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A coastal reservoir of biodiversity for Upper Pleistocene human populations: palaeoecological investigations in Gorham's Cave (Gibraltar) in the context of the Iberian Peninsula

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ABSTRACT

Palaeobotanical (pollen, charcoal) data from Gorham's Cave reveals a diversified landscape in the Gibraltar region during the Middle (c. 32 560–23 780 year BP) and Upper Palaeolithic (c. 18 440–10 880 BP). Inferred vegetation types include oak, pine, juniper, and mixed woodlands and savannahs, grasslands with heaths, heliophytic matorrals, phreatophytic formations (e.g. riverine forests, wetlands), and thermomediterranean coastal scrub. A revision of palaeoecological data suggests that patches of trees persisted even in northern and continental territories of the Iberian Peninsula during the cold stages of OIS3 and OIS2. However, a southern Mediterranean coastal shelf extending from Gibraltar to Málaga, and probably further north up to Murcia, was unique in its combination of thermo-, meso-, and supramediterranean plant and animal species. Given the composition of these assemblages, this shelf and its adjacent mountains represented a crucial reservoir of biodiversity during the Upper Pleistocene. It is within this physiographically complex context with its diversity of resources where the last Neanderthals extraordinarily survived until c. 24 000 BP, that is over 10 000 years later than the disappearance of Neanderthals from elsewhere in temperate Europe.

1. Introduction

This paper deals with palaeoecological investigations in Gorham's Cave in Gibraltar, southern Iberia (Fig. 1; Finlayson et al., 2006, in press) and presents new palynological data, which add substantially to the palaeobiological background in highlighting the coastal shelf of southern Iberia as a crucial reservoir of biodiversity during the Upper Pleistocene.

The key issue is one of "glacial refugia", a major theme in historical biogeography and evolution (Bennett et al., 1991; Hewitt, 2000; Willis and Whittaker, 2000; Carrión et al., 2003; Tzedakis, 2005). In the case of southern Iberia, the very persistence to the present-day of a number of thermophilous, Mediterranean and subtropical species (Ojeda et al., 2000; Arroyo et al., 2004) indicates that they survived the climatic fluctuations of the Pleistocene. This poses the problem of where they persisted. Their present-day distribution represents the changed conditions of the Holocene and the culmination of range expansion that began in the Late Pleistocene and was contingent on species availability and postglacial ecological processes such as migration, invasion, inertia, resilience, and competition (Carrión, 2001). This interest in glacial refugia extends to the potential for conservation practice, since the criteria for conservation may be influenced by, for example, the location of zones that acted as glacial refugia, or biodiversity 'hot-spots', during the environmental crises of the last 2 000 000 years (Tzedakis et al., 2002; Svenning, 2003; Petit et al., 2004). In other words, certain areas may have functioned as natural 'biosphere reserves' when climatic conditions were inhospitable elsewhere in present-day temperate and boreal regions.

It is within this refugium scenario that we place the survival of Iberian Neanderthals, a process that should be analyzed from the

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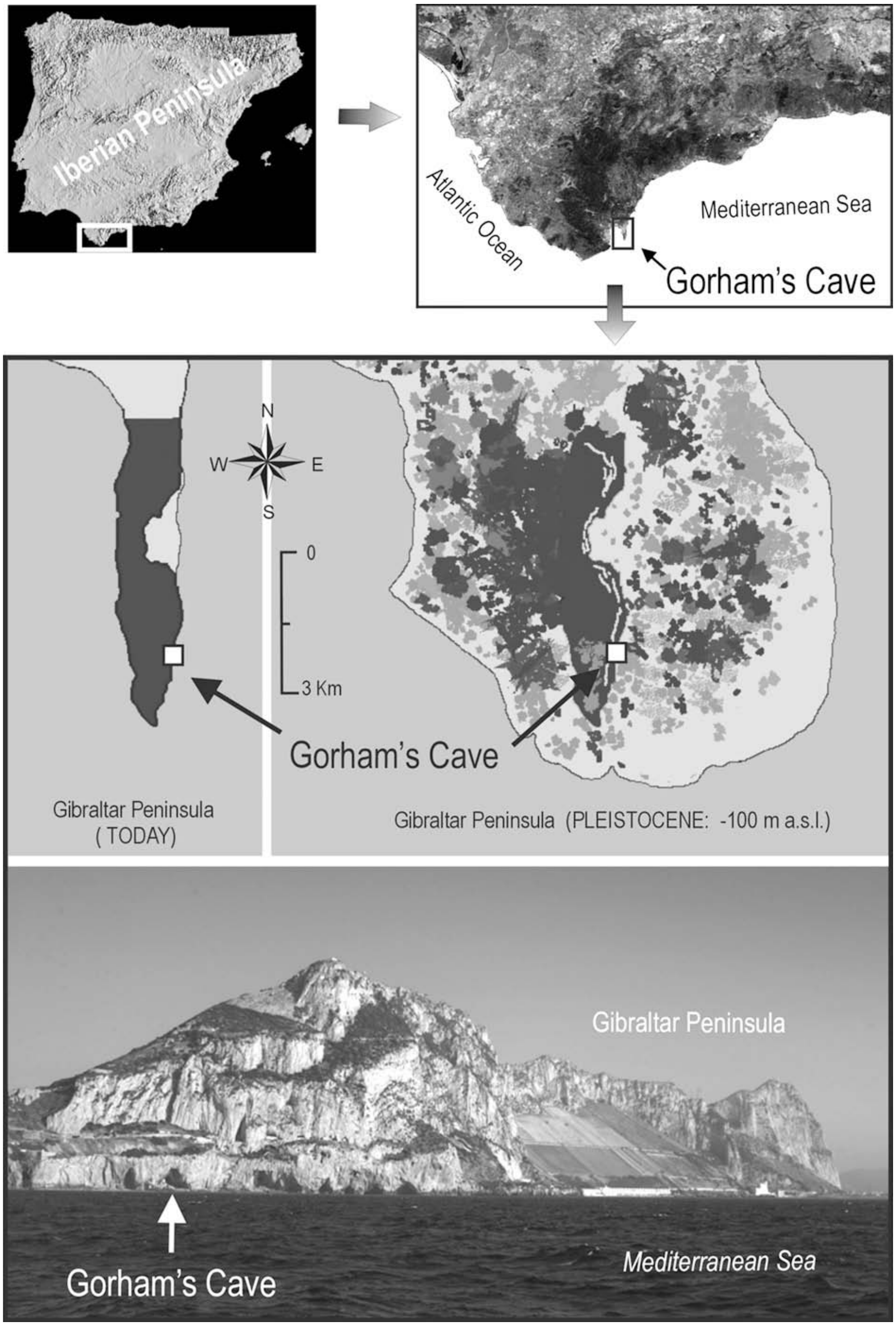

Fig. 1. Location of Gorham's Cave, Gibraltar, southern Iberia, and reconstruction of the Gibraltar Peninsula during the LGM when sea level was c. 100 m below the present-day position (Rodríguez-Vidal et al., 2004; Finlayson and Carrión, 2006).

perspective of wider evolutionary patterns and palaeoecological relationships rather than as a stage in some putative ladder of progress towards modern humans (Carrión, 2004; Finlayson, 2005). Thus, we shall contend here that the last Neanderthals, – like the first ''Moderns'' – are but a component of the Late Pleistocene biota in the southwest extreme of Europe, and that the apparently anomalous survival of the Neanderthals can be explained in terms of processes such as adaptation to climate change, and ecological interaction and behaviour.

2. Chronostratigraphy

Extensive excavations were carried out in Gorham's Cave between 1997 and 2004, affecting 29 m^2 of cave floor and producing a stratigraphy with four main levels (Finlayson et al., 1999, 2000, 2006). Levels I and II are thin and correspond to Phoenician to Neolithic horizons. Here we focus on Levels III and IV with Upper and Middle Palaeolithic lithic technologies, respectively. Level III (mean depth 62 cm) is sub-divided into a basal Solutrean and an upper Magdalenian horizon. Early Upper Palaeolithic technology such as Aurignacian and Gravettian are absent (Finlayson et al., 2006). Level III consists of a sandy sediment with dark brown clay in a sandy matrix. It has a strong organic component that includes discrete lumps of charcoal. The mean depth of Level IV is 41 cm but its base has not been reached except in a small corner of the cave. It is a beige-coloured pure clay horizon with an abundance of discrete lumps of charcoal and a hearth.

Table 1
Distribution of AMS dates from Gorham's Cave, (Gibraltar), by stratigraphic levels. Source: Finlayson et al. (2006)

Sample reference	AMS radiocarbon age (±2 σ)
Magdalenian horizon (Level III)	
Beta-185343	10 880 ± 80
Beta-181895	12 460 ± 100
Beta-184047	12 640 ± 100
Solutrean horizons (Level III)	
Beta-181893	16 420 ± 120
Beta-184042	18 440 ± 160
Late Mousterian horizon (Level IV)	
Beta-185345	23 780 ± 540
Beta-196775	24 010 ± 320
Beta-196773	26 400 ± 440
Beta-185346	27 280 ± 420
Beta-196770	28 170 ± 480
Beta-196791	28 570 ± 480
Beta-184048	29 210 ± 380
Beta-184049	29 240 ± 380
Beta-196792	30 310 ± 620
Beta-196776	30 560 ± 720
Beta-184045	31 110 ± 460
Beta-196768	31 290 ± 680
Beta-196772	31 780 ± 720
Beta-196769	31 850 ± 760
Beta-19671	32 560 ± 780
Basal Mousterian horizon (Level IV)	
Beta-184044	44 090 ± 2200
Beta-181894	46 540 ± 3600
Beta-184040	>47 410

The chronology of the Gorham's sequence is based on a stratigraphically-coherent series of AMS radiocarbon dates obtained from charcoal fragments. Level IV is largely dated between c. 32 560 and 23 780 BP. Three AMS dates from the back of the cave where Level IV thins out and meets the cave floor are greater than 41 900 BP. Level III is dated between c. 12 640 and 10 880 BP for the Magdalenian horizon, and between c. 18 440 and 16 420 BP for the Solutrean horizons (Table 1).

Geochemical and mineralogical analyses (X-ray diffraction, atomic absorption spectrometry, concentration and ratios of trace elements, XRF scanner) show that stratigraphical levels at Gorham's are clearly differentiated (Finlayson et al., 2006), and therefore support the chronological sequence. Sedimentation in the cave is relatively continuous, with Level IV having a particular composition that differs from the rest of the column.

3. The palaeoecological record of Gorham's Cave

3.1. Methodological considerations

Charcoal (Fig. 2) and pollen analysis of the cave sediments (Fig. 3), and pollen analysis of coprolites were initially carried out in Gorham's Cave (Gale and Carruthers, 2001; Carrión et al., in press). Here we combine this information with pollen analysis of eighteen additional coprolites (GEC) recovered from the 2005 excavation (Figs. 4 and 5). These are attributed to canids and, to a lesser extent, hyaenids (Scott et al., 2003; Carrión et al., in press).

In the laboratory, the coprolites were cut open with a steel spatula, and material from the centre was scraped out to minimise contamination from external surfaces, and weighed. Laboratory treatment was performed following conventional HF, HCl, KOH method and *Lycopodium clavatum* tablets containing a known quantity of spores were added to each sample prepared to enable a calculation of pollen concentration. Pollen grains were concentrated by means of heavy-liquid flotation.

