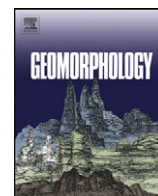




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Undrowning a lost world – The Marine Isotope Stage 3 landscape of Gibraltar

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ABSTRACT

The Rock of Gibraltar, at the south-western extreme of the Iberian Peninsula and 21 km from the North African coast, is a 6-km long limestone peninsula which was inhabited by Neanderthals from MIS 5e until the end of MIS 3. A total of 8 sites, either with Neanderthal fossils or their Mousterian lithic technology, have been discovered on the Rock. Two, Gorham's and Vanguard Caves, are the subject of ongoing research. These 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. They hold a unique archive of fauna and flora, in the form of fossils, charcoal and pollen, helping environmental reconstruction of now-submerged shelf landscapes. In addition, geological and geomorphological features – a 300-metre dune complex, elevated aeolian deposits, raised beaches, scree, speleothems – complement the biotic picture.

The work is further complemented by a study of the ecology of the species recorded at the site, using present-day observations. The species composition in this fossil record closely matches the present day fauna and vegetation of the Doñana National Park, SW Spain: a mosaic of pine groves, coastal dunes, shrubland and seasonal wetlands and currently the richest reserve in terms of biodiversity in the Iberian Peninsula, located only 100 km to the northwest from Gibraltar.

All this information permits, for the first time, the quantification of the vegetation structure of the ancient coastal plain and the modelling of the spatio-temporal dynamics of the MIS 3 coastal shelf off Gibraltar.

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1. Introduction

The Iberian Peninsula lies at the western end of the Mid Latitude Belt (MLB) (Finlayson, 2004), which runs from the Himalayas in the east to Portugal and Morocco in the west, and which was a biogeographical unit in terms of its topographical, faunal and vegetation features in the Tertiary and Early Quaternary (Finlayson, 2011). The distribution of Aurignacian-family industries closely matches the maximum geographical area occupied by the Neanderthals in Eurasia, which, in turn, matches the MLB (Finlayson and Carrión, 2007). It has been argued (Finlayson, 2009) that the Iberian Peninsula, and the South-west in particular, represent remnants of this ancient MLB. These landscapes have been dependent largely on the tectonic and eustatic-induced changes to the geomorphology, as well as on the edaphic substrate. Gibraltar lies at the extreme south west of the Iberian Peninsula. It represents a uniquely-preserved example that allows us to recreate a landscape that once typified large areas from Iberia to China. A multi-disciplinary approach to a high resolution reconstruction of

the Gibraltar coastal area in MIS 3 is presented, as a prime example of an MLB relict landscape.

The Mediterranean vegetation and mixed forest has been observed to have persisted in a number of Iberian Mediterranean localities during Marine Isotope Stage 3 (MIS 3) (e.g. Carrión, 1992a,b; Burjachs and Julia, 1994; Carrión et al., 1995; Carrión and Munuera, 1997) despite it having been the coldest and most unstable of the entire Pleistocene (Finlayson, 2003; Martrat et al., 2004; Finlayson and Carrión, 2007).

The rapid climate changes that occurred during the last glacial cycle (~125–10 ka BP) meant that the coastal fringes, that are below sea level at present, were exposed for most of that time (Bailey and Milner, 2002/3; Moreno et al., 2005). In the south of the Iberian Peninsula, the exposed coastal plains would have become available to species as southern refugia, especially given coincidence of sea-level fall and shelf exposure with moments of relative cooling.

The importance of coastal environments and of the coastal shelf as a zone of geographic expansion by modern humans (Lahr and Foley, 1998; Quintana-Murci et al., 1999; Walter et al., 2000) and the exploitation of intertidal, marine and aquatic resources are increasingly being accepted as having been a widespread characteristic of early human palaeoeconomies and not just restricted to the Holocene (Klein, 1999;

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Erlandson, 2001; Mannino and Thomas, 2002; Klein et al., 2004; Finlayson, 2006; Fa, 2008; Brown et al., 2011; Cortés-Sánchez et al., 2011). More than 300 submarine sites having been noted by Werz and Flemming (2001), dating from between 5,000 to >45,000 ka BP off the coasts of Europe, North America, Australia and Japan. These coastal fringes could have provided corridors for the movements of species, including humans, as well as having provided refugia for their survival (Bailey et al., 2008). Thus, the landscape described here had a major influence on the survival and spread of fauna and flora, including humans. It is a landscape that is today restricted to pockets along the coastal fringes of SW Iberia. The best-preserved example is the Doñana National Park, located only 100 km away to the northwest of Gibraltar (Fig. 1). Here we argue that it is a hitherto unappreciated relic of a lost world.

2. Rock of Gibraltar – emerged geological landscape

The Gibraltar Strait area is located in the Western Mediterranean at the Africa-Eurasia convergent plate boundary. The Africa-Eurasia collision promoted a westwards displacement of the internal zones of the Betic cordillera, mainly during the Early Miocene, and the generation of the so-called Gibraltar Arc (Sanz de Galdeano, 1990).

This structural development took place in concert with an important regional rock uplift (Zazo et al., 1999; Rodríguez-Vidal et al., 2004). Major faults interacting with the coast have NE-SW and NW-SE orientations and they mainly work as strike-slip faults separating crustal blocks with different associated uplifting or subsiding character (Goy et al.,

1995; Gracia et al., 2008). These largest lineations work as sinistral and dextral strike-slip faults, respectively, promoting consistent coast-line displacements in the Gibraltar Strait. The tectonic blocks, defined by NE-SW and NW-SE faults, have had a differential uplift rate so forming a pseudo horst-graben system. In the Rock of Gibraltar the more active faults were NW-SE with relative downthrown staircased blocks to NE (Isthmus) and mainly to SW (Southern Plateau and Vladi's Reef), towards Gibraltar/Algeciras Canyon and the Strait.

The Rock of Gibraltar is a small peninsula 5.2 km by 1.6 km having a total area of about 6 km² (Fig. 1). It has a north-south orientation, with highly eroded steep cliffs on the east while the west side consists of gentler slopes.

To the north of the peninsula, there is an isthmus consisting of Holocene sediments no higher than 3 m above sea level (a.s.l.) and linking it to the mainland. The Main Ridge of The Rock is composed of Early Jurassic limestone and dolomite rises up to three main peaks, two of which are above 400 m a.s.l. and form the central area. At the south end of the peninsula, the Southern Plateau is a staircased slope between 130 m and sea level (Rose and Rosenbaum, 1991), with a series of steep cliffs caused by Quaternary wave-cut erosion as a product of shoreline processes.

The tectonic structural movements that have determined the general shape and the surface erosional and depositional processes that have acted on the uplifted rocks have been identified by Rodríguez-Vidal and Gracia (1994, 2000) in the formation of this peninsula, and the complex geomorphological development and neotectonic uplift history has been described by Rodríguez-Vidal et al. (2004, 2007, 2010). These authors have provided a detailed analysis of the Rock's sedimentary record (uplifted marine terraces, windblown sands, scree breccias and karstic sediments) and its erosional landforms (cliffs, wave-cut platforms, staircased slopes and endokarstic systems) which show that the Rock's evolution has proceeded through a combination of tectonic uplift and eustatic sea-level change. Coastal cliffs that have been isolated from wave action when tectonic uplift has exceeded the rate of eustatic sea-level rise, or when the sea level has fallen, have been exposed to subaerial processes which have acted to degrade them further. Along the coast of Gibraltar the land has been uplifted at rates of 0.04 to 0.06 mm/yr in the last 100 ka (Goy et al., 1995).

