Climatic conditions for the last Neanderthals: Herpetofaunal record of Gorham's Cave, Gibraltar

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ABSTRACT

Gorham's Cave is located in the British territory of Gibraltar in the southernmost end of the Iberian Peninsula. Recent excavations, which began in 1997, have exposed an 18 m archaeological sequence that covered the last evidence of Neanderthal occupation and the first evidence of modern human occupation in the cave. By applying the Mutual Climatic Range method on the amphibian and reptile assemblages, we propose here new quantitative data on the terrestrial climatic conditions throughout the latest Pleistocene sequence of Gorham's Cave. In comparison with current climatic data, all mean annual temperatures were about 1.6–1.8 °C lower in this region. Winters were colder and summers were 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. The climate was Mediterranean and semi-arid (according to the Aridity Index of Dantin–Revenga) or semi-humid (according to the Aridity Index of Martonne). The atmospheric temperature range was higher during the latest Pleistocene, mainly due to lower winter temperatures. Such data support recent bioclimatic models, which indicate that high rainfall levels may have been a significant factor in the late survival of Neanderthal populations in southern Iberia. The Solutrean levels of Gorham's Cave and climate records from cores in the Alboran Sea indicate increasing aridity from Marine Isotope Stage (MIS) 3-2. Because Neanderthals seem to have been associated with woodland habitats, we propose that lessening rainfall may have caused the degradation of large areas of forest and may have made late surviving Neanderthal populations more vulnerable outside southern refuges like the Rock of Gibraltar.

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Introduction

The Neanderthal extinction and the possible implication of climate has long been the subject of intense debate (Stringer et al., 2003; Carrión, 2004; Finlayson et al., 2006; Tzedakis et al., 2007; among many others). Established views of the superiority of Anatomically Modern Humans (AMH) over Neanderthals (as the cause of the survival of the first and the extinction of the latter) are under scrutiny as numerous works show that Neanderthals were capable of behavior that is now regarded as modern. The extinction of the Neanderthals appears to have been a drawn-out, climate-related affair (Finlayson and Carrión, 2006; Müller et al., 2011). Neanderthals inhabited temperate Europe for more than 300,000 years and are thought to have disappeared between 40,000 and 28,000 years ago, around the time that the first modern humans arrived in Europe during a period of significant climatic oscillation (Finlayson, 2009). The Neanderthals are thought to have survived longest in southerly European regions such as the Balkans, Italy and Iberia (Carrión et al., 2011; Dennell et al., 2011).
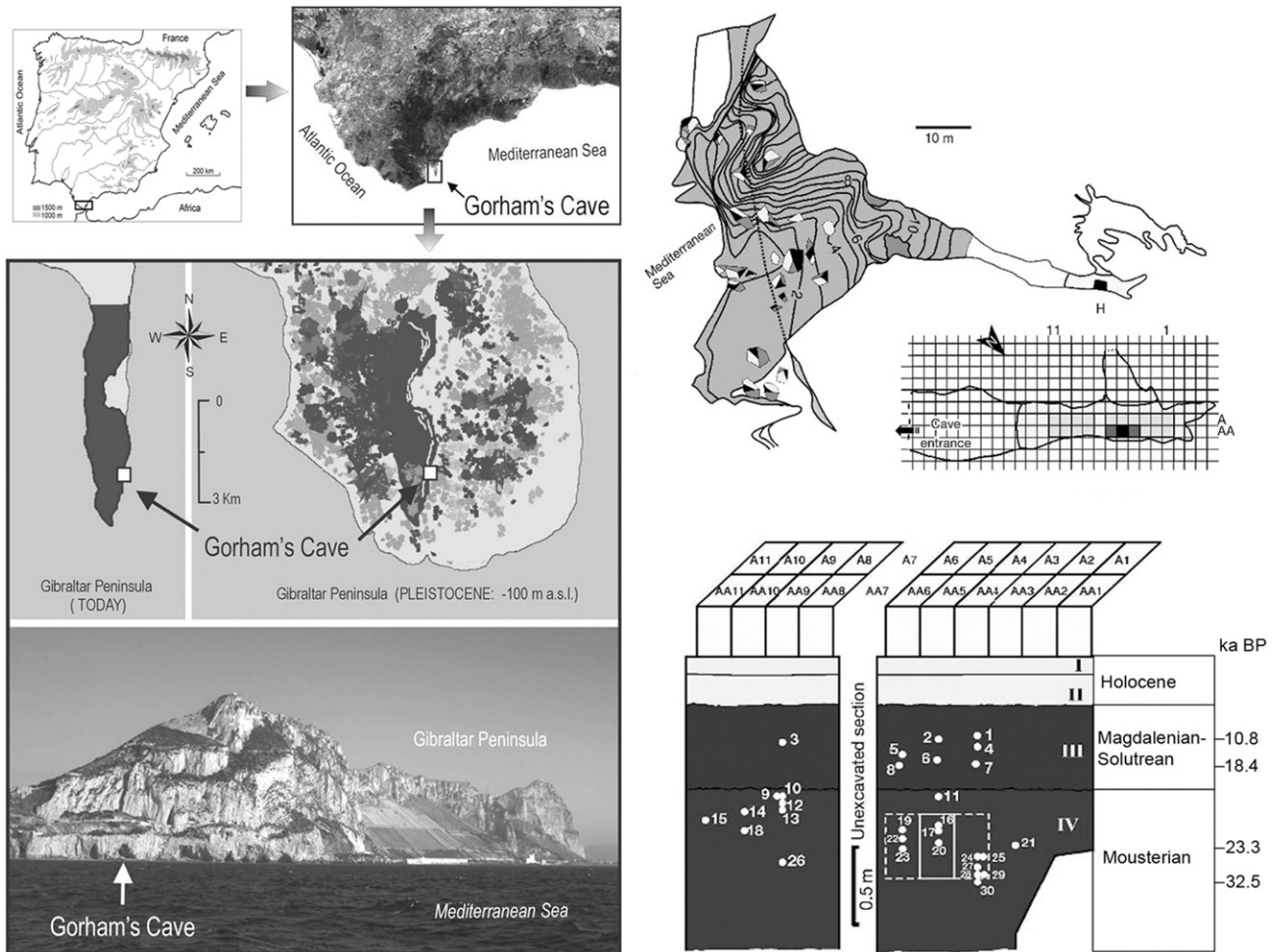
Figure 1. Left: Location of Gorham's Cave in southern Iberian Peninsula and reconstruction of the Gibraltar Peninsula during the Last Glacial Maximum, with sea level ca. 100 m below present-day position (modified from Carrion et al., 2008). Right-Top: General plan of Gorham's Cave showing the location of the excavated hearth site (H) and detail of excavated area with the hearth site (light grey and black). Right-Bottom: Stratigraphy of the excavated inner part of Gorham's Cave described in text. Numbered white dots indicate the positions of charcoal samples used for ^{14}C AMS dates. The white rectangle marks the position of the Mousterian hearth site. Hatched lines indicate the hearth's radius of influence indicated by charcoal concentrations. Modified from Finlayson et al., 2006.

