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LAST NEANDERTHALS IN THE WARMEST REFUGIUM OF EUROPE: PALYNOLOGICAL DATA FROM VANGUARD CAVE

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Abstract

This paper presents pollen analyses on hyaena coprolites from Vanguard Cave, Gibraltar, with the aim of depicting the vegetation landscapes of the southern Iberian Neanderthals during the MIS 3. The Palaeolithic vegetation in the surroundings included pine, oak, juniper, *Pistacia*, and mixed woodlands, savannahs, riverine forest patches, heliophytic matorrals, rocky scrub with chamaephytes and hemicryptophytes, grasslands with heaths, shrubby grasslands, steppe-like saltmarshes, and littoral vegetation. We compare our results to those of previous palaeobotanical study in the adjacent Gorham´s Cave providing data for the MIS 3 and MIS 2. Placing the palaeobotanical records of Vanguard and Gorham´s Caves in European context, the southern coasts of Iberia emerge as the most thermic refugium of the Late Quaternary, which has important implications for existing arguments about the long survival of Neanderthals in the Iberian Peninsula.

Keywords: Neanderthals, human evolution, palynology, palaeoecology, Quaternary, coprolites, Gibraltar, Iberian Peninsula

1 Introduction

Pollen analysis has proven to be a valuable method in the reconstruction of the floristic and vegetational components of past ecosystems (Ritchie, 1995; Bennett and Willis, 2001; Birks, 2005), including the contexts of hominin evolution (García-Antón and Sáinz-Ollero, 1991; Carrión and Scott, 1999; Burjachs, 2001; Bonnefille et al., 2004; Finlayson and Carrión, 2007; Bonnefille, 2010; Carrión et al., 2011; Messager et al., 2011; Bigga et al., 2015; McGee and DeMenocal, 2017). However, conventional polleniferous deposits (lakes and peat bogs) geographically close to hominin sites are rare, and palaeoecological reconstruction must therefore be based on archaeological sediments. The survival of pollen in these sediments is often unknown (Bottema, 1975; Davis, 1990; Coles and Gilbertson, 1994; Navarro et al., 2000, 2001; Carrión, 2002a). Within materials recovered from archaeological caves, rockshelters, and open-air palaeoanthropological sites, coprolites and other preserved food remains have played a crucial role in the history of Quaternary palynology (Davis and Anderson, 1987; Betancourt et al., 1989; Scott and Cooremans, 1992b; Scott and Vogel, 1992c; Scott, 1994; James and Burney, 1997; Akeret et al., 1999; Fernández-Jalvo, et al., 1999; Carrión et al., 1999b, 2000b, 2006; Alcover et al., 1999; Allen et al., 2000; Holmgren et al., 2001; Latorre et al., 2002; Hunt and Rushworth, 2005; Maher, 2006; Velázquez and Burry, 2012; De Porras et al., 2017; Marais et al., 2015; Williams et al., 2018) and in particular, hyaena coprolites have been a common resource (Scott, 1987; Horwitz and Goldberg, 1989; Carrión et al., 2000a, 2001, 2004, 2008; González-Sampériz et al., 2003; Scott et al., 2004; Yll et al., 2006; Villa et al., 2010; Gatta et al., 2016; Daura et al., 2017).

This paper presents pollen analyses performed on hyaena coprolites from Vanguard Cave, Gibraltar, with the aim of depicting the vegetation landscapes of the southern Iberian Neanderthals during the MIS 3 (c. 59-29 kya). A previous palaeobotanical study in the adjacent Gorham´s Cave provided data for the MIS 3 and MIS 2 (c. 29-14 kya) (Carrión et al., 2008), and a comparison of the palaeoecological records from both sites is needed. For the purposes of this special issue, it should be emphasized that the Gibraltar peninsula hosts the last known populations of Neanderthals (Finlayson et al., 2006; Finlayson and Carrión, 2007) and more information of their palaeobotanical context is required.

2 The site: stratigraphy, chronology, faunal and archaeological records

Vanguard Cave lies at 36º7´17´´N and 5º20´30´´W in the Gibraltar promontory on the southern Iberian Peninsula. It forms the northern shoreline of the Strait of Gibraltar which connects the Mediterranean Sea with the Atlantic Ocean. Several caves, including Vanguard, Gorham´s, Bennett´s, Hyaena and Boat Hoist Caves, form a limestone complex at the present-day sea-level facing onto Governor´s Beach (Fig. 1). Geomorphological studies demonstrate that the Gibraltar peninsula underwent tectonic uplifts and eustatic sea-level fluctuations during the Pleistocene, and it is now clear the cave complex formed in an emerged coastal shelf of upto 5 km, and contains deposits covering most of the MIS 5d-2 interval (Jiménez-Espejo et al., 2013; Rodríguez-Vidal et al., 2013).

Vanguard Cave has been archaeologically excavated over several seasons (Figs. 2, 3). The most extensive research was conducted in the 1990s and early 2000s by a team from the Natural History Museum, London, and the Gibraltar Museum as part of the Gibraltar Caves Project (see Barton et al., 2013 and references therein). This work focused on three major sections at different elevations of the Vanguard sedimentary sequence (Upper, Middle and Lower areas); without direct vertical continuity between them. Starting in 2012, a new excavation project aimed to: (i) re-analyse the data and excavation contexts, to (ii) establish a continuous stratigraphy of the sedimentary deposits allowing for a long-term, open-area excavation.

Vanguard Cave contains ~17m of sedimentary deposits, mainly composed of massive, coarse-to-medium sands intermixed with tabular-to-lenticular units of silts and silty sands (Macphail and Goldberg, 2000; Doerschner et al., 2018). The sands from the uppermost ~5m of the sequence are inter-digitated with black clay layers showing phosphatisation (Fig. 4). The abundance of phosphates seems to be related to bird and bat guano (Macphail et al., 2013). So far, the most recent excavation has allowed researchers to define 24 stratigraphical levels in the uppermost ~5m of the profile (see details in Doerschner et al., 2018). A comparison of this stratigraphy with former frameworks (Macphail et al., 2013) is ongoing.

Pettitt and Bailey (2000) analysed seven samples and concluded that the deposits were either close to, or beyond the limits of the radiocarbon dating method. Their results were confirmed by the multi-grain OSL dating on three sediment samples with a chronology from 46±3 ka to 112±10 ka. A subsequent study using six multi-grain and one single-grain OSL age estimate, pointed to an earlier depositional age of MIS 5 (~74–133 ka) (Rhodes, 2012). Recent research has provided new OSL results based on fifteen samples collected from the uppermost ~5m of the newly excavated Vanguard Cave profile (Doerschner et al., 2018). This study indicates that sediment probably accumulated during the last sea-level highstand in MIS 5 until when the cave was completely filled ~43 ka (MIS 3).

Pioneering faunal analyses of the Vanguard sequence showed low variation in the macro-mammal assemblage, indicating environmental stability during the deposition period. The faunal assemblage from the central area was characterised by the presence of ungulates, including ibex (*Capra pyrenaica*), red deer (*Cervus elaphus*) and wild boar (*Sus scrofa*), as well as marine mammals (Mediterranean monk seals *Monachus monachus* and dolphins *Delphinus delphis*, *Tursiops truncatus*) and carnivores (*Ursus arctos*) (Currant et al., 2013). Among the faunal fossils, it is worth mentioning the human-induced damage on a proximal phalanx and the scapula of a Mediterranean monk seal (Stringer et al., 2008). In addition to terrestrial and marine mammals, molluscan shells such as *Callista chione*, *Mytilus galloprovincialis*, *Acanthocardia tuberculata*, *Patella caerulea*, *Patella vulgare* and a few barnacles (*Balanus*), were also registered. The latest research in the upper part of the sedimentary sequence allowed for the observation of taxonomical and taphonomical differences between levels. The uppermost part of the profile (Levels 1–16) showed a predominance of small vertebrates, including Leporidae and birds. Many of the bones recovered were semi-articulated and showed no biostratinomic modifications, which suggests they were introduced naturally into the cave.

The presence of coprolites and hyaena bones (especially at Level 5) indicates, on the other hand, the use of the cave as a carnivore den (Fig. 5). The human presence seems to be occasional in this part of the stratigraphy with only a few stone tools in Levels 5–6, 9–12 and 14–16 (Fig. 3). In contrast, Levels 17–24 show a higher proportion of lithics and human-induced damage on bones. Stone tools were recovered in Levels 18, 20 and 22, as well as cut-marks, evidence of burning, and intentional percussion notches on ungulate (ibex and red deer) bones to access the marrow. As in the uppermost levels, natural intrusions and perturbations in the form of burrows were detected at Level 19. One hyena bone was identified at Level 18, which together with a coprolite from Level 20, reaffirms the alternation of hominids and carnivores in the cave.

Barton (2013) attributed the lithic artefacts from the Upper and Middle areas of the cave to the Middle Palaeolithic techno-complex. The lithic assemblage showed only slight variation throughout the sequence, with small changes in the prevailing percentages of quartzite over finer-grained cherts. Limestone from the cave bedrock was also used for making tools, a circumstance suggesting a significant expeditious behaviour. For Barton (2013), the low density of lithics in the assemblage, as well as the limited diversity of raw materials, was concordant with a succession of short-term human occupations at the cave.

3 Material and methods

53 samples of minerogenic sediment from Vanguard Cave Levels 1 to 24 were palynologically sterile. This failure in pollen analysis is not surprising taking into account the sedimentary texture of the deposit, dominated by sands. The absence of pollen in sandy stratigraphies of caves is quite common (Carrión et al., 1999a).

In contrast to the sediment samples, 17 out of 32 coprolite samples from Levels 4, 5, and 6b (Table 1), were polleniferous, and the current study is based on these samples (Fig. 5). Taking into account the OSL data by Doerschner et al. (2018) on Levels 4-6, the pollen data from these coprolites conform to the 45-60 ka period approximately. Coprolites were externally pale brown to yellowish, and internally pale brown to White. Most were relatively hard, although not permineralised, and they sometimes broke easily. Their surface showed straight cracks, up to 3 cm in length, sometimes intersecting each other in the inner region, giving a polygonal appearance to the matrix. A denser cortex, probably related to the intestinal lubricant (Horwitz and Goldberg, 1989), was macroscopically visible from the inner region of the coprolite. Several specimens contained corroded fragments of partially digested prey bones.

In the laboratory, the coprolites were cut open with a steel spatula, and material from the centre was scraped out to minimize contamination from external surfaces, and weighed. Laboratory treatment was performed following conventional HF, HCl, KOH method (Carrión et al., 2013) and *Lycopodium clavatum* tablets containing a known quantity of spores were added to each sample 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. 6-8). Percentages of each taxon for each sample were based on a pollen sum excluding hydro-hygrophytes and non-pollen microfossils.

Evergreen, deciduous, and cork-oak palynological types were discernible in most cases (Planchais, 1962; Carrión et al., 2000b), with the evergreen types predominant. We identified the occasional presence of maritime pine pollen (*Pinus pinaster*) (Fig. 6), although the pine pollen mostly belongs to a medium- (*P. pinea-halepensis*) to small-sized (*P. nigra-sylvestris*) morphotype (Carrión et al., 2000a). Fungal spores were not counted as they were largely sordariaceous ascospores, customarily occurring in fossil dung of different kinds (van Geel et al., 1989).