Pollen diagrams were constructed using p-simpoll software (Bennett, 2000) (Figs. 3–6). Percentages of each taxon for each sample were based on a pollen sum (c. 150–2000 grains) excluding hydro-hygrophytes and non-pollen microfossils. Even though evergreen, deciduous and cork-oak palynological types (Planchais, 1962; Carrión et al., 2000a) were discernible in the pollen slides, with evergreen predominant, we have represented a single sum for the oak pollen in view of the difficulties with many grains that showed intermediate characteristics (Fig. 4). This continuum in the palynotypes could be related to the high levels of interpopulational introgression among oak species in the region (Olalde et al., 2002; Petit et al., 2002; Jiménez et al., 2004). As regards pines, we are able to identify palynologically the occasional presence of cluster pine (*Pinus pinaster*) (Fig. 4), although the pine pollen belongs generally to a medium- (*P. pinea-halepensis*) to small-sized (*P. nigra-sylvestris*) morphotype (Carrión et al., 2000b). Like *Q. suber* and *P. pinaster*, *Frangula* and *Calluna* were eventually, but not always separable from *Rhamnus* and Ericaceae respectively (Fig. 4). Fungal spores were not counted as they were largely sordariaceous ascospores, customarily occurring in fossil dung of different kinds (Van Geel et al., 1989).

3.2. Palaeo-vegetation inferred from charcoal and pollen analysis

The charcoal sequence of the Mousterian Level IV is dominated by *Pinus pinea-pinaster*, with minor contributions of *Pinus nigra-sylvestris*, *Juniperus*, Fabaceae, Cistaceae, *Olea* and *Erica*. Upper Palaeolithic Level III is still dominated by strobili and charred wood of *Pinus pinea-pinaster*, accompanied by *Juniperus*, *Quercus*, *Arbutus unedo*, *Fraxinus*, Fabaceae, Cistaceae and *Pistacia lentiscus* (Fig. 2). Although the anthracological method is not particularly well suited to detecting the spatial relationships between forested and non-forested landscapes, these analyses at Gorham's Cave suggest that pines, junipers, oaks, olive trees, and lentiscs, together with other shrubs, grew close to the cave and were relatively accessible to the human occupants.

Cave sediment pollen spectra from Mousterian Level IV show relative high frequencies of *Juniperus*, *Pinus*, Ericaceae, Poaceae, Asteraceae, Cistaceae (*Helianthemum* and *Cistus-Halimium* types) and to a lesser extent, *Ilex aquifolium*, *Artemisia*, and Chenopodiaceae (Fig. 3). Among the AP components, *Olea* and *Pistacia* are worth mentioning, together with *Betula*, *Corylus*, *Fraxinus*, *Quercus* and *Salix*. Upper Palaeolithic Level III is characterised by overall increases of pine and grass pollen, decrease of juniper, and peaks of Ericaceae. Several minor components show slight increases with respect to Level IV: *Asphodelus*, *Olea*, Lamiaceae, *Salix*, and evergreen *Quercus*. Level III includes a diversity of trees and shrubs like *Abies*, *Acer*, *Alnus*, *Betula*, *Cedrus*, *Corylus*, *Fraxinus*, *Ilex*, *Juglans*, *Populus*, *Quercus*, *Hedera*, Thymelaeaceae, *Ephedra*, *Lonicera*, *Phillyrea* and *Viburnum*.

The pollen-bearing coprolites show great variability in the pollen percentages, with the main dominants being *Pinus*, Poaceae, *Quercus*, and *Juniperus* (Figs. 4–6). Other pollen taxa reach relatively high values in some samples, such as *Artemisia* (Goc-18, Goc-6, GORc-3), Cyperaceae (Goc-4), Cistaceae (GORc-8), *Plantago* (GORc-7), Ericaceae (Goc-11), and Asteraceae (GORc-6). A variety of trees, shrubs, and herbs is also apparent, including conifers (*Taxus*, *Pinus pinaster*), broad-leaf trees (*Corylus*, *Alnus*, *Betula*, *Castanea*, *Ulmus*, *Fraxinus*, *Acer*, *Salix*), Mediterranean scrub-understorey (*Arbutus*, *Olea*, *Phillyrea*, *Buxus*, *Viburnum*, *Rhamnus*), xerothermic scrub (*Maytenus*, *Myrtus*, *Calicotome*), and a number of heliophytes (e.g. Ericaceae, Genisteae, *Asphodelus*, *Artemisia*, *Plantago*).

Several groups of coprolites contain specimens collected at the same depth and excavation coordinates but with marked differences in the composition and dominant taxa. For example, Goc-17, Goc-18, and GORc-13 are dominated by *Pinus-Juniperus*, *Artemisia*-Asteraceae, and Poaceae-Ericaceae, respectively. Most other groups show similar variability, although the group formed by Goc-13,

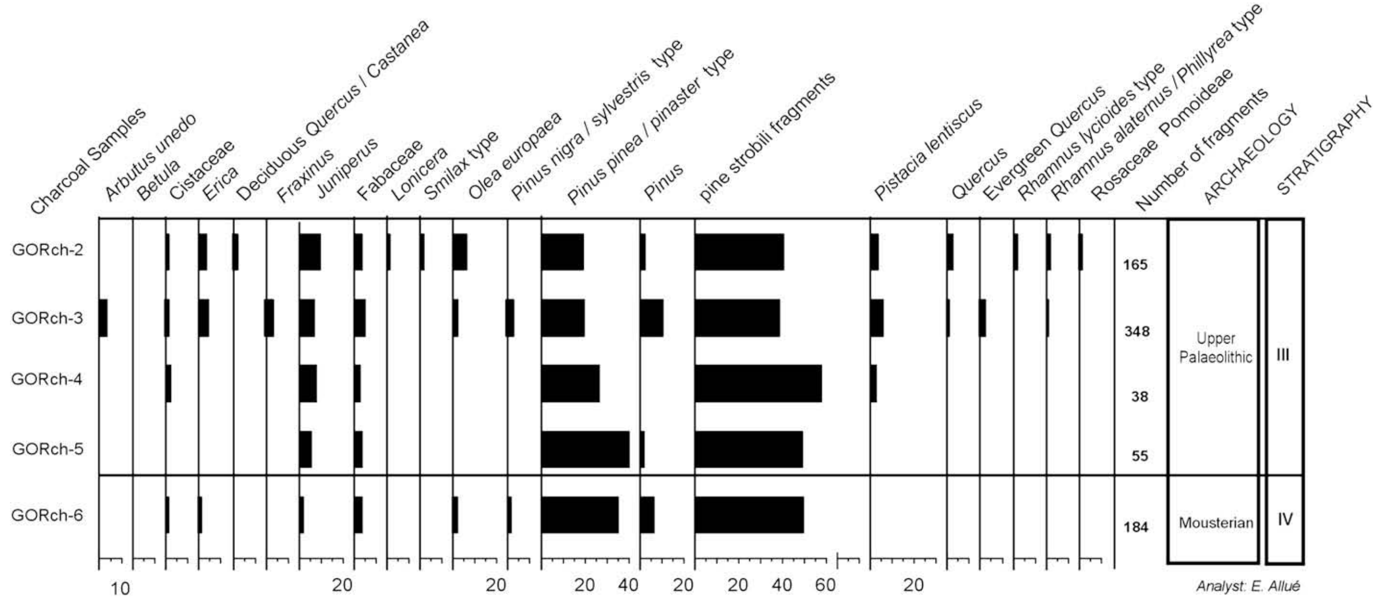

Fig. 2. Charcoal diagram of Gorham's Cave.

Goc-14 and Goc-15 is an exception with Poaceae pollen dominant in all cases.

Although coprolite pollen spectra in Figs. 4–6 are stratigraphically ordered along the vertical axis, their reconstructed environments should not be taken as a sequence of palaeoecological events. An overall interpretation for Mousterian *vs.* Upper Palaeolithic coprolite pollen appears more realistic. Indeed, the fact that coprolites collected at identical positions show different pollen spectra supports the view that they reflect different environments coexisting within a patchy landscape rather than a temporal record of different vegetation stages. Moreover, interpretation of coprolite pollen needs to take account of the variable behaviour of the animal that produced the coprolite. Several uncertainties are therefore involved in the production of coprolite pollen spectra, and this makes the current interpretation provisional pending further research. On the other hand, pollen analysis of coprolites may complement conventional methods of palynology, particularly in giving a more sensitive measure of the balance between forest and non-forest communities. Previous palynological investigations show that hyena coprolites produced *in situ* are likely to represent mosaic characteristics of landscapes, in physiographically complex territories (Scott et al., 2003). Experimental studies suggest further that most pollen is collected during hyaena movements away from home sites, with the composition of the pollen spectra depending on the vegetation of the particular areas visited (Scott, 1987; Scott and Brink, 1992).

So we tend to regard the differences between the charcoal and pollen sequences, and between the coprolites of the same level, as a help in the elaboration of a more complete palaeo-vegetation picture rather than an unwanted complication. Charcoal chiefly reflects the woody component, and sediment pollen the local environment including the herbaceous types. This suggests that the

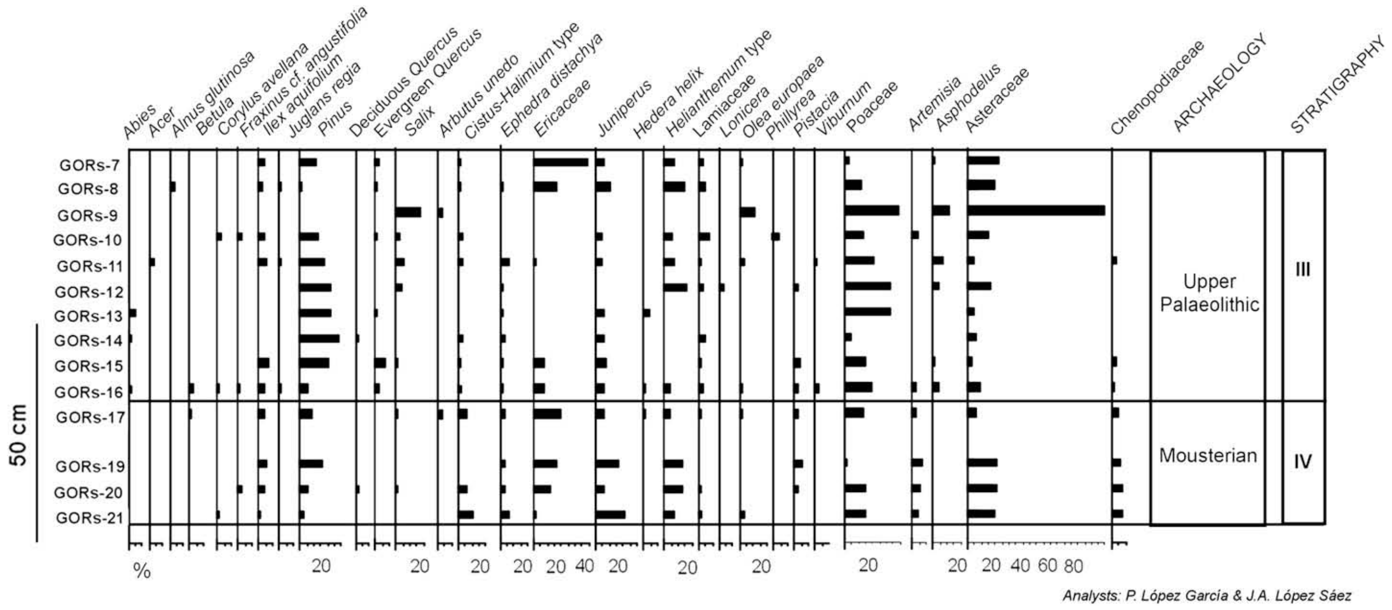

Fig. 3. Pollen diagram (selected taxa) from the excavated lithostratigraphical section in Gorham's Cave.

