Palaeobotany and Palynology 162, 458-475. Special issue: Carrión JS, Leroy S (Eds), Iberian Floras through Time: Land of Diversity and Survival

Carrión, J.S., Rose, J., Stringer, C., 2011. Early human evolution in the western Palearctic: ecological scenarios. Quat. Sci. Rev. 30, 1281–1295.

Carrión, J.S., Fernández, S., González-Sampériz, P., López-Merino, L., Peña, L., Burjachs, F., López-Sáez, J.A., García-Antón, M., Carrión-Marco, Y., Uzquiano, P., Postigo, J.M., Barrón, E., Allué, E., Badal, E., Dupré, M., Fierro, E., Munuera, M., Rubiales, J.M., García-Amorena, I., Jiménez-Moreno, G., Gil-Romera, G., Leroy, S., García-Martínez, M.S., Montoya, E., Fletcher, W., Yll, E., Vieira, M., Rodríguez-Ariza, M.O., Anderson, S., Peñalba, C., Gil-García, M.J., Pérez-Sanz, A., Albert, R.M., Díez, M.J., Morales, C., Gómez-Manzaneque, F., Parra, I., Ruiz-Zapata, B., Riera, S., Zapata, L., Ejarque, A., Vegas, T., Rull, V., Scott, L., Andrade, A., Pérez-Díaz, S., Abel-Schaad, D., Moreno, E., Hernández-Mateo, L., Ochando, J., Pérez Navarro, M.A., Sánchez Baena, J.J., Riquelme, J.A., Iglesias, R., Franco, F., Chaín, C., Figueiral, I., Grau, E., Matos, M., Jiménez-Espejo, F., Arribas, A., Garrido, G., Finlayson, G., Finlayson, C., Ruiz, M., Pérez-Jordá, G., Miras, Y., 2013. Paleoflora Ibérica: Plioceno-Cuaternario, 2 vols. Ministerio de Economía y Competitividad, Madrid. Universidad de Murcia y Fundación Séneca ISBN 84-616-6797-2.

Carrión, J.S., Ochando, J., Fernández, S., Munuera, M., Amorós, G., Blasco, R., Rosell, J., Finlayson, S., Giles, F., Jennings, R., Finlayson, G., Giles-Pacheco, F., Rodríguez-Vidal, J., Finlayson, C., 2018. Last Neanderthals in the warmest refugium of Europe: palynological data from Vanguard Cave. Review of Palaeobotany and Palynology, Special Issue (Carrión, J. S., deMenocal, P., Scott, L., eds.): Human evolution and palaeofloras: the contribution and potential of palaeobotany in the environmental reconstruction of hominin-bearing sites. Rev. Palaeobot. Palynol. 259, 63–80.

Carrión, J.S., Fernández, S., Jiménez, J., Munuera Giner, M., Ochando, J., Amorós, G., Ponce de León, M., Zollikofer, Ch., Martín-Lerma, I., Toro-Moyano, I., Hajdas, I., Walker, M.J., 2019a. The sequence at Carihuela Cave and its potential for research into Neanderthal ecology and the Mousterian in southern Spain. Quat. Sci. Rev. 217, 194–216.

Carrión, J.S., Scott, L., deMenocal, P. (Eds.), 2019b. Paleofloras, paleovegetation and human evolution. Rev. Palaeobot. Palynol. Special Issue. 267, 32–38.

Casas-Gallego, M., Lassaletta, L., Barrón, E., Bruch, A., Montoya, P., 2015. Vegetation and climate in the Eastern Iberian Peninsula during the pre-evaporitic Messinian (late Miocene). Palynological data from the Upper Turolian of Venta del Moro (Spain). Rev. Palaeobot. Palynol. 215, 85–99.

Casas-Gallego, M., Postigo-Mijarra, J.M., Rivas-Carballo, M.R., Valle-Hernández, M., Morín de Pablos, J., Barrón, E., 2021. Early evidence of continental aridity and open-habitat grasslands in Europe as revealed by the Middle Miocene microflora of the Madrid Basin. Palaeogeogr., Palaeoclimatol. Palaeoecol. 581, 110603.

Cheddadi, R., Fady, B., François, L., Hajar, L., Suc, J.-P., Huang, K., Demarteau, M., Vendramin, G.G., Ortu, E., 2009. Putative glacial refugia of Cedrus atlantica deduced from Quaternary pollen records and modern genetic diversity. J. Biogeogr. 36, 1361–1371.

Coles, G.M., Gilbertson, D.D., 1994. The airfall-pollen budget of archaeologically important caves: Creswell Crags, England. J. Archaeol. Sci. 21, 735–755.

Connor, S.E., Vannière, B., Colombaroli, D., Anderson, R.S., Carrión, J.S., Ejarque, A., Gil Romera, G., González-Sampériz, P., Hoefer, D., Morales-Molino, C., Revelles, J., Schneider, H., van der Knaap, W.O., Van Leeuwen, J.F., Woodbridge, J., 2019. Humans take control of fire-driven diversity changes in Mediterranean Iberia's vegetation during the mid–late Holocene. The Holocene 29, 886–901.

