Towards a Middle Pleistocene terrestrial climate reconstruction based on herpetofaunal assemblages from the Iberian Peninsula: state of the art and perspectives

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Abstract

The pattern of the varying climatic conditions in southern Europe over the last million years is well known from isotope studies on deep-ocean sediment cores and the long pollen records that have been produced for lacustrine and marine sedimentary sequences from Greece, Italy and the Iberian margin. However, although relative glacial and interglacial intensities are well studied, there are still few proxies that permit quantitative terrestrial temperature and precipitation reconstruction. In this context, fauna-based climate reconstructions based on evidence preserved in archaeological or palaeontological sites are of great interest, even if they only document short windows of that climate variability, because (a) they provide a range of temperature and precipitation estimates that are understandable in comparison with present climate; (b) they may allow the testing of predicted temperature changes under scenarios of future climate change; and (c) quantitative temperature and precipitation estimates for past glacials and interglacials for specific regions/latitudes can help to understand their effects on flora, fauna and hominids, as they are directly associated with those cultural and/or biological events. Moreover such reconstructions can bring further arguments to the discussion about important climatic events like the Mid-Bruhnes Event, a climatic transition between moderate warmths and greater warmths during interglacials. In this paper we review a decade of amphibian- and reptile-based climate reconstructions carried out for the Iberian Peninsula using the Mutual Ecogeographic Range method in order to present a regional synthesis from MIS 22 to MIS 6, discuss the climate pattern in relation to the Mid-Bruhnes Event and the thermal amplitude suggested by these estimates and finally to identify the chronological gaps that have still to be investigated.

Keywords: Vertebrates as climate proxy; Amphibian; Reptile; Mutual Ecogeographic Range; Middle Pleistocene; South-Western Mediterranean.

1. Introduction

Since Buffon, in his *Époques de la Nature* (1778), suggested that the climate of western Europe must have been much warmer in the past to support the elephants, hippos, big cats and rhinos that were found as fossils, the vertebrate record has been understood to provide information on past climatic conditions, via the use of analogy with modern representatives. At first, studies of fossil vertebrates involved only counting the number of taxa and organisms present in an archaeological or palaeontological excavation and interpretation of these data was done in a qualitative and descriptive way only. Since then there have been many advances in both the methods used for analysis of fossil vertebrate remains and a great increase in scope of the questions. They have been used to address quantitative palaeoenvironmental reconstructions (e.g. Chaline et al., 1995; Lyman and O’Brien, 2005; Villa et al. 2010; Lopes et al. 2013), effect of climatic variability on vertebrates (e.g. Blois and Hadly, 2009; Blois et al., 2010, 2013; Bryson et al. 2010; McDonald and Bryson, 2010), changes in the vertebrate communities over time (e.g. Stewart 2008, 2009; Hofreiter and Stewart, 2009), determination of refuge area (e.g. Stewart and Lister, 2001; Stewart and Cooper, 2008; López-García et al., 2010a), extinction and speciation processes (e.g. Lister, 2004; Nogués-Bravo et al., 2008; Gillespie et al. 2012), impact of vertebrates on flora (e.g. Johnson, 2009a, b; Gill et al., 2009, 2012; Faith, 2011; Brault et al., 2013), evolution of the ecological niches over time (e.g. Martínez-Meyer et al., 2004; Rödder et al., 2013) and finally the most advanced of these approaches involves quantitative reconstruction of palaeoclimatic conditions.

Methods for the quantitative inference of palaeoclimate using vertebrates dates back to the pioneering work of Brattstrom (1953, 1956), followed in the 1990's by an abundant literature (e.g. Markwick, 1994, 1998; Kay and Maden, 1996; Motuzco and Ivanov, 1996; Montuire et al., 1997; Aguilar et al., 1999; Montuire, 1999). The most commonly used vertebrates for palaeoclimatic reconstructions are mammals (of which small mammals dominate over herbivorous megafauna), followed by reptiles and amphibians. The parameters which can be reconstructed using vertebrate remains are principally temperature and precipitation (Table 1).