Interest in the Rock of Gibraltar in terms of palaeontology and paleoanthropology has been mentioned as early as 1798 by the Major Imrie (1798). The significance of the archaeological and paleontological record of Gibraltar's caves was first reported in the mid-nineteenth century with the discovery of a Neanderthal cranium at Forbes' Quarry in 1848 (Stringer, 2000a), and the subsequent discovery of a Neanderthal child cranium in 1926 at Devil's Tower (Garrod et al., 1928). Gorham's Cave was discovered by A. Gorham in 1907. Its long human occupation was first brought to light in the 1950s (Waechter, 1951, 1964), with work recommencing at this site in the early 1990s (Stringer et al., 1999; Stringer, 2000b). Research undertaken at Gorham's Cave over the past decade has confirmed that southern Iberia was an important glacial refuge for Neanderthal populations (see various references in Stringer, 2000a; Finlayson et al., 2006, 2008; Carrión et al., 2008, 2011). Archaeological evidence suggests that Neanderthals inhabited the cave possibly as late as 28,000 years ago (Finlayson et al., 2006). The last Neanderthals that occupied Gorham's Cave had access to a diverse community of plants and vertebrates on the sandy plains, open woodland and shrubland, wetlands, cliffs and coastal environments surrounding the site. According to Finlayson et al. (2006) and Carrión et al. (2008), such ecological diversity might have facilitated their long survival. The Neanderthals persisted in Mediterranean environments that had acted as glacial refuge for many species throughout the Quaternary period.

In fact, southern Iberia is widely regarded as having been one of the most significant glacial refuges in Europe during the Pleistocene period (Hewitt, 2000; Carrión et al., 2003; Gómez and Lunt, 2007; O'Regan, 2008; Carrión and Leroy, 2010; González-Sampériz et al., 2010; Rodríguez-Sánchez et al., 2010; Jennings et al., 2011). Factors that characterized southern Iberia as a glacial refuge were its southerly location, topographic heterogeneity, extensive coastlines, favorable weather patterns and proximity to Africa (Finlayson, 1999). Because there is some contradiction in the persistence of thermophilous fauna and flora in southern Iberia during the Pleistocene, and the possibility of climate deterioration as being the cause of the disappearance of the last Neanderthals, the aim of this paper is to present new quantitative data on the terrestrial climatic conditions throughout the latest Pleistocene sequence of Gorham's Cave using herpetofaunal assemblages.

Geological and chronological setting

The Rock of Gibraltar is a north-south orientated peninsula situated in the southernmost part of the Iberian Peninsula (36°N 05°W), 21 km from the coast of North Africa (Morocco) and with a total area
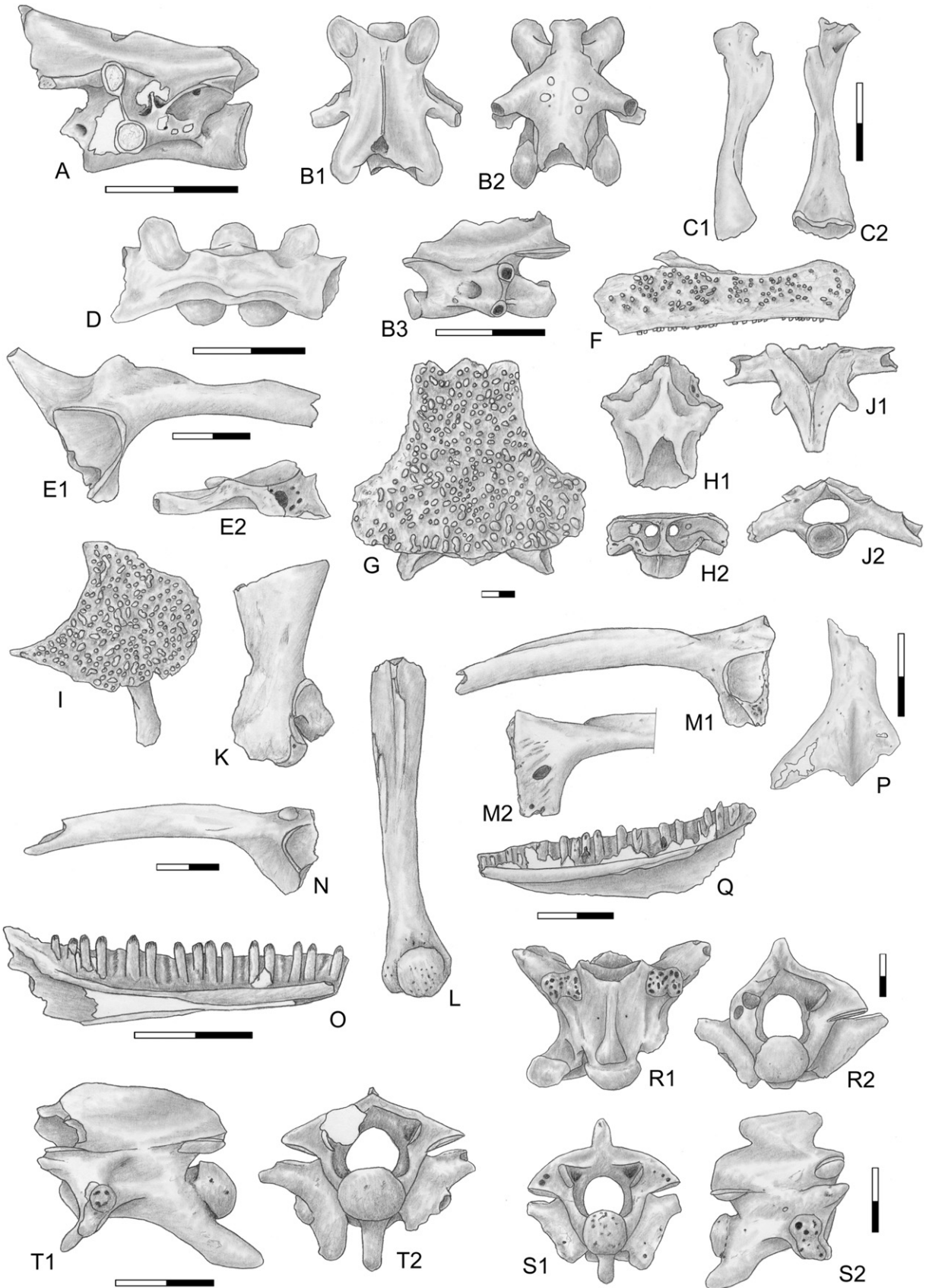
Figure 2. Some amphibians and squamates reptiles from Gorham's Cave. A: *Pleurodeles waltl*, trunk vertebra, right lateral view; B–C: *Triturus* cf. *pygmaeus*, B: Trunk vertebra, dorsal (B1), ventral (B2) and left lateral (B3) views, C: Humerus, lateral (C1) and ventral (C2) views; D–E: *Discoglossus* sp., D: Sacrum, dorsal view, E: Right ilium, lateral (E1) and posterior (E2) views; F–M: *Pelobates cultripes*, F: Right maxilla, lateral view, G: Fused frontoparietals, dorsal view, H: sphenethmoid, dorsal (H1) and anterior (H2) views, I: Right squamosal, lateral view, J: Third vertebra, dorsal (J1) and anterior (J2) views, K: Left scapula, dorsal view, L: Left humerus, ventral view, M: Left ilium, lateral (M1) and medial (M2) views; N: *Hyla* sp., left ilium, lateral view; O: *Chalcides striatus*, left dentary, medial view; P–Q: *Acanthodactylus erythrurus*, P: Fused frontals, dorsal view, Q: Right dentary, medial view; R: *Rhinechis scalaris*, trunk vertebra, ventral (R1) and posterior (R2) views; S: *Natrix maura*, trunk vertebra, posterior (S1) and right lateral (S2) views; T: *Vipera latastei*: Trunk vertebra, left lateral (T1) and posterior (T2) views. All scales = 2 mm.