Dallman, P., 1998. Plant Life in the World's Mediterranean Climates. University of California Press, Berkeley, CA.

de Deckker, P., Geurts, M., Julià, R., 1979. Seasonal rythmites from a Lower Pleistocene lake in northeastern Spain. Palaeogeogr. Palaeoclimatol. Palaeoecol. 26, 43–71.

De Villalta, J.F., Vicente, J., 1972. Una flora del Cuaternario antiguo en las cercanías de Crespià. Acta Geol. Hispan. 7, 120–128.

Dennell, R.W., 2009. The Palaeolithic settlement of Asia. Cambridge University Press, Cambridge.

Dennell, R.W., Roebroeks, W., 2005. An Asian perspective on early human dispersal from Africa. Nature 438, 1099–1104.

Desprat, S., Sánchez Goñi, M.F., Turon, J.-L., McManus, J.F., Loutre, M.F., Duprat, J., Malaize, B., Peyron, O., Peypouquet, J.-P., 2005. Is vegetation responsible for glacial inception during periods of muted insolation changes? Quat. Sci. Rev. 24, 1361–1374.

Desprat, S., Sánchez Goñi, M.F., Naughton, F., Turon, J.-L., Duprat, J., Malaize, B., Cortijo, E., Peypouquet, J.-P., 2007. Climate variability of the last five isotopic interglacials: direct land-sea-ice correlation from the multiproxy analysis of North-Western Iberian margin deep-sea cores. Dev. Quat. Sci. 7, 375–386.

Dimbleby, G.W., 1985. The Palynology of Archaeological Sites. Academic Press, London.

Domínguez-Rodrigo, M., 2014. Is the "Savanna Hypothesis" a dead concept for explaining the emergence of the earliest hominins? Curr. Anthropol. 55, 59–81.

Duval, M., Falguères, C., Bahain, J.-J., Grün, R., Shao, Q., Aubert, M., Hellstrom, J., Dolo, J.-M., Agustí, J., Martínez-Navarro, B., Palmqvist, P., Toro-Moyano, I., 2011. The challenge of dating Early Pleistocene fossil teeth by the combined uranium series-electron spin resonance method: the Venta Micena palaeontological site (Orce, Spain). J. Quat. Sci. 26, 603–615.

Duval, M., Falguères, C., Bahain, J.-J., Grün, R., Shao, Q., Aubert, M., Dolo, J.-M., Agustí, J., Martínez-Navarro, B., Palmqvist, P., Toro-Moyano, I., 2012. On the limits of using combined U-series/ESR method to date fossil teeth from two Early Pleistocene archaeological sites of the Orce area (Guadix-Baza basin, Spain). Quatern. Res. 77, 482–491.

Ehlers, J., Gibbard, P., 2008. Extent and chronology of Quaternary glaciation. Episodes 31, 211–218.

Erdtman, G., 1969. Handbook of Palynology. Hafner Publishing Company, Nueva York.

Espigares, M.P., Martínez-Navarro, B., Palmqvist, P., Ros-Montoya, S., Toro, I., Agustí, J., Sala, R., 2013. Homo vs. Pachycrocuta: earliest evidence of competition for an elephant carcass between scavengers at Fuente Nueva-3 (Orce, Spain). Quat. Int. 295, 113–125.

Espigares, M.P., Palmqvist, P., Ros-Montoya, S., García-Aguilar, J.M., Rodríguez-Gómez, G., Serrano, F., Martínez-Navarro, B., 2019. The earliest cut marks of Europe: a discussion on hominin subsistence patterns in the Orce sites (Baza basin, SE Spain). Sci. Rep. 9, 15408.

Fauquette, S., Guiot, J., Suc, J.P., 1998a. A method for climatic reconstruction of the Mediterranean Pliocene using pollen data. Palaeogeogr. Palaeoclimatol. Palaeoecol. 144, 183–201.

Fauquette, S., Quézel, P., Guiot, J., Suc, J.P., 1998b. Signification bioclimatique de taxons-guides du Pliocène méditerranéen. Geobios 31, 151–169.

Feddi, N., Fauquette, S., Suc, J.P., 2011. Histoire pliocène des écosystèmes végétaux de Méditerranée sud-occidentale: apport de l'analyse pollinique de deux sondages en mer d'Alboran. Géobios 44, 57–69.

Fiacconi, M., Hunt, C.O., 2017. Palynology of surface sediments from caves in the Zagros Mountains (Kurdish Iraq): patterns and processes. Rev. Palaeobot. Palynol. 239, 66–76.

García-Antón, M., 1995. Pollen analysis of Middle Pleistocene palaeovegetation at Atapuerca. In: Bermúdez, J.M., Arsuaga, J.L., Carbonell, E. (Eds.), Human Evolution in Europe and the Atapuerca evidence. Publicaciones de la Junta de Castilla y León 1, Valladolid, pp. 147–165.

García-Antón, M., Sainz-Ollero, H., 1991. Pollen records from the middle Pleistocene Atapuerca site (Burgos, Spain). Palaeogeogr., Palaeoclimatol. Palaeoecol. 85, 199–206.

García-Prieto, E., 2015. Dinámica paleoambiental durante los últimos 135.000 años en el Alto Jiloca: el registro lacustre de El Cañizar. (PhD Thesis)Universidad de Zaragoza, Spain.