4 Palynological record and taphonomical remarks

Values of the total pollen concentration, the pollen sum, the number of pollen taxa, and the percentages of indeterminable pollen are shown in Table 1. The number of palynomorphs extracted from the coprolites ranges between 0 and 89601 grains/g. Pollen preservation was generally good, allowing reliable pollen identifications and frequencies of indeterminable grains averaging 4,8%. Pollen taxa diversity is high, with 70 types in total, and exceeding 20 types in most samples. Sample VANc7, dominated by *Pinus*, only has 4 different types, and its pollen concentration is the lowest (Table 1).

Despite the doubts it may arise on the palaeoecological value of this sample, we have decided to include it in this study because experimental studies on the pollen taphonomy of coprolites are still scarce, and therefore we no not wish to lose any potentially relevant information for future research.

The pollen-bearing coprolites of Vanguard Cave show several pollen dominants: *Pinus*, Poaceae, Chenopodiaceae, and *Quercus* (Figs. 6, 7). Other pollen taxa may reach relatively high values in some samples, such as *Pistacia lentiscus*, *Artemisia*, (e.g. VANc1-3, c8, c9), and Cichorioideae (VANc1, c8, c10) (Fig. 7). A diversity of trees, shrubs, and herbs is also visible. Broad-leaf trees include deciduous *Quercus*, *Quercus suber*, *Alnus*, *Betula*, *Castanea sativa*, *Corylus avellana*, *Juglans regia*, *Fraxinus*, *Salix*, *Ulmus*, and *Sorbus*. Mediterranean woody shrubs and trees include *Olea europaea*, *Phillyrea*, *Buxus*, *Coriaria*, *Myrica*, and *Rhamnus*. Among the conifers, we have identified *Abies*, *Taxus baccata*, *Pinus pinaster*, *Cedrus* and *Juniperus*. Xerothermophytes include *Maytenus europaeus*, *Withania frutescens*, *Calicotome*, and *Myrtus communis* (Fig. 6). Indicators of saline substrates (Chenopodiaceae, *Tamarix*, *Limonium*, *Nerium oleander*), and heliophytes such as Ericaceae, Asteroideae, Cistaceae, *Ephedra fragilis* (VANc1-c4, VANc10-c15), *E. nebrodensis* (VANc7-c8), are also present (Fig. 7). In lower frequencies but still common, are Genisteae, Brassicaceae, Lamiaceae, *Asphodelus*, *Centaurea*, and *Plantago* (Fig. 7). Non-pollen palynomorphs suggesting the ingestion of stagnant water by the hyaenas or their prey, or perhaps water transport into the cavity include *Mougeotia*, *Zygnema*, *Pseudoschizaea*, and acritarchs, and probably *Equisetum*, *Polypodium* and other pteridophyte spores (Fig. 7).

It is noteworthy that several groups of coprolites collected at the same depths showed differences in the pollen spectra. For example, VANc2, VANc3 and VANc-4 are characterized by *Pinus*-Poaceae, Poaceae-Chenopodiaceae, and *Quercus*-*Pinus*-Chenopodiaceae, respectively; VANc8 is dominated by Poaceae, *Artemisia* and Cichorioideae while VANc9 records more pine and *Artemisia* (Figs. 6, 7). Although coprolite pollen samples are ordered stratigraphically, it is at first unlikely that the changes observed across the pollen diagram represent a diachronic sequence of palaeoecological events. These major differences between closely situated pollen samples might be reflecting different environments that coexisted within a patchy landscape mosaic that was visited by the hyenas rather than a temporal record of different vegetation stages. However, it cannot be discarded that the variation of pollen spectra below and above VANc11-VANc12 could be meaningful in terms of vegetation change: evergreen and deciduous *Quercus* are more frequent in the lower part, whereas *Pistacia*, *Olea*, Poaceae, *Artemisia*, and Cichorioideae increase in the upper part suggesting an opening of the landscape. In addition, *Pinus* is generally less frequent above VANc7, and Chenopodiaceae attains maximum values in VANc6 (Figs. 6, 7). The exclusive occurrence of the heliophytes *Calicotome*, *Myrtus*, *Buxus*, Apiaceae, Brassicaceae, *Bupleurum*, *Helianthemum*, Genisteae, *Hypericum*, Liliaceae, *Nerium oleander*, *Ononis*, Rubiaceae and Thymelaeaceae, from VANc-10 upwards (Figs. 6, 7), supports the occurrence of generally less forested environments. Likewise, the presence of *Ephedra nebrodensis* exclusively in VANc8 and VANc7 suggests not only more frequently open vegetation, but also climatic continentalization, and probably lower mean temperatures during the most recent accumulation of Level 5. This is a point that bears palaeoecological implications and shall be later discussed.

In the interpretation of coprolite pollen spectra, we need to take account of the variable behaviour of the animal that produced the coprolite. We know that hyaena coprolites produced *in situ* are likely to represent mosaic characteristics of landscapes in physiographically heterogeneous territories (Scott et al., 2003). Spotted hyenas range in the Namib Desert following the distribution of freshwater pools (Skinner and van Aarde, 1980). Prey diet would be partially reflected in the abundance of grasses, and especially the high diversity of herbaceous types. Furthermore, experimental studies show 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, which generally is rarely wider than 15 km and never more than 50 km from hyaena den (Scott, 1987; Scott and Brink, 1992a; Argant, 2004; Argant and Dimitrijevic, 2007).

Previous studies postulate that pollen may be incorporated into the hyaena coprolite (i) by ingestion of water, (ii) incidentally from the air, (iii) adhered to any item of the diet, (iv) by ingestion of vegetable matter, and (v) from the stomach contents of the prey. Determining the relative role of each is mostly speculative. Most hyaenas will try to eat almost everything, and subsist on a broad omnivorous diet including carrion, vegetable matter, mammals, and birds' eggs (Mills, 1989). However, when there is abundant supply, hyaenas seem to subsist primarily on meat, with a preference for large mammals. They are frequently primary defleshers (Kruuk, 1972). In this case, an important pollen source must be the stomach content of these large herbivores. This could be the case for coprolites with high pollen concentrations such as VANc9, VANc12, or VANc17 (Table 1). Prey may have consumed grass swards, which are excellent traps of regional pollen not influenced by the flowering season (Gutiérrez et al., 1998).

In general, coprolite pollen spectra may record occurrence 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 entomophilous-dominated vegetation in terms of occurrence of minor pollen taxa that are crucial for characterizing local floristic assemblages. This would apply to several taxa found in Vanguard, such as *Maytenus*, *Withania*, *Calicotome*, Genisteae, and *Asphodelus* (Figs 6, 7.). In fact, even the low frequencies of these pollen taxa may be linked to local abundance, as they are very poor dispersers (Carrión, 2002a).

5 Comparison between the pollen records of Vanguard and Gorham´s Cave, and inferences about the last glacial vegetation of the Gibraltar Peninsula

Altogether, the pollen records of Vanguard and Gorham´s (Levels III and IV) (Fig. 8) depict a glacial refugium for temperate trees, Mediterranean scrub, and especially Ibero-Maghrebian thermophytic formations. Although the chronology of both records has neither been finely, nor definitively established, it is clear that a great part of the MIS 4-2 dry-cold interval is captured (Carrión et al., 2008; Doerschner et al., 2018) without any relevant change in the composition of pollen assemblages. At most, if considering average values, we observe a slightly higher incidence of *Quercus*, Cistaceae, Ericaceae, and *Olea* in Gorham´s, and of *Pistacia* and Chenopodiaceae in Vanguard. Considering the presence/absence of woody taxa, only a few are exclusive for Gorham´s (e.g. *Frangula, Acer, Ilex, Arbutus, Viburnum, Prunus*) and Vanguard (e.g. *Withania*, *Abies*, *Myrica*, *Sorbus*, *Juglans*, *Nerium*), with both sites showing a considerably high rate of taxon coincidence (63%). All major taxa and those less frequent but with percentages higher than 5% are present in both pollen sequences.

Cave sediment from Gorham´s Cave provided pollen for Levels IV and III, showing abundant *Pinus*, *Juniperus*, Ericaceae, Poaceae, Cistaceae, Asteraceae, *Artemisia*, and Chenopodiaceae (Fig. 8). These sediment pollen spectra are probably more post-depositionally biased than those derived from coprolites, where preservation was more favourable allowing better pollen counts and palynological discrimination (Carrión et al., 2008). Macrobotanical remains from Gorham´s help complete the picture. Charcoal (strobili and charred wood) confirms the local presence of *Pinus pinea, Juniperus, Pistacia lentiscus, Olea europaea, Erica,* Cistaceae, *Arbutus unedo*, and *Fraxinus*, among other minor components (Carrión et al., 2008). A preliminary inspection of macroscopic charcoal in Vanguard also showed *Pistacia*, and *Olea* (Ward et al., 2013).

According the aforementioned data, the Palaeolithic vegetation surrounding the Gibraltar Caves would include pine, oak, juniper, *Pistacia*, and mixed woodlands, savannahs (*sensu* Grove and Rackham, 2001), riverine forest patches, heliophytic matorrals, rocky scrub with chamaephytes and hemicryptophytes, grasslands with heaths, shrubby grasslands, and steppe-like saltmarshes and littoral vegetation.

Savannas with pine, oak and juniper, and perhaps other taxa (e.g. *Pistacia lentiscus, P. terebinthus*, *Castanea sativa*, *Olea europea*, *Erica arborea*) in the arboreal layer may well have been widespread along the coastal shelf eastwards of the caves (Fig. 1). According present-day vegetation (Pérez and Bensusan, 2005), evergreen oak species such as *Quercus ilex/rotundifolia/coccifera* was prevalent. *Pinus pinea* was dominant in pine woodlands, and over coastal dunes, here accompanied of junipers.

Deciduous and mixed forests likely developed in the most humid enclaves, plausibly including a diversity of species like *Quercus faginea, Q. suber, Q. pyrenaica, Q. canariensis, Acer granatense, Ilex aquifolium, Corylus avellana, Betula celtiberica, Ulmus glabra, Fraxinus angustifolia, Sorbus domestica, Juglans regia, Castanea sativa, Erica arborea, Pistacia terebinthus, Phillyrea angustifolia, Viburnum tinus, Buxus sempervirens-balearica, Taxus baccata, Hedera helix, Ruscus hypophyllum*, and probably, although not represented in the pollen spectra, lauroid shrubs and ferns

(Cabezudo and Pérez Latorre, 2001). Most likely, these forests were widespread in the Pleistocene of the western mountains of the Gibraltar Strait facing North Africa.

Riparian forests possibly followed the courses of rivers and watercourses and ravines. Several species of *Salix, Fraxinus angustifolia, Populus alba, Alnus glutinosa, and Frangula alnus*, together with sedges like *Carex pendula*, are likely in these environments.

The abundance of chenopods in Vanguard is probably related with salt-marshes in the adjacent coastal shelf. Other pollen taxa represented in xero-halophytic communities of the littoral are *Tamarix, Withania, Frankenia, Plantago, Limonium, Nerium, Plantago,* and *Thymelaea*. Heliophytic shrublands likely were abundant with spiny and brush-like legumes (*Cytisus, Genista, Teline, Stauracanthus*), heaths (*Calluna, Erica*), and rock-roses (*Cistus, Halimium, Helianthemum, Fumana*).

The thermophilic character of the coastal communities is confirmed by the pollen occurrences of *Maytenus europaeus, Ephedra fragilis, Calicotome cf. villosa, Withania frutescens, Myrtus communis, Pistacia lentiscus*, and to a lesser extent, *Olea europaea, Phillyrea angustifolia-latifolia, Ephedra fragilis, Bupleurum cf. gibraltaricum, Tamarix cf. africana*, and *Asphodelus cf. albus*.