of approximately 6 km^2, a length of 5.2 km and a maximum natural width of 1.6 km (Rodriguez-Vidal et al., 2004, 2007; C. Finlayson et al., 2006, 2008, G. Finlayson et al., 2008) (Fig. 1). Gorham's Cave is located at the foot of this Gibraltar promontory, oriented to the south–east (36° 07′N 5° 21′W) and forms part of a complex of four caves (Bennett, Vanguard, Hyaena and Gorham's). Research into the geomorphological evolution of the Rock by Rodriguez-Vidal et al. (2004, 2007) has provided the framework for the reconstruction of the landscape at Gibraltar during the Quaternary. These authors have provided a detailed analysis of Gibraltar's sedimentary record and its erosional landforms, showing that the Rock evolved through a combination of tectonic uplift and eustatic sea level change.

The excavations in the inner part of the cave, which had not been systematically excavated previously, commenced in 1997, exposing an area of 29 m^2 of cave floor and producing a stratigraphy with four main occupation levels (C. Finlayson et al., 1999, 2006, 2008; G. Finlayson et al., 2008) (Fig. 1). Levels I and II are thin lenses and correspond to Phoenician and Neolithic horizons, respectively. Level III (mean depth of 62 cm) is sub-divided into a basal Solutrean (IIIb) and an upper Magdalenian (IIIa) horizon and consists of sandy sediment with dark brown clay in a sandy matrix. It has a strong organic component that includes discrete lumps of charcoal.

Another distinctive feature of this level is a layer of fallen angular limestone and speleothem fragments, which runs along the middle of this horizon and separates the Solutrean and Magdalenian occupational levels. Level IV (mean depth of 41 cm, but its base has not been reached) corresponds to a Mousterian horizon and is composed of a beige-colored pure clay horizon with an abundance of discrete lumps of charcoal and a hearth (C. Finlayson et al., 2006, 2008; G. Finlayson et al., 2008).

The archaeological remains associated with Level III consist of 240 Upper Palaeolithic artefacts using predominantly flint, chert and some quartzites as raw material. In contrast, Level IV contains 103 stone tools attributed to the Mousterian technocomplex also made using similar raw materials (Finlayson et al., 2006; Giles Pacheco et al., 2012).

The chronology of the Gorham's Cave sequence is based on a stratigraphically-coherent series of AMS radiocarbon dates obtained from charcoal fragments. Level III is dated between ca. 12,640 and 10,880 BP (before present) for the Magdalenian horizon (level IIIa), and between ca. 18,440 and 16,420 BP for the Solutrean horizon (level IIIb). Level IV is dated between ca. 32,560 and 23,780 BP (Finlayson et al., 2006).

Material and methods

Fieldwork and sorting

The herpetofauna fossil remains used for this study consist of disarticulated bone fragments collected by water-screening during the 1999–2005 excavation campaigns at Gorham's Cave (Fig. 2). All of the sediment was water-screened using superimposed 10, 5 and 0.5 mm mesh screens. The studied sample included more than 2000 fragments, representing 24 different taxa (Table 1). Tortoise remains and some larger bones have been collected on site from excavations.

Systematic attribution

Material from the 1999 to 2005 excavations was picked by Claire Valarino and identified by C. Gleed-Owen (Gleed-Owen, 2001; Gleed-Owen and Price, 2012). Since 2009, H.-A. Blain resumed study of Gibraltar herpetofaunal remains and identified part of the remaining material from Gorham's 2005 excavation campaign picked by J.M. López-García. The bones were identified following the general criteria given by Bailon (1991, 1999), Haller-Probst

(1997), Holman (1998), Ratnikov and Litvinchuk (2007) and Bailon et al. (2011) for amphibians, and Szyndlar (1984, 1991a, b), Barbadillo (1989), Bailon (1991), Barahona Quintana (1996), Barahona and Barbadillo (1997), Hervet (2000), Caputo (2004) and Blain (2005, 2009) for reptiles. Comparisons were drawn using the dry skeletal collections of the Museo Nacional de Ciencias Naturales (MNCN, Madrid, Spain) and our personal collections.

