



Glacial refugia of temperate, Mediterranean and Ibero-North African flora in south-eastern Spain: new evidence from cave pollen at two Neanderthal man sites

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ABSTRACT

Aim To locate glacial refugia of thermophilous plant species in Spain.

Location Two south-eastern Spanish Neanderthal man sites in Murcia; namely, the inland Cueva Negra del Estrecho del Río Quípar and the coastal Sima de las Palomas del Cabezo Gordo.

Methods We use pollen found in cave sediments as a source of palaeobotanical and palaeoecological information. The findings are discussed with regard both to animal remains from both sites, and also to other refugia in south-eastern Spain and elsewhere in the Iberian Peninsula.

Results Both sequences show persistence of abundant mesothermophilous trees during the last glacial stage, suggesting both localities were reservoirs of phytodiversity and woodland species. At both sites, deciduous and evergreen oaks are the most abundant components, followed by a wide variety

of deciduous trees and sclerophyllous shrubs, including Ibero-North African xerothermic scrub near the coast.

Conclusions Incomplete information underlies a common misapprehension that Iberian glacial refugia were confined to southernmost parts of the peninsula. A rather different picture of Quaternary refugia emerges from consideration of pollen sequences from caves (and other inputs such as macroscopic charcoal, spatial genetic structure of present-day populations, faunal remains, and present-day distribution of thermophilous species). This picture offers a view of numerous viable areas for woodland species in southern Spain, in addition to others in the mountain ranges, both in continental central Spain and those of northern Spain: these stretch from the Mediterranean coast of Catalonia to the westernmost extent of the Bay of Biscay.

Key words archaeobotany, glacial refugia, historical biogeography, Neanderthal, palaeoecology, Pleistocene, pollen analysis, Spain.

INTRODUCTION

It is of palaeoecological, biogeographical and evolutionary interest when pollen analysis identifies localities where temperate and Mediterranean woodland species survived during the last ice age (Comes & Kadereit, 1998; Willis & Whittaker, 2000). Although the Iberian Peninsula may have retained sclerophyllous and some broad-leaved species, the main

refugia for deciduous trees lay further east in the Italian and Balkan Peninsulas (Bennett *et al.*, 1991; Magri & Parra, 1997). This picture implies Europe-wide migration of temperate woodland species during lateglacial and early Holocene times (Huntley, 1990; Brewer *et al.*, 2002). However, new palaeobotanical findings and reinterpretation of old ones sit uneasily with this model — in particular, anthracological findings from Hungary (Willis *et al.*, 2000) indicate more northerly woodland survivals than hitherto supposed. This raises a worrying question of whether low tree-pollen percentages owe less to long-distance transport than to so-called 'deficient' pollen dispersal or production; central European pollen sites might thus

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be explained in terms of lateglacial regional expansion of 'stationary' populations, rather than of continent-wide spread from distant southern refugia.

What light can southern regions of the Iberian Peninsula throw on this question? Phytodiversity there today is remarkable with respect to the rest of Europe, in both arid Mediterranean south-eastern areas (Mota *et al.*, 1997; Sánchez-Gómez *et al.*, 1998) and humid Atlantic south-south-western ones (Ojeda *et al.*, 1996). Southern Spain today, moreover, has several thermophilous species of undoubtedly tropical or subtropical origin (e.g. *Maytenus europaeus*, *Withania frutescens*, *Periploca angustifolia*, *Ziziphus lotus*, *Chamaerops humilis*, *Tetraclinis articulata*, *Myrtus communis*, *Halogeton sativus*, *Launaea arborescens*, *Rhododendron ponticum*, *Myrica gale*, *Prunus lusitanica*, *Cosentinia vellea*, *Culcita macrocarpa*), implying the presence of Pleistocene refuges in the Iberian Peninsula that most likely were vestigial relics of an African Miocene biogeographical expansion into Europe during the so-called Messinian 'crisis' (Arroyo, 1997). How far does palaeopalynological research corroborate these inferences?

Upper Pleistocene palaeobotanical findings from Spain have tended to be somewhat patchy up to now. New pollen findings are discussed here from two south-eastern Spanish caves. Both have Neanderthal human remains, Middle Palaeolithic artifacts, and wide faunal variety. Together with findings at other sites, they show that south-eastern Spain contained significant centres of diversity during the last glacial stage for both deciduous and sclerophyllous trees and shrubs, including thermophilous Ibero-North African species.

Study sites

Cueva Negra del Estrecho del Río Quípar ('Black Cave of the River Quípar Gorge') is near the hamlet of La Encarnación within the township of Caravaca de la Cruz (Murcia) (Fig. 1). Today the climate is subhumid to semiarid, with 2600–2800 h of sunshine annually, mean January temperatures of 2–4 °C, and mean July ones of 20–22 °C. The north-facing rock-shelter extends some 12 m backwards from a 12-m-wide mouth, 4–5 m high.