Of the two prevailing winds in the Strait of Gibraltar, the easterly (Levante) and the westerly (Poniente), the former is by far the stronger. Rodríguez-Vidal et al. (2007) have described the effects on the build-up of dunes in the area of Gibraltar, particularly where large rampant type dunes accumulated against the steep slopes of the mountainous coast. The three main aeolian units identified on the Rock are the Monkey's Cave Sandstones, and the Alameda Sands and Catalan Sands on the west and east sides respectively (Rose and Hardman, 2000). From their geomorphological location and the dates of similar close sandy cave sediments (Rodríguez-Vidal et al., 2004, 2007) it can be inferred that these latter accumulations were generated during MIS 5 to 3, between 125 and 30 ka, originating from marine beaches, located between 6 m a.s.l. to 80 m b.s.l. (below sea level), before being blown inland to accumulate as topographic dunes.

For the better part of that last glacial cycle, the sea level remained on average 80 m below the present sea level, and at the Last Glacial Maximum fell to –120 m (Siddall et al., 2003). The landscape of Gibraltar was most affected on the east side of the Rock which is much shallower than to the west, and where a large coastal plain was exposed extending to up to 5 km from the present coastline (Fig. 2). There are a number of sites with archaeological evidence of human habitation along this side (Fig. 1), and we will attempt to provide insights into whether the shelf had emerged in MIS 3, and the biological species, water and lithic raw material resources that were present. The plain's substrate was windblown sands which accumulated against the limestone rock (Rodríguez-Vidal et al., 2007, 2010). Together, acidic sands and alkaline rocks created a geological ecotone which generated high ecological diversity.

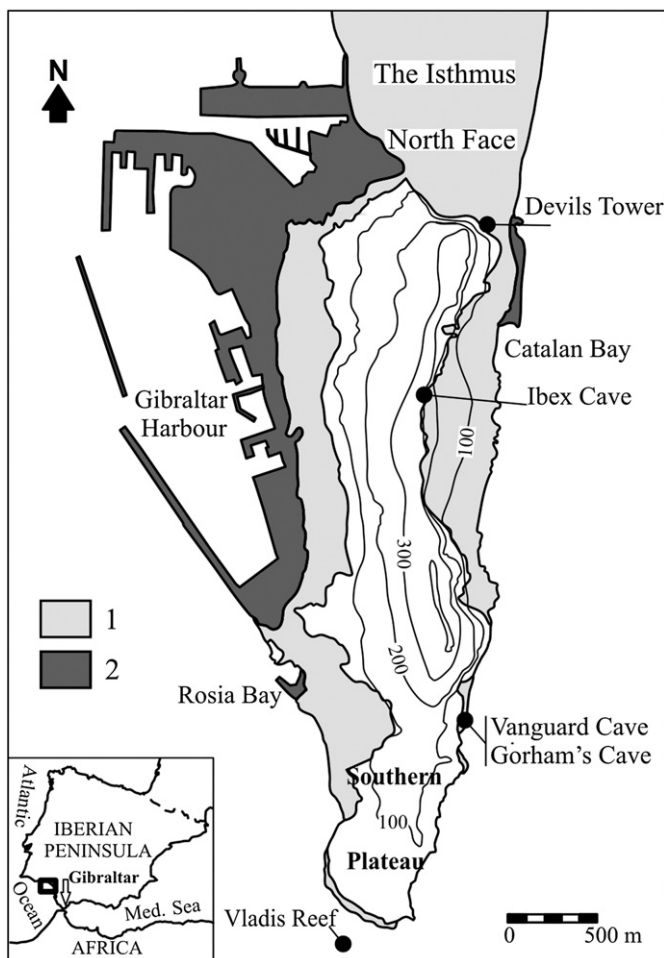


Fig. 1. Iberian Peninsula and the location of Gibraltar and Doñana area (rectangle). Simplified topographic map of the Gibraltar Peninsula. Contours at 100 m intervals. Legend: 1. Late Pleistocene morphosedimentary record. 2. Reclaimed land.

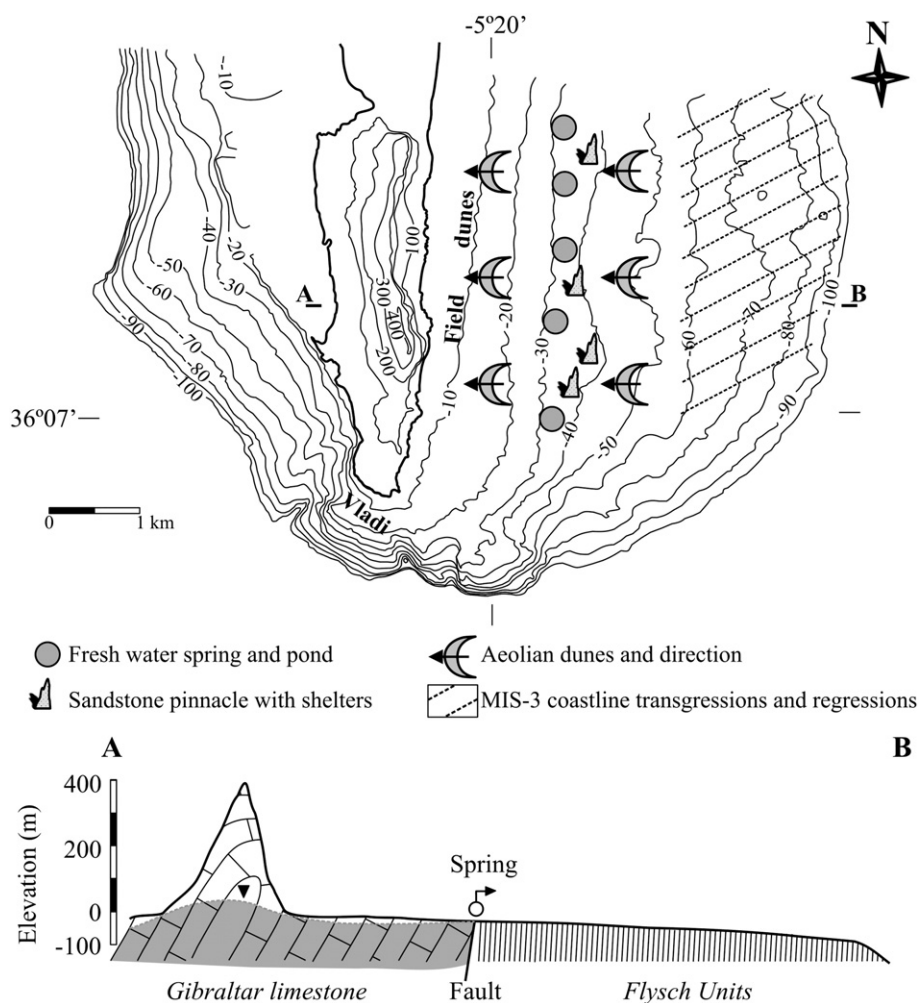


Fig. 2. Present topography-bathymetry of the Gibraltar Rock and submerged area (GIBRAMAR survey) with the main geomorphological features during MIS 3. The Rock contour at 100 m, and the drown area at 10 m intervals. E–W schematic section representing the geology and karst hydrology (grey is groundwater).