Gaussen, H., 1964. Les gymnospermes actuelles et fossiles. Travaux du Laboratoire Forestier de Toulouse 7, 321–480.

Geurts, M., 1977. Premières données à l'étude palynologique des dépôts calcareux quaternaires en Catalogne. Acta Geol. Hispán. 12, 86–89.

Geurts, M., 1979. Approche palynostratigraphique des depots calcareux quaternaires dans la region de Banyoles-Besalc (Catalogne). Actas de La IV Reunión Del Grupo de Trabajo Del Cuaternario, pp. 106–115.

Gibert, L., Ortí, F., Rosell, L., 2007. Plio-Pleistocene lacustrine evaporites of the Baza Basin (betic Chain, SE Spain). Sediment. Geol. 200, 89–116.

Gil-Romera, G., Carrión, J.S., McClure, S., Schmich, S., Finlayson, C., 2009. Holocene vegetation dynamics in Mediterranean Iberia: historical contingency and climatehuman interactions. J. Anthropol. Res. 65, 271–285.

Gil-Romera, G., Carrión, J.S., Pausas, J.G., Sevilla-Callejo, M., Lamb, H.F., Fernández, S., Burjachs, F., 2010. Holocene fire activity and vegetation response in South Eastern Iberia. Quat. Sci. Rev. 29, 1082–1092.

Girard, M., 1975. Prévèlement d`échantillons en grotte et station de terrain sec en vue de l`analyse pollinique. Bulletin de la Société préhistorique française 72, 158–160.

Girard, M., Renault-Miskovsky, J., 1969. Nouvelles techniques de preparation en palynologie appliques a trois sediments du Quaternaire final de l´Abri Corneille (Istres-Bouches-du-Rhone). Bulletin de l´Association Francaise pour l´Etude du Quaternaire 4, 275–284.

González-Sampériz, P., Leroy, S.A.G., Carrión, J.S., Fernández, S., García-Antón, M., Gil-García, M.J., Uzquiano, P., Valero-Garcés, B., Figueiral, I., 2010. Steppes, savannahs, forests and phytodiversity reservoirs during the Pleistocene in the Iberian Peninsula. Rev. Palaeobot. Palynol. 162, 427–457.

González-Sampériz, P., García-Prieto, E., Aranbarri, J., Valero Garcés, B.L., Moreno, A., Gil-Romera, G., Sevilla Callejo, M., Santos, L., Morellón, M., Mata, P., Andrade, A., Carrión, J., 2013. Reconstrucción paleoambiental del último ciclo glacial-interglacial en la Iberia continental: la secuencia del Cañizar de Villarquemado (Teruel). Cuadernos de investigación geográfica 49–76.

González-Sampériz, P., Gil-Romera, P., García-Prieto, E., Aranbarri, J., Moreno, A., Morellón, M., Sevilla-Callejo, M., Leunda, M., Santos, L., Franco-Múgica, F., Andrade, A., Carrión, J.S., Valero-Garcés, B.L., 2020. Strong continentality and effective moisture drove unforeseen vegetation dynamics since the last interglacial at inland Mediterranean areas: the Villarquemado sequence in NE Iberia. Quat. Sci. Rev. 242, 106425.

Gould, S.J., 1989. Wonderful Life. Norton, New York.

Gould, S.J., 2002. The Structure of Evolutionary Theory. Cambridge, Massachusetts, Belknap.

Granados, A., Oms, O., Anadón, P., Ibáñez-Insa, J., Kaakinen, A., Jiménez-Arenas, J.M., 2021. Geochemical and sedimentary constraints on the formation of the Venta Micena Early Pleistocene site (Guadix-Baza Basin, Spain). Sci. Rep. 11, 22437.

Haberland, C., Gibert, L., Jurado, M.J., Stiller, M., Baumann-Wilke, M., Scott, G., Mertz, D.F., 2017. Architecture and tectono-stratigraphic evolution of the intramontane Baza Basin (Bétics, SE-Spain): constraints from seismic imaging. Tectonophysics 709, 69–84.

Hably, L., Kvacek, Z., 1998. Pliocene mesophytic forests surrounding crater lakes in western Hungary. Rev. Palaeobot. Palynol. 101, 257–269.

Hunt, C.O., Fiacconi, M., 2018. Pollen taphonomy of cave sediments: what does the pollen record in caves tell us about external environments and how do we assess its reliability? Quat. Int. 485, 68–75.

Hüsing, S.K., Oms, O., Agustí, J., Garcés, M., Kouwenhovene, T.J., Krijgsman, W., Zachariasse, J., 2010. On the late Miocene closure of the Mediterranean–Atlantic gateway through the Guadix basin (southern Spain). Palaeogeogr., Palaeoclimatol. Palaeoecol. 291, 167–179.

Jiménez-Moreno, G., 2003. Análisis polínico de las secciones de Barranco León y Fuente Nueva de Orce (Granada). Primeros resultados. In: Toro, I., Agustí, J., Matínez-Navarro, B. (Eds.), El Pleistoceno inferior de Barranco León y de Fuente Nueva, 3, Orce (Granada). Memoria Científica Campañas 1999-2002, pp. 173–181.