The sedimentary fill represents both erosion products of the fossiliferous sandy limestone in which the cave was formed and a significant proportion of fine, angular, microscopically pitted, silt-sized particles, similar to wind-blown loess. There are no sorted river gravels, but thermoclastic scree is very abundant. Five lithostratigraphical units are present in the cave (Fig. 2). Unit 1 is superficial, disturbed, powdery soil of grey hues containing modern artifacts and sheep droppings. Unit 2 is a compact yellowish layer comprising diffuse reddish brown lateritic lenses, eroded sand and bioclasts, and 15% of loess-size particles. Its upper part is cemented by calcium carbonate. Unit 3 is a yellow to greyish sediment with 10–15% loess-size wind-blown particles and thermoclastic scree. At

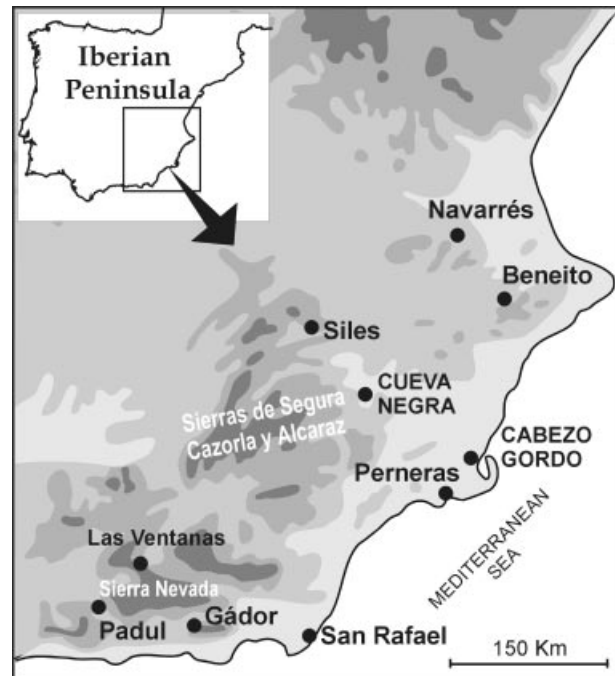


Fig. 1 Study sites and location of other pollen sequences from glacial refugia in south-eastern Spain.

the top, it shows calcrete breccia layers. Unit 4 includes broken calcrete slabs covering sediments similar to the preceding unit. Unit 5 comprises allochthonous cobbles, and calcrete slabs in a loess-size matrix (Walker *et al.*, 1998, 1999).

Some 8 teeth and bones of *Homo sapiens neanderthalensis*, numerous Middle Palaeolithic artifacts, and abundant faunal remains have been recovered from units 2–5 within an area of 25 square metres under methodical excavation since 1990 (Walker *et al.*, in press).

The rock-shelter lies at 780 m above sea level, in a rocky escarpment 40 m above the River Quípar at 1°48'10"E, 38°2'5"N, where the river leaves a gorge ('Estrecho') that runs from south to north, before bending sharply eastwards today. Although formed by karstic processes in Upper Miocene biocalcarene, the rock-shelter was raised up with respect to the river by Middle Pleistocene tectonics, along with the rest of the east flank of the gorge, such that it has come to lie slightly higher than the glacial-terrace B sediments of the opposite bank, to which the Cueva Negra sedimentary fill very likely corresponds (Walker *et al.*, 1998, 1999). Glacial-terrace B is a formation of calcretes, silts, loess, and gravels, which occurs widely dating from the early Upper Pleistocene in the Segura and Vinalopó drainage basins (Walker & Cuenca, 1977). Its upper units seem to be just within the range of radiocarbon dating, around 40 000 BP, whilst lower ones formed during the period from c. 115 000–40 000 BP (Cuenca