3. Rock of Gibraltar – submerged geological landscape

The rocks exposed in Gibraltar are of two principal types: limestone and shale. [Rose and Rosenbaum \(1991\)](#) ascribe the Mesozoic rocks exposed to the Gebel Tariq Group, divided into four formations: Little Bay Shale, Gibraltar Limestone, Catalan Bay Shale and Dockyard Shale.

The South and Southwestern part of The Rock is formed by dolostone, part of the Gibraltar Limestone Formation, subdivided into the Bleak, Europa, Keightley and Buffadero Members ([Rose and Rosenbaum, 1991](#)). The dolo-limestone formation extends offshore on either side of The Rock as submerged platforms of various depths. To the east it is bound by a Flysch unit with a tectonic contact ([Fig. 2](#)).

The seabed to the east of The Rock has a shallower gradient than that recorded in the west. It has a gentle slope continuing over 5 km from the eastern edge of The Rock in its widest part. The depth of seabed reaches 100–110 m before the slope angle doubles ([Fig. 2](#)). The plateau represents the footprint of what was once a much larger geomorphological feature.

Vladi's Reef is the name given to the cliffs on the north of Europa Reef, a submerged platform off Europa Point ([Fig. 2](#)), where archaeological work has been carried out by the project "Underwater Archaeological Excavations (GIBRAMAR)". The reef drops from –19.0 m at the top of the cliff to –22.0 m at its northeast limit ([Fig. 3](#)). Caves are located at the foot of the cliff which is highly eroded with large fractured blocks, some of which have become detached forming a boulder field to the north of the reef. The interior of the caves contains beach-worn

cobbles with borings and encrusted marine organisms, which have provided a date range of cal 667–541 yr BP covered by a fine sandy deposit with a high proportion of gravels and low proportion of silts and clays (21%). The larger, coarser fraction is composed of bioclastic fragments and small subangular dolomite pebbles which forms the present seabed, and numerous shell fragments that date to cal 360–179 yr BP ([Table 1](#)). This area has been heavily eroded by sea currents and possible Late Pleistocene deposits are gone. Sediments excavated from the caves are more recent and have been interpreted as relics of the AD 1755 Atlantic earthquake-tsunami ([Rodríguez-Vidal et al., 2011](#)).

The Vladi's Reef outcrop is formed by angular poligenetic breccia with fragments of dolostone and limestone ([Fig. 4B–G](#)). The matrix is micrite ([Fig. 4C, D, G](#)), with little fragments of bedrock, and envelops the lithoclast, from which a late micrite origin can be inferred. Rather than to be of sedimentary source, the micrite-size matrix and lithoclasts are suggested to have a tectonic origin: derived from the abrasion of pre-existing calcium grains. Sparitic cementation of drusy calcite infills the fissures and replaces the matrix ([Fig. 4F–H](#)). The different shape of calcite growth framework suggests a fresh water vadose cementation – not marine or phreatic. The original bedrock for this submerged breccia would be the upper part of Keightley Member and/or the transition to Buffadero Member.

The morphological marine features of Vladi's Reef, the visual aspect of rock samples and their microscopical observations indicate a tectonic origin for the outcrop of the reef bedrock rather than a brecciated sedimentary formation (i.e. is not a scree breccia). Tectonic breccias were formed in the Cenozoic when The Rock was thrust

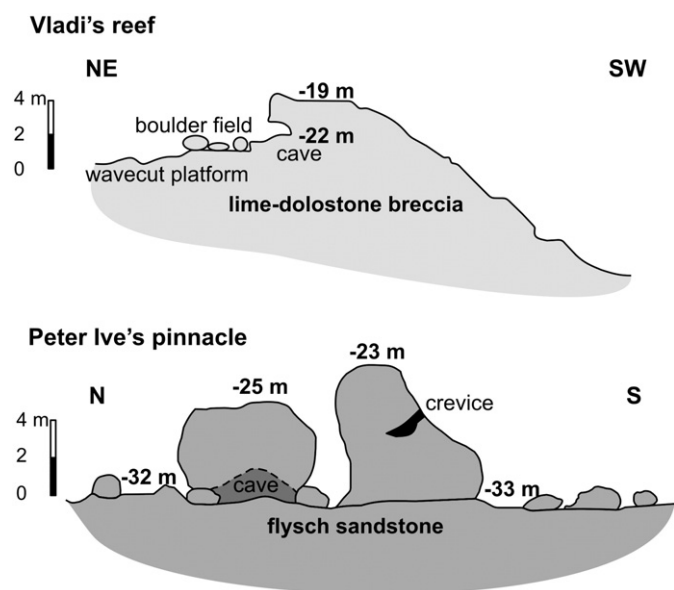


Fig. 3. Schematic sections across Vladí's Reef and Peter I've's pinnacle (modified from GIBRAMAR survey and Smith and Fa, 2004, respectively).

to its present position, typically associated with faults and also occurring as zones of crushed rock within the limestone mass.

A good example of this tectonic breccia occurs in the Rosia Bay area (Fig. 1). Here breccias occur in which the adjacent fragments clearly come from the same original bed, and follow the line of bedding along the outcrop (Fig. 4A). This implies that the rock has been brecciated in place rather than formed by erosion and transport as in scree breccias. The pervasive extent of this autobrecciation, coincident with development of a high porosity, is consistent with the deformation taking place without a great pressure from rocks above, and therefore at shallow depth within the Earth's crust. Intense and pervasive brecciation is also consistent with high pore fluid pressures. When high enough, such pressures will crack and brecciate rock in a process called hydrofracture (Rose and Rosenbaum, 1991).

The Vladí's Reef breccia has proved to be terrestrial in origin, and its late calcrete cementation (Fig. 2B) have been dated to 34,840 – 36,280 cal yr BP (Table 1), thus providing direct evidence that these reefs at –22 m a.s.l. were above sea level at the time of late Neanderthal occupation of Gorham's and Vanguard Caves (Finlayson et al., 2006; Stringer et al., 2008). In addition, several sandstone pinnacles have been identified off the east side of Gibraltar at –30 to –40 m (Figs. 2 and 3). The pinnacles are the tectonic relic of vertical Flysch sandstone strata isolated by the differential erosion of marginal shales. These were rockshelters and potential sites of lithic extraction for Neanderthals (Giles Pacheco et al., 2012) and are associated with freshwater springs, veritable MIS 3 coastal oases (Faure et al., 2002) for humans and fauna. Such springs align along the N–S fault contact between the Gibraltar calcareous rocks and the siliceous Flysch Units (Fig. 2). During MIS 3, in the presently submerged areas, such springs were probably feeding freshwater coastal lakes and ponds, as is detected in the Gorham's Cave

stratigraphy (Finlayson et al., 2008a). An analogous example exists in Doñana National Park (Spain) today, the area known as La Vera, which is the most ecologically rich part of the reserve. It follows that the pinnacles and springs may have attracted a high biological diversity during MIS 3.