Climatic reconstruction

Paleoclimatic interpretations are based on the presence of herpetofauna species from each level. The Mutual Climatic Range (MCR) method (see Blain et al., 2009) was used to quantify palaeotemperatures and palaeoprecipitation. We simply identified the geographic region (divided into 10 × 10 km UTM squares) where all of the species present in the locality or in a stratigraphical level currently live. Careful attention has been paid so that real current distribution corresponds to potential ecological/climatic distribution, and is not strongly affected by other limiting or perturbing parameters, such as urbanization, landscape anthropization, predation, competition with other species, etc. In the case of the tortoise *Testudo hermanni*, for example, its current distribution in the Iberian Peninsula is strongly reduced by human activities and does not correspond to its potential climatic/environmental range (e.g., Llorente et al., 1995). Consequently *T. hermanni* has not been included in the MCR, although results have been contrasted with the climatic requirements of its geographically nearest extant representatives (mean annual temperature higher than 14 °C and mean annual precipitation lower than 700 mm; Llorente et al., 2004).

Analysis of the MCR in each level is based on the distribution atlases of the Iberian herpetofauna (Godinho et al., 1999; Pleguezuelos et al., 2004). Climatic parameters have been estimated for each 10 × 10 km UTM square, using various climatic maps of the Iberian Peninsula (Ninyerola et al., 2005). A total of 26 climatic parameters have been calculated for this study (Table 2).

For comparison with current climatic data, we extrapolated the climatic values (1970–2001) near the entrance of Gorham's Cave from the Iberian Peninsula climatic database (Ninyerola et al., 2005).

To measure aridity, we used Gaussen, Dantin–Revenga and De Martonne indices. The Gaussen Index ($P < 2 \times T$) considers that a month is dry if the pluviometric amount in a month (P), considered in mm, is lower than two times the value of the average temperature in °C of that month (T). The Index of Dantin–Revenga ($100 \times$ MAT/MAP) and the Aridity Index of Martonne MAP/ (MAT + 10) are calculated using the variables of mean annual temperature (MAT) and mean annual precipitation (MAP).

Results

Amphibian and reptile assemblages

The amphibian and reptile bone remains include more than 2000 elements, representing at least 24 taxa, including newts, toads, frogs, tortoises, turtles, lacertid and scincid lizards, geckos, and several snakes. In its entirety, the Gorham's Cave sequence documents a large part of the high herpetofaunal diversity observed today in Gibraltar (Table 1; Edgar, 2010) and neighboring parts of Andalusia (Pleguezuelos et al., 2004). Nevertheless, some taxa currently present in Gibraltar are not represented in the Gorham's fossil record, such as marine turtles, *Testudo graeca*, *Trachemys scripta* (introduced from North America), *Blanus mariae*, *Chamaeleo chamaeleon*, *Hemidactylus turcicus* and *Podarcis hispanica*. Such an absence may be explained by taphonomic or environmental reasons (marine turtles, *B. mariae* and *P. hispanica*) or may be by the fact that some species are known or thought to be

Table 1
List of the amphibians and reptiles currently represented in Gibraltar (according to Edgar, 2010) and their distribution as fossils in each level from Gorham's Cave.

	Species name	Common name	Today	IIIa	IIIb	IV
Amphibians	*Pleurodeles waltl*	Sharp-ribbed Salamander	i	x	x	
	Triturus pygmaeus	Pygmy Marbled Newt		cf.	cf.	cf.
	Lissotriton sp.	Indeterminate Newt		x	x	x
	Discoglossus sp.	Indeterminate Painted Frog			x	
	Alytes sp.	Indeterminate Midwife Toad			x	
	Pelobates cultripes	Western Spadefoot	e	x	x	x
	Bufo spinosus	Common Toad	i	x	x	x
	Epidalea calamita	Natterjack Toad	x	x	x	x
	Hyla meridionalis	Stripeless Tree Frog	i			sp.
	Pelophylax perezi	Perez's Marsh Frog	i			
Reptiles	*Caretta caretta*	Loggerhead Turtle	x			
	Chelonia mydas	Green Turtle	x			
	Dermochelys coriacea	Leathery Turtle	x			
	Testudo hermanni	Hermann's Tortoise			x	x
	Testudo graeca	Spur-thighed Tortoise	i			
	Emys orbicularis	European Pond Terrapin	i			indet.
	Mauremys leprosa	Stripe-necked Terrapin	i			
	Trachemys scripta	Red-eared Slider	i			
	Blanus mariae	Iberian Worm Lizard	x			
	Chamaeleo chamaeleon	Chameleon	i			
	Chalcides bedriagai	Bedriaga's Skink	x		x	
	Chalcides striatus	Three-toed Skink	x	x		
	Hemidactylus turcicus	Turkish Gecko	x			
	Tarentola mauritanica	Moorish Gecko	x	x		x
	Acanthodactylus erythrurus	Spiny-footed Lizard	e	x	x	
	Timon lepidus	Ocellated Lizard	x	x	x	x
	Podarcis hispanica	Iberian Wall Lizard	x			
	Psammodromus algirus	Algerian Sand Racer	x		sp.	
	Coronella girondica	Southern Smooth Snake	x	x	x	x
	Hemorrhois hippocrepis	Horseshoe Whip Snake	x	x	x	x
	Rhinechis scalaris	Ladder Snake	x	x	x	x
	Malpolon monspessulanus	Western Montpellier Snake	x	x	x	
	Macroprotodon brevis	False Smooth Snake	x		x	
	Natrix maura	Viperine Snake	e	x	x	x
	Natrix natrix	Grass Snake	x	x		
	Vipera latastei	Lataste's Viper	x	x	x	x

(x): presence; (i): introduced; (e): now extinct.

introduced in the Iberian Peninsula in historic times (like *H. turcicus*, *T. graeca*, *T. scripta* and *Ch. chamaeleon*). Conversely, some species are thought to be recently introduced by humans in Gibraltar but are well represented in Gorham's (*Pleurodeles waltl*, *Bufo spinosus*, *Hyla* and unidentified terrapin). In addition, a higher diversity during Pleistocene times is documented by the presence of two newts (*Triturus* cf. *pygmaeus* and *Lissotriton* sp.), *Discoglossus*, *Alytes*, *Pelobates cultripes*, *T. hermanni*, *Acanthodactylus erythrurus* and *Natrix maura*. This higher diversity, aside from the disturbance caused today by the urbanization, suggests that Gibraltar and the southernmost part of the Iberian coasts really acted as a refuge during the latest Pleistocene for both strictly thermophilous Mediterranean taxa (*Discoglossus*, *P. cultripes*, *T. hermanni*, and *A. erythrurus* among other) and some western 'Atlantic' taxa (*Triturus* cf. *pygmaeus* and *Lissotriton* sp.).