Jiménez-Moreno, G., Fauquette, S., Suc, J., 2008. Vegetation, climate and palae- oaltitude reconstructions of the Eastern Alps during the Miocene based on pollen records from Austria, Central Europe. J. Biogeogr. 35, 1638–1649.

Jiménez-Moreno, G., Fauquette, S., Suc, J.-P., 2010. Miocene to Pliocene vegetation reconstruction and climate estimates in the Iberian Peninsula from pollen data. Rev. Palaeobot. Palynol. 162, 403–415.

Jiménez-Moreno, G., Pérez-Asensio, J.N., Larrasoaña, J.C., Sierro, F.J., Garcia-Castellanos, D., Salazar, A., Salvany, J., Ledesma, S., Mata, M.P., Mediavilla, C., 2019. Early Pliocene climatic optimum, cooling and early glaciation deduced by terrestrial and marine environmental changes in SW Spain. Global Planet. Change 180, 89–99.

Jiménez-Moreno, G., Anderson, R.S., Ramos-Román, M.J., Camuera, J., Mesa-Fernández, J.M., García-Alix, A., Jiménez-Espejo, F.J., Carrión, J.S., López-Avilés, A., 2020. The Holocene Cedrus pollen record from Sierra Nevada (S Spain), a proxy for climate change in N Africa. Quat. Sci. Rev. 242, 106468.

Julià, R., Suc, J.P., 1980. Analyse pollinique des dépots lacustres du Pléistocène Inférieur de Banyoles (Bañolas, site de la Bòbila Ordis-Espagne: un élément nouveau dans la reconstitution de l'histoire paléoclimatique des régions méditerranéennes d' Europe occidentale). Geobios 13, 5–19.

Kahlke, R.-D., García, N., Kostopoulos, D.S., Lacombat, F., Lister, A.M., Mazza, P.P.A., Spassov, N., Titov, V.V., 2011. Middle Pleistocene inferred from large mammal communities, and implications for hominin dispersal in Europe. Quat. Sci. Rev. 30, 1368–1395.

Kovar-Eder, J., Kvaček, Z., Martinetto, E., Roiron, P., 2006. Late Miocene to Early Pliocene vegetation of southern Europe (7-4 Ma) as reflected in the megafossil plant record. Palaeogeogr., Palaeoclimatol. Palaeoecol. 238, 321–339.

Leroy, S.A.G., 1987. Analyse palynologique de deux nouvelles sections du Pléistocène Inférieur de Banyoles (Catalogne). Actas del VI Simposio de Palinologia, APLE, Salamanca 1987, 303–313.

Leroy, S.A.G., 1988. Image pollinique d' une steppe du Pliocène supérieur à Bobila Ordis, Banyoles (Catalogne). Institut Français de Pondichéry, Travaux Scientifiques et Techniques. Actes deuxième symposium APLF, Bordeaux, t. XXV, pp. 197–207.

Leroy, S.A.G., 1990. Paléoclimats Plio-Pléistocènes en Catalogne et Languedoc d'après la palynologie de formations lacustres Ph.D. Thesis. Université Catholique de Louvain, Faculté des Sciences. Belgique.

Leroy, S.A.G., 1997. Climatic and non-climatic lake-level changes inferred from a Plio-Pleistocene lacustrine complex of Catalonia (Spain): palynology of the Tres Pins sequences. J. Paleo. 17, 347–367.

Leroy, S.A.G., 2008. Vegetation cycles in a disturbed sequence around the Cobb- Mountain subchron in Catalonia (Spain). J. Paleo. 40, 851–868.

Leroy, S.A.G., Arpe, K., Mikolajewicz, U., 2011. Vegetation context and climatic limits of the Early Pleistocene hominin dispersal in Europe. Quat. Sci. Rev. 30, 1448–1463.

López-Sáez, J.A., López-García, P., Burjachs, F., 2003. Arqueopalinología: síntesis crítica. Universidad de Córdoba.

López-Sáez, J.A., López-García, P., Cortés Sánchez, M., 2007. Paleovegetación del Cuaternario reciente: Estudio arqueopalinológico. In: Cortés Sánchez, M. (Ed.), Cueva Bajondillo (Torremolinos). Secuencia cronocultural y paleoambiental del Cuaternario reciente en la Bahía de Málaga. Centro de Ediciones de la Diputación de Málaga, Junta de Andalucía, Universidad de Málaga, Fundación Cueva de Nerja y Fundación Obra Social de Unicaja, Málaga, pp. 139–156.

Lozano-Fernandez, I., Blain, H.A., López-García, J.M., Agustí, J., 2015. Biochronology of the first hominid remains in Europe using the vole Mimomys savini: Fuente Nueva 3 and Barranco León D, Guadix-Baza Basin, south-eastern Spain. Hist. Biol. 27, 1021–1028.

Luzón, C., Courtenay, L.A., Yravedra, J., Saarinen, J., Blain, H.A., DeMiguel, D., Viranta, S., Azanza, B., Rodríguez-Alba, J.J., Herranz-Rodrigo, D., Solano, J.A., Oms, O., Agustí, J., Fortelius, M., Jiménez Arenas, J.M., 2021. Taphonomic and spatial analyses from the Early Pleistocene site of Venta Micena 4 (Orce, Guadix-Baza Basin, southern Spain). Sci. Rep. 11, 13977.