4. Rock of Gibraltar – Late Pleistocene landscape

The Last Interglacial is represented in The Rock by several highstand sea-level deposits, clearly visible in the eastern flank. Many pre-existing caves were widened by wave action (e.g. Gorham's and Vanguard Caves), and beach deposits accumulated within them or at the toes of the Northern and Eastern cliffs. During maximum highstand, The Rock was isolated from mainland Iberia. Intermediate cold pulses promoted relative sea-level falls, which favoured faunal passes from the land to the Rock, occupying narrow coastal lowlands. During this generally warm and humid period dune deposits covered the shore platform (Rodríguez-Vidal et al., 2010) and speleothems formed in the caves, both covering previous units.

During sea-level fall and lowstand of MIS 4–2, sea level was always below highstand heights. Many coastal cliffs became inactive, i.e. affected by terrestrial processes only. The Gibraltar island transformed into a tombolo, with a permanent isthmus that promoted faunal interchanges, probably accompanied by a stable human occupation (Neanderthals), mostly in caves (Fig. 5) and shelters at the cliff toes close to where feeding resources were more available.

Small easterly dunes coming from nearby beaches formed in the bays and entered into certain caves. The last intensive period of Catalan Bay climbing dune development was between 50 and 40 ka (Rodríguez-Vidal et al., 2004), related to the latest sandy sediments of Ibex Cave, and the late filling of Gorham's and Vanguard Caves (Goldberg and MacPhail, 2000; Pettitt and Bailey, 2000). The period of maximum aeolian activity was probably linked with the MIS 3 highstand shoreline (Jiménez-Espejo et al., 2013), now submerged on both sides of the Rock (Fig. 2).

In Table 2 we present the lists of species of plants and animals which have been identified from MIS 3 levels at Gorham's Cave (after Finlayson et al., 2006 and Finlayson, 2006, see Fig. 5) with additional data from Vanguard and Ibex Caves, and Devil's Tower Rock Shelter (Fig. 1). They span the time period 55–28 ka, i.e. MIS 3. These species are arranged in accordance with the habitats that they occupy at present. These results, combining independent data from a range of taxa, indicate that the geological diversity of the MIS 3 landscape was reflected in a high ecological diversity. In particular, there are components related to the limestone Rock of Gibraltar and others related to the acidic sandy environment of the coastal plain and its dunes. The nearest analogue of the latter in existence today is the Doñana National Park in SW Spain (Fig. 1).

The main habitat types identified by the MIS 3 species in the caves are (i) Cliffs, screes and rocky habitats on limestone substrate; (ii) Stone Pine *Pinus pinea* woodland/savannahs, Juniper scrub woodland and mixed Pine/juniper woodland, *Cistus* and *Erica* shrubland with patches of open grasslands, on sandy substrates; (iii) mobile dunes and associated seasonal wetlands; and (iv) coastal habitats:

- (i) Cliffs, screes and rocky habitats on limestone substrate: The Rock of Gibraltar is densely covered with olive *Olea europaea* woodland which grows extensively on the limestone, and which is well represented in the fossil record. The indicators of this habitat include a range of plants that still grow on the Rock of Gibraltar (*O. europaea*, *Pistacia lentiscus*, *Rhamnus* spp., *Calicotome* spp., *Ephedra fragilis*, *Asphodelus* spp.). Moorish Gecko *Tarentola mauritanica* and Iberian wall Lizard *Podarcis hispanica* are typical reptiles that persist on the Rock today. A number of the larger raptors (e.g. Lammergeyer *Gypaetus barbatus*, Egyptian Vulture *Neophron percnopterus*) have disappeared as breeding species in historical times but the birds reflect species that would be

Table 1

Calibrated AMS dates of terrestrial¹ and marine² samples from Vladí's Reef (Gibraltar). Radiocarbon Laboratory: (Beta) Beta Analytic Inc., Miami, USA, and (OxA) Oxford Radiocarbon Accelerator Unit, U.K. Calibration IntCal09.14c (Reimer et al., 2009), (*) $\Delta R = -135 \pm 20$ ¹⁴C years (Soares and Martins, 2010).

Field code	Lab. code	Sample material	$\delta^{13}\text{C}_{\text{‰}}$	¹⁴ C age (yr BP)	Calibrated yr BP IntCal09 (2-σ)
VLA-37	Beta-290907	Calcrete ¹	–1.9	30,870 ± 200	34,840–36,280
VLA-44	OxA-15824	Encrustation ²	+1.4	907 ± 27	541–667*
VLA-47	OxA-15864	Shell ²	+0.9	491 ± 22	179–360*

expected in such habitats today. Among the mammals, Mouse-eared Bat *Myotis myotis* and Schreiber's Bat *Miniopterus schreibersii*, are still present on the Rock while Spanish Ibex *Capra pyrenaica* disappeared in historical times (Finlayson, 2006; López-García et al., 2011).

- (ii) Woodland/savannahs on sandy substrates: The vegetation associated with the more stabilised dunes in the Doñana National Park

today, with thicker woodland habitats are associated with the genus *Juniperus* which is found in both the charcoal and pollen record in the Gibraltar caves, and whilst it is not possible to identify the species from these, *J. phoenicea* grows in warm sandy substrates. Depending on the depth of the water table under the sands, the wettest dunes are associated with *Myrtus* and *Arbutus unedo*, parklands with the presence of *O. europaea* and *Quercus*