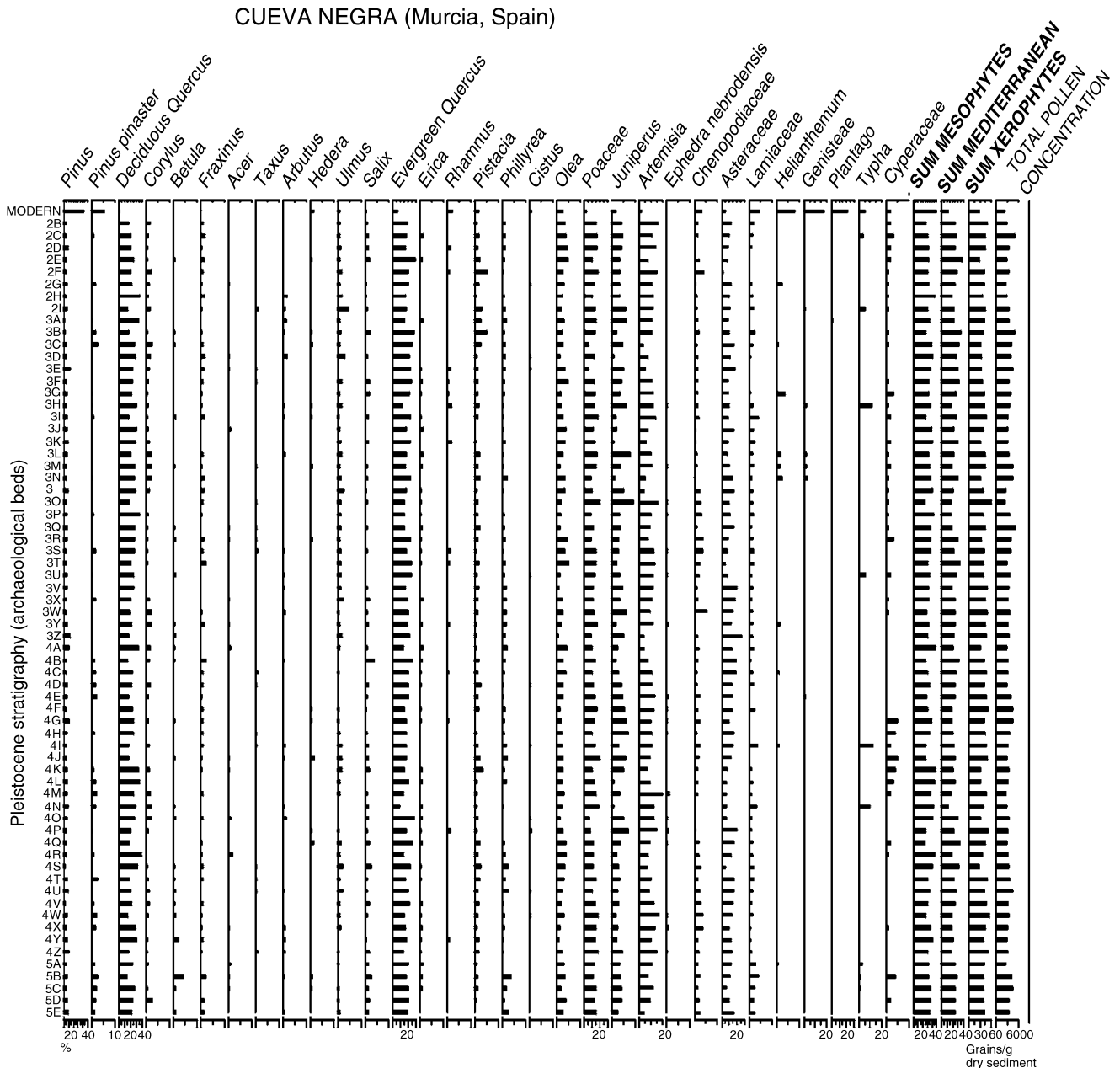


Fig. 2 Cueva Negra del Estrecho del Río Quípar pollen diagram (Murcia, Spain).

et al., 1986). This chronostratigraphic context, together with the type of Palaeolithic industry, and the abundance of thermoclastic scree, suggest that the study deposit is of last glacial age, most likely early to mid Upper Pleistocene (Walker *et al.*, in press).

Sima de las Palomas del Cabezo Gordo ('Dove Hole on Big Hill') is at $0^{\circ}53'53''\text{W}$, $37^{\circ}47'54''\text{N}$, in Torre Pacheco township (Fig. 1), at 80 m above sea level on the S-facing

flank of Cabezo Gordo, a steep 310-metre-high hill of Permo-Triassic (Nevado-Filábride) marbled limestone, which rises from the coastal plain as an isolated block lying E-W. The 'Sima' is a natural karstic shaft that contains the remains of a breccia fill, which was largely removed by iron miners. A column of breccia remains that runs 18 m down the shaft from the uppermost entrance to the floor of the Main Chamber. Nowadays the climate here is semiarid, with 3000 h