Climate reconstruction

The Gibraltar region features a Mediterranean climate with mild winters and warm and dry summers. Two main prevailing winds affect the climate of Gibraltar throughout the year: an easterly wind known as Levante (usually late summer, autumn and early spring) causes humid weather and warmer sea temperatures, while the westerly Poniente brings in cooler air and lowers the sea temperature. Precipitation, though concentrated in the autumn and spring, can be observed throughout the year. The MAT is 17.9 °C and MAP is 798 mm (Ninyerola et al., 2005). The average difference between the warmest (August) and coldest (January) months (MTW and MTC respectively), is 13.1 °C. The arid period is particularly long, lasting from May to September (five consecutive months).

Past climatic parameters were obtained from the use of the MCR method on the fossil herpetofauna assemblages (Table 2). Overlaps obtained correspond to various areas within the Iberian Peninsula as represented in Fig. 3. Climatograms have been made to better visualize the monthly evolution of temperature and precipitation, and respecting the scales $T = 2 \times P$ to evaluate directly the Gaussen Index (Fig. 4). Our climatic interpretation is synthesized in Table 3.

The overlap gives respectively 67 UTM squares for level IV, 20 squares for level IIIb and 22 squares for level IIIa (Table 2; Fig. 3). These squares occur in central-western and south-western Iberia for levels IIIa and IIIb, but for level IV, the overlap is extended and reaches the Catalan Mediterranean seashore at the north (Fig. 3). MAT ranges from 16.1 to 16.3 °C, and MAP from 685 to 763 mm (Table 2). The climate was warm with a high atmospheric temperature range. Summer was rather warmer, and winter was temperate. Rainfall was low and its distribution mainly irregular throughout the year (with its highest amounts during winter and spring), with four dry months during the summer and early autumn (from June to September) with rainfall lower by 40 mm. Aridity indexes suggest a semi-arid ombroclimate (Fig. 4; Table 3).

In comparison with current climatic data, all MCR-estimated MATs are about 1.6–1.8 °C lower than today. Similarly, winters were colder (difference for MTC = 3.3–3.9 °C) and summers were similar in warmth to today. MAP was slightly lower (35–113 mm) than today, but according to the Aridity Index of Gaussen there were only four dry months during the Late Pleistocene, as opposed to five dry months currently. The climate remained Mediterranean and semi-arid (according to the Aridity Index of Dantin–Revenga) or semi-humid (according to the Aridity Index of Martonne). Finally, continentality (or atmospheric temperature range) was

Table 2
Climatic values (1970–2001) from the vicinity of Gorham's Cave (obtained from Ninyerola et al., 2005) and climatic parameters calculated (in °C for temperature and mm for precipitation) by the Mutual Climatic Range method.

| | | Temperature | | | | | | | | | | | | | Precipitation | | | | | | | | | | | | |
| | | | MA | | | | | | | | | | | | | MA | | | | | | | | | | | |
		T	J	F	M	A	M	J	J	A	S	O	N	D	P	J	F	M	A	M	J	J	A	S	O	N	D
Level IV	N	67	67	67	67	67	67	67	67	67	67	67	67	67	67	67	67	67	67	67	67	67	67	67	67	67	67
	Mean	16.1	8.6	9.3	12.6	14.0	16.4	20.6	24.8	25.5	21.6	16.4	12.0	8.9	763	98	77	62	65	50	31	12	14	34	77	103	126
	SD	1.8	2.3	1.7	2.5	1.9	1.3	1.5	1.2	1.3	1.6	2.3	2.0	2.5	159	26	23	19	17	14	14	4	10	14	17	23	28
	Min	12	4	6	8	10	14	18	22	22	18	10	8	4	600	60	40	40	40	40	10	10	10	20	60	60	80
	Max	18	12	12	16	16	18	22	26	28	24	18	14	12	1100	140	120	110	110	100	60	30	60	80	120	140	170
Level IIIb	N	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20
	Mean	16.3	8.0	9.4	12.0	14.1	16.7	20.6	25.7	25.6	22.4	16.4	12.4	8.9	685	91	73	64	60	49	20	12	12	31	71	102	120
	SD	1.9	2.1	2.5	2.1	2.1	1.3	1.6	1.2	1.1	1.8	1.8	1.8	1.8	163	18	18	20	17	14	13	4	4	12	16	17	16
	Min	12	4	6	8	10	14	18	22	22	18	12	8	6	600	70	50	50	40	40	10	10	10	20	60	80	90
	Max	18	10	12	14	16	18	22	27	27	24	18	14	11	1200	130	120	100	90	100	60	20	20	60	120	140	150
Level IIIa	N	22	22	22	22	22	22	22	22	22	22	22	22	22	22	22	22	22	22	22	22	22	22	22	22	22	22
	Mean	16.3	8.0	8.9	11.6	13.5	16.1	20.5	24.6	24.6	21.5	15.4	11.8	8.0	709	94	79	58	54	56	26	12	12	30	74	104	118
	SD	1.5	2.9	2.1	2.5	2.4	1.6	1.6	1.5	1.5	2.5	2.6	2.5	1.9	148	14	18	21	18	17	16	4	4	12	19	20	17
	Min	14	4	6	8	10	14	18	22	22	18	12	8	5	600	80	60	40	40	40	10	10	10	20	60	80	90
	Max	18	11	11	14	16	18	22	26	26	24	18	14	10	1000	130	110	100	90	90	50	20	20	60	110	140	160
1970–2001		17.9	11.9	12.8	14.5	15.7	18.3	21.5	24.4	25.0	22.9	19.4	15.5	12.9	798.0	134.1	107.1	73.9	68.3	37.9	22.0	10.0	10.0	12.4	62.9	129.8	172.8

Mean annual temperature (MAT), mean annual precipitation (MAP), N = number of 10 × 10 km UTM squares of the overlap, SD = standard deviation, Min = minimum, Max = maximum.

higher during the Late Pleistocene than today, mainly due to lower winter temperatures.