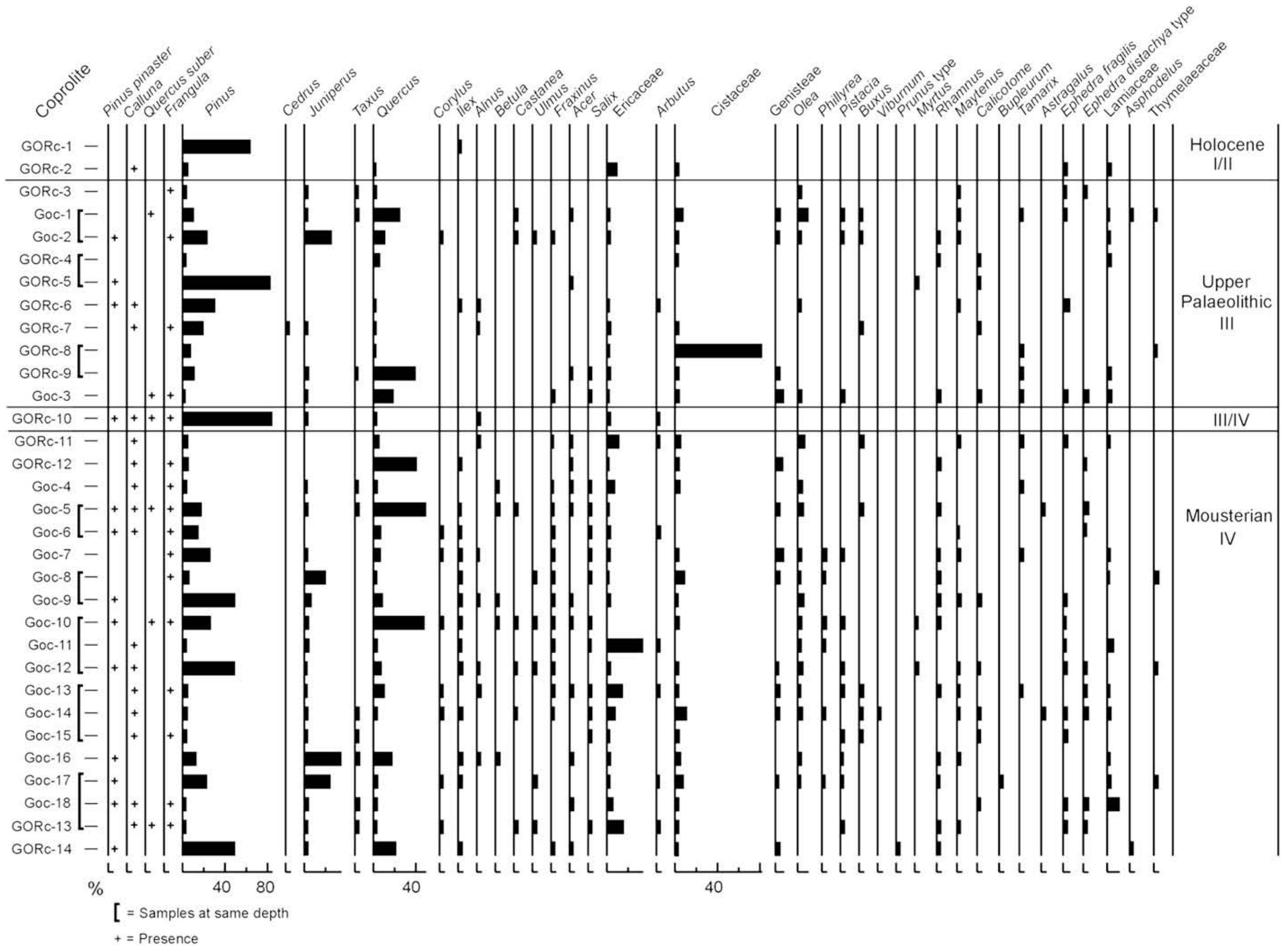

Fig. 4. Pollen diagram of coprolites from Gorham's Cave (i).

Palaeolithic landscapes surrounding Gorham's Cave were characterised by stands of pine and, to a lesser extent, juniper, with grasses, composites, and other shrubs and herbs, and patches of woodland comprising a variety of taxa.

Coprolite pollen is likely to reflect the diversity of vegetation types across the region (Scott et al., 2003; Carrión et al., 2004) (Table 2). Thus, during the period from c. 32 560 to 23 780 BP, the Strait of Gibraltar region would have embraced an extraordinary diversity of vegetation types including oak, pine, juniper, and mixed woodlands, savannahs (*sensu* Grove and Rackham, 2001), riverine forest patches, heliophytic matorrals, rocky scrub with abundant chamaephytes and hemicryptophytes, grasslands with heaths, shrubby grasslands, and steppe-like saltmarshes and littoral vegetation. Savannahs with pine, oak and juniper in the arboreal layer may well have been widespread along the coastal shelf eastwards of Gorham's Cave (Fig. 1). With regard to oaks, an evergreen species such as *Quercus ilex/rotundifolia* was most likely prevalent, with *Pinus pinea* dominant in pine woodlands.

Humid forests would have developed in favourable stations, plausibly including such species like *Quercus faginea*, *Q. pyrenaica*, *Q. canariensis*, *Q. suber*, *Q. lusitanica*, *Pinus pinaster*, *Acer granatense-monspessulanum*, *Ilex aquifolium*, *Corylus avellana*, *Betula celtiberica*, *Ulmus glabra*, *Castanea sativa*, even *Erica arborea*, *Pistacia terebinthus*, *Phillyrea angustifolia*, *Viburnum tinus*, *Buxus sempervirens-balearica*, *Taxus baccata*, *Hedera helix*, and probably, although not represented in the pollen spectra, lauroid shrubs and ferns (Cabezudo and Pérez Latorre, 2004). The abundance of *Ilex aquifolium* pollen in the cave sediment (Fig. 3) and its presence in the coprolites (Fig. 4) suggests that subhumid forest patches were relatively close to Gorham's Cave. On waterlogged and pseudogley soils, riparian forests would be expected with several species of *Salix*, *Fraxinus angustifolia*, *Populus alba*, *Alnus glutinosa*, and *Frangula alnus*, together with sedges like *Carex pendula*.

The Mousterian pollen record from coprolite samples also suggests the existence of heliophytic matorrals dominated by spiny and brush-like legumes (*Cytisus*, *Genista*, *Teline*, *Stauracanthus*), heaths (*Calluna*, *Erica*), and rock-roses (*Cistus*, *Halimium*, *Helianthemum*, *Fumana*) (Figs. 4–6). The thermophilic character of the coastal communities is assessed by the pollen occurrences of *Maytenus europaeus*, *Calicotome cf. villosa*, *Myrtus communis*, and to a lesser extent, *Olea europaea*, *Phillyrea angustifolia-latifolia*, *Ephedra fragilis*, *Bupleurum cf. gibraltaricum*, *Tamarix cf. africana*, *Asphodelus albus* and *Pistacia lentiscus*.

Vegetational landscapes of Gibraltar did not experience notable changes in the Upper Palaeolithic period from c. 18 440 to 10 880 BP, although pine-dominated ecosystems, and grasslands may have somewhat extended, while juniper and heath generally declined (Figs. 3–6). Locally, open pine woodlands with juniper, woody legumes, wild olive, evergreen oak, buckthorn, heath, and Cistaceae understorey would have been characteristic. Regionally, oaks persisted in patches, and the diversity of the aforementioned mesothermophilous taxa remained high. Indicators of the thermomediterranean coastal scrub

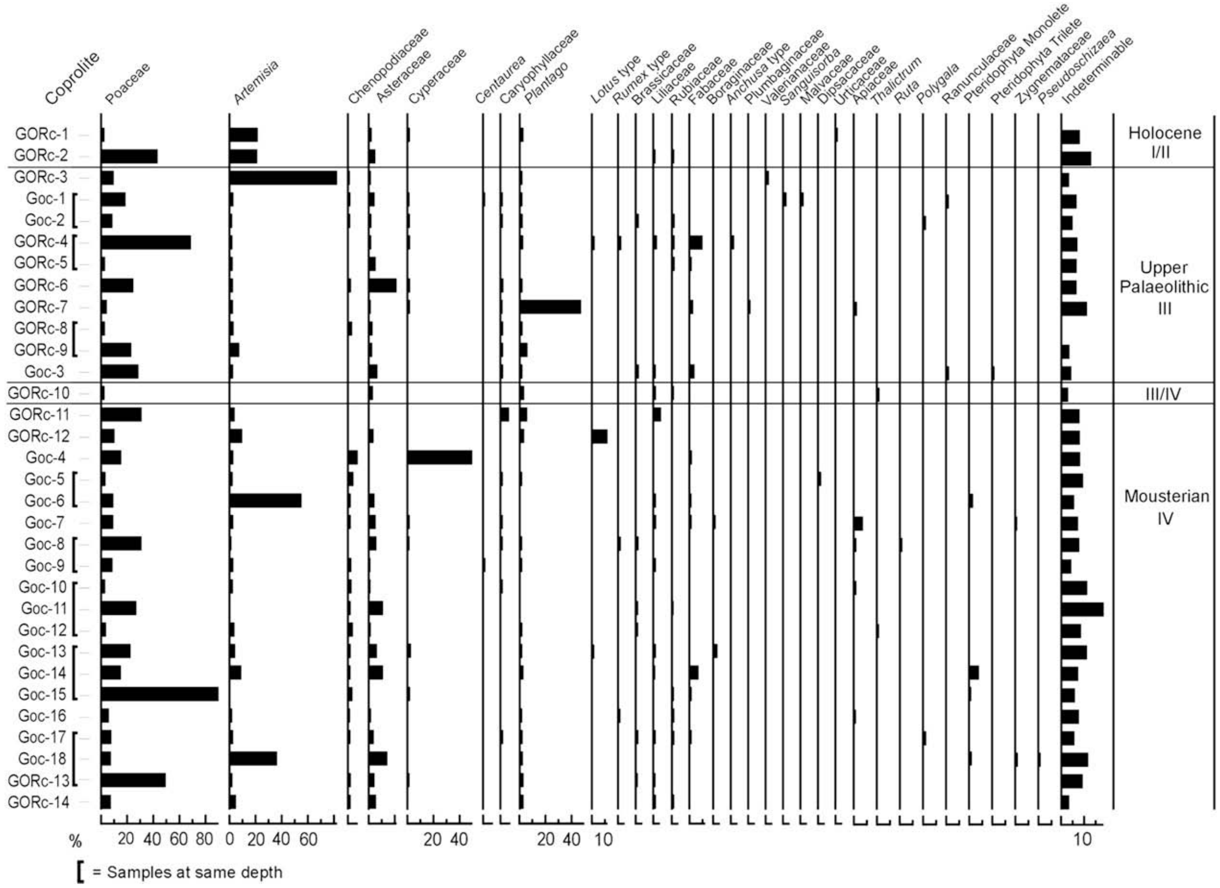

Fig. 5. Pollen diagram of coprolites from Gorham's Cave (ii).

are still present in the Upper Palaeolithic (Table 2). This allows us to conclude that the Gibraltar region was a unique territory in its abundance and diversity of temperate and Mediterranean trees and shrubs during the OIS3 and LGM.

3.3. *The faunal record*

Gorham's Cave excavations have provided an impressive amount of faunal remains, often with potential for palaeoenvironmental reconstruction. Amphibians and reptiles are both well-represented in the Palaeolithic levels and show a dominant thermo-mesomediterranean profile with species like the western spadefoot toad (*Pelobates cultipres*), stripeless tree frog (*Hyla meridionalis*), sharp-ribbed salamander (*Pleurodeles waltl*), Hermann's tortoise (*Testudo hermanni*), the stripe-necked terrapin (*Mauremys leprosa*), the Moorish gecko (*Tarentola mauritanica*), the spiny-footed lizard (*Acanthodactylus erythrurus*), and the horseshoe whip snake (*Coluber hippocrepis*), together with species more characteristic of supramediterranean and humid biotopes like the pygmy marbled newt (*Triturus marmoratus* subsp. *pygmaeus*), and a number of generalists like Mediterranean common toad (*Bufo bufo* subsp. *spinosus*), natterjack toad (*Bufo calamita*), large psammodromus (*Psammodromus algirus*), and viperine snake (*Natrix maura*) (Gleed-Owen, 2001; Finlayson and Carrión, 2006).