The vegetation landscapes of Gibraltar did not experience meaningful changes between the Middle Palaeolithic (Gorham´s level IV, Vanguard Levels 4-6) and Upper Palaeolithic periods (Gorham´s level III) (Fig. 8). The Gibraltar region was a unique territory in its abundance and diversity of temperate and Mediterranean trees and shrubs during the MIS3 and the Last Glacial Maximum (LGM).

This point, of paramount importance from palaeoecological and biogeographical perspectives, is confirmed here by the occurrence of *Maytenus senegalensis*, which together with *Withania, Periploca, Calicotome, Osyris, Lycium*, and *Myrtus*, is also found in southern (López-Sáez et al., 2007), and southeastern Spain during the cold late Pleistocene (Carrión et al., 1995b; Carrión et al., 2003b), indicating frost-free conditions. Beyond the indication of a warm climate in the region during the cold phases of the Upper Pleistocene, these findings give support to the ideas by Mota et al. (1996), and Cabezudo and Pérez-Latorre (2001), about the importance of the palaeotropical element in the composition of pre-anthropic shrub communities of the southeastern coastal mountains of Iberia. In Sierra de Gádor, Almería, such taxa like *Maytenus, Myrtus, Phillyrea* and *Buxus* parallel deciduous *Quercus* and the mesophytic forest optimum during the middle Holocene (Carrión et al., 2003b). *Maytenus senegalensis subsp. europaea* (Celastraceae), originally from tropical savannas, is today a Tertiary relict distributed in North Africa and the south of Spain (Málaga, Almería, Granada, and Murcia provinces), adapted to Mediterranean climates with a distinctly thermophilous character, forming part of coastal shrublands and inland not above 300 m a.s.l. (Díez-Garretas et al., 2005; Mendoza-Fernández et al., 2015). The species, vulnerable today, is not currently growing on Gibraltar (Galán de Mera et al., 2000).

6 Neanderthals surviving in the warmest refugium

Placing the palaeobotanical records of Vanguard and Gorham´s Caves in European context, the southern coasts of Iberia emerge as the most thermic refugium of the Late Quaternary (Fig. 9, Table 2). The occurrence of warmth-loving plant communities during the MIS3 and the LGM in the extreme south of Iberia is supported by the Mediterranean pollen sequence of Bajondillo (Torremolinos, Málaga), which shows evergreen and deciduous *Quercus* accompanied by *Corylus, Fraxinus, Juglans, Pinus pinaster, Olea, Phillyrea, Myrtus, Lycium, Pistacia*, and significantly, the thermophytes *Withania frutescens, Cosentinia vellea*, and *Selaginella denticulata* (López-Sáez et al., 2007). 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). Together with pine, charcoal remains of *Quercus*, *Juniperus*, *Cistus*, *Rhamnus-Phillyrea*, *Prunus*, and *Sorbus-Crataegus* have been found (Badal, 1998). In the southeastern Spanish coast, pollen spectra of mesothermophilous taxa have been recovered from Middle Palaeolithic deposits of Cueva Perneras (Carrión et al., 1995a), and Sima de las Palomas (Walker, 2001; Carrión et al., 2003b). These show abundant Quercus and Oleaceae, and frequent presence of thermophytes (*Myrtus*, *Erica arborea*, *Pistacia*, *Buxus*, *Periploca*, *Maytenus*, *Osyris*, *Withania*, *Lycium*, *Calicotome*, *Ephedra fragilis*, *Cosentinia vellea*, *Selaginella denticulata*, *Ruta*).

The plant record, however, is only a part of the evidence. The Gibraltar Peninsula is a puzzling geological ecotone ranging from acidic sands to highly alkaline rocks which would generate high ecological diversity analogous to the current Doñana National Park in southwestern Spain (Rodríguez-Vidal et al., 2013). The impressive record of vertebrates includes thermophilous herpetofauna (*Pelobates cultipres*, *Hyla meridionalis*, *Pleurodeles waltl*, *Testudo hermanni*, *Mauremys leprosa*, *Tarentola mauritanica*, *Acanthodactylus erythrurus*, *Coluber hippocrepis* (Gleed-Owen, 2001; Finlayson and Carrión, 2006), avifauna from multiple biotopes (Cooper, 1999; Sánchez-Marco, 2004; Finlayson, 2006), with an important contribution of savannah species, representation of thermo- to oromediterranean belts, and dry to hyperhumid ombrotypes, as well as species indicative of high productivity in the coastal shelf. There are no substantial differences between the bird assemblages recovered from Middle and Upper Palaeolithic horizons (Carrión et al., 2008).

Among the mammals, it is important to note the total absence of cold fauna, such as woolly mammoth *Mammuthus primigenius*, and woolly rhinoceros *Coelodonta antiquitatis* (Finlayson, 2004). *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). Among the carnivores, the most common are Iberian 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*).

Several faunal analyses support the view that thermicity was a crucial factor in the maintainance of this biodiversity stronghold. By applying the Mutual Climatic Range method on the amphibian and reptile assemblages, Blain et al. (2013) presented quantitative data on the terrestrial climatic conditions throughout the latest Pleistocene sequence of Gorham's Cave. Inferred mean annual temperatures were about 1.6-1.8 °C lower than present-day in this region, while winters would have been slightly colder and summers similar to today. Mean annual precipitation was slightly lower, but according to the Aridity Index of Gaussen there were only four dry months during the latest Pleistocene as opposed to five dry months today during the summer. In sum, the climate was still semi-arid, and thermo-Mediterranean.

The Neanderthal palaeoecology described for Vanguard fits into a pattern that could be widely generalized to other *Homo* species. Finlayson et al. (2011) provided a quantitative reconstruction by using a database of *Homo* occupation sites with associated bird fossils from the Palaearctic region. An inspection of the frequencies of habitat categories showed a close association between human occupation and wetland sites, including lakes, lagoons and marshes. There is a clear association between *Homo* and ecologically rich, semi-open savannah-type ecotonal and mosaic landscapes, such as shown in Gibraltar.

The geological setting, and the topography in particular, is a determinant factor for this ecological scenario. Bailey and King (2011) used field and remote sourced imagery from Africa and the Red Sea region to investigate the relationship of active tectonics and complex topography with archaeological and fossil material. They concluded that geologically dynamic regions, despite their potential for catastrophic events, will favour the creation and maintenance of mosaic habitats through time. It follows that coastlines will be ecologically attractive to humans. The coastal zones, doubtless, would have been a corridor for past human expansion (Bailey et al., 2008; Stringer et al., 2008). In the case of Vanguard and Gorham´s, the location of the caves was surely influential. In the Gibraltar Peninsula a total of 8 sites, either with Neanderthal fossils or their Mousterian lithics, have been discovered. Gorham's and Vanguard Caves are currently at sea level, but during MIS 3 faced an emerged coastal shelf with the shoreline as far as 5 km away at times, and sea level remaining on average 80 m below the present level (Siddall et al., 2003; Rodríguez-Vidal et al., 2013). From all the above, it is not surprising that Gibraltar, a tectonically active area, may have represented a refugial territory for Neanderthals during the cold stages of the Pleistocene, and indeed it seems predictable that the progressive Neanderthal extinction followed a clear continental to oceanic direction, ending in southern Iberia (Finlayson, 2008; Carrión et al., 2008).

The conclusion by Carrión et al. (2011), showing that the appearance of evolutionary novelties within hominins and long permanence of populations is concentrated in regions of highest worldwide biological diversity, is also pertinent. It was assumed that the current areas occupied by hotspots are the remnants of larger territories that have been functioning like engineers of plant and animal diversity over the entire Quaternary and probably long before (Kikvidze and Ohsawa, 2001; Carrión et al., 2006). The Horn of Africa hotspot and its southern fringes in Kenya and Tanzania, together with southern Africa, would have embraced most of the earliest occurrences for genera and species of fossil hominins. Within the western Palaearctic, the Caucasus and the Mediterranean Region were very significant in this respect. The key factors activating evolutionary change may have been geological instability, and a shifting physiographical heterogeneity in association with high biodiversity and ecological interaction.

These palaeoenvironmental considerations have important implications for existing arguments about the long survival of Neanderthals in the Iberian Peninsula (Carrión, 2004; Stewart, 2005; Finlayson and Carrión, 2007; Jiménez-Espejo et al., 2007). Neanderthals lived here in a singularly diverse environment. Former revisions of the palaeoecological data for the Iberian and European Pleistocene (Carrión et al., 2008, 2013; González-Sampériz et al., 2010) show that the southern coasts of Iberia are unique in showing the co-existence of thermo-, meso-, and supramediterranean plant and animal species, including dry and humid, forested and treeless biotopes. In addition, 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.

7 Evolutionary and ecological remarks

One of the issues on which more ink has been poured into the scientific literature on human evolution has been that of Neanderthal extinction. So far in this paper, we have conciously avoided discussing this matter because the data from Vanguard do not add substantial evidence. However, it is singular that neither its origin nor Neanderthals´s long survival have excited the imagination of the researchers as the disappearance of a species (Finlayson, 2010, 2014). Clearly, the Neanderthals disappeared in a cold context, but one that was especially marked by having great climatic variability at the end of the MIS3 or beginning of the LGM (Finlayson and Carrión, 2006, 2007; Jiménez-Espejo et al., 2007). At this moment we are faced with a monumental problem of scale in the interpretation of the process and in the temporal definition of the patterns. This problem has generated much confusion and, in some forums, interpretations based on the neo-Darwinian tradition of competitive exclusion between species. The idea that our species would have a clear biological and cultural superiority over the Neanderthals is part of the traditional paleoanthropological culture (Banks et al., 2008, Gilpin et al., 2016), but perhaps we are mixing problems of cultural transit, biological transitions (in a taxonomic sense) and paleoenvironmental models in a somewhat prejudiced way.

The Neanderthal occupations of the southern coast of the Iberian Peninsula provide an excellent record for the species and, in particular, they provide strong evidence for its long survival, regardless the current discussion about the best method for radiocarbon dating of the last Neanderthal sites (Wood et al., 2013; Higham, 2014; Zilhao et al., 2017). In this regard we note that no site within the southern Iberian coastal refugium has been redated. The interpretation of southern highland sites and others falling firmly within the central Iberian tablelands as representative of the topographically-rich southern Iberian Peninsula, is naïve and incorrect. It does not refute the overwhelming existence of a glacial refugium of great significance to many species along the coastal strip of southern Iberia. The geological, floristic and faunal repertoire is of outstanding richness and suggests coastal platforms occupied by a vegetation mosaic with an extensive biome of "Mediterranean savannah". The

Neanderthals who occupied this coastal environment were omnivorous, ambush hunters, including among their prey marine animals and numerous birds (Finlayson and Carrión, 2006, 2007). It is evident that they had a deep knowledge of the environment in which they lived. In the same way, we now know that they decorated themselves with feathers (Finlayson et al., 2012), made ornaments (Welker et al., 2016), painted on the walls of the caves (Rodríguez-Vidal et al., 2014; Hoffman et al., 2018), and carried out organized, knowledgeable, and caring healthcare (Spikins et al., 2018). Perhaps the cognitive revolution that brought us to the evolutionary theatre is nothing more than a historical contingency (Gould, 2002).