Magri, D., Parra, I., 2002. Late Quaternary western Mediterranean pollen records and African winds. Earth Planet. Sci. Lett. 200, 401–408.

Magri, D., Di Rita, F., Aranbarri, J., Fletcher, W., González-Sampériz, P., 2017. Quaternary disappearance of tree taxa from Southern Europe: timing and trends. Quat. Sci. Rev. 163, 23–55.

Maldonado-Garrido, E., Piñero, P., Agustí, J., 2017. A catalogue of the vertebrate fossil record from the Guadix-Baza Basin (SE Spain). Span. J. Palaeontol. 32, 207–235.

Martínez-Monzón, A., Sánchez-Bandera, C., Fagoaga, A., Oms, O., Agustí, J., Barsky, D., Solano-García, J., Jiménez-Arenas, J.M., Blain, H.-A., 2022. Amphibian body size and species richness as a proxy for primary productivity and climate: the Orce wetlands (Early Pleistocene, Guadix-Baza Basin, SE Spain). Palaeogeogr., Palaeoclimatol. Palaeoecol. 586, 110752.

Martínez-Navarro, B., Turq, A., Oms, O., 1997. Fuente Nueva-3 (Orce, Granada, Spain) and the first human occupation of Europe. J. Hum. Evol. 33, 611–620.

Martínez-Navarro, B., Espigares, M.P., Ros, S., 2003. Estudio preliminar de las asociaciones de grandes mamíferos de Fuente Nueva-3 y Barranco León-5 (Orce, Granada, España). In: Toro Moyano, I., Agustí, J., Martínez-Navarro, B. (Eds.), El Pleistoceno inferior de Barranco León y de Fuente Nueva 3, Orce (Granada), Junta de Andalucía. Consejería de Cultura, Sevilla, pp. 115–136.

Mercado, F.G., Tendero, F.V., 1988. Mapa de vegetación actual de la Sierra de Baza. Granada University, Spain.

Messager, E., Lebreton, V., Marquer, L., Russo-Ermolli, E., Orain, R., Renault Miskovsky, J., Lordkipanidze, D., Despriée, J., Peretto, C., Arzarello, M., 2011. Palaeoenvironments of early hominins in temperate and Mediterranean Eurasia: new palaeobotanical data from Palaeolithic key-sites and synchronous natural sequences. Quat. Sci. Rev. 30, 1439–1447.

Navarro, C., Carrión, J.S., Navarro, J., Munuera, M., Prieto, A.R., 2000. An experimental approach to the palynology of cave deposits. J. Quat. Sci. 15, 603–619.

Navarro, C., Carrión, J.S., Munuera, M., Prieto, A.R., 2001. A palynological study of karstic cave sediments on the basis of their potential for palaeoecological reconstruction. Rev. Palaeobot. Palynol. 117, 245–265.

Navarro, C., Carrión, J.S., Prieto, A.R., Munuera, M., 2002. Modern cave pollen and its application to describe the palaeorecords in an arid environment. Complutum 13, 7–18.

Nogueira, C., Bugalho, M.N., Pereira, J.S., Caldeira, M.C., 2017. Extended autumn drought, but not nitrogen deposition, affects the diversity and productivity of a Mediterranean grassland. Environ. Exp. Bot. 138, 99–108.

Ochando, J., Carrión, J.S., Blasco, R., Fernández, S., Amorós, G., Munuera, M., Sañudo, P., Fernández Peris, J., 2019. Silvicolous Neanderthals in the Far West: the Mid-Pleistocene palaeoecological sequence of Bolomor Cave (Valencia, Spain). Quat. Sci. Rev. 217, 247–267.

Ochando, J., Carrión, J.S., Blasco, R., Rivals, F., Rufà, A., Amorós, G., Munuera, M., Fernández, S., Rosell, J., 2020a. The Late Quaternary pollen sequence of Toll Cave, a palaeontological site with evidence of human activities in Northeastern Spain. Quat. Int. 554, 1–14.

Ochando, J., Carrión, J.S., Blasco, R., Rivals, F., Rufá, A., Demuro, M., Arnold, L.J., Amorós, G., Munuera, M., Fernández, S., Rosell, J., 2020b. Neanderthals in a highly diverse, Mediterranean-Eurosiberian forest ecotone: the Pleistocene pollen record of Teixoneres Cave. Northeastern Spain. Quat. Sci. Rev. 241, 106429.

Ochando, J., Carrión, J.S., Rodríguez-Vidal, J., Jiménez-Arenas, J.M., Fernández, S., Amorós, G., Munuera, M., Scott, L., Stewart, J.R., Knul, M.V., Toro-Moyano, I., Ponce de León, M., Zollikofer, C., 2020c. Palynology and chronology of hyaena coprolites from the Piñar karstic Caves Las Ventanas and Carihuela, southern Spain. Palaeogeogr., Palaeoclimatol. Palaeoecol. 552, 109771.

Ochando, J., López-Sáez, J.A., Pérez-Díaz, S., Ramos-Fernández, J., Munuera, M., Fernández, S., Galacho-Jiménez, F.B., Luelmo-Lautenschlaeger, R., Carrión, J.S., 2020d. A new pollen sequence from southern Iberia suggesting coastal Pleistocene phytodiversity hotspot. Rev. Palaeobot. Palynol. 281, 104281.