If we combine records from Gorham's Cave, Vanguard Cave and Devil's Tower Rock Shelter, the avifauna diversity reaches 145 species, which makes Gibraltar a singular region in the context of Mediterranean palaeontology (Cooper, 1999; Sánchez-Marco, 2004; Finlayson, 2006). Overall, this Pleistocene diversity suggests the existence of multiple biotopes, with an important contribution of savannah species, representation of thermo- to oromediterranean belts, and dry to hyperhumid ombrotypes, and no substantial differences between the assemblages recovered from Middle and Upper Palaeolithic horizons (Tables 3a–c).

The large number of raptors and scavengers suggest a high productivity in the coastal shelf, which would have been the primary hunting area. Seabirds would have been available including petrels, shearwaters, cormorants, auks and gulls. Species that still breed in the rocky Mediterranean or nearby Atlantic coasts, albeit in more remote areas, include the storm petrel (*Hydrobates pelagicus*), the Balearic shearwater (*Puffinus mauretanicus*) and the Cory's shearwater (*Calonectris diomedea*). The presence of the flightless and now extinct great auk (*Pinguinus impennis*) suggests the presence of breeding colonies. It is also worth mentioning the co-occurrence of *Melanitta nigra*, *Mergus cf. serrator*, *M. merganster*, *Somateria*, *Melanitta fusca*, *Clangula hyemalis*, *Gavia stellata*, *Fulmarus glaciaris* and *Alle alle*, that is, a combination of Arctic, Atlantic and Mediterranean species that has no modern analogue.

The raptors that breed in trees are abundant; these species would have made use of the pine and oak woodlands for nesting and as posts from which to oversee the coastal shelf, in the same way as they do today on the wetlands of the Guadalquivir River. The red kite (*Milvus milvus*), is the most common species together with the black kite (*Milvus migrans*), the booted eagle (*Hieraetus pennatus*), the buzzard (*Buteo buteo*), the hobby (*Falco cf. subbuteo*), and the tawny owl (*Strix aluco*). Other species, such as the goshawk

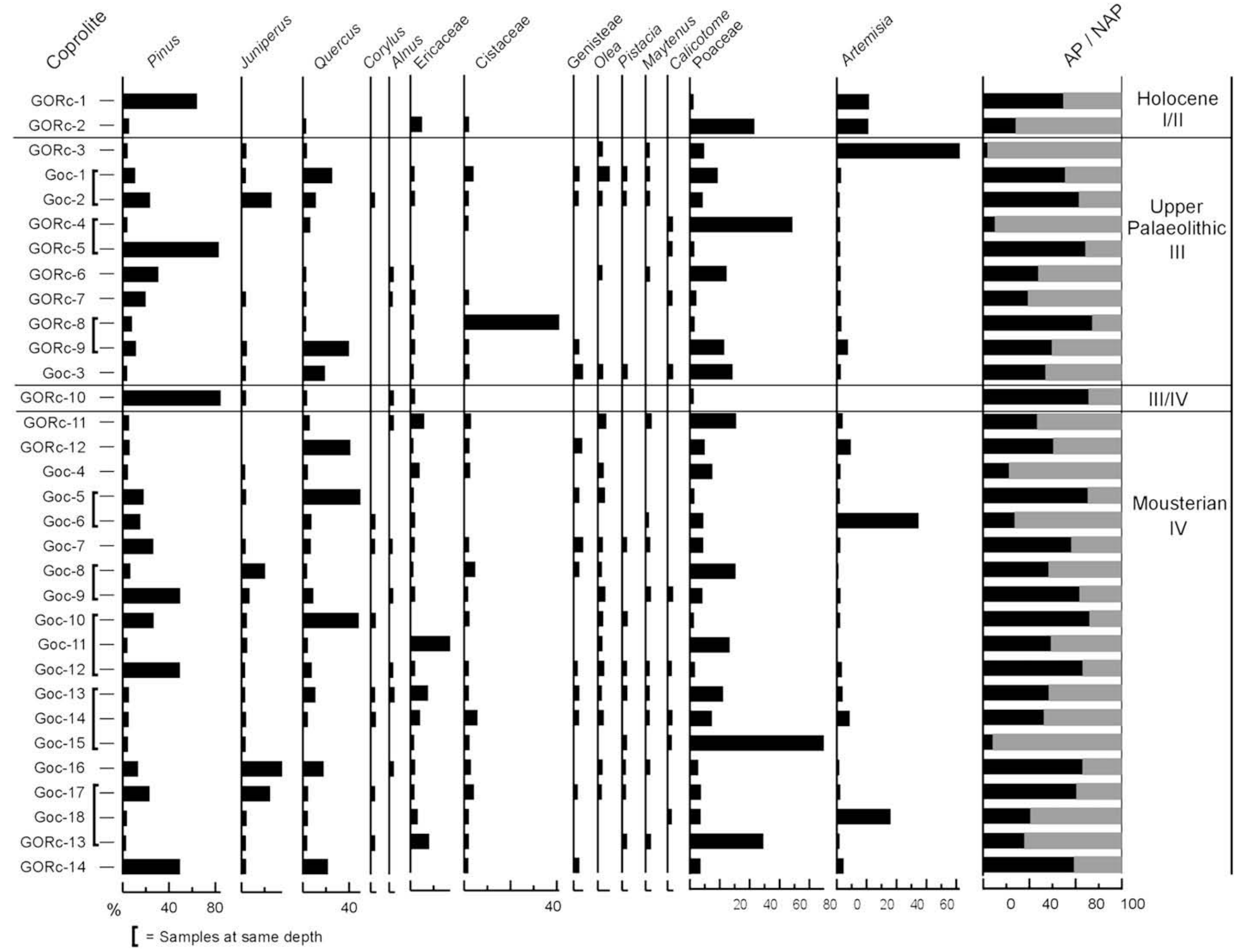

Fig. 6. Synthetic pollen diagram of coprolites from Gorham's Cave.

(*Accipiter gentiles*) and the sparrowhawk (*Accipiter nisus*), the woodcock (*Scolopax rusticola*) and various *Sylvia* warblers, indicate copses of closed woodland and scrub.

The great diversity of waterbirds equally reflects a variety of seasonal wetlands (pools, small lakes, lakelets, and marshes). Among these waterbirds are grebes, duck, coot, waders, pratincoles and marsh terns. Areas of meadows and scrublands would have favoured other species, with the red-legged partridge (*Alectoris rufa*) among the most common in the record. Other typical species are quail (*Coturnix coturnix*), stone curlew (*Burhinus oedicnemus*) and the hoopoe (*Uppupa epops*). The great bustard (*Otis tarda*) points to the presence of open plains. There are only a few terrestrial species, such as the snowy owl (*Nyctaea scandiaca*) and the rough-legged buzzard (*Buteo lagopus*), which indicate a cold climate, and in any case, these species appear in low frequencies, in contrast with the marked presence of Mediterranean species, such as the lesser kestrel (*Falco naumanni*) and the European roller (*Corracias garrulus*) which would have arrived from tropical Africa in spring (Cooper, 1999).

Oryctolagus cuniculus, *Capra pyrenaica* and *Cervus elephus* are abundant among the mammals, together with minor occurrences of *Sus scrofa*, *Bos primigenius*, *Equus caballus*, and *Stephanorhinus hemitoechus* (Currant, 2001; Finlayson, 2006). This record is consistent with the results from palaeobotany, that is, a Mediterranean mosaic landscape with an abundance of savannahs and shrubby grasslands, with large herbivores occupying the coastal shelf and caprids on the cliffs. It is important to note the total absence of cold fauna, such as mammoth, and woolly rhinoceros. Not even the chamois is recorded in these sites, although they are present in other Pleistocene sites of the Betic Cordillera (Finlayson, 2004). Among the carnivores, the most common in the Palaeolithic record at Gorham's Cave are lynx (*Lynx pardina*), wild cat (*Felis sylvestris*), spotted hyaena (*Crocuta crocuta*), leopard (*Panthera pardus*), wolf (*Canis lupus*), brown bear (*Ursus arctos*) and monk seal (*Monachus monachus*).

3.4. The Neanderthal record

Ever since a Neanderthal cranium was discovered at Forbes's Quarry in 1848, and especially with the discovery of a second in 1926 from Devil's Tower Rock Shelter associated with Mousterian lithics, the Gibraltar caves have become renowned among European palaeoanthropologists (Garrod et al., 1928; Waechter, 1964; Mellars, 1996). Today, few would deny the close association of Neanderthals and Mousterian technology (Finlayson, 2004), and the Mousterian sequence at Gorham's Cave therefore indicates the presence of Neanderthals in Gibraltar between c. 47 000 and 23 780 BP, and earlier (Table 1).

The stratigraphic distribution of AMS dates in the Late Mousterian horizon of Gorham's Cave suggests a continuous occupation

Table 2
Main inferred landscapes from coprolite pollen spectra in Gorham's Cave, and palaeoecological indicators.

Sample	Level	Main inferred landscapes	TH	LM	HR
GORc-1	I	Pine woodlands + *Artemisia* patches	−	−	+
GORc-2	II	Poaceae-*Artemisia* steppes with heaths	−	+	−
GORc-3	III	*Artemisia*-dominated shrubland	+	+	+
Goc-1	III	*Quercus*-dominated Mediterranean shrubby savannah	+	+	+
Goc-2	III	*Juniperus*–*Pinus*–*Quercus* woodland	+	+	+
GORc-4	III	Shrubby grassland	+	−	−
GORc-5	III	Pine woodland	+	+	+
GORc-6	III	*Pinus*-Poaceae-Asteraceae savannah	+	+	+
GORc-7	III	Heliophytic matorral with stands of pines	+	−	+
GORc-8	III	Cistaceae shrubland	−	−	−
GORc-9	III	*Quercus*-Poaceae savannah	−	−	+
Goc-3	III	*Quercus*-Poaceae open savannah	+	+	+
GORc-10	IV–III	Pine woodland	−	−	+
GORc-11	IV	Scrub-grasslands with hearths and olives	+	+	+
GORc-12	IV	Open oak woodland	−	−	+
Goc-4	IV	Cyperaceae-dominated wetland	−	+	+
Goc-5	IV	Oak woodlands with pines	+	+	+
Goc-6	IV	*Artemisia*-dominated shrubland	+	+	+
Goc-7	IV	Mediterranean scrub with pine stands	+	+	+
Goc-8	IV	Juniper savannah	−	+	+
Goc-9	IV	Pine woodlands with oaks	+	+	+
Goc-10	IV	Oak woodlands with pines	+	+	+
Goc-11	IV	Heath grassland-scrub	−	+	+
Goc-12	IV	Pine woodland	+	+	+
Goc-13	IV	Oak-heath savannah	+	+	+
Goc-14	IV	Mediterranean open scrub	+	+	+
Goc-15	IV	Grassland	+	+	+
Goc-16	IV	*Juniperus*–*Quercus* woodlands	+	+	+
Goc-17	IV	*Juniperus*–*Pinus* woodlands	−	+	+
Goc-18	IV	*Artemisia* shrubland with composites	+	+	+
GORc-13	IV	Heath grassland	+	+	+
GORc-14	IV	Pine-oak open woodland	−	+	+

TH, thermic coastal scrub, is indicated by *Maytenus*, *Calicotome* and/or *Myrtus*. LM, thermo- to lower mesomediterranean vegetation belt, is indicated by *Olea*, *Phillyrea*, *Pistacia*, *Myrtus* and/or *Ephedra fragilis*. HR, humid and riparian forest trees, are indicated by *Frangula*, *Taxus*, *Corylus*, *Ilex*, *Alnus*, *Betula*, *Castanea*, *Ulmus*, *Fraxinus*, *Acer*, and/or *Salix*. Thick lines indicate groups of coprolite specimens collected from the same depth.

ending abruptly at c. 23 780 BP. This is at least 4000 years later than the latest currently available date elsewhere in Europe and over 10 000 years later than the disappearance of Neanderthals across much of temperate Europe (Finlayson et al., 2008). In contrast to the Mousterian levels, the Upper Palaeolithic Level III, which follows the Mousterian after a 5 ka gap, appears to indicate rather more sporadic visits.