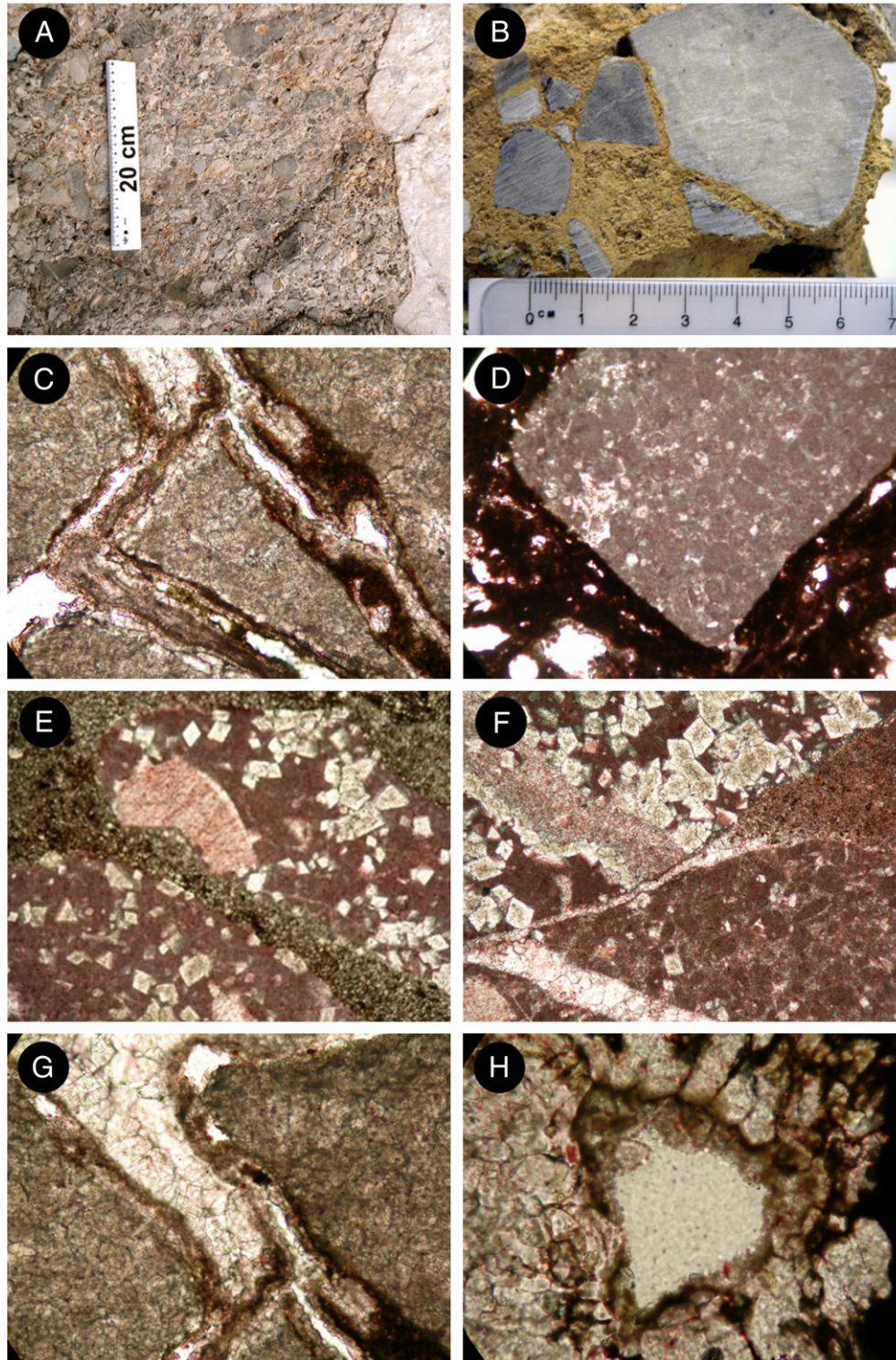


Fig. 4. The visu similarities between the surficial Rosia Bay tectonic breccia (A1 breccia, A2 hardrock) and Vladi's Reef breccia from submerged VLA-37 sample (B). The poligenetic lithoclasts within the Vladi's thin sections are formed by angular–subangular fragments of fractured dolostone (C), peloidal grainstone (D), and dolomitized peloidal limestone (E, F). Neomorphism processes affecting to the clastic bedrock (F, G, H): The carbonate mud between the clasts is replaced by fine calcite (F), blocky mosaic of several drusy calcite and fine micrite layers infilling the clastic contact (G), geopetal calcite growth into a little cavity (H).

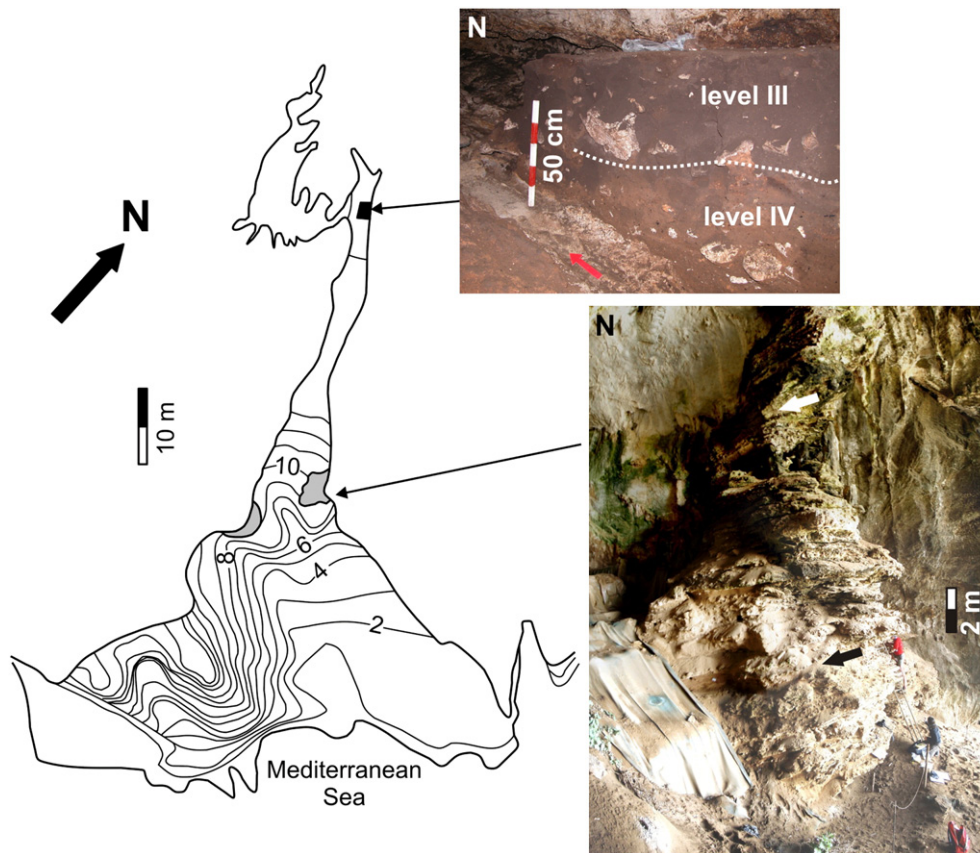


Fig. 5. Gorham's Cave topography and photo-stratigraphic sections at the Entrance and the Upper area. The first section is 21 m high of blown sand record with Mousterian lithic remains (Waechter, 1964), arrow is the lee-face dip of coastal dune. The second one is the inner archaeological section excavated by Finlayson et al. (2006) with the Middle (level IV) and Upper Palaeolithic (level III) occupation evidence.

suber, and *P. lentiscus* is usually found in the driest soils. The more stabilised sandy substrates are characterised by the presence of Juniper scrub woodland and mixed Pine/juniper woodland, while *Cistus* and *Erica* shrubland are found in the patches of open grasslands, on sandy substrates.

This landscape component is missing today in Gibraltar as the coastal plain is submerged (Fig. 6). The range of plants and animals observed in the caves record is a close match to the species found today in Doñana (Finlayson, 2006). The exceptions are the extinct Narrow-nosed Rhinoceros *Stephanorhinus hemitoechus* and Au-rochs *Bos primigenius* and a range of carnivores that have disappeared in historical times, notably the Wolf *Canis lupus*, last seen in Doñana in the mid 20th century. Brown Bear *Ursus arctos*, Spotted Hyaena *Crocota crocuta* and Leopard *Panthera pardus* would have also potentially occupied these habitats. The Spanish Lynx *Lynx pardina* remains in Doñana today.