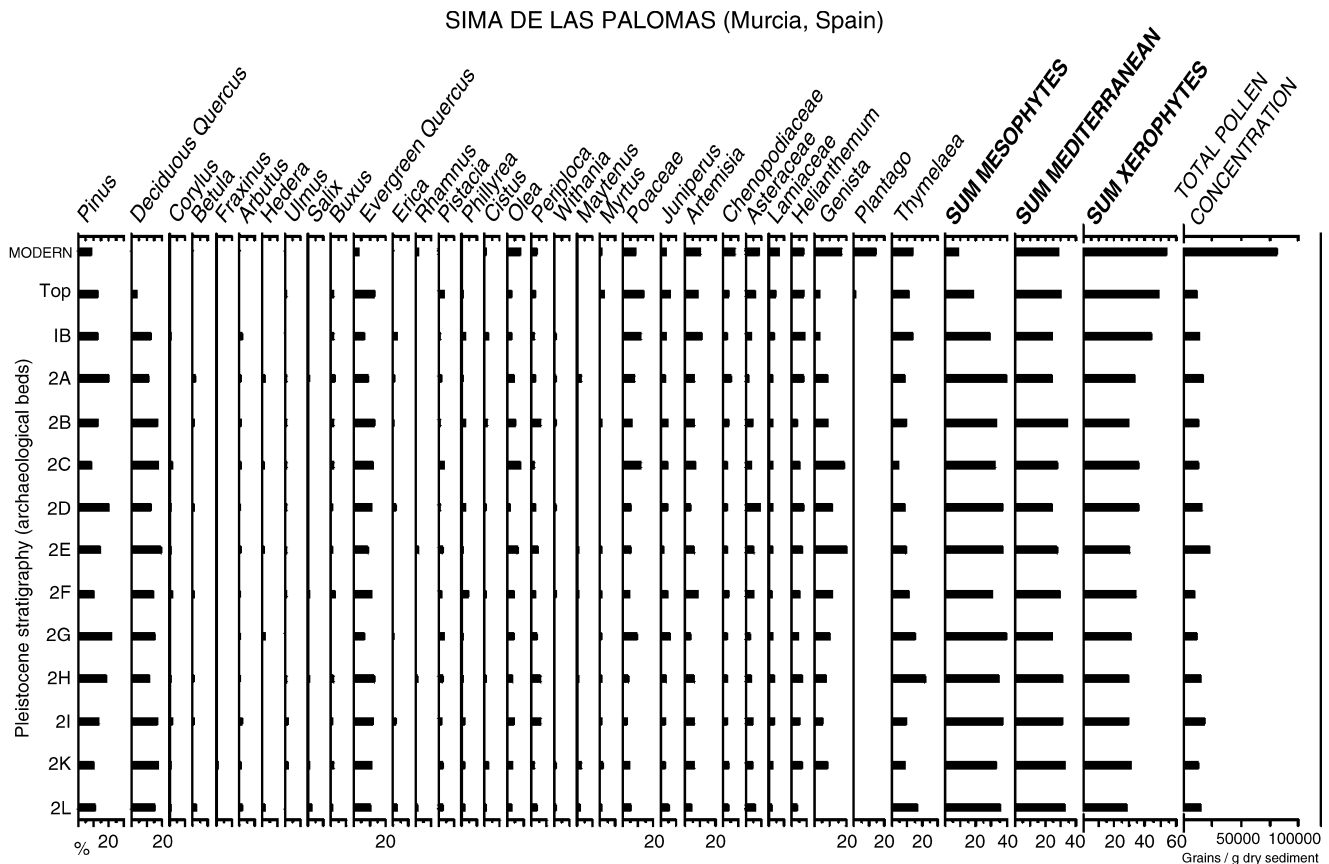


Fig. 3 Sima de las Palomas del Cabezo Gordo pollen diagram (Murcia, Spain).

of sunshine annually, a winter temperature never below 10 °C, and a mean July temperature of 26 °C.

Two lithostratigraphical units have been recognized in the uppermost 1.8 m of the column under excavation since 1994. Unit 1 is a yellowish cemented breccia and scree adhering to the overhang. Unit 2 is characterized by horizontal accumulation of angular scree in a clayey matrix with fine layers of burnt soil. Both units are rich in bones, including remains of *Homo sapiens neanderthalensis*, and Mousterian artifacts. Thorium-Uranium and AMS radiocarbon dating assign these deposits to about 60 000–40 000 years ago. The bottom of the column, below unit 2, has Thorium-Uranium determinations of about 125 000 years (Walker *et al.*, in press). The study deposit is therefore likely to be synchronous with the Cueva Negra section, that is, early to mid Upper Pleistocene. Details on the chronological context of both sites are presented elsewhere (Walker *et al.*, in press).

METHODS

Sampling of vertical sections was done in close relationship to the stratigraphy; each recognizable archaeological bed

was sampled, generally only one sample per bed, that is at 3–5 cm intervals. Control for modern pollen rain was done by means of two samples, each made up of 5 subsamples from the surface of the soil at the respective sites. Laboratory treatment was performed following the conventional HCl, HF and KOH method, and *Lycopodium clavatum* tablets containing a known quantity of spores were added to each sample prepared to enable estimation of pollen concentration. Pollen grains were concentrated by heavy-liquid flotation. Residues were mounted in silicone oil. Pollen identification was performed by comparison with the reference collection at Murcia University. Identification criteria for conflicting taxa are described elsewhere (Carrión, 2002a). Total sums of 230–490 and 351–536 pollen grains and spores were obtained for Cueva Negra and Sima de las Palomas, respectively. Pollen diagrams were constructed by using progressively the programs Tilia, TiliaGraph, TGView, and CorelDraw 9.0 (Figs 2 and 3). Internal separation of pollen zones has not been undertaken for the pollen diagrams, because visual inspection reveals only slight variation. Nomenclature for plant taxa follows Sánchez-Gómez *et al.* (1998).

RESULTS

Cueva Negra pollen records

Pollen spectra are codominated by two well-differentiated groups of *Quercus*, with percentages of around 15% and 35%, respectively (Fig. 2). One is of deciduous species which, given the local limestone substrate, was no doubt mainly *Quercus faginea*. The other is an evergreen group, which could indicate the presence of *Quercus ilex/rotundifolia* or *Q. coccifera*. *Quercus* is more abundant than any other tree or shrub species, although pine (*Pinus*), juniper (*Juniperus*), and wild olive (*Olea*), consistently reach levels over 2–3%. Low frequency oscillations throughout the sections are shown for hazel (*Corylus*), birch (*Betula*), cluster pine (*Pinus pinaster*), ash (*Fraxinus*), elm (*Ulmus*), willow (*Salix*), lentisk (*Pistacia*), and *Phillyrea*. Sporadically present are field maple (*Acer*), yew (*Taxus*), strawberry tree (*Arbutus*), ivy (*Hedera*), and rock-roses (*Cistus*). Although there is a significant herbaceous component of wormwood (*Artemisia*), Poaceae, and Asteraceae, and to a lesser extent Chenopodiaceae, Lamiaceae, and Cyperaceae, the abundance of those taxa is nonetheless low when compared to Pleistocene pollen spectra from other Mediterranean parts of Spain (Carrión *et al.*, 2000).

Pollen analyses at Cueva Negra show steppe vegetation coexisting with woodland species. Determining the geographical location of plant species through pollen analysis is complicated due to methodological pitfalls (Birks, 1993), so we can but speculate about the composition of plant formations at the time, although some light may be shed on this matter by regional topography and the ecology of those taxa identified. Thus, it seems likely that upland plateaus were open ground where grasses and wormwood scrub (*Artemisia*) predominated, sometimes with juniper bushes and occasionally pine trees, whilst valleys and gorges (like that of the Quípar) gave shelter to most of the woodland flora and mesothermophilous shrubs. Thus, Cueva Negra pollen frequencies imply mixed copses of both deciduous and evergreen oaks with cluster pines for the most part, along with representatives of other deciduous species such as hazel or beech that are no longer found there and only linger on in sheltered valleys of the high Sierra del Segura, 50 km away to the NW (Fig. 1). Many of these trees probably behaved as phreatophytes, growing on river banks and valley floors near water-courses. Thermophilous taxa such as *Olea*, *Pistacia* and *Phillyrea* show striking abundance for the last glacial-stage mesomediterranean enclave around Cueva Negra.