4. Gorham's Cave in its wider phytogeographical context

4.1. Taphonomic considerations

Table 3b
Habitat attribution for bird species found in the Gorham's Cave fossil record

Cultural attribution	Wetlands (%)	Coastal (%)	Marine (%)	Rocky (%)	Terrestrial (%)
Middle Palaeolithic ($n = 117$)	20.51	20.51	9.40	30.77	61.54
Upper Palaeolithic ($n = 50$)	18.00	24.00	10.00	34.00	60.00

Table 3c
Analysis of terrestrial habitats by vegetation structure

Cultural attribution	Open[a] (%)	Intermediate (%)	Closed (%)
Middle Palaeolithic ($n = 31$)	16.13	64.52	19.35
Upper Palaeolithic ($n = 12$)	16.67	75.00	8.33

[a] Open refers to structurally simple habitats (e.g. grasslands); closed are structurally complex habitats (e.g. dense forests); Intermediate habitats include savannah-type parkland and shrublands.

In order to assess the significance of Gibraltar as a potential reservoir of phytodiversity, we need to place the Gorham's sequence in its Iberian context and evaluate the wider distribution of temperate and thermophilous taxa during the cold stages of the Upper Pleistocene (Fig. 7). It needs emphasising, however, that the available evidence is likely to under-represent the real occurrence of temperate woody plant populations, not only because of limited investigations, but also because isolated populations of trees tend to be invisible in palynological records. Tree pollen productivity can also be affected by bad weather/climate and low CO_2 (Leroy, 2007). Willis and van Andel (2004) examined 151 ^{14}C-dated and identified pieces of macrofossil charcoal wood from 40 localities in central and eastern Europe, and demonstrated that during the last Full-glacial, populations of coniferous and deciduous trees grew much further north and east than previously assumed. In fact, coniferous and broad-leaf trees were continuously present throughout the period 32 000–14 000 BP.

So, unfortunately, any account will be subject to many uncertainties because of reliance on pollen data, which are usually relatively insensitive to local detail and problematic with respect to the spatial origin of the pollen. To detect local variability, plant macrorfossils -including charcoal – are preferable, but suitable records are rare. It is also worth re-emphasising the potential of coprolite palynology to detect local occurrences of plant species that are seldom registered in pollen analysis of lacustrine, peaty, lagoonal, and marine sediments. Carrión (2002a) showed that dung pollen spectra give the best reflection of coastal vegetation of Murcia and Almería in terms of occurrence of minor pollen taxa that are crucial for characterising local floristic assemblages. This would be the case with *Maytenus*, *Periploca*, *Withania*, *Ziziphus*, *Calicotome*, *Genista*, *Cytisus*, *Asphodelus* and *Osyris*, among others (Fig. 8). Pollen analysis of cave infills, speleothems, and archaeological sediments in general, which represent another usual source of palaeoenvironmental information in glacial Iberia, also carry pitfalls that have been repeatedly emphasised, such as differential stratigraphic resolution, preservation, percolation, reworking and other biases (Coûteaux, 1977; Turner and Hannon, 1988; Sánchez-Goñi, 1994). Even so, studies of modern samples demonstrate that there is potential for elucidating the composition and relative abundance of

Table 3a
Bioclimatic attribution for bird species found in the fossil record for Gorham's Cave, according to Finlayson (2006)

Cultural attribution	OM SH	SM SH	MM D	MM SH	MM H	MM HH	TM D	TM SH	TM H	SM D
% Middle Palaeolithic ($n = 35$)	17.14	40.00	80.00	74.29	62.86	8.57	57.14	71.43	28.57	25.71
% Upper Palaeolithic ($n = 25$)	28.00	52.00	80.00	60.00	60.00	4.00	56.00	64.00	28.00	20.00

The data were collected from 860 1-hectare study plots, randomly selected from a grid made up of 20 100 km^2 units centred on the southernmost region of the Iberian Peninsula. Each plot was given a bioclimatic attribution. A census of bird species within these study plots provides the bioclimatic attribution for each species. Only species recorded throughout the study with a frequency of over 20 were used for the analysis. (Thermo-types: OM, oromediterranean; SM, supramediterranean; MM, mesomediterranean; TM, thermomediterranean; Ombrotypes: D, dry; SH, subhumid; H, humid; HH, hyperhumid).

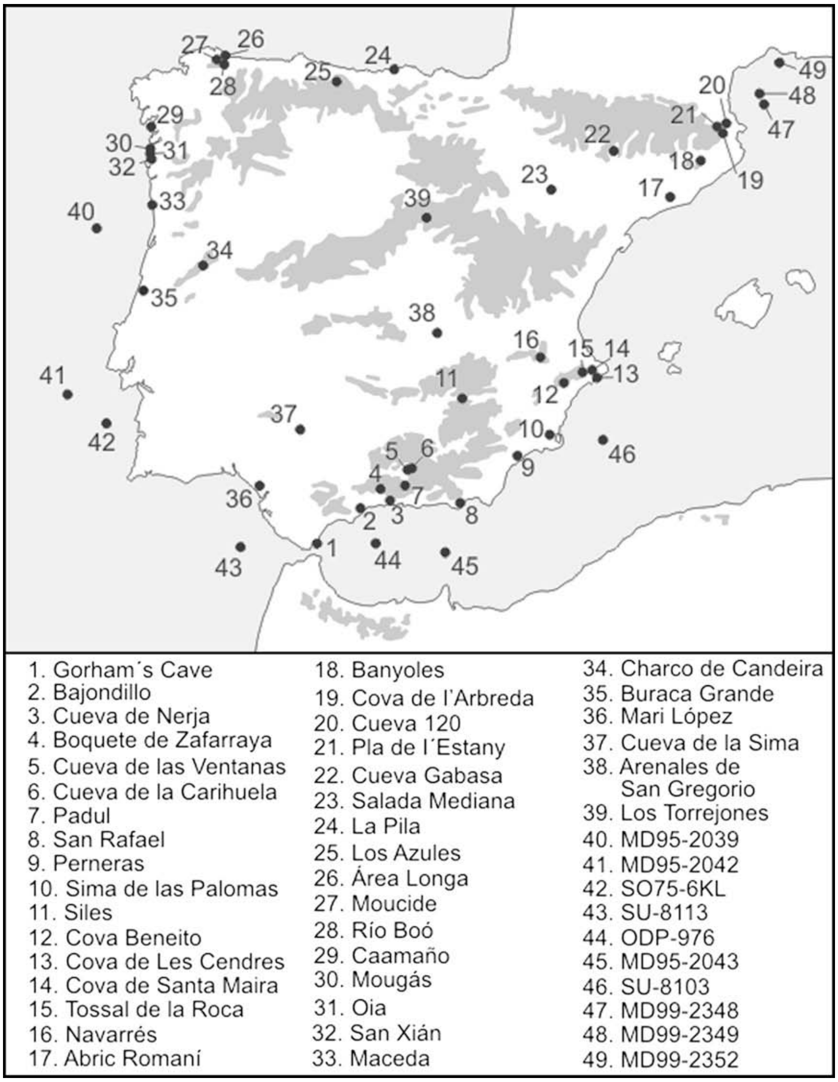

Fig. 7. Important localities in the Iberian Peninsula with palaeobotanical information indicating the location of glacial refugia of temperate, Mediterranean, and thermophilous woody taxa.

plant communities in the surrounding catchment (Coles et al., 1989; Davis, 1990; Navarro et al., 2000; McGarry and Caseldine, 2004).

Offshore pollen sequences have provided useful approaches of past vegetation and climate for long, continuous periods of the Cenozoic for which terrestrial sequences are not available (Leroy and Dupont, 1994; Sánchez-Goñi et al., 2002; Dupont and Behling, 2005; Roucoux et al., 2006). However, marine sequences are limited by a sampling resolution of c. 200 years in measuring the synchronicity of the vegetation response to suborbital climate change (Tzedakis, 2005). Comparison between past land and marine records is further complicated as the errors in dating each record can be larger than the lag times that are being studied. On the other hand, the events in these pollen records are generally controlled through GRIP-derived time scales, but only a few studies (e.g. Allen et al., 1999) have developed independent calendar-year chronology to allow comparison of different types of records.

Given the proximity of north Africa, a major challenge with lagoon, deltaic, and offshore southern Iberian sediments, is the definition of the pollen source area. Magri and Parra (2002) have measured the incidence of pollen from African origin in marine sites of the western and central Mediterranean. Apart from high values of *Cedrus*, the African input is so significant that Combretaceae pollen (typical from sub-Saharan savannahs) was able to reach a latitude of 42º 06′ in the core 9103 offshore Murcia (Parra, 1994). Furthermore, sedimentary contexts at the margin of arid lands are liable to deposition of pollen brought in from great distances by rivers and sea currents, which can mask dry vegetation of the nearby coastal territories. In modern sediments of the Dead Sea, for example, desert plant pollen was greatly outnumbered by pollen of Mediterranean vegetation carried in via the River Jordan (Rossignol, 1969). In the Bay of Elat in southern Israel, modern pollen spectra contain up to 80% of pollen derived from sea-bottom muds off Lebanon and northern Israel, not to mention pollen carried by sea currents flowing across 25–30° of latitude (Horowitz, 1992). In the central Negev, wadi sediments contain up to 77% Chenopodiaceae, and 19% Poaceae-Cyperaceae, while dust collected from the surface on nearby highlands showed Poaceae-Cyperaceae 91%, Chenopodiaceae 6%, and Fabaceae 2% (Horowitz, 1979). As concerns the Alborán sea cores, it must not be forgotten that one of the largest source of terrigenous matter to the Western Mediterranean Sea is the Sahara Desert (Weldeab et al., 2003). In general, to understand the meaning of the pollen signal in marine sequences, we need to distinguish between the terrigenous and autochthonous sediments (Beaudoin et al., 2007), which requires the incorporation of palyno-taphonomical research using present-day marine sediments.