- (iii) Mobile dune systems and associated seasonal wetlands: The dominant tree species here is Stone Pine *P. pinea*, and it characterises shifting sand dune systems, being the only tree species that can mature at a rate that is fast enough to keep up with the pace of the mobile dunes. Other species associated with mobile dunes are *Halimium* spp. which can be found in the dune slacks, and which is also present in the fossil record for the area. The associated seasonal wetlands are found in the areas between dune ridges where the water table is very high, and where there are often temporary lakes and ponds (Fig. 6). These would have been separated by the mobile dunes from the sea, as in Doñana today. The species range observed in the Gibraltar Caves matches the species of the Doñana dunes and pools today.
- (iv) Coastal habitats: The coastal habitats represented sandy and rocky shorelines. A wide range of marine molluscs typical of rocky and

sandy intertidal and subtidal shorelines is represented (Fa, 2008). Of interest is a range of bird species that are rarely found in the area today, and which appear to reflect cooler winters (see discussion) and cold conditions in the north: Red-throated Diver *Gavia stellata*, Northern Fulmar *Fulmarus glacialis*, Eider *Somateria* spp., Velvet Scoter *Melanitta fusca*, Long-tailed Duck *Clangula hyemalis* and Goosander *Mergus merganser*. Of note is the presence of Bald Ibis *Geronticus eremita*, a species now confined to a small remnant population in Morocco, but that has been reintroduced recently in the Spanish province of Cádiz, near Gibraltar, and as of 2011 is breeding successfully in at least three separate coastal locations (M. Cuadrado, Zoo of Jerez, personal communication). The White-tailed Eagle *Haliaeetus albicilla* probably became extinct in the area in historical times, as did the Monk Seal *Monachus monachus*. The Great Auk *Pinguinus impennis* became globally extinct in the 19th century.

5. Discussion

Finlayson (2006) developed new forms of data collection and combined multi-scale ecological datasets of present-day distributions of species with plant and bird fossil data in a quantitative reconstruction of habitats and landscapes, and in 2008(b) Finlayson et al. used this method for quantitative reconstruction of bioclimate, demonstrated that the prevailing climate during the Last Glacial Maximum (LGM) varied only slightly with present-day climate, and drew attention to the generally underestimated importance of small-scale refugia during glacials. Ferguson et al. (2011) have later demonstrated that the seasonal range of Sea Surface Temperature (SST) was greater than today during the last glacial by $\sim 2^\circ\text{C}$ as a result of greater winter cooling, by measuring the Mg/Ca and oxygen isotope ($\delta^{18}\text{O}$) ratios in present

Table 2

Habitat types represented in the MIS 3 landscape of Gibraltar inferred from a range of plant and animal indicators excavated in its caves (after Finlayson et al., 2006 and Finlayson, 2006).