The extinction of Neanderthals and its connection with the arrivals of Modern Humans to western Europe is not yet clear, and the old debate continues about whether climate changes, assimilation into genetic pool (Zilhao et al., 2010) or competition with Modern Humans played the pivotal role in driving Neanderthals to disappearance. Wolf et al. (2018) have studied a high-resolution loess record from the Upper Tagus Basin in central Spain, and demonstrated that the Neanderthal abandonment of inner Iberian territories 42 kyr ago coincided with the development of hostile environmental conditions, while archaeological evidence testifies that this desertion took place regardless of modern humans' activities. Plausibly the process is heterogeneous both temporal and spatially and would cause an episodic fragmentation of the great western Palaearctic metapopulation of the species (Finlayson, 2010). In this context, the work by Kolodny and Felman (2017) introduces an alternative to the old dialectics: a neutral model of evolution in which Neanderthal replacement was determined by repeated migration of modern humans from Africa into Eurasia, followed by random species drift.

Whatever the case, while there is no new paleoanthropological linked to firm chronological evidence, our species cannot be considered as a direct cause of the extinction of the last Neanderthal populations, simply because there is no evidence of cohabitation in the regions where Neanderthals showed exceptional survival, such as in southern Iberia. Here, in the far south, the Neanderthals disappeared thousands of years before the first Modern Humans arrived and Modern Humans arrived late, with the representative cultures of the earliest Modern Humans in Europa being absent altogether (Finlayson et al., 2004, 2006, 2008; Fernández et al., 2007). It should be stressed that, as a species and in the context of human evolution, the Neandertals had a particularly long biological existence, because they formed part of the Middle Pleistocene faunal community, reaching the end of the Upper Pleistocene, disappearing with one of the most climatically critical episodes in Earth's climate history.

The biological realities at this time seem genealogically more promiscuous and the geneticists have arrived at a precious moment to help us understand that there was much more gene flow (successful reproductions) than was assumed among all hominin populations investigated. The most unexpected result of the eastern localities comes from the hand of ancient DNA (both mitochondrial and nuclear) and suggests that there was a different human population (the Denisovans) that lived in Siberia at the same time as the Neanderthals and also at the time when these went extinct (Krause et al., 2010). Moreover, Denisovan sequences of mitochondrial DNA obtained from the same site are more diverse than those known to Neanderthals (Stringer and Barnes, 2015). In addition there were other species in Eurasia before (*H. erectus*, *H. floresiensis*, *H. heidelbergensis*), but the relationship with Neanderthals and Denisovans may not be known until we have old DNA from these species. It is also true that Neanderthals, Denisovans and other species hybridized (Varki, 2016). In the first discovery of an ancient- human hybrid, Slon et al. (2018) have reported the genome from an individual who had a Neanderthal mother and a Denisovan father. There are also “ghost species”, species for which we do not have bone records. We also know that there are Neanderthal and Denisovan genes that continue to be expressed in the immune systems of our species (Dannemann et al., 2016; Deschamps et al., 2016). In the DNA of Europeans and Asians there is up to 4% of Neanderthal DNA. Perhaps, therefore, talk about the Neanderthal extinction at this point has become frivolous.

These results reveal just how little we know about recent human evolution. From the monotonic Modern Human-Neanderthal scenario, recent results are revealing the complexity of the situation in the Pleistocene. Yet, instead of humbly accepting the huge gaps that must still exist we tweak the narratives to incorporate the new results, disregarding the lack of evidence of phenotypic variation which single fossils cannot provide nor indeed our inadequacy at providing fossil ancestor-descendant sequences with such limited material.

A major part of the problem has been the inability to situate palaeoanthropological and archaeological results in ecological context, so critical to presenting a solid base for human behaviour and evolution. This paper shows, by providing a detailed botanical perspective of the environments in which the Gibraltar Neanderthals lived, just how crucial such information is. To obtain such a detailed record of Neanderthal vegetation habitats and their changes (or lack of) through time is admittedly rare but this should not mean that we can gloss over such important contextual data in sites that are deficient in this respect. Unfortunately, the treatment of Iberian and other sites for purposes of dating as though they existed in an ecological vacuum, has only served to return us to the errors of the past. The simple and unrealistic linear Modern Human replacement of Neanderthals in Europe is being revisited from the microscopic perspective of those who seek to understand the phenomenon from the reductionist perspective of a detailed date provided by a piece of bone or charcoal. Such information is only useful if placed in a firm ecological context of the kind presented in this paper.

So it is usual to look at the morphological variation of fossils in the mirror of biology and the technological variation of tools in that of culture. But there is some overlap and the tools could be under some genetic control in the same way that the morphological variation could reflect a certain degree of plasticity, not necessarily a taxonomic essence. The Neanderthal, like the other species, is a fortunate and highly unlikely evolutionary accident that forms a terminal part of the rugged estuary with which we could iconograph the evolution of humans and their relatives.

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Figure 1. Location of Vanguard and Gorham´s Caves, 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., 2014; Finlayson and Carrión, 2006)

Figure 2. Plan view map of the Vanguard Cave site. Redrawn from Doerschner et al. (2018)

Figure 3. Profiles sampled for pollen analysis in Vanguard Cave

Figure 4. Uppermost part of Vanguard Cave´s current excavation (Levels 1-6)

Figure 5. Hyaena coprolites from Vanguard Cave. Chronology: c. 45-60 ka, according OSL data by Doerschner et al. (2018)

Figure 6. Pollen diagram of coprolites from Vanguard Cave (i)

Figure 7. Pollen diagram of coprolites from Vanguard Cave (ii)

Figure 8. Synthetic pollen diagram of coprolites from Gorham´s and Vanguard Caves. Horizontal columns show average percentages per archaeological level. The chronology

of the levels including coprolites is c. 41-11 ka in Gorham´s (Levels IV-III) and c. 60-45 ka in Vanguard Cave

Figure 9. Full glacial (MIS 4 to MIS 2) distribution of: i) Mesothermophilous taxa (deciduous *Quercus*, *Corylus*, *Alnus*, *Tilia*, and *Fagus*); ii) Mesothermophilous taxa including Sclerophyllous elements (evergreen *Quercus*, *Olea*, *Pistacia*, *Phillyrea*, *Myrtus*, *Buxus*, and *Rhamnus*); and iii) Mesothermophilous taxa including sclerophyllous elements and Ibero- Maghrebian scrub (*Maytenus*, *Periploca*, *Ziziphus*, *Withania*, *Lycium*, and *Calicotome*). The background shows the current bioclimatic belts of the Iberian Peninsula. Updated from González-Sampériz et al. (2010): see Table 2 for sites.

Table 1. Polleniferous coprolite samples from Vanguard Cave. Coordinates and palynological characteristics

Coprolite	Level	Nº	Coordinates	Weight (g)	Concentration (grains/g)	Indeterminable (%)	Pollen sum	Number of taxa
VANc1	4	70	K61 x18 y17	7,1	12704	5,91	254	21
VANc2	5	13	L60C x18 y17	6,2	14055	2,69	372	21
VANc3	5	14	L60C x22 y17	6,2	6736	9,85	203	21
VANc4	5	69	K60D x76 y17	6,3	7223	4,43	271	28
VANc5	5	27	L59A x37 y60	7,1	9884	4,76	399	30
VANc6	5	25	L60A x10 y69	4,6	13478	4,28	397	20
VANc7	5	24	L60A x8 y70	6,4	1954	0,00	133	4
VANc8	5	26	L60A x5 y78	7,0	9722	7,34	177	19
VANc9	5	27	L60A x9 y78	7,0	89601	7,56	225	19

VANc10	5	28	L60A x12 y100	6,8	10179	3,17	221	24
VANc11	5	22	K60B x80 y82	7,3	7326	0,00	353	11
VANc12	5	23	L60B x81 y82	6,5	23392	5,00	60	13
VANc13	5	28	L59A x44 y88	7,0	10958	11,86	194	15
VANc14	5	10	K59A x1 y90	6,9	11993	3,02	331	21
VANc15	5	39	L60A x15 y96	7,0	12280	2,56	313	30
VANc16	6b	49	K59B x70 y56	3,5	17214	5,22	268	15
VANc17	6b	50	K59B x69 y90	4,9	27856	4,23	284	22

Table 2 . Geographic coordinates, fossil material, and chronostratigraphy of the sites mapped in Figure 9. Asteriks for sites added to the work by González Sampériz et al. (2010)

No. in Fig. 11	Site	Coordinates	Material	Chronostratigraphy (only Pleistocene)	References
Northern Iberia					
1	Altamira cave (Cantabria)	43°22′N 4°06′W 75 (m) asl	Charcoal	MIS 2	Uzquiano (1992a,b)
2	Area Longa (Lugo)	43°36′N 7°18′W 0 (m) asl	Pollen	MIS 5 to MIS 3	Gómez-Orellana et al. (2007)
3	Cobrante cave (Cantabria	43°18′N 3°32′W 600 (m) asl	Pollen Charcoal	MIS 3–MIS 2	Ruiz-Zapata et al. (2005), Uzquiano (2005, 2008)
4	Covalejos cave (Cantabria)	43°24′N 3°56′W 80 (m) asl	Pollen Charcoal	MIS 3	Ruiz-Zapata et al. (2005), Uzquiano (2005, 2008)
5	Cualventi cave	43°23′N	Charcoal	MIS 2	Uzquiano

	(Cantabria)	4°08′W 75 (m) asl			unpublished data
6	El Castillo cave (Cantabria)	43°17′N 3°58′W 170 (m) asl	Charcoal	MIS 4–MIS 3	Uzquiano (2005, 2007, 2008)
7	El Conde cave (Asturias)	43°16′ N 5°58′W 600 (m) asl	Charcoal	MIS 3	Uzquiano et al. (2008)
8	El Esquilleu cave (Cantabria)	43°12′N 4°36′W 350 (m) asl	Charcoal	MIS 3	Uzquiano (2005, 2008)
9	El Linar cave (Cantabria)	43°20′N 4°10′W 120 (m) asl	Charcoal	MIS 2	Uzquiano (2016)
11	La Pila cave (Cantabria)	43°25′N 4°01′W 25 (m) asl	Charcoal	MIS 2	Uzquiano (1992a, 1995, 1998)
12	Lago de Ajo (Asturias)	43°02′ N 6°08′W 1570 (m) asl	Pollen	MIS 2	Allen et al. (1996)
13	Lago Enol	43°16′N	Pollen	MIS 2	Moreno et al.