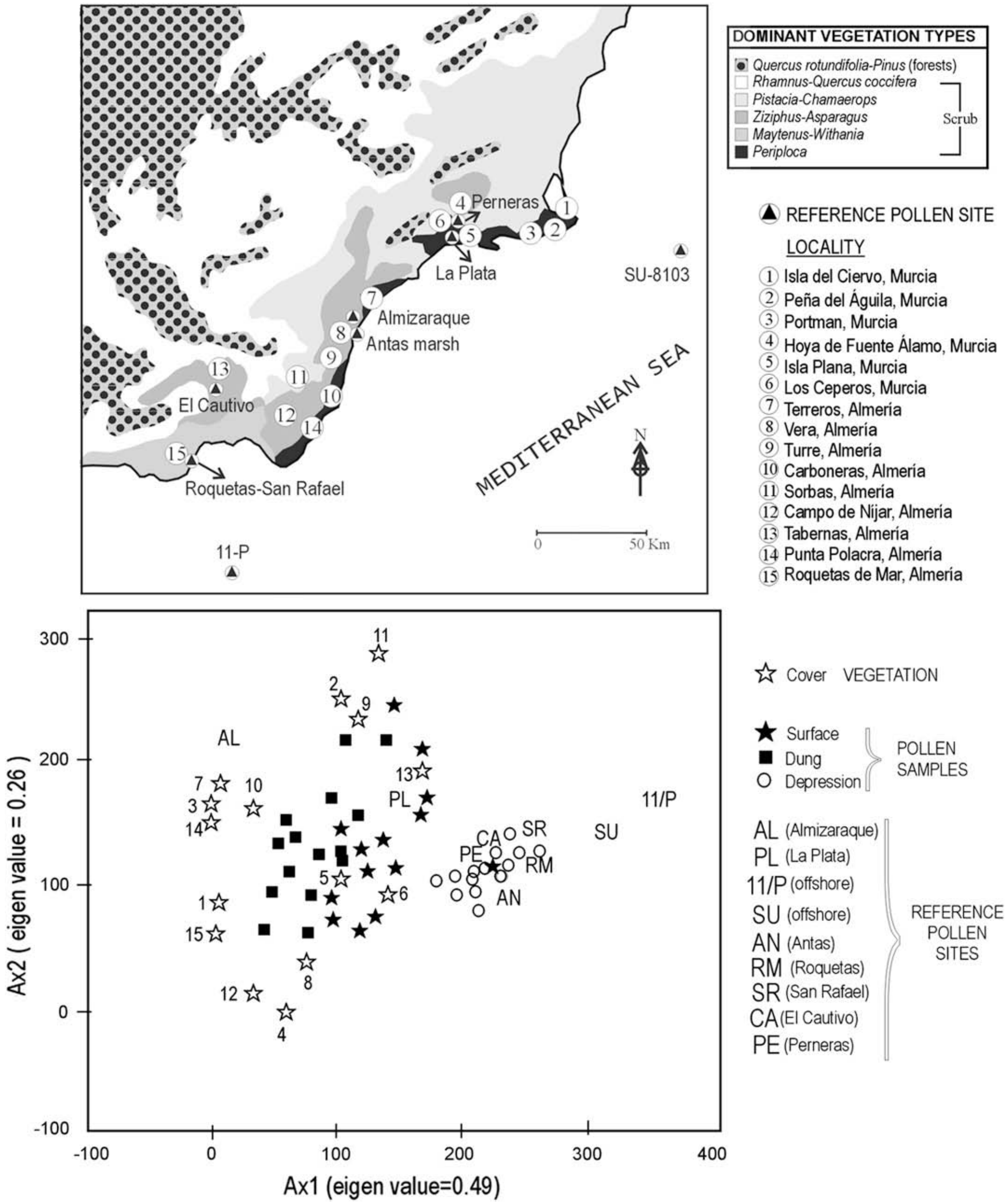

Fig. 8. Coastal plant communities in southeastern Spain are characterised by insect-pollinated scrub species, which fail to occur in Quaternary pollen sequences from valleys, marshlands and marine cores. Here is shown a detrended correspondence analysis (DCA) including cover values, pollen percentages of surface, dung, and depression samples, and average pollen percentages of selected taxa in regional reference pollen sequences. Pollen spectra from biogenic materials of animal origin are the best analogues of local and regional vegetation. Insight into Quaternary vegetation of southern Iberian regions demands complementary pollen analysis of coprolites and cave sediments with preserved biotic remains, in addition to water-lain sediments. Redrawn from Carrión (2002b).

4.2. Palaeobiological data

4.2.1. Southern Atlantic coast and Portugal

Pleistocene pollen sequences from the Atlantic coast of southern Spain rarely extend back to the Pleistocene, but Yll et al. (2004) have recovered a Pleniglacial pollen sequence in the Mari López marshland, Doñana Park, about 15 km from the coastline. Although fragmentary, this record shows a continuous presence of *Quercus* and *Olea* between c. 47 000 and 31 370 BP. Further north, in eastern Portugal, a lacustrine deposit in Charco da Candieira, Serra da Estrela, displays a continuous record of *Quercus* pollen between c. 14 800 and 9525 BP (Van der Knaap and van Leeuwen, 1997). Charcoal from Palaeolithic deposits at Buraça Grande, Portuguese Estremadura, demonstrate the survival in the LGM from c. 23 920 to 17 580 BP of *Pinus sylvestris*, Leguminosae, and *Olea europaea*, as dominant taxa together with the presence of *Quercus*, *Arbutus unedo*, *Erica*, *Pistacia lentiscus*, *Prunus spinosa*, *Phillyrea*/*Rhamnus*, and *Crataegus* (Figueiral and Terral, 2002).

4.2.2. Littoral of Málaga and Almería

The presence and eventual dominance of warm-loving plant associations during the OIS3 and LGM in the extreme south of Iberia is supported by the Mediterranean pollen sequence of Bajondillo (Torremolinos, Málaga), which shows continuous occurrences of evergreen and deciduous *Quercus*. Both fluctuate in frequency, but are never absent from the pollen record, with maxima during the Last Interglacial, OIS3 and Holocene, and minima during the OIS4, and OIS2 (López-Sáez et al., 2007). Oaks are accompanied by *Abies*, *Alnus*, *Betula*, *Corylus*, *Fraxinus*, *Juglans*, *Pinus pinaster*, *Salix*, *Ulmus*, *Erica*, *Genista*, *Hedera*, *Ilex*, *Juniperus*, *Olea*, *Phillyrea*, *Myrtus*, *Lycium*, *Pistacia*, and *Rhamnus*. Minor but significant amounts of the thermomediterranean *Withania frutescens*, *Cosentinia vellea*, and *Selaginella denticulata* are recorded in the Mousterian and early Upper Palaeolithic levels.

Charcoal fragments, pine cone remains, and pine kernel shells in Nerja Cave, show the presence of three pine species in the coast of Málaga during the Upper Palaeolithic between c. 24 000 and 17 500 BP: *Pinus pinea*, *Pinus nigra* and *Pinus halepensis*, with the first predominant, and the Aleppo pine appearing from the Solutrean onwards (Badal, 1998). These findings not only support the autochthonous character of these three species, and the co-occurrence of at least meso to supramediterranean conditions, but also the use of pine kernels for food. Together with pine, charcoal remains of *Quercus*, *Juniperus*, *Cistus*, *Rhamnus-Phillyrea*, *Prunus*, and *Sorbus-Crataegus* have been found (Badal, 1998).

As at Gorham's, the fauna of Palaeolithic Nerja includes abundant *Oryctolagus cuniculus*, together with *Capra pyrenaica*, *Cervus elaphus*, and to a lesser extent, *Equus*, *Hyaena*, *Lynx*, *Sus scropha*, *Capreolus capreolus* and *Bos primigenius* (Aura et al., 2002). Further east, at San Rafael on the Almerian coast, a pollen sequence from a marshland shows continuous curves for evergreen and deciduous *Quercus* and *Olea* during the LGM and the Lateglacial (Pantaleón-Cano et al., 2003).

4.2.3. *Inland Andalucía and the eastern Betic cordillera*

Continental Andalucía shows more oscillating pollen sequences for the glacial stages. The Boquete de Zafarraya (1022 m a.s.l), inland from Málaga, has abundant charcoal of *Juniperus* alternating with *Olea*–Quercus–Rhamnus assemblages in Mousterian levels (30–45 ka) (Vernet and Terral, 2006), while pollen shows an open landscape with very low proportion of trees (Lebreton et al., 2006), and the fauna is dominated by 80% of *Capra pyrenaica* (Barroso et al., 2006). Between c. 43 000 and 26 300 BP, the pollen record of Cueva de la Sima at Constantina (Sevilla) shows *Castanea*, *Corylus*, *Juglans*, evergreen *Quercus*, *Olea*, *Myrtus*, *Phillyrea* and *Pistacia*. These taxa occur more episodically during the subsequent stage (26 300–9300 BP), which is characterised by herbaceous assemblages (Rodríguez-Vidal et al., 2003).

The Padul peatbog and Carihuela Cave have provided long pollen sequences for the late Quaternary of Granada (Pons and Reille, 1988; Carrión, 1992; Carrión et al., 1999; Fernández et al., 2007). Padul shows small frequencies of *Quercus* throughout the Upper Pleistocene in stages equivalent to OIS4, OIS3 and OIS2. In addition, for the Pleniglacial phase between c. 29 300 and 13 200 BP, this pollen sequence includes episodic occurrences of *Juniperus*, *Betula*, *Alnus*, *Hippophae*, and *Erica arborea* (Pons and Reille, 1988). Between c. 45 200 and 21 430 BP, the Carihuela pollen record shows peaks of Poaceae, *Artemisia* and *Pinus*, while the last Neanderthals, after c. 28 000 BP, occurred in open pine woodland environment with reduction of mesothermophilous taxa. The Lateglacial pollen spectra of Carihuela, starting at c. 15 700 BP, show the immigration of oaks into a grass-dominated open landscape with juniper, and several other tree and shrub taxa (Fernández et al., 2007). An early oak colonisation is also visible in Padul after c. 15 200 BP (Pons and Reille, 1988), which suggests the proximity of refugia for evergreen and deciduous *Quercus* together with other trees and shrubs. Lateglacial tree pollen is also recorded in coprolites of spotted hyena (*Crocuta crocuta*) at Cueva de las Ventanas, near Carihuela. Here, about 10 670 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* (Carrión et al., 2001c).

Refugia like the former might be located in the Betics. The lacustrine pollen site of Siles, at 1320 m a.s.l in an intramontane valley of the Sierra de Segura in Jaén (Carrión, 2002b), dating from upper Pleniglacial times (c. 17 030 BP), includes *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*. This group increases in Lateglacial times. The persistence of warmth-demanding species like *Pistacia*, *Arbutus*, and *Olea* in the interior of the Iberian Peninsula at such altitudes is surprising, and may perhaps indicate absence or rarity of snowfall. In any case, this is consistent with the hypothesis of Bennett et al. (1991), that mountain ranges would have been important areas for the survival of trees by facilitating rapid altitudinal displacements in response to climatic pulses.

4.2.4. *Murcian coast*

Pollen spectra of mesothermophilous taxa have been recovered from Middle Palaeolithic deposits in Cueva Perneras (Carrión et al., 1995), and Sima de las Palomas (Walker, 2001; Carrión et al., 2003). These show abundant *Pinus*, *Quercus* 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*, *Maytenus*, *Osyris*, *Withania*, *Lycium*, *Calicotome*, *Ephedra fragilis*, *Cosentinia vellea*, *Selaginella denticulata*, *Ruta*). As with *Maytenus* and *Calicotome* in Gorham's Cave, most of these taxa have not been found in nearby lagoonal and offshore pollen sequences (Nogueras et al., 2000; Sánchez-Goñi et al., 2002; Pantaleón-Cano et al., 2003; Yll et al., 2004). However, although minor components of the pollen spectra (they are clearly underrepresented), these thermophytes are important indicators of frost-free conditions (Mota et al., 1997).

4.2.5. *Alicante–Valencia*

To the north of Murcia, pollen findings come from sites in inland mesomediterranean environments, from deposits spanning Middle–Upper Palaeolithic transition at Cova Beneito in Alicante (Carrión and Munuera, 1997), and from the Navarrés peat bog in Valencia (Carrión and van Geel, 1999). However, mesothermophilous taxa are not continuously present; indeed, most of the deciduous trees and Mediterranean shrubs reduce markedly during OIS2, following expansion during the OIS3.

Fullglacial and Lateglacial pollen spectra from the Villena peatbog in Alicante are dominated by pine, but with a continuous curve of *Quercus ilex-coccifera* type (Yll et al., 2003). Other taxa (minor accounts and discontinuous occurrences) include *Juniperus*, *Abies*, *Carpinus*, *Betula*, *Alnus*, *Salix*, *Ulmus*, *Acer*, *Tilia*, *Fraxinus*, deciduous *Quercus*, *Corylus*, *Olea, Phillyrea*, *Buxus*, *Pistacia*, Ericaceae, *Cistus* and *Rhamnus*.