Habitat type	Floral indicator	Faunal indicator
Cliffs, screes and rocky habitats on Limestone substrate	<i>Abies</i> ; <i>Acer</i> ; <i>Lonicera</i> ; <i>Smilax</i> ; <i>Olea europaea</i> ; <i>Pinus nigra</i> / <i>sylvestris</i> ; <i>Cedrus</i> ; <i>Taxus</i> ; <i>Pistacia</i> ; <i>Buxus</i> ; <i>Prunus</i> ; <i>Myrtus</i> ; <i>Rhamnus</i> ; <i>Maytenus</i> ; <i>Calicotome</i> ; <i>Bupleurum</i> ; <i>Ephedra fragilis</i> ; <i>E. distachya</i> ; <i>Hedera helix</i> ; <i>Phillyrea</i> ; <i>Viburnum</i> ; <i>Asphodelus</i> .	Reptilia: <i>Tarentola mauritanica</i> ; <i>Podarcis hispanica</i> . Aves: <i>Phalacrocorax aristotelis</i> ; <i>Gypaetus barbatus</i> ; <i>Neophron percnopterus</i> ; <i>Gyps fulvus</i> ; <i>Aquila fasciata</i> ; <i>A. chrysaetos</i> ; <i>Falco naumanni</i> ; <i>F. tinnunculus</i> ; <i>F. eleonorae</i> ; <i>F. peregrinus</i> ; <i>Larus michahellis</i> ; <i>Columba livia</i> ; <i>Bubo bubo</i> ; <i>Athene noctua</i> ; <i>Apus apus</i> ; <i>A. pallidus</i> ; <i>Tachymarptis melba</i> ; <i>Hirundo rustica</i> ; <i>Ptyonoprogne rupestris</i> ; <i>Delichon urbica</i> ; <i>Prunella collaris</i> ; <i>Oenanthe leucura</i> ; <i>O. oenanthe</i> ; <i>O. hispanica</i> ; <i>Monticola</i> sp.; <i>Phoenicurus ochruros</i> ; <i>Pyrrhocorax graculus</i> ; <i>P. pyrrhocorax</i> ; <i>Corvus monedula</i> ; <i>C. corax</i> ; <i>Petronia petronia</i> . Mammalia: <i>Myotis myotis</i> ; <i>M. nattereri</i> ; <i>Miniopterus schreibersii</i> ; <i>Capra pyrenaica</i> .
Stone Pine <i>Pinus pinea</i> woodland/savannah Juniper scrub woodland and mixed Pine/juniper woodland <i>Cistus</i> and <i>Erica</i> shrubland Patches of open grasslands. These habitats are on sandy substrates	<i>Arbutus unedo</i> ; <i>Cistus</i> / <i>Halimium</i> ; <i>Calluna</i> ; <i>Erica</i> ; <i>Fraxinus</i> ; <i>Juniperus</i> ; <i>Pinus pinea</i> / <i>pinaster</i> ; <i>Betula</i> ; <i>Castanea</i> ; <i>Ulmus</i> ; <i>Corylus avellana</i> ; <i>Ilex aquifolium</i> ; <i>Juglans regia</i> ; <i>Salix</i> ; <i>Quercus suber</i> ; <i>Frangula</i> ; <i>Helianthemum</i> .	Reptilia: <i>Testudo hermanni</i> ; <i>Psammmodromus algirus</i> ; <i>Timon lepidus</i> ; <i>Blanus cinereus</i> ; <i>Malpolon monspessulanus</i> ; <i>Coluber hippocrepis</i> ; <i>Elaphe scalaris</i> ; <i>Natrix natrix</i> ; <i>Coronella girondica</i> ; <i>Vipera</i> sp. Aves: <i>Milvus migrans</i> ; <i>M. milvus</i> ; <i>Gypaetus barbatus</i> ; <i>Neophron percnopterus</i> ; <i>Gyps fulvus</i> ; <i>Circus cyaneus</i> ; <i>Accipiter gentilis</i> ; <i>A. nisus</i> ; <i>Buteo buteo</i> ; <i>B. lagopus</i> ; <i>Aquila fasciata</i> ; <i>A. chrysaetos</i> ; <i>Hieraetus pennatus</i> ; <i>Falco naumanni</i> ; <i>F. tinnunculus</i> ; <i>F. subbuteo</i> ; <i>Alectoris rufa</i> ; <i>Coturnix coturnix</i> ; <i>Otis tarda</i> ; <i>Burhinus oedicephalus</i> ; <i>Vanellus vanellus</i> ; <i>Scolopax rusticola</i> ; <i>Columba oenas</i> ; <i>C. palumbus</i> ; <i>Streptopelia turtur</i> ; <i>Otus scops</i> ; <i>Strix aluco</i> ; <i>Caprimulgus ruficollis</i> ; <i>Coracias garrulus</i> ; <i>Upupa epops</i> ; <i>Picus viridis</i> ; <i>Dendrocopos major</i> ; <i>Melanocorypha calandra</i> ; <i>Calandrella</i> sp.; <i>Galerida cristata</i> ; <i>Lullula arborea</i> ; <i>Alauda arvensis</i> ; <i>Anthus pratensis</i> ; <i>A. spinoletta</i> / <i>petrosus</i> ; <i>A. compestris</i> ; <i>Motacilla alba</i> ; <i>M. flava</i> ; <i>Prunella modularis</i> ; <i>Oenanthe oenanthe</i> ; <i>O. hispanica</i> ; <i>Erethacus rubecula</i> ; <i>Phoenicurus ochruros</i> ; <i>Ficedula hypoleuca</i> ; <i>Sylvia melanocephala</i> ; <i>S. atricapilla</i> ; <i>Parus major</i> ; <i>Certhia</i> sp.; <i>Lanius meridionalis</i> ; <i>Cyanopica cooki</i> ; <i>Pica pica</i> ; <i>Corvus corone</i> ; <i>Sturnus unicolor</i> ; <i>Petronia petronia</i> ; <i>Fringilla coelebs</i> ; <i>Coccothraustes coccothraustes</i> ; <i>Carduelis carduelis</i> / <i>cannabina</i> ; <i>Chloris chloris</i> ; <i>Pyrrhula pyrrhula</i> ; <i>Passer</i> sp.; <i>Emberiza citrinella</i> ; <i>E. hortulana</i> ; <i>E. calandra</i> . Mammalia: <i>Crocodylus russula</i> ; <i>Iberomys cabrerarum</i> ; <i>Terricola duodecimcostatus</i> ; <i>Sorex minutus</i> ; <i>Sorex gr. coronatus-araneus</i> ; <i>Talpa occidentalis</i> ; <i>Apodemus sylvaticus</i> ; <i>Eliomys quercinus</i> ; <i>Arvicola sapidus</i> ; <i>Oryctolagus cuniculus</i> ; <i>Cervus elaphus</i> ; <i>Equus ferus</i> ; <i>Sus scrofa</i> ; <i>Bos primigenius</i> ; <i>Stephanorhinus hemitoechus</i> ; <i>Ursus arctos</i> ; <i>Crocota crocuta</i> ; <i>Canis lupus</i> ; <i>Vulpes vulpes</i> ; <i>Felis sylvestris</i> ; <i>Lynx pardina</i> ; <i>Panthera pardus</i> . Amphibia: <i>Pleurodeles waltl</i> ; <i>Triturus marmoratus pygmaeus</i> ; <i>Discoglossus</i> sp.; <i>Pelobates cultripes</i> ; <i>Bufo bufo spinosus</i> ; <i>B. calamita</i> ; <i>Hyla meridionalis</i> ; <i>Rana</i> sp. Reptilia: <i>Mauremys leprosa</i> ; <i>Acanthodactylus erythrurus</i> ; <i>Chalcides</i> sp.; <i>Blanus cinereus</i> ; <i>Malpolon monspessulanus</i> ; <i>Coluber hippocrepis</i> ; <i>Elaphe scalaris</i> ; <i>Natrix maura</i> ; <i>Coronella girondica</i> ; <i>Vipera</i> sp. Aves: <i>Podiceps cristatus</i> ; <i>P. auritus</i> ; <i>Phalacrocorax carbo</i> ; <i>Plegadis falcinellus</i> ; <i>Geronticus eremita</i> ; <i>Branta bernicla</i> ; <i>Tadorna</i> sp.; <i>Anas platyrhynchos</i> ; <i>A. crecca/querquedula</i> ; <i>Marmaronetta angustirostris</i> ; <i>Netta rufina</i> ; <i>Aythya ferina</i> ; <i>A. fuligula</i> ; <i>Milvus migrans</i> ; <i>M. milvus</i> ; <i>Haliaeetus albicilla</i> ; <i>Rallus aquaticus</i> ; <i>Porzana porzana</i> ; <i>Fulica atra</i> ; <i>Himantopus himantopus</i> ; <i>Glareola pratincola</i> ; <i>Charadrius hiaticula</i> ; <i>Vanellus vanellus</i> ; <i>Pluvialis squatarola</i> ; <i>Gallinago</i> sp.; <i>Limosa limosa</i> ; <i>Tringa totanus</i> ; <i>Calidris alpina</i> ; <i>Larus michahellis</i> ; <i>Chroicocephalus ridibundus</i> ; <i>Chlidonias niger</i> ; <i>A. spinoletta</i> / <i>petrosus</i> ; <i>Motacilla alba</i> ; <i>M. flava</i> . Mammalia: <i>Arvicola sapidus</i> .
Mobile dunes and associated seasonal wetlands	<i>Pinus pinea</i> ; <i>Juniperus</i> ; <i>Alnus glutinosa</i> ; <i>Salix</i> ; <i>Artemisia</i> ; <i>Tamarix</i> ; <i>Poaceae</i> .	Mollusca: <i>Acanthocardia tuberculatum</i> ; <i>Anomia</i> sp.; <i>Callista chione</i> ; <i>Cardita calyculata</i> ; <i>Chamelea</i> sp.; <i>Charonia nodifera</i> ; <i>Cypraea spurca</i> ; <i>Fissurella</i> sp.; <i>Gibbula</i> sp.; <i>Glycimeris bimaculata</i> ; <i>Littorina obtusata</i> ; <i>L. saxatilis</i> ; <i>Lucina borealis</i> ; <i>Modiolus modiolus</i> ; <i>Osilinus turbinatus</i> ; <i>O. articulatus</i> ; <i>Mytilus galloprovincialis</i> ; <i>M. edulis</i> ; <i>Nassarius reticulatus</i> ; <i>Nucella lapillus</i> ; <i>Patella caerulea</i> ; <i>P. depressa</i> ; <i>P. ferruginea</i> ; <i>P. ulissiponensis</i> ; <i>P. vulgata</i> ; <i>Pecten jacobaeus</i> ; <i>P. maximus</i> ; <i>Semicassis undulata</i> ; <i>Siphonaria pectinata</i> ; <i>Spondylus gaederopus</i> ; <i>Stramonita haemastoma</i> ; <i>Trivia monacha</i> ; <i>Venerupis decussata</i> . Aves: <i>Gavia stellata</i> ; <i>Fulmarus glacialis</i> ; <i>Pterodroma</i> sp.; <i>Calonectris diomedea</i> ; <i>Puffinus mauretanicus</i> ; <i>Hydrobates pelagicus</i> ; <i>Morus bassanus</i> ; <i>Phalacrocorax carbo</i> ; <i>P. aristotelis</i> ; <i>Geronticus eremita</i> ; <i>Tadorna</i> sp.; <i>Somateria</i> sp.; <i>Clangula hyemalis</i> ; <i>Melanitta nigra</i> ; <i>M. fusca</i> ; <i>Mergus merganser</i> ; <i>M. serrator</i> ; <i>Haliaeetus albicilla</i> ; <i>Haematopus ostralegus</i> ; <i>Pluvialis squatarola</i> ; <i>Limosa limosa</i> ; <i>Numenius phaeopus</i> ; <i>N. arquata</i> ; <i>Tringa totanus</i> ; <i>Calidris canutus</i> ; <i>C. alpina</i> ; <i>C. maritima</i> ; <i>Phalaropus fulicarius</i> ; <i>Larus marinus</i> ; <i>L. michahellis</i> ; <i>Chroicocephalus ridibundus</i> ; <i>Rissa tridactyla</i> ; <i>Chlidonias niger</i> ; <i>Pinguinus impennis</i> ; <i>Alle alle</i> ; <i>Uria aalge</i> ; <i>Alca torda</i> ; <i>Fratercula arctica</i> ; <i>Anthus spinoletta</i> / <i>petrosus</i> . Mammalia: <i>Delphinus delphis</i> ; <i>Tursiops truncatus</i> ; <i>Monachus monachus</i> .
Coastal		



Fig. 6. Highstand present-day view of the east side of Gibraltar, and photographic lowstand reconstruction of the MIS 3 landscape.

day limpet (*Patella*) shells and comparing them to similar measurements taken from fossil limpets from Gibraltar. Overall, such an increase in temperature range had little impact on the landscape and its components. The cold fauna never reached Gibraltar (Finlayson and Carrión, 2007) and only the occasional wintering Arctic birds indicate a slight change of conditions.