	(Asturias)	4°59′W 1070 (m) asl			(2011); López-Merino (2009)
14	Lagoa de Lucenza (Lugo)	42°35′N 7°07′W 1375 (m) asl	Pollen	MIS 3–MIS 2	Muñoz-Sobrino et al. (2001)
15	Las Aguas cave (Cantabria)	43°22′N 4°11′W 100 (m) asl	Charcoal	MIS 2	Uzquiano unpublished data
16	Las Caldas cave (Asturias)	43°19′N 5°55′W 160 (m) asl	Charcoal	MIS 2	Uzquiano unpublished data
17	Lezetxiki cave (Guipuzcoa)	43°4′N 2°31′W 350 (m) asl	Pollen	Middle Pleistocene—MIS 3	Sánchez-Goñi (1993); Arrizabalaga et al. (2004)
18	Los Azules cave (Asturias)	43°21′N 5° 06′W 600 (m) asl	Charcoal	MIS 2	Uzquiano (1992a,b); López-García (1981)
19	Moucide (Lugo)	43°35′N 7°19′W	Pollen	MIS 3	Ramil-Rego and Gómez-

		90 (m) asl			Orellana et al. (2001)
20	PRD-4*	42°32′ N 8°31′ W 260 (m) asl	Pollen	MIS 2	López-Merino et al. (2012)
21	Oia (Pontevedra)	41°59′N 8°52′W 5 (m) asl	Pollen	MIS 3–MIS 2	Gómez-Orellana (2002)
22	Pozo de Carballal (Lugo)	42° 42′N 7°06′W 1330 (m) asl	Pollen	MIS 2	Muñoz-Sobrino et al. (1997)
23	Sopeña rockshelter (Asturias)	43°19′N 4°58′W 450 (m) asl	Charcoal	MIS 3	Uzquiano, unpublished data
West–Northwestern Iberia					
24	Buraca Escura (Portuguese Extremadura)	39°54′N 8°35′W 350 (m) asl	Charcoal	MIS 2	Aubry et al. (2001)
25	Buraca Grande (Portuguese Extremadura)	39°55′N 8°36′W 350 (m) asl	Charcoal	MIS 2	Figueiral and Terral (2002)
26	Cabeço de	39°20′N	Charcoal	MIS 3–MIS 2	Figueiral

	Porto Marinho (Portuguese Extremadura)	8°56′W 70 (m) asl				(1993); Zilhão et al. (1995a,b)
27	Charca da Candiera (Serra da Estrela Portugal)	40°20′N 7°34′W 1409 (m) asl	Pollen	MIS 2		van der Knaap and van Leeuwen (1997)
28	Gruta do Caldeirao (Portuguese Extremadura)	39°38′N 8°24′W 120 (m) asl	Charcoal	MIS 2		Figueiral, unpublished data
29	Algarve*	37°6′N 8°21′W 0 (m) asl	Pollen	MIS 2		Scheneider et al. (2016)
30	Guadiana Estuary (Beliche Portugal)	37°16′N 7°27′W 24 (m) asl	Pollen	MIS 2		Fletcher et al. (2007)
31	El Asperillo*	04' 16'' N, 20 88' W 0-30 (m) asl	Pollen	MIS 2		Stevenson (1984); Postigo-Mijarra (2010)
32	Cancela de la Aulaga*	36°59'N 6°25'W	Pollen	MIS 2		Manzano et al. (2018)

	(Huelva)	0 (m) asl			
33	La Roya (Zamora)	42°07′N 6° 42′W 1608 (m) asl	Pollen	MIS 2	Allen et al. (1996); Muñoz-Sobrino et al. (2004)
34	Lagoa de As Lamas (Orense)	42°45′N 6°53′W 1360 (m) asl	Pollen	MIS 2	Maldonado (1994)
35	Lagoa de Marinho (Portugal)	41°49′N 7°56′W 1150 (m) asl	Pollen	MIS 2	Ramil-Rego et al. (1993)
36	Laguna Sanguijuela (Zamora)	42°08′N 6°42′W 1080 (m) asl	Pollen	MIS 3–MIS 2	Muñoz-Sobrino et al. (2004)
37	Lapa do Anecrial (Portuguese Extremadura)	39°35′N 8°47′W 350 (m) asl	Charcoal	MIS 2	Figueiral, unpublished data
38	Lleguna (Zamora)	42°07′N 6°43′W 1050 (m) asl	Pollen	MIS 2	Muñoz-Sobrino et al. (2004)

Iberian Range and Central Iberia					
39	Arenales de San Gregorio (Ciudad Real)	39°18′N 3°02′W 640 (m) asl	Pollen	MIS 3–MIS 2	Ruiz-Zapata et al. (2000)
40	Buena Pinta cave (Madrid)	40°56′N 3°46′W 1100 (m) asl	Charcoal	MIS 4	Uzquiano, unpublished data
41	Camino (Madrid)	40°36′N 3°16′W 1100 (m) asl	Charcoal	MIS 4	Uzquiano, unpublished data
42	Fuentillejo (Ciudad Real)	38°56′N 4°03′W 635 (m) asl	Pollen	MIS 3–MIS 2	Vegas et al. (2008)
43	Hoyos de Iregua (La Rioja)	42°01′N 2°44′W 1780 (m) asl	Pollen	MIS 2	Gil-García et al. (2002)
44	Laguna del Hornillo (Soria)	41°58′N 2°50′W 1820 (m) asl	Pollen	MIS 2	Gómez-Lobo (1993)

45	Laguna Grande (Soria)	42°02 N 3°01′W 1510 (m) asl	Pollen	MIS 2	Vegas et al. (2001)
46	Mesa de Ocaña (Madrid)	39°55′N 3°29′W 700 (m) asl	Pollen	MIS 2	Ruiz-Zapata et al. (2000)
47	Quintanar de la Sierra (Burgos)	42°01′N 3°01′W 1470 (m) asl	Pollen	MIS 2	Peñalba (1994); Peñalba et al. (1997)
48	TD — Tablas de Daimiel (Ciudad Real)	39°09′N 3°42′W 600 (m) asl	Pollen	MIS 3–MIS 2	Valdeolmillos et al. (2003)
49	Torrejones (Guadalajara)	41°00′N 3°15′W 1100 (m) asl	Pollen	MIS 4	Carrión et al. (2007)
Pyrenees and northeastern Iberia					
50	Abric Romaní (Barcelona)	41°32′N 01°17′W 300 (m) asl	Pollen Charcoal	MIS 4–MIS 3	Burjachs and Julià (1994); Burjachs and Allué (2003)
51	Banyoles	42°07′N	Pollen	Early–Middle	Elhaï, (1966);

	(Girona)	02°45′E 173 (m) asl		Pleistocene — MIS 2	Pérez-Obiol and Julià (1994)
52	Cova 120 (Girona)	42°16′N 2° 36′E 460 (m) asl	Charcoal	MIS 3	Agustí et al. (1987)
53	El Portalet (Huesca)	42°48′ N 0°23′ W 1980 (m) asl	Pollen	MIS 3–MIS 2	González-Sampériz et al. (2006)
54	Gabasa cave (Huesca)	42°00′N 4°06′E 780 (m) asl	Pollen	MIS 3	González-Sampériz et al. (2003)
55	Estanya*	42°02′N, 0°32′E, 670 (m) asl	Pollen	MIS 2	Vegas-Vilarrubia et al. (2013); González-Sampériz et al. (2017)
56	L'Abreda cave (Girona)	42°09′N 02°44′W 200 (m) asl	Pollen Charcoal	MIS 3–MIS 2	Ros Mora (1987); Burjachs (1993)
57	Pla de l'Estany (Girona)	42°11′N 2°32′E 520 (m) asl	Pollen	MIS 6 to MIS 2	Burjachs (1990)

58	Salada de Mediana (Zaragoza)	41°30′N 0°44′W 350 (m) asl	Pollen	MIS 2	Valero-Garcés et al. (2000a,b); González-Sampériz et al. (2008)
59	San Juan de Mozarrifar (Zaragoza)	41°44′N 2°51′W 220 (m) asl	Pollen	MIS 3	Valero-Garcés et al. (2004)
60	Tramacastilla palaeolake (Huesca)	42°43′N 0°23′W 1640 (m) asl	Pollen	MIS 2	González-Sampériz et al. (2005)
61	Villarquemado* (Teruel)	40°30′N; 1°18′W 1000 (m) asl	Pollen	MIS 2	Arambarri et al. (2014)
South–southeastern Iberia					
62	Cueva Antón	38° 3'N 1°29'W 350 (m) asl	Pollen	MIS 5-3	Zilhão et al. (2016)
63	Algarrobo cave (Murcia)	37°38′N 1°17′W 290 (m) asl	Pollen	MIS 2	Munuera and Carrión (1991)
64	Ambrosio cave	37°49′N	Charcoal	MIS 2	Rodríguez-

	(Almería)	2°5′W 950 (m) asl			Ariza (2005)
65	Bajondillo (Málaga)	36°38′N 4°29′W 0 (m) asl	Pollen	MIS 3–MIS 2	López-Sáez et al. (2007)
66	Boquete de Zafarraya (Málaga)	36°56′N 4°07′W 1022 (m) asl	Pollen Charcoal	MIS 3	Lebreton et al. (2006); Vernet and Terral (2006)
67	Carihuela cave (Granada)	37°26′N 3°25′W 1020 (m) asl	Pollen Charcoal	MIS 5 to MIS 2	Carrión (1992a); Carrión et al. (1998, 1999); Fernández et al. (2007)
68	Cova Beneito (Alicante)	38°48′N 0°28′W 680 (m) asl	Pollen Charcoal	MIS 3–MIS 2	Carrión (1992b); Carrión and Munuera (1997); Uzquiano, unpublished data
69	Cova Bolumini (Alicante)	38°50′N 0°00′W	Charcoal	MIS 2	Badal (1991)

		170 (m) asl			
70	Cova de Les Cendres (Alicante)	38°41′N 0°09′E 45 (m) asl	Charcoal	MIS 3–MIS 2	Badal (1991); Vernet (1997); Badal and Carrión (2001)
71	Vanguard	36° 7'N 5°20'W 0 (m) asl	Pollen	MIS 3	In this paper
72	Gorham's cave (Gibraltar)	36°07′N 5°20′W 5 (m) asl	Pollen Charcoal	MIS 3–MIS 2	Carrión et al. (2008)
73	Hoyo de la Mina cave (Málaga)	36°42′N 4°19′W 100 (m) asl	Charcoal	MIS 2	Uzquiano, unpublished data
74	La Ratlla del Bubo (Alicante)	38°16′N 0°48′W 200 (m) asl	Charcoal	MIS 2	Badal (1991)
75	Laguna de San Benito (Valencia)	38°56′N 1°06′W 671 (m) asl	Pollen	MIS 3–MIS 2	Dupré et al. (1996)
76	Laguna de Villena (Alicante)	38°37′N 0°55′W 502 (m) asl	Pollen	MIS 4 to MIS 2	Yll et al. (2003)
77	Las Ventanas	37°26′N	Pollen	MIS 2	Carrión et al.

	cave (Granada)	3°26′W 1056 (m) asl			(2001)
78	Malladetes cave (Valencia)	39°00′N 0°17′W 500 (m) asl	Pollen	MIS 3–MIS 2	Dupré (1988)
79	Navarrés (Valencia)	39°06′N 0°41′W 225 (m) asl	Pollen	MIS 3– MIS 2 MIS 2	Carrión and Dupré (1996); Carrión and Van Geel (1999)
80	Nerja cave (Málaga)	36°45′N 3°50′W 110 (m) asl	Charcoal	MIS 2	Badal (1991); Vernet (1997); Aura et al., (2002)
81	Padul (Granada)	37°00′N 3°36′W 723 (m) asl	Pollen	MIS 11 to MIS 2	Florschütz et al. (1971); Pons and Reille (1988); Ortiz et al. (2004)
82	Perneras cave (Murcia)	37°32′N 1°25′W 100 (m) asl	Pollen	MIS 3–MIS 2	Carrión et al. (1995)
83	Salines (Alicante)	38°30′N 0°53′W	Pollen	MIS 2	Giralt et al. (1999)

		470 (m) asl			
84	Alfaix (Almería)	37° 8'N 1°56'W 90 (m) asl	Pollen	MIS5-3	Schulte et al. 2008
85	San Rafael (Almería)	36°46′N 2°37′W 8 (m) asl	Pollen	MIS 2	Pantaleón-Cano et al. (2003)
86	Santa Maira (Alicante)	38°43′N 0°13′W 650 (m) asl	Charcoal	MIS 2	Aura et al. (2005)
87	Siles lake (Jaén)	38°23′N 2°30′W 1320 (m) asl	Pollen	MIS 2	Carrión (2002a)
88	Sima de Las Palomas (Murcia	37°47′N 0°53′W 120 (m) asl	Pollen	MIS 3–MIS 2	Carrión et al. (2003)
89	Tossal de La Roca (Alicante)	38°47′N 0°15′W 650 (m) asl	Pollen Charcoal	MIS 2	López-Sáez and López-García (1999); Uzquiano (1988)
90	Túnel dels Sumidors (Valencia)	38°53′N 0°41′W 500 (m) asl	Pollen	MIS 2	Dupré (1988)