The rockshelter pollen sequence of Tossal de la Roca in the Sierra de Foradada (Alicante) also shows continuous presence of oaks, albeit in low frequencies, during the Fullglacial and Lateglacial, between c. 15 360 and 12 000 BP (Uzquiano, 1990; Cacho et al., 1998; López-Sáez and López-García, 1999). Charcoal analyses in Cova de Les Cendres (Teulada-Moraira, Alicante), radiocarbon dated between c. 24 000 and 13 000 BP, show low frequencies of *Quercus ilex-coccifera*, and rarely deciduous *Quercus* within a landscape dominated by *Pinus nigra* and *Juniperus*. Accompanying taxa include *Crataegus*, *Erica multiflora*, *Pistacia*, *Prunus*, *Salix-Populus*, *Thymelaea*, and Fabaceae (Badal and Carrión, 2001). Lateglacial and early Holocene (c. 11 600–9700 BP) sediments at Cova de Santa Maira (Castell de Castells, Alicante) contain very abundant oak charcoal, both from evergreen and deciduous species (Badal and Carrión, 2001; Aura et al., 2005).

4.2.6. *Northeastern Spain*

Palaeobotanical evidence of temperate and Mediterranean trees during the Last Glacial stage is not restricted to southernmost locations of Iberia. At Abric Romaní rockshelter, near Barcelona, tree pollen percentages reach 40–60% between about 70 000 and 40 000 BP, with continuous presence of *Juniperus*, *Rhamnus*, *Quercus*, *Olea-Phillyrea*, *Syringa*, *Alnus*, *Salix*, *Juglans*, *Betula*, *Fagus*, *Betula*, *Coriaria*, *Pistacia* and *Vitis* (Burjachs and Julià, 1994). Level D from this site (c. 44 400 BP) shows charcoal with high percentages of *Pinus sylvestris/nigra* accompanied by *Acer*, *Hedera*, *Olea europaea*, deciduous *Quercus* and *Vitis* (Allué, 2002). *Sambucus* and *Prunus* occur at levels N and O (c. 56 000 BP).

Lacustrine sediment pollen from Pla de l'Estany (Olot, Girona), shows the occurrence of *Quercus* and other trees (*Abies*, *Fagus*, *Carpinus*, *Betula*, *Corylus*, *Alnus*, *Tilia*, *Ilex*, *Ulmus*, *Fraxinus*, *Populus*) after c. 30 000 BP (Burjachs, 1990). A pollen sequence in the Castel sa Sala rockshelter, Vilanova de Sau, Cataluña shows very abundant *Quercus ilex-coccifera* during the Lateglacial after c. 16 000 BP (Yll, 1987). Oaks, *Acer monspessulanum*, *A. opalus*, *Prunus*, and *Rhamnus cathartica/saxatilis* are all well-represented in pollen and charcoal remains from the Middle and early Upper Palaeolithic deposits of Cova de l'Arbreda (Serinyà, Girona) during a period assignable to the OIS3. Additionally, the Solutrean level (c. 22 590 BP) yields charcoal of deciduous *Quercus*, *Fagus sylvatica*, *Ilex aquifolium*, *Buxus sempervirens* and Pomoideae (Ros, 1987; Burjachs, 1993, 1994; Maroto, 1994). Similarly, abundant charcoal of deciduous *Quercus* and evergreen *Quercus*, together with *Buxus*, *Rhamnus*, *Prunus*, *Corylus avellana*, *Juniperus* and *Pinus sylvestris* has been identified in the Middle Palaeolithic Cueva 120 (Alta Garrotxa) (Agustí et al., 1987; Allué, 2002). From 30 000 to 27 000 BP, *Quercus* is visible in the Banyoles pollen diagram (Pérez Obiol and Julià, 1994). Burjachs and Allué (2002) review sequences in northeastern Spain from 12 000 to 9000 BP. *Pinus sylvestris/nigra*, *Juniperus*, *Betula*, *Acer*, *Sambucus*, *Rhamnus cathartica/saxatilis*, *Prunus*, and *Quercus* are common features of the charcoal record throughout.

Continental Aragón, in northeastern Spain, also shows the successful persistence of tree populations during climatically-stressful episodes of the Upper Pleistocene. Pollen in coprolites of spotted hyena from Gabasa Cave (González-Sampériz et al., 2003; González-Sampériz, 2004) shows the presence of evergreen and deciduous *Quercus* during the middle part of the last glacial stage in the Huesca Pre-Pyrenean basin. Other taxa include *Juniperus*, *Betula*, *Corylus*, *Ulmus*, *Fagus*, *Hedera*, *Ilex* and *Lonicera*. Around 20 000 BP, palaeolacustrine deposits at 1500–1600 m a.s.l in the Pyrenees (Formigal and Tramacastilla) show minor pollen contributions of *Pinus*, *Abies*, *Juniperus*, *Betula*, *Corylus*, *Alnus* and *Quercus* (González-Sampériz et al., 2005). Lateglacial sediments of the Salada Mediana playa-lake in the Ebro River Basin, exhibit continuous curves of *Corylus* and evergreen *Quercus* together with deciduous *Quercus*, *Alnus*, *Betula*, *Salix*, *Ulmus*, *Juglans* (Valero-Garcés et al., 2000; González-Sampériz et al., 2004). Like other cases, this is not a Fullglacial site, but given the scarcity of records, a useful approach to locating glacial refugia is to identify Lateglacial pollen records that show relatively rapid responses of forest vegetation to deglaciation.

4.2.7. Cantabrian coast and northwestern Iberia

From a survey of tree pollen occurrences in Lateglacial sites of central and northern Iberia, Peñalba (1994) suggested that *Quercus*, *Corylus*, *Alnus*, *Taxus* and *Pinus* had a wide distribution in the northern Iberian Peninsula during pre-Holocene times as patchy refugia situated at medium elevations, a conclusion confirmed by subsequent studies. Thus, the new pollen diagram from Area Longa (Fazouro, Lugo, 0 m a.s.l) is crucial to demonstrate the occurrence of refugial areas for trees in the NW littoral (Gómez-Orellana et al., 2007). Within an overall dominance of *Calluna*–Erica–Poaceae assemblages, Level II pollen spectra show the OIS4 persistence of *Picea*, *Quercus robur* type, *Corylus*, *Fagus*, *Carpinus*, *Ulmus* and *Ilex*). The possibility of long-distance pollen transport in this zone is unlikely mainly because more than 20% of all terrestrial pollen is arboreal. *Quercus robur* type is also continuously recorded along the OIS3 Level III pollen spectra.

The oscillations observed in Area Longa parallel changes in the shorter OIS3 pollen records of Moucide, San Xián, and Santa María de Oia (Gómez-Orellana, 2002). Upper Pleniglacial (e.g. Lagoa de Lucenza, Río Boó, Caamaño, Maceda) and Lateglacial pollen sequences of the Cantabrian and north Atlantic littoral of Iberia show intermittent pollen occurrences of trees, but rapid Holocene colonisation by angiosperm forests suggest nearby enclaves of forest tree populations during the Fullglacial stages (Iriarte et al., 2005; Muñoz-Sobrino et al., 2004).

The Cantabrian coast and northern slopes of the adjacent mountain ranges could have also offered refuges for trees, according to pollen analyses of peaty and lacustrine basins (Ramil-Rego et al., 1998a,b; Muñoz-Sobrino et al., 2001, 2004) and macroscopical charcoal from La Pila in Cantabria and Los Azules in Asturias (Uzquiano, 1992; Arnanz and Uzquiano, 1997). Pleniglacial and Lateglacial pollen includes mostly low percentages of *Pinus*, *Betula*, *Juniperus*, *Corylus*, *Quercus*, *Fraxinus*, *Alnus*, *Ulmus*, *Tilia*, *Salix*, *Juglans*, *Fagus* and *Castanea*. Charcoal comes from *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*. Plausibly, these northern refugia would have been in areas of sheltered topography that provided suitable and stable microclimates.

4.2.8. Central Iberia

Fullglacial landscapes of central Iberia have been little investigated. Recent pollen analyses of spotted hyena coprolites in the palaeontological sites of Villacastín (Segovia) and Los Torrejones (Tamajón, Guadalajara), suggest the existence of populations of woody taxa (*Quercus*, *Taxus*, *Betula*, *Castanea*, *Prunus*, Ericaceae, *Juniperus*) during the late Mid Pleistocene and early Upper Pleistocene (Carrión et al., 2006). Based on biocorrelation of macrofaunal and microfaunal remains, the sequence of Los Torrejones have been assigned to the period between c. 80 000 and 60 000 BP (Arribas et al., 1997). The faunal assemblage includes *Equus caballus*, *Bos/Bison* sp., *Sus scrofa*, *Stephanorhinus hemitoechus*, *Cervus elaphus*, *Capreolus capreolus*, *Crocuta crocuta* subsp. *spelaea*, *Ursus arctos*, *Panthera pardus*, *Vulpes vulpes*, *Homo sapiens*, *Canis lupus*, *Lacerta lepida*, *Microtus nivalis*, *Microtus arvalis*, *Eliomys*, *Oryctolagus cuniculus*, *Meles meles*, *Erinaceus europaeus*, and *Testudo hermanni*. A palynological study in Arenales de San Gregorio, an eolian deposit near Tomelloso (Ciudad Real), OSL dated at 22 000–23 000 BP, shows minor but continuous occurrences of *Corylus*, *Alnus*, *Betula*, *Castanea*, *Fagus*, *Olea*, *Juglans*, *Fraxinus*, *Salix*, and *Ulmus* (Valdeolmillos et al., 2000).

According to the available palaeobotanical information (Dupré, 1988; García-Antón et al., 1990; García-Antón and Sainz-Ollero, 1991; Peñalba, 1994; Blanco et al., 1997; Peñalba et al., 1997), central Iberia during the cold stages of the Quaternary could have contained a diversity of trees and shrubs within a mixture of open and closed habitats favourable to mammalian diversity, in particular ungulate faunas including red deer (*Cervus elaphus*), fallow deer (*Dama clactoniana*), roe deer (*Capreolus capreolus*), horses (*Equus caballus*), ass-like horses (*Equus hydruntinus*), narrow-nosed rhinoceros (*Stephanorhinus hemitoechus*), large bovids (*Bos primigenius*, *Bison* sp.), and wild boar (*Sus scrofa*). Diverse and productive grasslands may account for the abundance of grazers like horses, while more densely forested episodes tempered by locally open spaces are in keeping with the appearance of mixed-feeding ungulates such as the fallow deer and narrow-nosed rhino.

4.2.9. Offshore pollen records

Marine palynology gives support to the idea that tree vegetation, although episodically contracted, was present across the Iberian Peninsula during glacial stages. Deep-sea pollen cores from NW margin (MD95-2039) (Roucoux et al., 2005), Gulf of Lyons (MD99-2348, MD99-2349, MD99-2352) (Beaudoin et al., 2007), offshore Portugal (SO75-6kl: Boessenkool et al., 2001), the southern Atlantic margin (MD95-2042, SU-8113) and the Alborán Sea (MD95-2043, ODP-976, SU-8103) (Parra, 1994; Sánchez-Goñi et al., 2000, 2002; Comborieu-Nebout et al., 2002), show oscillating but continuous occurrences of Mediterranean and temperate trees and shrubs throughout the cold stages of the Pleistocene, including OIS3 and the LGM. In Alborán, these spectra are mainly represented by deciduous and evergreen *Quercus*, *Quercus suber*, *Alnus*, *Abies*, *Betula*, *Corylus*, *Ulmus*, *Fraxinus*, *Pistacia*, *Olea*, *Phillyrea*, *Cistus*, and *Coriaria* (Targarona, 1997; Sánchez-Goñi et al., 2002; Kageyama et al., 2005). In the Gulf of Lyons, they contain high amounts of pollen of Cupressaceae, *Abies*, *Picea*, and deciduous *Quercus* suggesting their presence in the emerged shelfs of southern France, and the Rhone and Pyreneo-Languedocian drainage basins (Beaudoin et al., 2007). Recent pollen analyses of the 25 000 year-long, Galician margin composite core MD99-2331 and MD03-2697 show the occurrence of deciduous oaks during the LGM and Lateglacial (Naughton et al., 2007), which strongly reinforces the view of multiple refugia across Iberia during the Pleistocene.