Discussion

During MIS3–MIS2 up to the onset of the Last Glacial Maximum (LGM) (60–24 ka [thousands of years ago]), the climate is thought to have been rapidly fluctuating, and was harsher than the present day. The climate then became cooler and drier but more stable during the LGM (24–18 ka) (Fletcher and Sánchez-Goñi, 2008). According to Sánchez-Goñi and d'Errico (2005), in the Mediterranean region during the cold episodes of the latest Pleistocene, MAP was 400 mm lower and MTC were 6–13 °C lower than present. However, during the temperate phases, the pollen-based estimations suggest that MAP and MTC were similar to today. During the coldest episodes of MIS3 and MIS2, the occurrence of Ibero-North African xerothermic scrub (*Maytenus*, *Ziziphus*, *Periploca*, *Withania*, *Osyris*, among others) was recorded in coastal Murcia (Walker et al., 2011), Málaga (Fernández et al., 2007) and the southernmost extreme in the Gibraltar Peninsula (Carrión et al., 2008). The most striking feature is the broad occurrence of tree populations throughout the whole region, including continental territories. Genera like *Corylus*, *Quercus*, *Pinus* (e.g., *Pinus pinaster*), *Fraxinus*, *Alnus*, *Betula*, *Castanea*, *Taxus*, *Abies*, *Fagus*, *Salix*, *Sorbus*, *Juglans*, *Olea*, *Pistacia* and *Ulmus*, among others, are common components of Pleistocene pollen assemblages throughout the Iberian Peninsula (Carrión et al., 2003, 2008, 2011; González-Sampériz et al., 2010).

Climate in Gorham's Cave

The large terrestrial and marine mammal assemblages at Gorham's Cave include *Cervus elaphus*, *Capra pyrenaica*, *Equus caballus* and *Monachus monachus*, all of which show conclusive evidence of anthropic predation, including cut-marks, breakage, and disarticulation, which was further substantiated by the absence of carnivore damage or post-depositional taphonomic modifications. Both faunal assemblages from Levels III and IV show no significant differences in prey species present, and indicate mild and relatively humid Mediterranean conditions, similar to that found in southern Iberia today (Stringer et al., 2008; Riquelme Cantal and Cortés Sánchez, 2009). This is further substantiated by the herpetofauna, avifauna, pollen and charcoals analyses, which show that the Pleistocene landscape outside Gorham's Cave was dominated by a thermo-mesomediterranean subhumid profile with the existence of multiple biotopes (Gleed-Owen, 2001; Sánchez-Marco, 2004; Finlayson and Carrión, 2006; Finlayson et al., 2006; Carrión et al., 2008; Gleed-Owen and Price, 2012). The paleobotanical findings of meso- and thermo-Mediterranean plant species such as *Pinus pinea*, *Maytenus senegalensis*, *Myrtus communis*, *Olea europea*, *Pistacia lentiscus*, *Withania frutescens* and *Calicotome* in the Pleistocene pollen record of Gibraltar (Carrión et al., 2008) support this premise. Greater cooling would have led to the disappearance of thermo-Mediterranean temperatures, something that cannot have happened for any length of time in the past, because plants and terrestrial animals adapted solely to this thermotype survive in the region today (Hewitt, 2000; Finlayson, 2006). Consequently, Jennings et al. (2011) suggested that MATs in the southern Iberian Peninsula lowered by only 2.0 °C during the cold-dry phase of the latest Pleistocene.

However, some proxies indicate that the climate may have been harsher during the latest Pleistocene in Gibraltar. Analysis of Mg/Ca and oxygen isotope (δ^{18}O) ratios in a suite of fossil limpet *Patella* shells from Gorham's Cave showed that sea–surface temperature seasonality was greater during the last glacial by approximately 2 °C as a result of a greater cooling (Ferguson et al., 2011). Also, MCR
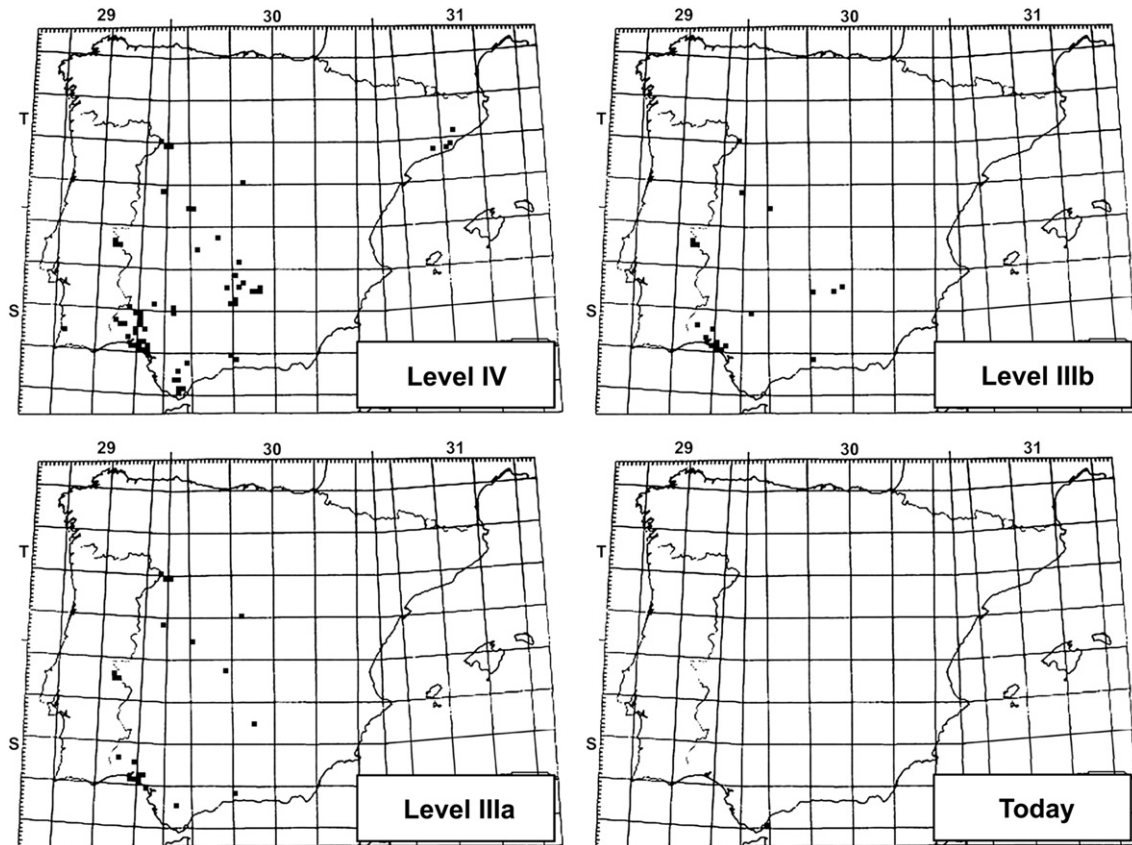
Figure 3. Overlaps of the current distribution of the taxa represented as fossils in each level from Gorham's Cave and living today in Gibraltar. Principal grid comprises 100 × 100 km UTM squares.