Marine records					
91	8057B (Portugal)	37°41′N 10°5′W 2811 water depth (m)	Pollen	MIS 2	Hooghiemstra et al. (1992)
92	MD03-2697 (Galicia)	42°09′N 9°42′W 2164 water depth (m)	Pollen	MIS 2	Naughton et al. (2007); Sánchez-Goñi et al. (2008)
93	MD95-2039 (Portugal)	40°34′N 10°20′W 3381 water depth (m)	Pollen	MIS 4 to MIS 2	Roucoux et al. (2001, 2005)
94	MD95-2042 (Portugal)	37°43′N 10°12′W 3146 water depth (m)	Pollen	MIS 6 to MIS 2	Sánchez-Goñi et al. (1999, 2008)
95	MD95-2043 (Alborán sea)	36°08′N 2°37′W 1841 water depth (m)	Pollen	MIS 3–MIS 2	Sánchez-Goñi et al. (2002); Fletcher and Sánchez-Goñi (2008)
96	MD99-2331 (Galicia)	42°09′N 9°40′W 2110 water	Pollen	MIS 5 to MIS 2	Sánchez-Goñi et al. (2005); Naughton et al.

		depth (m)			(2007)
97	ODP 976 (Alborán sea)	36°09′N 4°08′W 1107 water depth (m)	Pollen	MIS 54 to MIS 2	Combourieu-Nebout et al. (1999, 2002, 2009); Bout-Roumazeilles et al. (2007);
98	SO75-6KL (Portugal)	37°56′N 9°30′W 2181 water depth (m)	Pollen	MIS 2	Boessenkool et al. (2001)

Highlights

- Pollen in hyaena coprolites from Vanguard Cave contribute to previous palaeoecological studies
- A detailed perspective of last Neanderthals environments is provided
- The geobiological repertoire indicate marked diversity
- Coastal platform with a vegetation mosaic in "Mediterranean savannah" biome

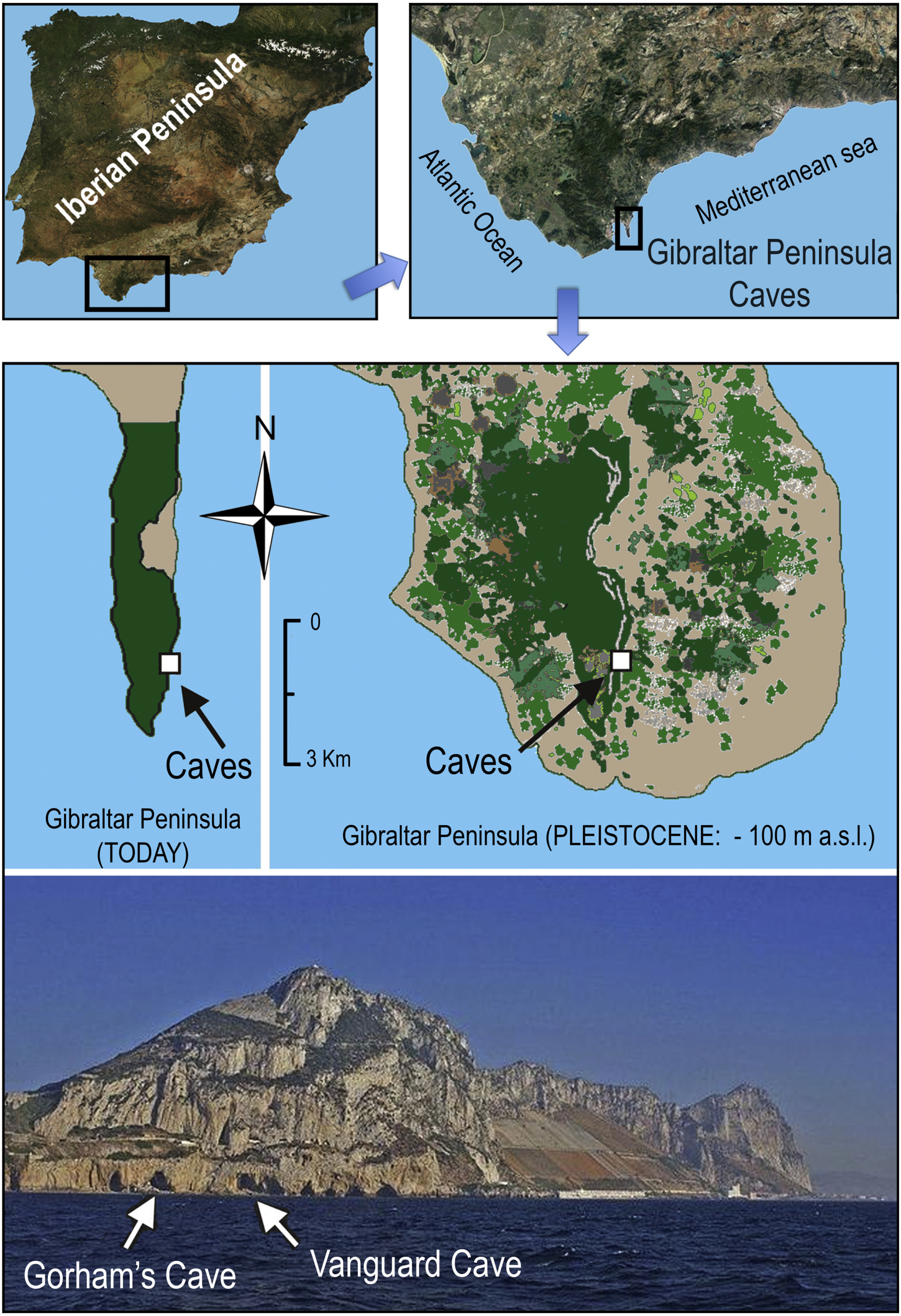
Iberian Peninsula
Atlantic Ocean
Mediterranean sea
Gibraltar Peninsula
Caves
N
0
3 Km
Caves
Caves
Gibraltar Peninsula
(TODAY)
Gibraltar Peninsula (PLEISTOCENE: - 100 m a.s.l.)
Gorham's Cave
Vanguard Cave

Figure 1

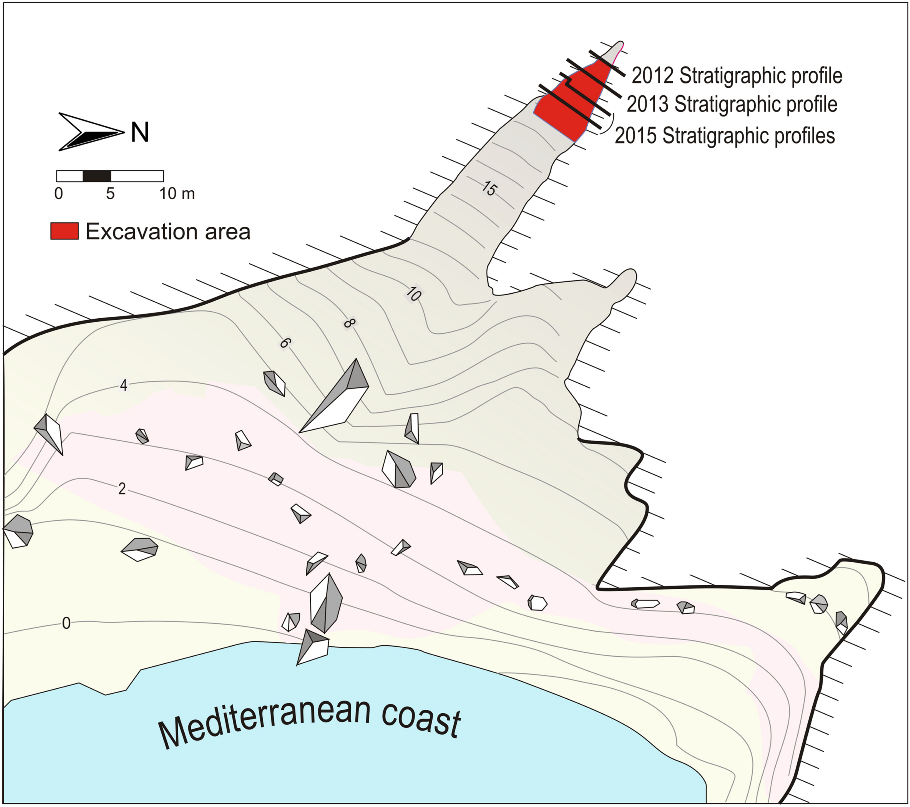
N
0
5
10 m
🟥 Excavation area
2012 Stratigraphic profile
2013 Stratigraphic profile
2015 Stratigraphic profiles
15
10
8
6
4
2
0
Mediterranean coast

Figure 2

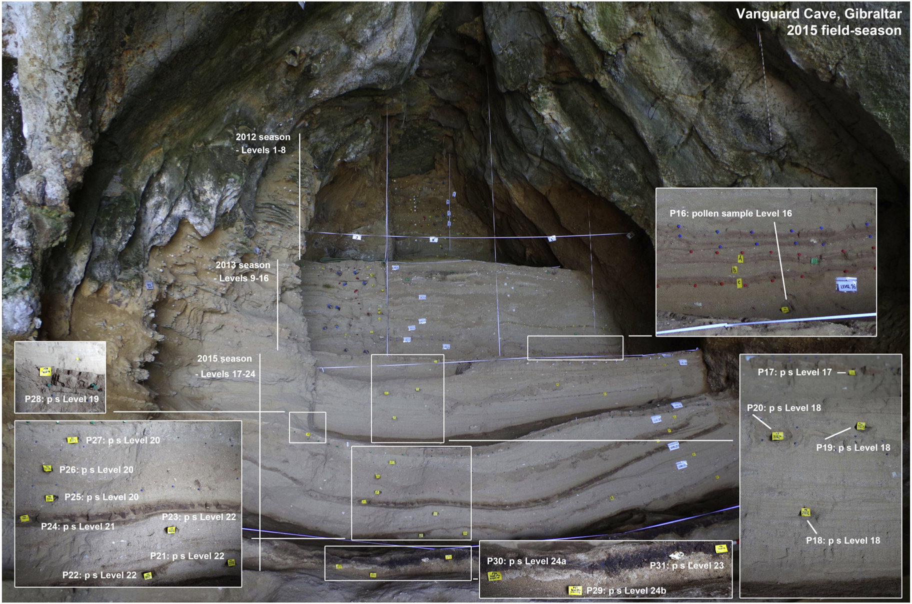
Vanguard Cave, Gibraltar
2015 field-season
2012 season
- Levels 1-8
2013 season
- Levels 9-16
2015 season
- Levels 17-24
P16: pollen sample Level 16
P28: p s Level 19
P27: p s Level 20
P26: p s Level 20
P25: p s Level 20
P23: p s Level 22
P24: p s Level 21
P21: p s Level 22
P22: p s Level 22
P17: p s Level 17
P20: p s Level 18
P19: p s Level 18
P18: p s Level 18
P30: p s Level 24a
P31: p s Level 23
P29: p s Level 24b