Methods for palaeoclimatic reconstructions based on vertebrates have increased both in number and accuracy in recent decades. However the application of most of these methods is restricted to a period or a biome/geographical location, is limited by the availability of a particular proxy or ecometric and in most cases does not permit a reconstruction of both temperature and rainfall. For example, in the case of palaeoclimatic reconstructions with thermal ecology (Brattstrom, 1956; Markwick, 1994, 1998; Böhme, 2006, 2008) and the relation size-temperature-metabolic rate (Denny et al., 2009; Makarieva et al., 2005; Sniderman, 2009; Head et al., 2009a, b, 2013), only temperature parameters can be inferred. In the case of reconstructions based on hypsodonty (Fortelius et al., 2002, 2006; Damuth et al., 2002; Eronen and Rook, 2004; Eronen et al., 2010b, 2011) it is only possible to infer precipitation, a factor that is always subject to large uncertainties for the past (Porch, 2010). Another limitation of some of these methods is that they can only be applied to a species that presents the necessary ecometric, such as the large size of *Titanoboa* (Head et al., 2009a), *Beelzebufo* (Makarieva et al., 2009) and *Barbaturex* (Head et al., 2013) or to a taxon that is restricted today to tropical environments such as Crocodylia (Markwick, 1994, 1998).

Finally, there are other methods that can only be used for more recent periods, such as the Mutual Ecogeographic Range (Martínez-Solano and Sanchiz, 2005; Blain et al., 2009, 2016a), a variant of the numerous methodologies for climate reconstruction which use the modern distribution of species such as the Mutual Climatic Range and the Modern Analogue Technique (see Birks et al., 2010 for a synthesis and comparison), due to the fact that it is necessary to have extant representatives for the species recovered from archaeological sites. This method has been applied mainly to the late Middle and Late Pleistocene-Holocene for small-mammals (e.g. López-García et al., 2008, 2010b, 2011a, b, c, d, 2013a, b; Bañuls et al., 2012, 2013, 2014; Fernández-García and López-García, 2013; Fernández-García, 2014; Rey-Rodríguez et al., 2016; Fagoaga et al., 2017, in press) and back to the earliest Pleistocene for herpetofauna (e.g. Martínez-Solano and Sanchiz, 2005; Blain, 2005, 2009, 2012-14; Blain et al., 2007, 2008a, 2009, 2010, 2011a, b, 2012a, b, 2013a, b, c, 2014a, b, c, 2015, 2016a, 2017a, b; Blain and Corchón Rodríguez, 2017; Agustí et al., 2009; Marquina et al., 2017; Villa et al., 2018a, b). Using this method in older periods with extinct taxa (especially mammals) and relating them to their closest current representatives could increase the error in palaeoclimatic reconstruction since the extinct taxon may not necessarily have had the same niche as its current representatives (Rödder et al., 2013), and during the past the biological communities were not necessarily analogous with present ones (Williams and Jackson, 2007; Semken et al., 2010; Urban et al., 2012; Correa-Metrio et al., 2012) and this disparity increases further back in time (Stewart, 2008). The presence of non-analogous or disparate communities is also a problem when reconstructions are based on current biomes or ecoregions, as in the case of the transfer function method (Hernández-Fernández, 2001; Hernández-Fernández and Peláez-Campomanes, 2003, 2005; Hernández-Fernández, 2006; Hernández-Fernández and Vrba, 2006; Hernández-Fernández et al., 2007) and the variant of the mutual climate range method of Polly and Eronen (2011), as in the past these biomes or ecoregions did not necessarily exist as today.

The Mutual Ecogeographic Range (MER) has been applied, under different names (see Lyman, 2016), to fossil amphibians and reptiles at a regional level (Catalonia) or for some Spanish provinces (Granada, Murcia, Burgos, Castellón and Valencia) by Blain (2005, 2009) and at a peninsular scale first by Martínez-Solano and Sanchiz (2005) and since then by Blain et al. (2009) and subsequent publications. According to Birks et al. (2010), the Mutual Climatic Range is part of indicator-species approaches (based on the "presence/absence of one or few taxa") whereas Modern Analogue Technique is part of assemblage approaches (based on the "presence/absence of many taxa"). As a bioclimate envelope approach is not generated for each taxon, MER seems to be closest to a Modern Analogue Technique. Moreover in contrast to the indicator species approaches, the assemblage approach considers the fossil assemblage as a whole (as we do, even if we are aware that generally a very few ecologically strong indicator species have more weight in such reconstruction than other more ubiquitous ones) and the relative abundances of all the different fossil taxa. In contrast to Modern Analogue Technique it is assumed (as in Mutual Climatic Range approaches) that a taxon has an equal probability of occurrence anywhere within its climate range (Hupper and Solow, 2004; Horne and Mezquita, 2008) even if this has been shown not to be true in many empirical studies.