on the small mammal assemblages from Gorham's Cave suggested lower MATs (around 4 °C lower than present temperatures) and higher MAP than at present (23–75 mm). Summer was temperate (0.2 °C lower than today) and winter was harsher (8.7 °C lower than today) (López-García, 2008, 2011; López-García et al., 2011b). Similar climate values have been estimated from small vertebrate analysis in other sites such as Sala de las Chimeneas (Maltravieso Caves, southwestern Spain; Bañuls Cardona et al., 2012). For Gorham's Cave, such analysis is principally based on the presence of two shrews that currently only live in northern Spain ('Atlantic' mid-European chorotype): *Sorex minutus* and *Sorex* gr. *coronatus-araneus* (López-García, 2008, 2011; López-García et al., 2011b). Although MCR-estimated climatic parameters using herpetofauna assemblages do not imply such harsh temperatures, the presence of 'Atlantic' taxa (*Triturus* cf. *pygmaeus*, *Lissotriton* sp. and *Chalcides striatus*) accords well with the concept that Gibraltar acted as a refuge for northern Atlantic species too during the latest Pleistocene. Conversely, the predominance of strictly Mediterranean fauna and flora in Gorham's Cave clearly suggests that temperatures were not very harsh, despite winters being colder than today. This is also in accordance with the concept of 'refugia within refugia' (Gomez and Lunt, 2007).

In conclusion, herpetofaunal-based MCR-estimated climatic parameters fit quite well with other proxies, with estimated MATs about 1.6–1.8 °C lower than today. This is consistent with the persistence of terrestrial animals adapted solely to the thermo-Mediterranean thermotype in Gorham's Cave, as stressed by Jennings et al. (2011). In a similar way to small-mammal-based MCR-estimated climatic parameters, winters were colder and summers were similar to today. MAP was slightly lower (35–

113 mm) than today, but according to the Aridity Index of Gaussen there were only four dry months during the Late Pleistocene, as opposed to five currently, suggesting that the climate remained Mediterranean and semi-humid (according to the Aridity Index of Martonne). Our data suggest increased continentality during the latest Pleistocene (by around 3.5–4.6 °C), which is consistent with the greater sea–surface temperature seasonality estimated by Ferguson et al.'s (2011) analysis of Mg/Ca and $\delta^{18}O$ from limpets.

Climate in southern Iberian refuge and the extinction of the Neanderthals

What about the apparent contradiction in the persistence of thermophilous fauna and flora in southern Iberian refuge and the possibility of climate deterioration as being the cause of the disappearance of the last Neanderthals? As stressed by Jennings et al. (2011), the persistence of good rainfall levels may have been a significant factor in the late survival of Neanderthal populations in parts of southern Iberia. Even if the climatic fluctuations occurring in northern Europe and northern Iberia seem to have been less severe, in the southernmost part of the Iberian Peninsula Gorham's Cave records a slightly lower (−78 mm) level of rainfall in the Solutrean level IIIb (Fig. 4). Such a decrease in precipitation matches pollen records (e.g., MD95-2043 located in the Alboran Sea; Fletcher and Sánchez-Goñi, 2008; Carrión et al., 2012, Fig. 4) that show a strong decrease in arboreal pollen from approximately 31 to 15 ka. The lowest arboreal pollen percentage corresponds to the end of Heinrich Event 2, at approximately 24.5 ka (Fletcher and Sánchez-Goñi, 2008). This is also supported by the geochemical analyses of marine sediments from the Balearic basin (ODP Site
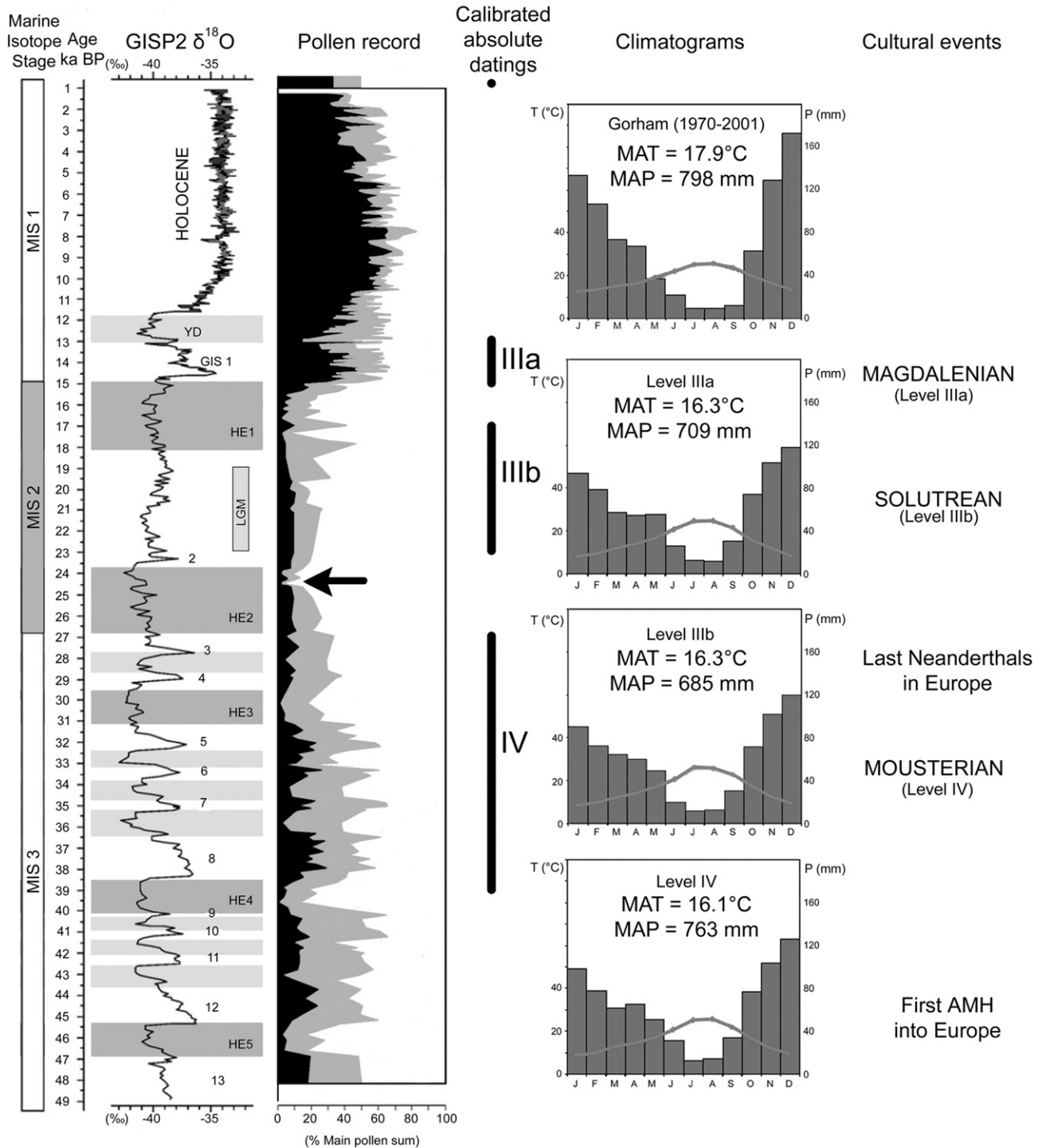
Figure 4. Comparison of Gorham's climatograms obtained from the MCR analysis with the pollen (Core MD95-2043) and GISP2 oxygen isotope records (modified from Fletcher and Sánchez-Goñi, 2008) and associated cultural events in Europe. For the pollen record, black area represents Mediterranean forest and grey area other arboreal taxa. Arrow indicates the lowest arboreal pollen percentage at approximately 24.5 ka. Abbreviations: AMH: Anatomically Modern Humans; GIS: Greenland Interstadial; HE: Heinrich Event; LGM: Last Glacial Maximum; MAT: Mean Annual Temperature; MAP: Mean Annual Precipitation. YD: Younger Drias.