Sima de las Palomas pollen records

Sima de las Palomas pollen spectra are dominated by two groups of *Quercus* as at Cueva Negra (Fig. 3). The deciduous

palynotype is more variable in shape, size, and exine ornamentation, perhaps reflecting a mosaic of underlying ecological factors, or several species coexisting in a context where soils show greater diversity than at Cueva Negra (in more humid mountainous regions than Murcia *Q. faginea*, *Q. canariensis* and *Q. pyrenaica* occur today in southern regions of the Iberian Peninsula). Pine is more prominent than at Cueva Negra, but which species cannot yet be determined. Likely candidates are black pine (*P. nigra*), Aleppo pine (*P. halepensis*), and umbrella pine (*P. pinea*); anthracology has shown *P. nigra* occurred from c. 25 000–13 000 year BP in Palaeolithic settlements in Alicante and Valencia (Badal & Carrión, 2001).

Given that today large parts of coastal Murcia on average get less than 200 mm of rain a year, with very high levels of evapo-transpiration (Sánchez-Gómez *et al.*, 1998), it is striking that Pleistocene pollen spectra show abundant pollen of deciduous oaks at Sima de las Palomas, alongside trees requiring damp-temperate conditions such as *Corylus avellana*, *Fraxinus*, *Arbutus unedo*, *Buxus*, and *Betula*. The oaks most likely grew nearby because their pollen frequencies of 15–20% exceed those involving long-distance pollen transport to south-eastern Spanish caves (Navarro *et al.* 2001). Was local climate damper than now in the upper Pleistocene? Or is a combination of Holocene climate changes and anthropogenic intervention to blame for the recent decline in deciduous trees? These are not exclusive possibilities, but the latter is supported (Carrión *et al.*, in press) by a Holocene sequence from Gádor (Almería), by archaeological findings, and by historical evidence (García Latorre & García Latorre, 1996; Giménez, 2000).

A far broader mosaic of plant communities may be envisaged in the local Pleistocene landscape than exists today. It would have contained both pine woods, and mixed evergreen and deciduous *Quercus* woodland, as well as deciduous trees in shady zones, gorges, and beside water-courses, all contributing to a rich undergrowth of Mediterranean species, with heliophilous formations on thinner soils. The latter would include *Periploca angustifolia*, *Osyris quadripartita*, *Asphodelus*, Labiates, Composites, Cistaceae, *Thymelaea hirsuta*, *Calicotome intermedia* and other Genistas. Last but not least there would have been marshlands and coastal saltpans characterized by Chenopodiaceae, *Lycium* and *Whitania frutescens*. The widespread presence of thermophytes, including species such as *Periploca angustifolia* and *Maytenus europaeus*, which readily succumb to frost, indicate that local climate can scarcely have been colder than today. Moreover, those taxa, along with *Whitania*, *Pistacia*, *Phillyrea*, *Calicotome*, and *Osyris*, are all clearly under-represented in both external and internal pollen rain (Carrión, 2002a), hence their abundance in the neighbourhood was undoubtedly greater than pollen spectra imply at first glance.

DISCUSSION

Palaeoecological value of the cave pollen spectra studied

Doubts have been raised about the palaeoecological value of palynological information obtained from archaeological studies from caves and rock-shelters (e.g. Turner & Hannon, 1988), but this issue has been discussed elsewhere (Davis, 1990; Carrión & Scott, 1999; Carrión *et al.*, 1999a). Four palaeopalynological aspects need stressing with regard to our region. First, it lacks lake, swamp, or peat deposits, hence vegetational reconstruction must resort to either marine sequences (Targarona, 1997) or deposits in caves or rock-shelters. Secondly, there are no reasons, *a priori*, to dismiss results obtained from considerations of pollen-rain representativeness as regards the external vegetation. At least, this is what can be concluded experimentally after analysing surface sediments at caves of different shapes and sizes, both within our region (Navarro *et al.*, 2000, 2001) and outside it (Burney & Burney, 1993). Thirdly, with regard to conventional sediments, those from the very same caves have an advantage in that they are able to collect those entomophilous species that make up most of the local vegetation but are conspicuous by their absence from lake-bed deposits (Carrión, 2002a): here, indeed, any chance at all of biotic transport to a site is of far more help than hindrance to palaeopalynologists.

Lastly, it is essential that there are palynological indicators both for analytical quality and palaeoecological coherence, so as to be able to detect possible skewing of pollen spectra due to such postdepositional processes as destruction of pollen, percolation, or reworking (Sánchez-Goñi, 1994). In this regard, it is noteworthy that in both series analysed (Figs 2 and 3) have been identified very many types, including some not always readily preserved (e.g. *Taxus*, Genistaceae, *Buxus*, *Calicotome*, *Periploca*), or whose identification demands precise exine characteristics, available only in nonoxidized palynomorphs (e.g. *Coris*, *Smilax*, *Maytenus*, *Withania*). Total concentrations of pollen are not especially high, being greater at Sima de las Palomas (between *c.* 9487 and 23 137 grains g⁻¹) than at Cueva Negra (between *c.* 2342 and 5150 grains g⁻¹), but they are nevertheless comparable to those often reported from surface sediments in caves (Davis, 1990; Navarro *et al.*, 2001), so there is no need to interpret them as being due to loss caused by destructive processes.