This observation is supported by the changes to the vegetation in Gibraltar during the Late Pleistocene which were relatively minor in comparison with patterns in other parts of Europe (Finlayson and Carrión, 2007). The arid steppes never reached this site (in fact *Artemisia* pollen is scarce) and montane pines, *P. sylvestris* and *P. nigra*, are present at times but are never abundant. Instead the predominant vegetation, with *P. pinea*, *O. europaea* and *P. lentiscus*, indicated predominantly Thermo to Meso-Mediterranean conditions and a humidity regime that varied between Sub-Humid and Dry (Finlayson, 2006).

The refugial bioclimatic conditions of south-western coastal Iberia — within a larger Iberian refugium — have become evident from the data and analyses presented by Finlayson (2006). These results highlight the special refugial conditions of the Gibraltar Pleistocene sites. These

results support studies based on analysis of extant woody plant taxa. Various authors have described present communities in the Strait and have described the area as a biodiversity hotspot (e.g. Ojeda et al., 1996; Arroyo et al., 2004). They have also described several relict communities in the Sierra de Algeciras on the western side of the Bay of Gibraltar, where rhododendrons (*Rhododendron ponticum* ssp. *baeticum*) and other relicts from the Tertiary still survive, and which also include species that are endemic to the region. Arroyo et al. (2004) comment that the evidence available for the existence of glacial refugia in the Strait area comes from the presence of certain taxa of Ibero-North African, or Iberian–Tingitanian species such as *Quercus lusitanica*, *Q. canariensis*, *R. ponticum* ssp. *baeticum* (only present today on the north shore of the Strait Ojeda et al., 1996), *Lonicera periclymenum* ssp. *hispanica*, *Ruscus hypophyllum*, *Cistus populifolius* ssp. *major*, *Genista tridentata*, *Genista triacanthos*, *Thymelaea villosa*, *Halimium alyssooides* and *Davallia canariensis*. Phylogeographical evidence suggests that the Laurel (*Laurus nobilis*) may also have survived the LGM in the Atlantic coast and the area of the Strait of Gibraltar (Arroyo-García et al., 2001; Arroyo et al., 2004). Carrión et al. (2000)

point out that given the bioclimatic requirements of *Q. suber*, the area of south-western Iberia may have been a key glacial refugium for this species especially in the intra-montane valleys and the coastal plains.

Ojeda et al. (2001), have identified the woods and matorrals on both sides of the area of the Strait of Gibraltar as being a hotspot of biodiversity, despite the fact that unlike other hotspots, this area has neither a limestone substrate, nor high isolated mountains, nor has the area been subjected to comparatively great climatic changes during the Pleistocene. Yet the flora of the area contains numerous endemics and populations with disjunct distributions, which they attribute to the ecological isolation of the area (also Arroyo, 1997; Arroyo et al., 2004).

The MIS 3 landscape outside the Gorham's Cave complex could essentially be described as a savannah-type mosaic – a complex of patches of trees with scattered shrubs, with a rich ground layer of forb and grass. Sand dunes, seasonal wetlands, coastal habitats and the cliffs and screes of the Rock itself made up this diverse landscape (Fig. 6). The results from different levels from the Gorham's and Vanguard Caves sequences show that this was the norm for most of the last glacial cycle (MIS 5d-2) (Finlayson et al., 2006; Finlayson and Carrión, 2007; Carrión et al., 2008).

The landscape described here – composed of open savannah-type parkland with a mosaic of shrubs – has no present-day equivalent in Iberia other than in the Stone Pine, *P. pinea*, habitats of the SW coast. However, it could be argued that the 'man-made' ecosystems characterised by their savannah-like physiognomy, and which are known as 'dehesas', demonstrate a close parallel (Infante et al., 1997; Joffe et al., 1999). Whilst these dehesas are not natural, and the dominant trees are evergreen oaks (mainly Holm Oak *Q. ilex rotundifolia* but also Cork Oak *Q. suber*), Joffe et al. (1999) have shown that their structure has adjusted over the long-term and corresponds to an optimal functional equilibrium for particular hydrological conditions.

The limiting factor for the habitats in refugial conditions described here, has been demonstrated to be the rainfall regimes, and these tend towards dry-semiarid. Joffe and Rambal (1993) have demonstrated that evapotranspiration is more dependent on the annual precipitation regimes in oak-savannah systems than in relatively close-canopy forests, making the savannah trees more vulnerable to prolonged drought. It therefore appears that the key limiting factor in MIS 3 was water and not temperature and this is borne out by the violent changes in aeolian deposition and variable river input observed from marine cores in the Sea of Alboran, just east of Gibraltar (Jiménez-Espejo et al., 2007). It is highly probable that it was drought which most seriously affected the flora and fauna of these landscapes. Most notably, drought may have pushed the last Neanderthals over the brink in this region. These sand-based, seasonal, environments were largely lost with the Holocene sea-level rise and historical overdevelopment of the coast. Today, they are relict landscapes on the verge of extinction. The Doñana National Park remains as the flagship of these ancient landscapes. It has to be noted, however, that Doñana, as we see it today, originated very recently in geological time – about 4500 yr ago – when the first Holocene coastal progradation occurred and mobile dunes emerged (Rodríguez-Ramírez et al., 1996). In other words, Doñana's landscapes, plus its fauna and flora, are reliable proxies of the Gibraltar of the past when sea level was much lower, but they never coexisted as parallel ecosystems. As climatic conditions are similar at present to those at the time when scattered pine woods and lagoons surrounded the Rock of Gibraltar, the same set of plant and animal species that had been present there were able to colonize Doñana a few millennia later, practically in historic time. The correspondence is particularly striking in the case of birds, not surprisingly perhaps, as this taxon has suffered the fewest local extinctions in the Holocene (Finlayson, 2011).

6. Conclusions

The reconstructed palaeolandscape outside the Gorham's Cave complex during MIS 3, now part of the submerged platform around Gibraltar,

bears a strong similarity to the few remaining sandy habitats that still remain in the south of the Iberian Peninsula of which the most extensive example is within the Doñana National Park. This landscape was set within a Thermo to Meso-Mediterranean, Sub-Humid to Dry, climate. The open savannah-type parkland with a mosaic of shrubs described here for the Gorham's Cave complex, however, has no present-day equivalent in Iberia other than in the Stone Pine, *P. pinea*, habitats of the SW coast. In this paper we have highlighted the presence of sources of fresh water which would have been critical when aridity (not temperature) was the primary limiting factor in the refugial area that was South Iberia. The caves and shelters at the base of the cliffs at Europa Reef and Eastern pinnacles were formed when the sea levels were lower than today. Their inventories provide direct evidence of the state of the emerged landscape at the time of the Neanderthals.

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