Oms, O., Parés, J.M., Martínez-Navarro, B., Agustí, J., Toro, I., Martínez Fernández, G., Turq, A., 2000. Early human occupation of Western Europe: paleomagnetic dates of two paleolithic sites in Spain. Proc. Natl Acad. Sci. USA 97, 10666–10670.

Oms, O., Anadón, P., Agustí, J., Julià, R., 2011. Geology and chronology of the continental Pleistocene archeological and mammal sites of the Orce Area (Baza Basin, Spain). Quat. Int. 243, 33–43.

Orain, R., Lebreton, V., Ermolli, E.R., Combourieu-Nebout, N., Sémah, A.-M., 2013. Carya as marker for tree refuges in southern Italy (Boiano basin) at the Middle Pleistocene. Palaeogeogr., Palaeoclimatol. Palaeoecol. 369, 295–302.

Owen-Smith, N., 2021. Only in Africa. Cambridge University Press, Cambridge, p. 376.

Palmqvist, P., Espigares, M., Pérez-Claros, J., Figueirido, B., Guerra-Merchán, A., Ros-Montoya, S., Rodríguez-Gómez, G., García-Aguilar, J., Granados, A., Martínez-Navarro, B., 2022. Déjà vu: a reappraisal of the taphonomy of quarry VM4 of the Early Pleistocene site of Venta Micena (Baza Basin, SE Spain). Sci. Rep. 12, 705.

Pontini, M.R., Bertini, A., 2000. Late Pliocene vegetation and climate in Central Italy: high-resolution pollen analysis from the Fosso Bianco succession (Tiberino Basin). Geobios 33, 519–526.

Popescu, S.-M., Biltekin, D., Winter, H., Suc, J.-P., Melinte-Dobrinescu, M.C., Klotz, S., Rabineau, M., Combourieu-Nebout, N., Clauzon, G., Deaconu, F., 2010. Pliocene and Lower Pleistocene vegetation and climate changes at the European scale: long pollen records and climatostratigraphy. Quat. Int. 219, 152–167.

Postigo-Mijarra, J.M., 2003. Contribución al conocimiento de la vegetación pleistocena de la Península Ibérica. Estudio paleobotánico de macrorrestos vegetales fósiles. Ph. D. ThesisUniversidad Autónoma de Madrid, Facultad de Ciencias.

Postigo-Mijarra, J.M., Barrón, E., 2017. Génesis y evolución de los paisajes ibéricos cuaternarios. Fenómenos y persistencia, cambio y extinción florística. Enseñanza de las Ciencias de la Tierra 25, 35–47.

Postigo-Mijarra, J.M., Burjachs, F., Gómez Manzaneque, F., Morla, C., 2007. A palaeoecological interpretation of lower–middle Pleistocene Cal Guardiola site (Tarrasa, Barcelona, NE Spain) from the comparative study of wood and pollen samples. Rev. Palaeobot. Palynol. 146, 247–264.

Postigo-Mijarra, J.M., Gómez-Manzaneque, F., Morla, C., 2008. Survival and long-term maintenance of tertiary trees in the Iberian Peninsula during the Pleistocene: first record of *Aesculus* L. (Hippocastanaceae) in Spain. Veg. Hist. Archaeobotany 17, 351–364.

Postigo-Mijarra, J.M., Barrón, E., Gómez-Manzaneque, F., Morla, C., 2009. Floristic changes in the Iberian Peninsula and Balearic Islands (south-west Europe) during the Cenozoic. J. Biogeogr. 36, 2025–2043.

Postigo-Mijarra, J.M., Morla, C., Barrón, E., Morales-Molino, C., García, S., 2010. Patterns of extinction and persistence of Arctotertiary flora in Iberia during the Quaternary. Rev. Palaeobot. Palynol. 162, 416–426.

Potts, R., Faith, J.T., 2015. Alternating high and low climate variability: the context of natural selection and speciation in Plio-Pleistocene hominin evolution. J. Hum. Evol. 87, 5–20.

Ramos-Román, M.J., Jiménez-Moreno, G., Camuera, J., García-Alix, A., Scott Anderson, R., Jiménez-Espejo, F.J., Sachse, D., Toney, J.L., Carrión, J.S., Webster, C., Yanes, Y., 2018. Millennial-scale cyclical environment and climate variability during the Holocene in the western Mediterranean region deduced from a new multi-proxy analysis from the Padul record (Sierra Nevada, Spain). Global Planet. Change 168, 35–53.

Revelles, J., Burjachs, F., van Geel, B., 2016. Pollen and non-pollen palynomorphs from the Early Neolithic settlement of La Draga (Girona, Spain). Rev. Palaeobot. Palynol. 225, 1–20.

Rivas-Martínez, S., 1987. Memoria del Mapa de Series de Vegetación de España. ICONA, Serie Tecnica, Madrid.

Rivas-Martínez, S., Arnaiz, C., Barrero, E., Crespo, A., 1977. Apuntes sobre las provincias corológicas de la Península Ibérica e Islas Canarias. Opusc. Bot. Pharm. Complutensis 1, 1–48.