At both sites, surface pollen spectra reflect wholly modern, but never Pleistocene, vegetation. Cueva Negra surface samples predominantly show *Pinus* (including considerable amount of *P. pinaster* type), *Helianthemum*, Genistaceae and *Plantago*, whilst Pleistocene ones show clear-cut predominance of *Quercus*, Poaceae, *Artemisia* and Asteraceae (Fig. 2). Sima de las Palomas surface samples show greater percentage similarity, but while its surface sediment lacks *Quercus* (absent today in this coastal region), *Quercus* pollen nevertheless is

very abundant in Pleistocene samples from the site. Likewise utterly absent from surface samples are other minority pollen grains identified nonetheless in the Pleistocene samples, such as *Corylus*, *Betula*, *Fraxinus*, *Arbutus*, *Ulmus*, *Salix*, *Erica* and *Ephedra distachya-nebrodensis* (Fig. 3). Last, but not least, our failure to detect either bed-rock Miocene spores at Cueva Negra, or Permo-Triassic ones at Sima de las Palomas is worth mentioning; nor were there differences in staining or preservation in pollen spectra from either site, such as are common when reworking or sediment mixing have taken place in a cave (Carrión *et al.*, 1995).

The new findings in the context of previous palynological studies

Cueva Negra pollen results are comparable with those slightly further west, from Siles, at 1320 m above sea level in an intermontane valley of the Sierra de Segura in Jaén (Carrión, 2002b) (Fig. 4). In deposits dating from upper pleniglacial times (*c.* 20 000–17 000 cal year BP), were found *Pinus pinaster*, deciduous *Quercus*, evergreen *Quercus*, Ericaceae, *Corylus*, *Betula*, and *Fraxinus*, in pollen percentages always above 2%, and frequently also *Acer*, *Taxus*, *Arbutus*, *Buxus*, *Salix*, *Ulmus*, *Phillyrea*, *Pistacia*, and *Olea*. All of these contingents were better represented at Siles in lateglacial times (*c.* 17 000–11 900 cal year BP) and especially in mid-Holocene times (*c.* 7400–5300 cal year BP), although pine woods appear to have predominated during the early Holocene (*c.* 11 900–7400 cal year BP).

Although not being synchronous, the similarity between the Cueva Negra and Siles spectra is important because both sites lie in closely related biogeographical areas between which migration is eminently feasible (Fig. 1); not for nothing have mountains near Cueva Negra been regarded by some plant biogeographers as an eastern extension of the Sierra de Segura (Sánchez-Gómez & Alcaraz, 1993). The Siles and Cueva Negra pollen records show that tree species survived at quite high places in southern European mountains during the last glacial stage. This agrees with a hypothesis put forward by Bennett *et al.* (1991) that tree survival would have been especially important in mountain ranges, such as those of the Balkans, allowing rapid altitudinal displacements of tree populations in response to climatic pulses (Willis, 1994). Owing to their roughly N-S orientation, the Segura mountains, like the Balkans, would have readily allowed altitudinal movements of tree populations to take place. Moreover, other indications that mountains in southern Spain contained significant tree reservoirs during the last ice age come from consideration of the genetic structure of European tree populations today (Herrán *et al.*, 1999; Jiménez, 2000; Salvador *et al.*, 2000).

Other pollen sequences in the Iberian Peninsula, with comparable incidences of mesothermophilous flora to Siles or