4.3. Neontological studies

The presence today in Cataluña and Cantabrian coast of such species as *Laurus nobilis*, *Prunus lusitanica*, *Viburnum tinus*, *Hypericum androsaceum*, *Tamus communis*, *Smilax aspera*, *Woodwardia radicans*, *Culcita macrocarpa*, and *Osmunda regalis* (Blanco et al., 1997) gives support to the existence of glacial refugia in these northern areas of Iberia. The same is applicable in the extreme south if due regard is taken of the presence of *Quercus lusitanica*, *Q. canariensis*, *Rhododendron ponticum* subsp. *baeticum*, *Lonicera periclymenum* subsp. *hispanica*, *Ruscus hypophyllum*, *Cistus populifolius* subsp. *major*, *Genista tridentata*, *G. triacanthos*, *Thymelaea villosa*, *Halimium alyssoides*, and *Davallia canariensis*.

Climate modelling by Leroy and Arpe (2007) has provided a plausible picture of distribution of tree growth during the Last-glacial Maximum for Europe and SW Asia. Warm summer-green trees would have survived in several areas of the Iberian Peninsula (not only the extreme south), Italy, the Balkans, in the Pindos, east of Rhodopes, at some places along the south and east coasts of the Black Sea and along the south coast of the Caspian Sea. For cool summer-green trees, the distribution area seems even larger. This study is crucial at filling the important gaps between sites with merely observational data.

This perspective is reinforced by genetic studies of animal and plant species. For example, the genetic structure of the populations of the European grasshopper (*Chortippus parallelus*) suggests refugia in the Cantabrian Mountains (Cooper et al., 1995), *Oryctolagus cuniculus* in northwestern and southwestern Iberia (Branco et al., 2002), *Capreolus capreolus* and *Lynx pardinus* south of Cádiz (Johnson et al., 2004), the cluster pine (*Pinus pinaster*) in the southern Iberian system and Betic cordilleras (Salvador et al., 2000), *Pinus halepensis* spread over several mountain ranges (Agúndez et al., 1997), like *P. sylvestris* (Soranzo et al., 2000), and *Frangula alnus* (Hampe et al., 2003); *Laurus nobilis* on the Atlantic coast and Strait of Gibraltar (Arroyo-García et al., 2001), and *Senecio gallicus* in the southwest (Comes and Abbott, 1998).

Oak species are particularly interesting. López de Heredia et al. (2007) have analyzed the cpDNA geographic structure of the Iberian evergreen *Quercus* complex (*Quercus suber*, *Q. ilex*, and *Q. coccifera*) pointing to the presence of glacial refugia of *Q. suber* in Portugal and eastern Iberia. In addition, there is strong evidence of multiple refugia of *Q. ilex-coccifera*, including central and northern Iberia. Interestingly, the degree of differentiation of cpDNA haplotypes suggests that these refugia may have endured from pre-Würmian times.

There are other reasons why it is likely that tree populations were able to persist in many areas of Iberia during Fullglacial stages. Longevity coupled with phenotypic plasticity, maintenance of high levels of genetic diversity (e.g. allozyme variation) in marginal populations, and a large incidence of polymorphic loci (68% more than herbs) mean that trees, in contrast to other plant species, are uniquely able to withstand directional environmental changes and respond to long-term environmentally imposed selection pressures (Hamrick, 2004).

5. Ecological implications for survival of human populations

The pattern of disappearance of Neanderthals across the Iberian Peninsula suggests a strong north to south trend (Finlayson et al., 2006; Finlayson and Carrión, 2007). Fifteen of the Gibraltar dates (Table 1) and one at Caldeirao in southwest Portugal are the only known dates that go beyond the 30 ka boundary. Interestingly, both sites fall within the modern thermomediterranean bioclimatic belt. Meso to supramediterranean Carihuela lithostratigraphical Unit V, dated between c. 28 000 and 22 000 BP (Fernández et al., 2007), and containing Mousterian lithics and a parietal fragment of a 35–40 year old Neanderthal male, is an exception. These Carihuela Neanderthal-bearing beds require re-excavation (Vega-Toscano, 1988), and the current dates should be viewed with caution. However, they may provisionally support the view that the transition from the Middle to the Upper Palaeolithic took the form of a long and diffuse spatio-temporal mosaic involving populations at low density.

These palaeoenvironmental considerations have important implications for existing arguments about the survival and ultimate extinction of the Neanderthals in the Iberian Peninsula (Zilhao, 2001; D'Errico and Sánchez Goñi, 2003; Carrión, 2004; Finlayson et al., 2004; Stewart, 2005; Vega-Toscano, 2005; Finlayson and Carrión, 2007; Jiménez-Espejo et al., 2007). They cast particular doubt on those hypotheses that presuppose that, during OIS3, extensive territories of the Peninsula alternated between steppe and forested vegetation. Arboreal landscapes were probably widespread in meso and thermomediterranean zones and reached the supramediterranean zone by following mountainous valleys. Abrupt changes towards treeless landscapes may have occurred in continental and high-elevation biotopes near the treeline or the arid fringes. But testing this hypothesis is challenging: even in the south, peatbogs and lacustrine deposits extending back the Lateglacial are rare (Pons and Reille, 1988), or interrupted during the coldest stages (Carrión and van Geel, 1999), and it is difficult to detect abrupt changes in vegetation from cave sequences, where hiatuses are common (Fernández et al., 2007). Marine pollen records, on the other hand, may easily produce the impression that terrestrial vegetation and oceanic water composition experienced synchronous changes in response to climate. However, plant species distributions are more affected by minimum temperatures, growth season, and precipitation than sea surface temperatures, or sea water chemistry (Robinson et al., 2006). In addition, correlation of marine pollen signals with abrupt climate changes such as those exemplified by the Dansgaard–Oeschger events may rest on a weak chain of assumptions (Wunsch, 2006).

We do not know how much inertia and/or resilience to global and regional climate change exists in Mediterranean woody formations. These vegetation types are made up of very resilient taxa, and many species possess physiological mechanisms that buffers the effects of global climatic changes (Bergkamp, 1998).

Carrión et al. (2001a), and Carrión (2002b), though reporting on Holocene rather than Pleistocene conditions, show that in the Mediterranean context the vegetation response to climatic changes can be delayed for centuries to millennia if an ecological threshold has to be crossed. Similar conclusions were reached in the tropics, specifically concerning to responses to Heinrich events (Jennerjahn et al., 2006). In contrast, high-elevation pollen sequences in ecotonal regions near the treeline show abrupt vegetation changes in response to Lateglacial (González-Sampériz et al., 2006) and even Holocene climatic changes (Carrión et al., 2001b).

Our review suggests that the Iberian Pleistocene must have been a period of complexity in landscapes, ecosystems, and biotic responses to climate changes, including some territories with a high degree of resilience, and others with extreme sensitivity to disturbance. The overall case is that Mediterranean populations of temperate tree species seem to have exchanged few genes with nearby populations during both glacial and interglacial periods (Petit et al., 2003), thus suggesting that they have been generally very stable over time. This is particularly applicable to highly heterogeneous landscapes, where recovery from disturbance has proved faster (Lavorel, 1999).

The new data presented here demonstrate that, at least in the extreme south of Iberia, the last Neanderthals and the first "Moderns" lived for many thousands of years in a singularly diverse environment. The Gibraltar Peninsula and just a few sites along the coastal shelf are unique in showing the co-existence of thermo-, meso-, and supramediterranean plant and animal species, including dry and humid, forested and treeless biotopes (Tables 2 and 3a–c). Although mesothermophilous, Mediterranean, and temperate woody taxa occurred patchily in the Iberian Peninsula during the cold stages of the Pleistocene (excluding pines), most fossil localities fall within the coastal domain (Fig. 7). Yet, the most thermophilous plant taxa (*Maytenus*, *Calicotome*, *Withania*, *Periploca*, *Osyris*, *Olea*, *Pistacia*) only co-occur in the southernmost fossil sites in coastal areas extending from Murcia to Gibraltar. Notwithstanding doubts about whether or not the Perneras and Sima de las Palomas pollen records fall within OIS3 (D'Errico and Sánchez Goñi, 2003), we can suggest that at least the coastal shelf between Málaga and Gibraltar represented a favourable territory for the survival of the greatest diversity of environments in the Iberian Peninsula during the period within OIS3 which encompassed the late survival and ultimate extinction of the Neanderthals, and for a long time after that into the LGM. For Gibraltar, this suggestion is strengthened by the faunal record, which includes an impressive avifaunal diversity, and thermophilous animal species sharing the taphocoenosis with mesomediterranean, and supramediterranean indicators (Tables 3a–c). Accepting considerations by Walker (2001) on the chronology of Sima de las Palomas, that coastal corridor might have been extended northwards by a further 450 km.

Neanderthals, then, would have persisted right to the onset of the Lastglacial Maximum in Mediterranean environments that had acted as glacial refugia for many species throughout the Quaternary. The hypothesis that Modern Humans succeeded Neanderthals because of their behavioural superiority is difficult to test in these southern territories. First, although coexistence and admixture appears possible in Portugal (Zilhao, 2001), to the far south the Neanderthals disappeared thousands of years before the first Modern Humans arrived (Table 1), so that these could not have been the cause of the disappearance of the former. Secondly, archaeological and taphonomic studies show scarcely any detectable differences between the behaviour of either group (Finlayson et al., 2006). Thirdly, evidence of Moderns in Europe prior to 30 ka is scant (Trinkaus, 2005), and overall, diagnostic and well-dated AMH fossils are not found west of the Iron Gates of the Danube prior to 32 ka (Finlayson and Carrión, 2007). Furthermore, the genetic data provide very limited evidence of AMH in Europe before the appearance of the Gravettian culture (Richards et al., 2000; Forster, 2004).

In Gibraltar, the Neanderthals may have had access to more than 140 caves that can be found in this karstic system, as well as those which may be submerged (Fa et al., 2000, 2001; Rodríguez-Vidal et al., 2004). The extensive coastal shelf to the east of the Rock of Gibraltar, now submerged, should be emphasised (Fig. 1; Finlayson, 2006). This emerged shelf could have had an area of >3000 hectares during the LGM, and would have continued towards the northeast in the direction of Malaga and presented an environment during the Pleistocene that is not available today. In addition to providing an extensive range of resources, this shelf would have allowed the movement of human groups along a coastal corridor that avoided the steep and abrupt terrain of the coastal mountain ranges, which must have been particularly inhospitable under Pleistocene climatic conditions.

The evidence available indicates that the human occupants of Gorham's Cave, regardless of their taxonomic status, consumed a large variety of resources, including most commonly ibex, but also marine mammals such as monk seals and even dolphins, and fish, mussels and limpets (Finlayson, 2006). The presence of burnt pine nuts in Neanderthal hearths dating to some 40 000 BP strongly suggests the collection of plants (Carrión et al., in press). A large number of rabbits and a great variety of birds – especially quail, duck and rock dove – suggest that the trapping of these small animals was also of great importance.

This paper therefore supports the hypothesis of a correlation between continuous human occupation and coastal shelves, and emphasises that in many cases hominins had a certain preference for landscapes with a variety of biotopes. The human populations that occupied these coastal areas in the Gibraltar region were omnivores and without doubt had a deep understanding of the environment in which they operated and the ability to take advantage of its many resources.

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