Rodríguez, J., Allué, E., Burjachs, F., Cáceres, I., Cuenca, G., Expósito, I., García, N., García-Antón, M., Huguet, R., van Made, J., Mosquera, M., Ollé, A., Pérez-González, A., Rodríguez, X.P., Rosell, J., Sala, R., Saladié, P., Vallverdú, J., Bermúdez de Castro, J.M., Carbonell, E., 2011. One million years of environmental changes and cultural evolution at Atapuerca (Burgos, Spain). Quat. Sci. Rev. 30, 1396–1412.

Rodriguez-Ariza, M.O., 1992. Human-plant relationships during the Copper and Bronze Ages in the Baza and Guadix basins (Granada, Spain). Bulletin de la Société Botanique de France. Actual. Bot. 139, 451–464.

Roiron, P., 1983. Nouvelle étude de la macroflore plio-pleistocène de Crespià (Catalogne, Espagne). Geobios 16, 687–715.

Roiron, P., 1992. Flores, végétation et climats du Neogène Mediterranéen: apports de macroflores du Sud de la France et du Nord-Est de l'Espagne. PhD ThesisUniversite´ de Montpellier II, Montpellier.

Rook, L., Martínez-Navarro, B., 2010. Villafranquian: the long story of a Plio-Pleistocene European large mammal biochronologic unit. Quat. Int. 219, 134–144.

Ros-Montoya, S., Bartolini-Lucenti, S., Espigares, M.P., Palmqvist, P., Martínez-Navarro, B., 2021. First review of Lyncodontini material (Mustelidae, Carnivora, Mammalia) from the Lower Pleistocene archaeo-palaeontological sites of Orce (Southeastern Spain). Rivista Italiana de Paleontologia e Stratigrafia 127, 33–47.

Saarinen, J., Oksanen, O., Žliobaitė, I., Fortelius, M., DeMiguel, D., Azanza, B., Bocherens, H., Luzón, C., Solano-García, J., Yravedra, J., Courtenay, L.A., Blain, H.-A., Sánchez-Bandera, C., Serrano-Ramos, A., Rodríguez-Alba, J.J., Viranta, S., Barsky, D., Tallavaara, M., Oms, O., Agustí, J., Ochando, J., Carrión, J.S., Jiménez-Arenas, J.M., 2021. Pliocene to Middle Pleistocene climate history in the Guadix-Baza Basin, and the environmental conditions of early *Homo* dispersal in Europe. Quat. Sci. Rev. 268, 107132.

Sánchez-Bandera, C., Oms, O., Blain, H.-A., Lozano-Fernández, I., Bispal-Chinesta, J.F., Agustí, J., Saarinen, J., Fortelius, M., Titton, S., Serrano-Ramos, A., Luzón, C., Solano-García, J., Barsky, D., Jiménez-Arenas, J.M., 2020. New stratigraphically constrained palaeoenvironmental reconstructions for the first human settlement in western Europe: the early Pleistocene herpetofaunal assemblages from Barranco León and Fuente Nueva 3 (Granada, SE Spain). Quat. Sci. Rev. 243, 106466.

Sánchez-Bandera, C., Fagoaga Moreno, A., Serrano-Ramos, A., Solano-García, J., Barsky, D., DeMiguel, D., Ochando, J., Piñero, P., Saarinen, J., Lozano-Fernández, I., Courtenay, L.A., Titton, S., Luzón, C., Bocherens, H., Yravedra, J., Fortelius, M., Agustí, J., Carrión, J.S., Oms, O., Blain, H.-A., Jiménez-Arenas, J.M., 2022. Glacial/interglacial climate variability in Southern Spain during the late Early Pleistocene and climate backdrop for early *Homo* in Europe. Gondwana Res. (submitted).

Sánchez-Goñi, M.F., Eynaud, F., Turon, J.L., Shackleton, N.J., 1999. High resolution palynological record off the Iberian margin: direct land-sea correlation for the Last Interglacial complex. Earth Planet. Sci. Lett. 171, 123–137.

Suc, J.P., 1980. Contribution a la connaissance du Pliocène et du Pleistocène inferieur des régions mediterranéennes d'Europe Occidentale par l'analyse palynologique des dêpots du Languedoc-Roussillon (Sud de la France) et de la Catalogne (Nord-Est de l'Espagne). PhD ThesisUniversité de Montpellier II, Montpellier, p. 198.

Suc, J.P., Cravatte, J., 1982. Etude palynologique du Pliocène de Catalogne (Nord-Est de l ´Espagne). Paléobiologie continentale XIII 1, 1–31.

Suc, J.P., Popescu, S.M., 2005. Pollen records and climatic cycles in the North Mediterranean region since 2.7 Ma. In: Head, M.J., Gibbard, P.L. (Eds.), Early–Middle Pleistocene Transitions: The Land–Ocean Evidence. Geological Society247, pp. 147–158.

Svenning, J.-C., 2003. Deterministic Plio-Pleistocene extinctions in the European cool-temperate tree flora. Ecol. Lett. 6, 646–653.

Titton, S., Barsky, D., Bargalló, D., Vergès, J.M., Guardiola, M., García-Solano, J., Jiménez-Arenas, J.M., Toro-Moyano, I., Sala, R., 2018. Active percussion tools from the Oldowan site of Barranco León (Orce, Andalousie, Spain): the fundamental role of pounding activities in hominin lifeways. J. Archaeol. Sci. 96, 131–147.