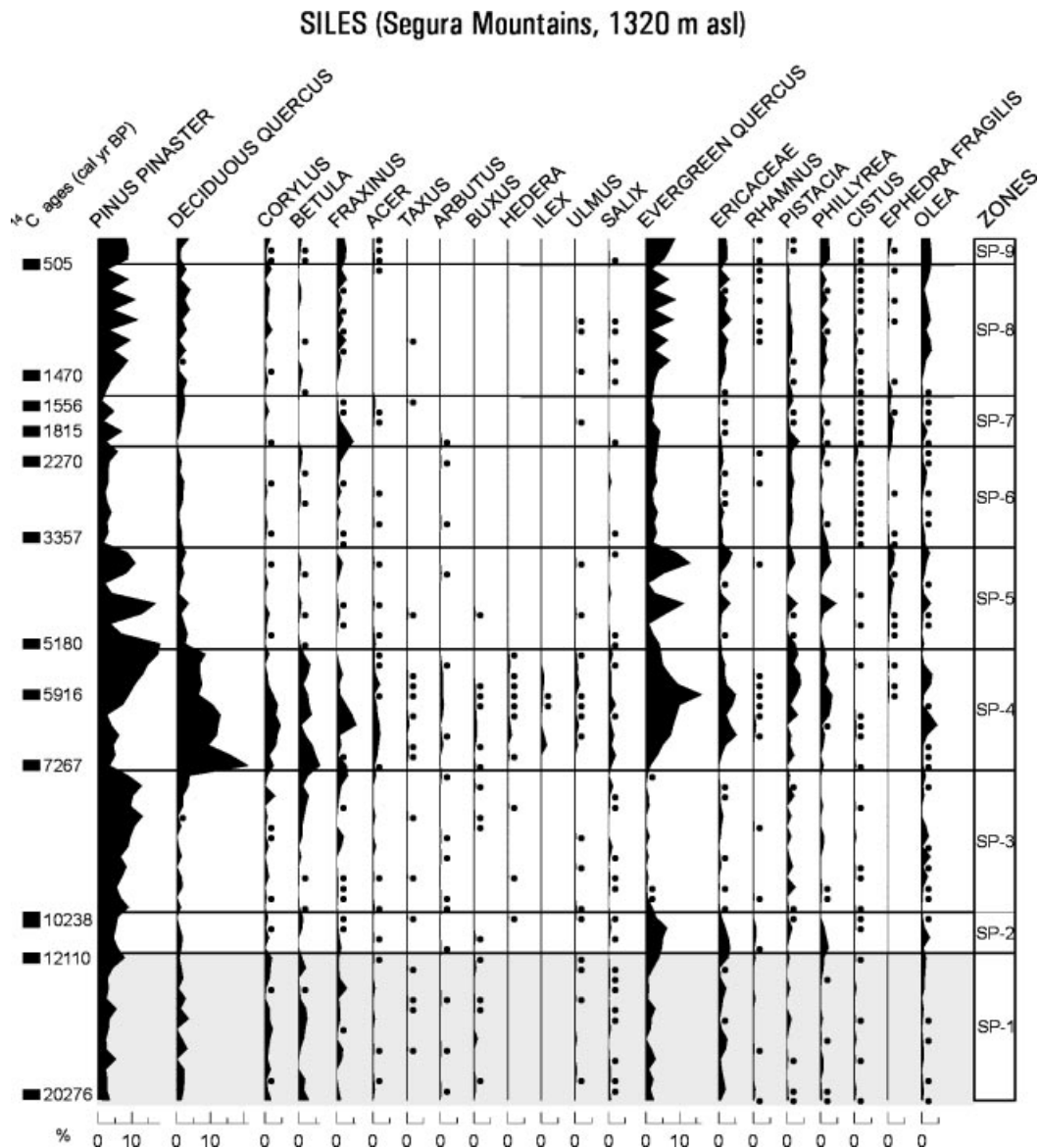


Fig. 4 Reference pollen diagram from the lake at Siles (Jaén, Spain), which includes mesothermophilous trees and shrubs (shaded zones correspond to the last glacial stage; black dots refer to percentages below 2%).

Cueva Negra, only occur at lower altitudes, as is the norm elsewhere in southern Europe (Willis, 1994; Leroy *et al.*, 1996; Van Andel & Tzedakis, 1996; Magri & Parra, 1997). The Murcian coast offers another important pollen record from the Middle-Upper Palaeolithic transition at Cueva Perneras (Carrión *et al.*, 1995). Although tree pollen was less important than at Sima de las Palomas, Cueva Perneras deposits contained abundant pollen of *Pinus*, *Quercus ilex-coccifera* and Oleaceae, and continuous or frequent presence of broad-leaved trees (*Fraxinus*, *Alnus*, *Corylus*, *Juglans*, *Ulmus*, *Salix*) and thermophytes (*Myrtus*, *Erica arborea*,

Pistacia, *Buxus*, *Periploca*, *Withania*, *Lycium*, *Ephedra fragilis*, *Cosentinia vellea*, *Selaginella denticulata*, *Ruta*).

To the south of Murcia, at San Rafael on the Almerian coast, a pollen sequence shows continuous curves for evergreen and deciduous *Quercus* and *Olea* during the last glacial maximum and tardiglacial (Pantaleón-Cano *et al.*, in press). Another pollen sequence showing lateglacial tree presence comes from coprolites of spotted hyaena (*Crocuta crocuta*) at Cueva de las Ventanas in Granada, where, about 12 780 cal year BP, there were pine woods, wormwood steppe with juniper, grassland, and mixed woodland of *Quercus*

with *Betula*, *Abies*, *Corylus*, *Alnus*, *Acer*, *Taxus*, *Myrtus*, *Buxus*, *Sorbus*, *Olea*, *Erica arborea*, *Pistacia*, *Ephedra fragilis*, *Viburnum*, *Sambucus*, *Cistus* and *Rhamnus*.

To the north of Murcia, relevant pollen findings come from sites in inland Mesomediterranean environments, namely, the dated Middle-Upper Palaeolithic transition at Cova Beneito in Alicante (Carrión & Munuera, 1997), and the Navarrés peat bog in Valencia (Carrión & van Geel, 1999). However, their thermophilous components show oscillations rather than uninterrupted presence: indeed, most of their deciduous trees and Mediterranean shrubs fell away markedly during the upper pleniglacial stage, after having advanced together during oxygen-isotope stage 3. In the north-eastern Mediterranean part of the Iberian Peninsula, Abric Romaní, near Barcelona, shows tree pollen percentages of 40–60% between about 70 000 and 40 000 year BP, with continuous presence of *Juniperus*, *Rhamnus*, *Quercus*, *Olea-Phillyrea*, *Syringa*, *Alnus*, *Salix*, *Juglans*, *Betula*, *Fagus*, *Betula*, *Coriaria*, *Pistacia* and *Vitis* (Burjachs & Julià, 1994).