Figure 3

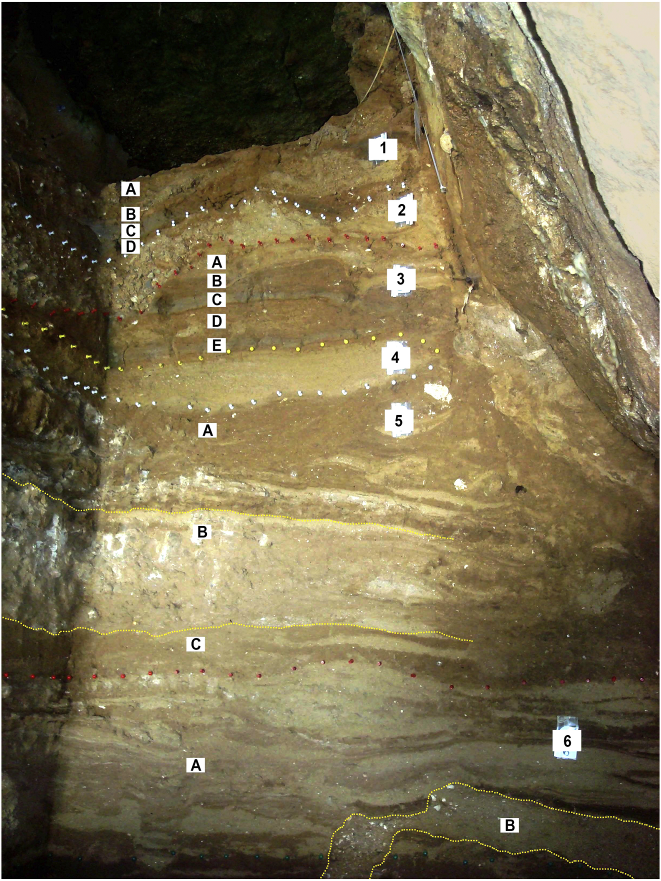

Figure 4

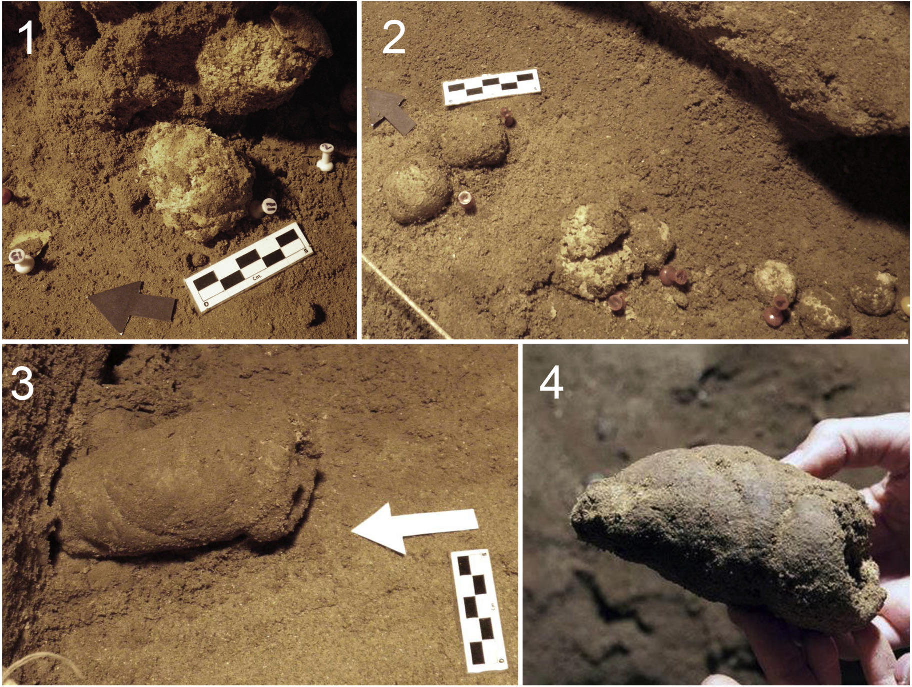

Figure 5

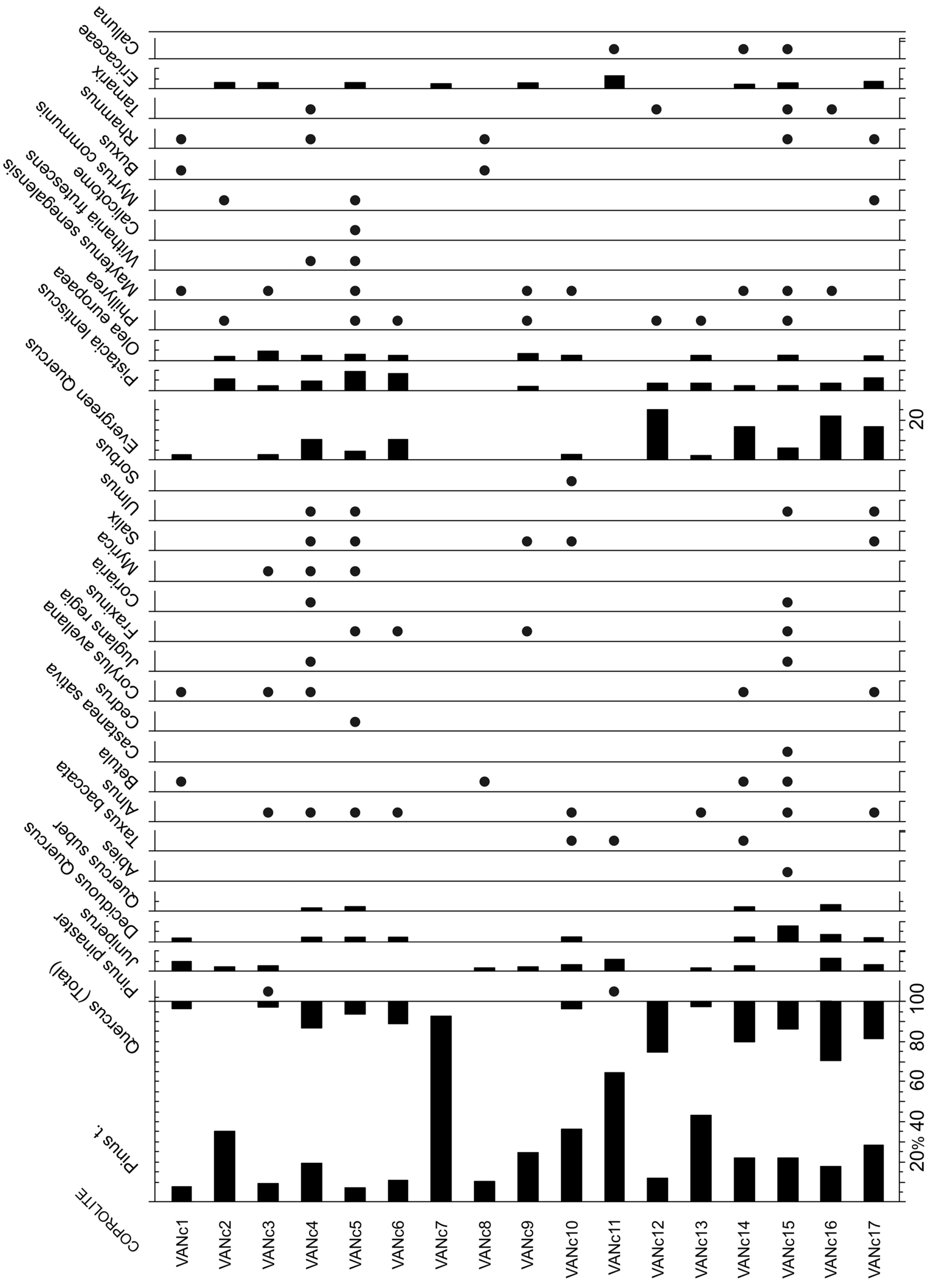
Calluna
Ericaceae
Tamarix
Rhamnus
Buxus
Myrtus communis
Calicotome
Withania frutescens
Maytenus senegalensis
Phillyrea
Olea europaea
Pistacia lentiscus
Evergreen Quercus
Sorbus
Ulmus
Salix
Myrica
Coriaria
Fraxinus
Juglans regia
Corylus avellana
Castanea sativa
Cedrus
Betula
Alnus
Taxus baccata
Abies
Quercus suber
Deciduous Quercus
Juniperus
Pinus pinaster
Quercus (Total)
Pinus t.
COPROLITE
VANc1
VANc2
VANc3
VANc4
VANc5
VANc6
VANc7
VANc8
VANc9
VANc10
VANc11
VANc12
VANc13
VANc14
VANc15
VANc16
VANc17
20
100
80
60
40
20%

Figure 6

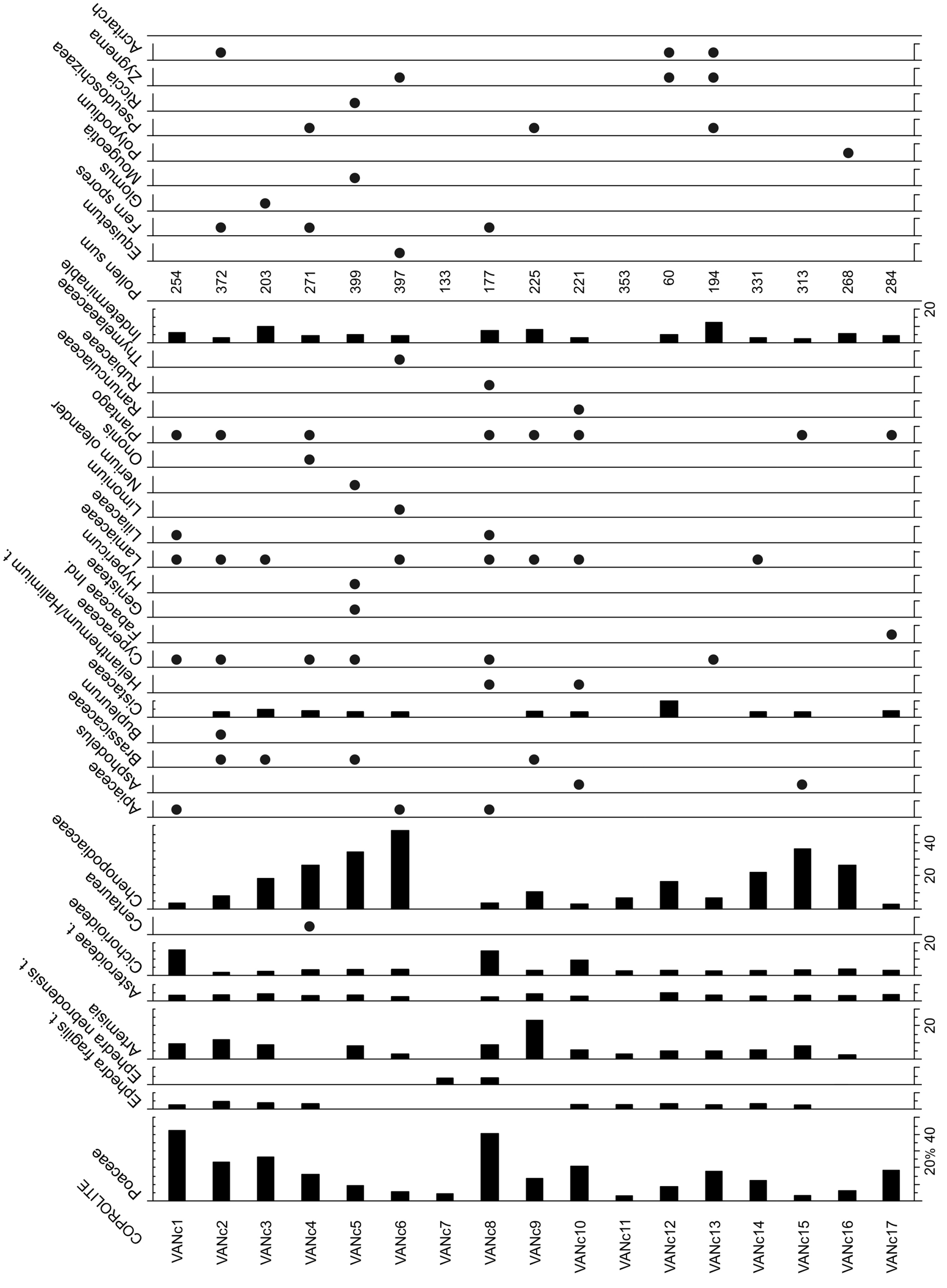
COPROLITE
VANc1
VANc2
VANc3
VANc4
VANc5
VANc6
VANc7
VANc8
VANc9
VANc10
VANc11
VANc12
VANc13
VANc14
VANc15
VANc16
VANc17
Poaceae
Ephedra fragilis t.
Ephedra nebrodensis t.
Artemisia
Asteroideae t.
Cichorioideae
Centaurea
Chenopodiaceae
Apiaceae
Asphodelus
Brassicaceae
Bupleurum
Cistaceae
Helianthemum/Halimium t.
Cyperaceae
Fabaceae Ind.
Genisteae
Hypericum
Lamiaceae
Liliaceae
Limonium
Nerium oleander
Ononis
Plantago
Ranunculaceae
Rubiaceae
Thymelaeaceae
Indeterminable
Pollen sum
254
372
203
271
399
397
133
177
225
221
353
60
194
331
313
268
284
Equisetum
Fern spores
Glomus
Mougeotia
Polypodium
Pseudoschizaea
Riccia
Zygnema
Acritarch
20% 40
20
40
20
40
20
20