975; Jiménez-Espejo et al., 2007) showing that conditions in southern Iberia were inhospitable (with MAT lowering about 4 or 6 °C compared with current temperatures) at approximately 24 ka cal BP (thousands of years ago calibrated before present). Hence, because the Neanderthals seem to have been associated with woodland habitats (see for example López-García et al., 2008, 2011a,b; 2012a,b; Burjachs et al., 2012; among others), the

disappearance of large forest tracts may have made them vulnerable, except in some small refuges in southern Iberia (e.g., the Rock of Gibraltar). Extreme aridity pulse as cause of local extinction has also been proposed by Shea (2008) for the Neanderthals of the Levant at 45 ka. The implication of these extinction events is that either the advantages of the coastal zone were not sufficient to buffer against episodes of extreme climate, or that the favored

Table 3
Climatic interpretation of the climatograms obtained for the different levels of Gorham's Cave.

		Level IV		Level IIIb		Level IIIa		Today	
Temperature	Mean annual temperature	16.1 °C	Warm	16.3 °C	Warm	16.3 °C	Warm	17.9 °C	Warm
	Atmospheric temperature range	16.9 °C	High	17.7 °C	High	16.6 °C	High	13.1 °C	Medium
	Summer temperature	2 months > 22 °C	Warm	3 months > 22 °C	Warm	2 months > 22 °C	Warm	3 months > 22 °C	Warm
	Winter temperature	MTC = 8.6 °C	Temperate	MTC = 8.0 °C	Temperate	MTC = 8.0 °C	Temperate	MTC = 11.9 °C	Mild
Rainfall	Mean annual precipitation	763 mm	Low	685 mm	Low	709 mm	Low	798 mm	Low
	Distribution of rainfall	Fairly regular	Winter	Irregular	Winter	Irregular	Winter	Irregular	Winter
	Type of precipitation	Rain		Rain		Rain		Rain	
Aridity	Gaussen Index	4	Mediterranean	4	Mediterranean	4	Mediterranean	5	Mediterranean
	Dantin-Revenga Index	2.1	Semi-arid	2.4	Semi-arid	2.3	Semi-arid	2.2	Semi-arid
	De Martonne Index	29.2	Semi-humid	26.0	Semi-humid	27.0	Semi-humid	28.6	Semi-humid

refugia contracted to an area too small to support viable populations.

Conclusions

The aim of this paper was to propose new quantitative data on the terrestrial climatic conditions throughout the latest Pleistocene sequence of Gorham's Cave using herpetofauna assemblages.

During the latest Pleistocene, the reconstructed climate was warm with a high atmospheric temperature range. Summers were warm and winters were temperate. Rainfall was lower, and its distribution irregular throughout the year (highest during winter and spring), with four dry months (June to September).

In comparison with current climatic data, all MCR-estimated MATs were 1.6–1.8 °C lower. Winters were colder (difference for MTC = 3.3–3.9 °C) and summers similar to today. Total rainfall was 35–113 mm lower than today, but according to the Aridity Index of Gaussen there were only four dry months during the Late Pleistocene compared with the five current months of dryness during the summer. The climate remained Mediterranean and semi-arid (according to the Aridity Index of Dantin–Revenga) or semi-humid (according to the Aridity Index of Martonne). Finally, the atmospheric temperature range was higher during the latest Pleistocene than today, mainly due to lower winter temperatures.

Such data reinforce the theory that high rainfall levels were a significant factor in the late survival of Neanderthals in southern Iberia. Lower rainfalls registered in the subsequent level IIIa, in agreement with pollen data and oxygen isotope records, suggest that increasing aridity during MIS 2 may have caused the loss of extensive forest tracts, thus making Neanderthals, if they were still surviving in southerly refugia by this late stage, more vulnerable.

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