Further afield, even the Cantabrian coast and adjacent mountain ranges seem to have offered refuges for trees during the last ice age, according to pollen analyses (Dupré, 1988; Ramil-Rego *et al.*, 1998a,b) and macroscopical charcoal (Uzquiano, 1992). Pleniglacial pollen samples include low frequencies of *Pinus*, *Betula*, *Juniperus*, *Corylus*, *Quercus*, *Fraxinus*, *Alnus*, *Ulmus*, *Tilia*, *Juglans*, *Fagus* and *Castanea*. Charcoal samples contain *Pinus sylvestris*, *P. uncinata*, *Juniperus*, *Betula alba*, *B. pendula*, *Corylus avellana*, *Quercus robur*, *Q. petraea*, *Tilia platyphyllos*, *T. cordata*, *Fraxinus excelsior*, *Sambucus nigra*, *Viburnum tinus*, *Cornus sanguinea*, *Quercus ilex*, *Fagus sylvatica*, *Sorbus aria*, *S. aucuparia*, *S. torminalis*, *S. domestica*, *Castanea sativa*, *Quercus suber*, *Arbutus unedo*, *Erica arborea*, *Crataegus monogyna*, and several species of *Prunus* and *Rhamnus*. Hunter-gatherers may have gathered hazelnuts, acorns and wild fruit (e.g. mazzard, *Prunus avium*) (Uzquiano, 1992). The palaeobotanical findings concur with the genetical structure of populations of Iberian brown oak (Olalde *et al.* 2002), and some palaeoecological inferences drawn from the abundant megafauna of the Biscay coast (Altuna, 1972).

For continental parts of the Iberian Peninsula, there exists both pollen and palaeobotanical evidence of mesophilous taxa in glacial and late glacial contexts (Dupré, 1988; Pons & Reille, 1988; García-Antón *et al.*, 1990; García-Antón & Sainz-Ollero, 1991; Carrión & Sánchez-Gómez, 1992; Pérez-Obiol & Julià, 1994; Blanco *et al.*, 1997). When cave pollen is considered along with reference pollen sequences and charcoal findings, everything seems to point less to refugia restricted to the far south (Brewer *et al.*, 2002), than to survival of stationary tree populations in many parts of the Peninsula, particularly in intramontane valleys in the Baetic, pre-Baetic, Iberian and other coastal ranges, with expansion and contraction in the central uplands.

To conclude, palynology at archaeological cave sites often raises doubts over contemporaneity between pollen and the layer containing it, and anthracology often seems closer to palaeobotanical orthodoxy than to palaeoecology. Nevertheless, both approaches together can build up a solid weight of evidence. Furthermore, some reference pollen sequences have undeniable counterparts in some cave pollen sequences (Carrión, 2002b) (Fig. 4). Our models about glacial refugia require far more information; several sites need to be restudied, their chronologies need refinement, and the present estimates of continental palaeotemperatures during the upper Pleistocene should be viewed with caution. Moreover, faunal remains, especially birds and small mammals, must be taken far more into consideration whenever revision of glacial refugia of temperate trees is undertaken, concerning palaeoclimatic inferences.

Relationships with palaeontological findings and human remains

Palynological findings at Cueva Negra del Estrecho del Río Quípar and Sima de las Palomas del Cabezo Gordo sit easily with the faunal evidence. At Cueva Negra, avian palaeontologist Anne Eastham's findings (Walker *et al.*, 1998; in press), point to five different environmental biotopes coexisting near this upland site, which today is in an open, arid landscape crossed by a small stream undeservedly called the 'River' Quípar. These are: (i) wetlands with a depth of lake-water necessary for ruddy shelducks, mallards, wigeons, teals, gadwalls, red-crested pochards, common pochards, ferruginous ducks, wild geese, little stints, and sandpipers; (ii) riverine and damp valley floors where soft sediments offered cover suitable for the bee-eaters and sand martins at Cueva Negra; (iii) *Quercus* woodland suitable for autumnal acorn-eaters such as the cave's Pleistocene jays and wood pigeons, where its owls, nightjars, woodpeckers, woodlarks, and several species of thrushes finches must have found their prey; (iv) steppe and open country preferred by larks, partridges, plovers, choughs, eagles, buzzards, kestrels, and falcons, whose bones are all well represented; and (v) the craggy mountainsides and cliffs around the cave itself, offering roosting places for the omnipresent choughs, rock doves, crag martins, swallows, swifts, and rock thrushes. Reptiles are especially well represented by tortoise remains. Numerous skeletal parts of small and large mammal species excavated support such a variety of biotopes around the rock-shelter: carnivores such as hyaena, brown bear, wolf, a small feline, omnivores such as macaque and wild boar; herbivores such as steppe rhinoceros, elephantids, giant deer, red deer, a smaller cervid, aurochs, bison, horse, and wild goat. Bats, hedgehogs, and shrews were also found.

At Sima de las Palomas, the correlation for the early to mid-upper Pleistocene between fauna and ancient habitats is

less clear-cut. Cementation of excavated breccia makes for slow progress in palaeontological research. Fewer bird species have been identified than at Cueva Negra (13 species as against 66) (Walker *et al.*, in press). There are, of course, craggy mountainsides around the cave. Below the site, the coastal plain surrounding Cabezo Gordo, nowadays dry and open, must have contained mixed woodland and grassland, with gallery woodland and swamps beside erstwhile streams feeding nearby wetlands and saltmarshes behind coastal sand dunes (where the Mar Menor coastal lagoon is today), even though marine regressions must have repeatedly drained these for many millennia each time. Mammals include carnivores such as panther, lynx, spotted hyaena, brown bear, fox and badger, and herbivores such as hippopotamus, elephantids, wild horses and asses, aurochs, red deer, wild goats and abundant lagomorphs. Tortoise is again common in the deposits.

The two Upper Pleistocene sites considered here from a palaeoecological standpoint of flora and fauna corroborate a proposal that long-term human presence may occur preferentially where several different biotopes coincide.

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