Figure 7

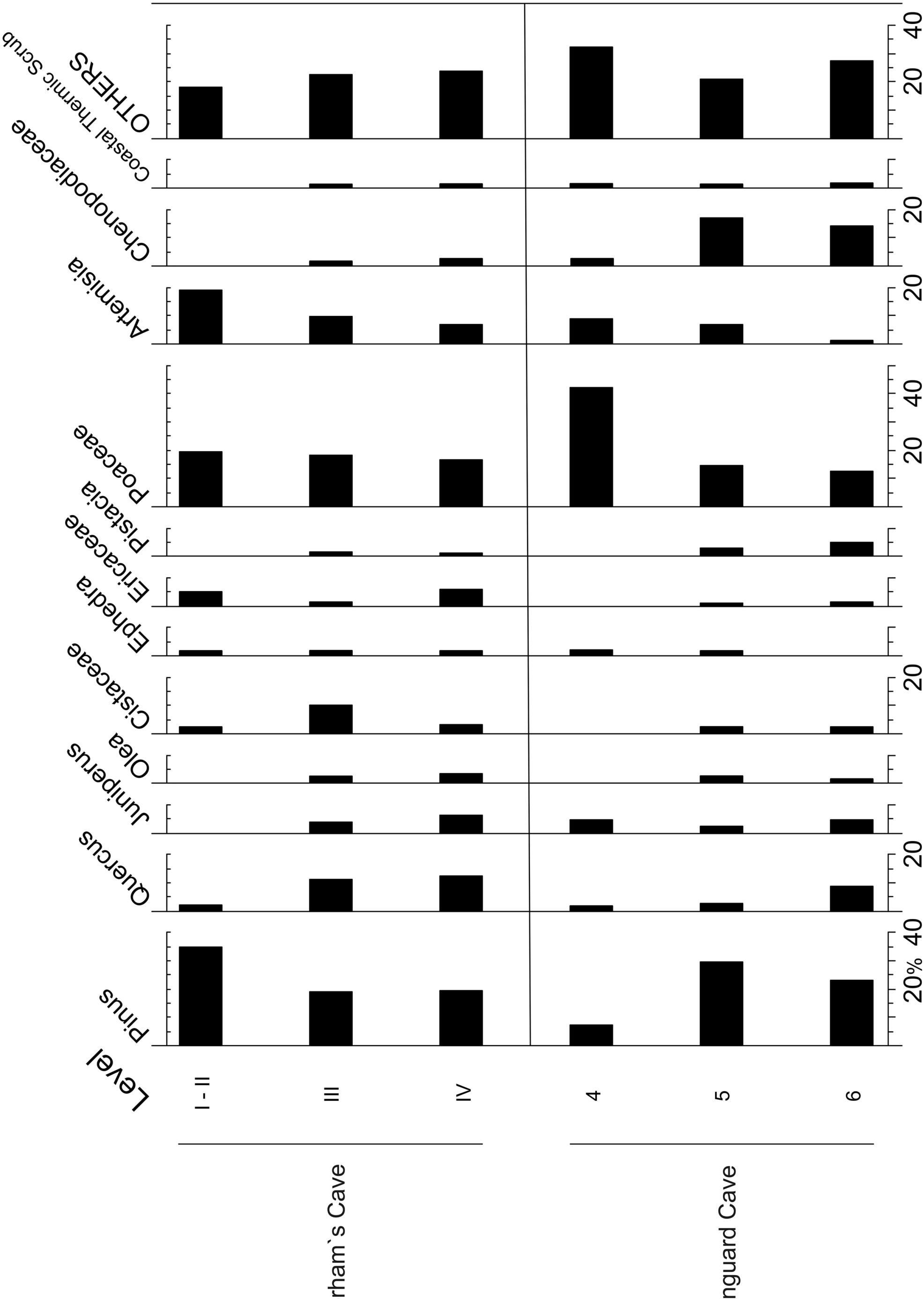
Level
I - II
III
IV
4
5
6
Gorham`s Cave
Vanguard Cave
Pinus
Quercus
Juniperus
Olea
Cistaceae
Ephedra
Ericaceae
Pistacia
Poaceae
Artemisia
Chenopodiaceae
Coastal Thermic Scrub
OTHERS
20%
40
20
20
20
40
20
20
20
40

Figure 8

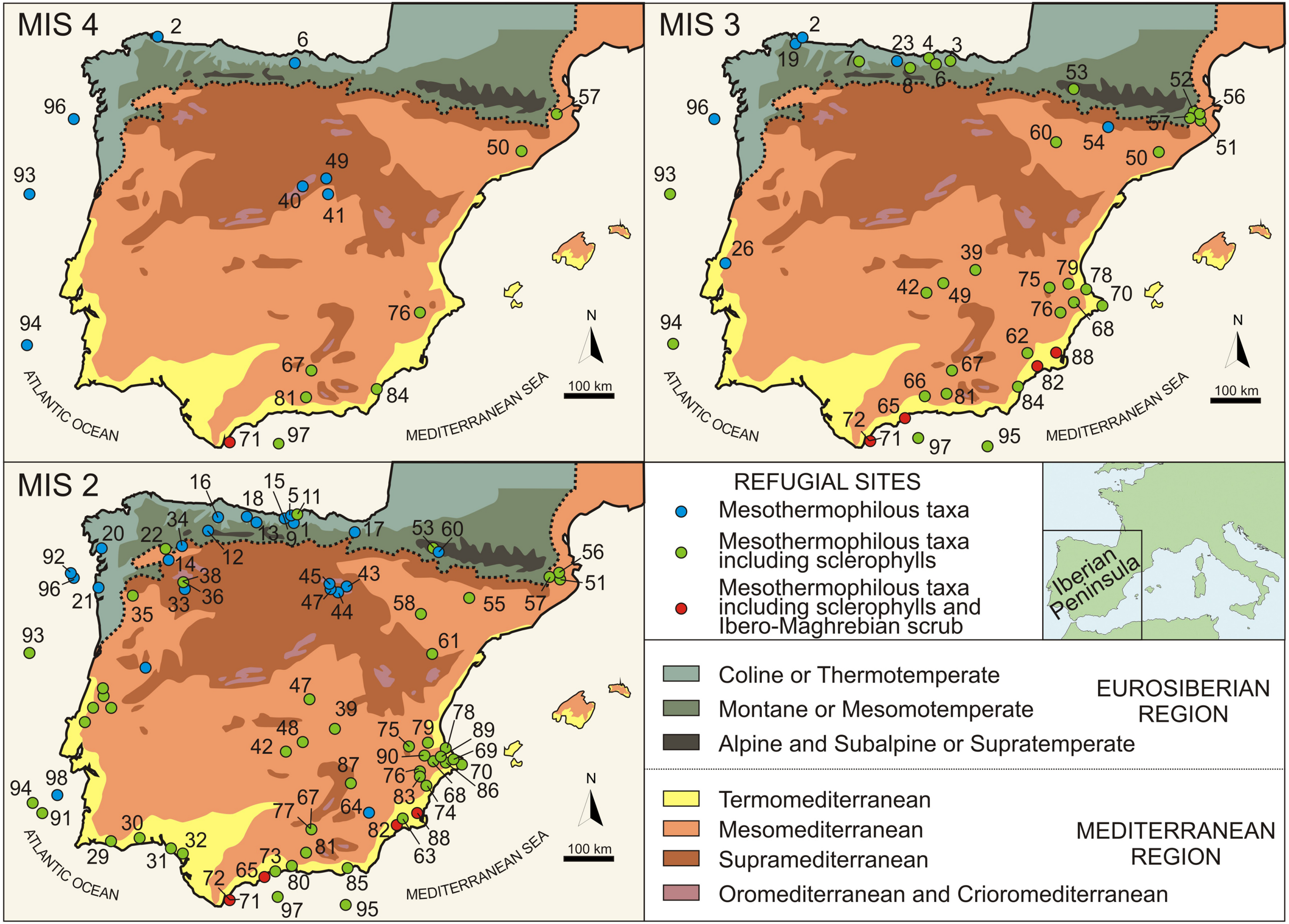
MIS 4
2
6
96
93
94
57
50
49
40
41
76
67
81
84
71
97
ATLANTIC OCEAN
MEDITERRANEAN SEA
N
100 km
MIS 3
2
19
23
4
3
7
8
6
53
52
56
57
51
96
60
54
50
93
26
39
42
49
75
79
78
70
76
68
94
62
88
82
67
66
81
84
65
72
71
97
95
ATLANTIC OCEAN
MEDITERRANEAN SEA
N
100 km
MIS 2
16
15
5
11
18
13
9
1
17
53
60
20
22
34
12
92
96
21
14
38
36
33
35
45
43
47
44
58
55
57
56
51
93
61
47
39
48
42
75
79
78
89
69
90
70
76
86
68
83
74
87
94
98
91
30
29
31
32
67
77
64
82
88
63
81
73
65
72
71
80
85
97
95
ATLANTIC OCEAN
MEDITERRANEAN SEA
N
100 km
REFUGIAL SITES
● Mesothermophilous taxa
● Mesothermophilous taxa including sclerophylls
● Mesothermophilous taxa including sclerophylls and Ibero-Maghrebian scrub
Iberian Peninsula
Coline or Thermotemperate
Montane or Mesomotemperate
Alpine and Subalpine or Supratemperate
EUROSIBERIAN REGION
Termomediterranean
Mesomediterranean
Supramediterranean
Oromediterranean and Crioromediterranean
MEDITERRANEAN REGION

Figure 9