Titton, S., Barsky, D., Bargalló, A., Serrano-Ramos, A., Vergès, J.M., Toro-Moyano, I., Sala, R., García-Solano, J., Jiménez-Arenas, J.M., 2020. Subspheroids in the lithic assemblage of Barranco León (Spain): recognizing the late Oldowan in Europe. PLoS One 15, e0231036.

Titton, S., Oms, O., Barsky, D., Bargalló, A., Serrano-Ramos, A., Solano-García, J., Sánchez-Bandera, C., Yravedra, J., Blain, H.-A., Toro-Moyano, I., Jiménez-Arenas, J.M., Sala-Ramos, R., 2021. Oldowan stone knapping and percussive activities on a raw material reservoir deposit 1.4 million years ago at Barranco León (Orce, Spain). Archaeol. Anthropol. Sci. 13, 108.

Toro-Moyano, I., de Lumley, H., Fajardo, B., Barsky, D., Celiberti, V., Grégoire, S., Martínez-Navarro, B., Espigares, M.P., Ros-Montoya, S., 2009. L'industrie lithique des gisements du pleistocène inférieur de Barranco León et Fuente Nueva 3, Granade, Espagne. L'Anthropologie 113, 111–124.

Toro-Moyano, I., De Lumley, H., Barrier, P., Barsky, D., Cauche, D., Celiberti, V., Grégoire, S., Lebégue, F., Mestour, B., Moncel, M.-H., 2010. Les industries lithiques archaïques de Barranco León et de Fuente Nueva 3. CNRS éditions, Paris.

Toro-Moyano, I., Barsky, D., Cauche, D., Celiberti, V., Grégoire, S., Lebegue, F., Moncel, M.H., de Lumley, H., 2011. The archaic stone-tool industry from Barranco León and Fuente Nueva 3, (Orce, Spain): evidence of the earliest hominin presence in southern Europe. Quat. Int. 243, 80–91.

Toro-Moyano, I., Martínez-Navarro, B., Agustí, J., Souday, C., Bermúdez de Castro, J.M., Martinón-Torres, M., Fajardo, B., Duval, M., Falguères, C., Oms, O., Parés, J.M., Anadón, P., Julià, R., García-Aguilar, J.M., Moigne, A.M., Espigares, M.P., Ros-Montoya, S., Palmqvist, P., 2013. The oldest human fossil in Europe, from Orce (Spain). J. Hum. Evol. 65, 1–9.

Trauth, M.H., Maslin, M.A., Deino, A., Strecker, M.R., Bergner, A.G.N., Dühnforth, M., 2007. High- and low-latitude forcing of Plio-Pleistocene African climate and human evolution. J. Hum. Evol. 53, 475–486.

Valle, F., Navarro, F.B., Jiménez, M.N., 2004. Datos botánicos aplicados a la gestión del medio natural andaluz I: Bioclimatología y biogeografía. Consejería de Medio Ambiente. Junta de Andalucía, Sevilla.

Verdú, M., Pausas, J., Postigo-Mijarra, J.M., Barrón, E., Casas-Gallego, M., Arroyo, J., Carrión, J.S., 2020. Phylogenetic diversity in the Iberian Peninsula throughout the Cenozoic. Environ. Exp. Bot. 170, 103888.

Vieira, M.C., 2009. Palinologia do Pliocénico da Orla Ocidental Norte e Centro de Portugal: Contributo para a compreensão da cronostratigrafia e da evolução paleoambiental. Tesis doctoralUniversidad do Minho, Braga, Portugal, p. 389.

Villalta, J.F., Vicente, J., 1972. Una flora del Cuaternario antiguo en las cercanías de Crespià. Acta Geol. Hispán. 7, 120–128.

Walker, M.J., Gibert, J., López, M.V., Vincent, A., Pérez-Pérez, A., Zapata, J., Ortega, J., Higham, T., Pike, A., Schwenninger, J.L., Zilhão, J., Trinkaus, E., 2008. Late Neanderthals in southeastern Iberia: Sima de las Palomas del Cabezo Gordo, Murcia, Spain. Proc. Natl. Acad. Sci. 105, 20631–20636.

Yravedra, J., Solano, J.A., Herranz-Rodrigo, D., Linares-Matás, G., Saarinen, J., Rodríguez-Alba, J.J., Titton, S., Serrano-Ramos, A., Courtenay, L., Mielgo, C., Luzón, C., Cámara, J., Sánchez-Bandera, C., Montilla, E., Toro-Moyano, I., Barsky, D., Fortelius, M., Agustí, J., Blain, H.-A., Oms, O., Jiménez-Arenas, J.M., 2022. Unravelling Hominin Activities in the Zooarchaeological Assemblage of Barranco León (Orce, Granada, Spain). J. Paleolithic Archaeol. 5, 6.

Zhu, Z., Dennell, R., Huang, W., Wu, Y., Qiu, S., Yang, S., Rao, Z., Hou, Y., Xie, J., Han, J., Ouyang, T., 2018. Hominin occupation of the Chinese Loess Plateau since about 2.1 million years ago. Nature 559, 608–612.