Assuming niche conservatism, MER involves finding the modern sample(s) that is (are) most similar to the fossil assemblage. Then the past climatic conditions are inferred from the climate variable(s) for the analogous modern sample(s). Application of MER to the Spanish fossil record is possible because most of the fossil Pleistocene amphibians and reptiles belong to extant species, with only a few exceptions (see Blain et al., 2016b for a recent review). The climate reconstruction is then based on the mean of the whole analogous modern samples (expressed here as 10 x 10 km UTM squares) without any weighting as usually the distribution of the obtained values is normal (see for example Martínez-Solano and Sanchiz, 2005). Such a method, based only on absence/presence (and not abundance), is consequently free from taphonomical bias and over-representation of some species in the fossil assemblages that may be more linked with the diet preference of the agent of accumulation or to the close proximity of a particular environment (rocky areas for karst sites or water biotopes for lake sites) than with climate.

Lobo et al. (2016) verified the assumption that current ecological niches for amphibians represent a reliable inference tool for past environmental conditions. This assumption can also certainly be extended to reptiles. Lobo et al. (2016) also demonstrate that for direct raw inferences, the combined taxa sets do not improve in accuracy with the number of species included (above a certain sample size threshold), but that the precision, however, is quite variable among taxa, reflecting sometimes the effect of non-climatic distributional constraints.

In the last decade, a number of publications dealt with climate reconstruction from various Pleistocene localities within the Iberian Peninsula based on their preserved fossil amphibians and reptiles (Fig. 1, Table 2). This work enables a regional synthesis of the palaeoclimatic data obtained to date from the herpetofaunal assemblages of the Iberian Peninsula from MIS 22 to MIS 6, i.e. since the first supposed cold glacial to the penultimate glacial. This time period is an interesting interval because it encompasses the last part of the Early-Middle Pleistocene transition (a major transition in climate cyclicity), and shows stronger climatic fluctuations (higher intensity of cold and warm periods) and also intriguing climatic phenomena: the Early-Brunhes and the Mid-Brunhes Events. So, even if microvertebrate based climatic reconstruction is still fragmentary, they remain important and interesting because (a) they provide a range of temperature and precipitation estimates that are understandable in comparison with present climate; (b) they allow the testing of predicted temperature changes under scenarios of future climate change; and (c) quantitative temperature and precipitation estimates for past glacials and interglacials for specific regions/latitudes can help to understand their effects on flora, fauna and hominids, as they are directly associated with those cultural and/or biological events. All these issues will be discussed here in the light of herpetofauna-based temperature estimates and their suggested thermal amplitude and concluding by identifying the chronological gaps that have still to be investigated.

2. Material and methods

Most of the climatic estimates used in this synthesis were obtained using the same standardized nomenclature and methods, hence we did not encounter any of the problems of differing taxonomy or methods which can often affect synthetic work.

2.1. Small vertebrate sampling and taxonomical identification

Standardized techniques for the recovery of small vertebrates in Pleistocene archaeological sites are now applied by vertebrate palaeontologists over the whole Iberian Peninsula, independently of archaeological research teams. The small vertebrate fossil remains recovered from studied sites mainly consist of disarticulated bone fragments collected by wet-sieving during field work campaigns. Depending on the excavated surface or sampling strategies, the sediment was water-screened using superimposed 10, 5 and 0.5 mm (or 0.7 mm in some cases) mesh screens and bagged by square, layer and excavation levels. The microfossils were processed, sorted and taxonomically classified with the naked-eye in the larger size fractions and with the help of a binocular microscope under 10x magnification for the smaller size fractions. The resulting cranial and post-cranial elements have been checked by a palaeoherpetologist who separated amphibian and reptile remains from the bones of other small vertebrates.

The fragments were identified mainly following the general criteria given by Böhme (1977), Bailon (1991, 1999), Sanchiz (1984), Esteban and Sanchiz (1985, 1990), Sanchiz et al. (1993, 2002), Holman (1998) and Gleed-Owen (1998 and 2000) for frogs and toads, Barahona Quintana (1996), Barahona and Barbadillo (1997) for lizards, and

Bailon (1991), Szyndlar (1984) and Blain (2005) for snakes. Comparisons were made using the dry skeleton collections mainly of the Museo Nacional de Ciencias Naturales (MNCN, Madrid, Spain), the Muséum national d'Histoire naturelle (MNHN, Anatomie Comparée, Paris, France), and reference collections held at IPHES (Tarragona, Spain). Specific attribution of this material rests principally on the best diagnostic elements. Descriptions and illustrations of the fossil elements for each of the represented species are presented in the source publications (Table 2).

2.2. Mutual Ecogeographic Range

As described in the source papers (see Table 2), the MER analysis for each site is based on the distribution atlases of the Iberian herpetofauna (Pleguezuelos et al., 2004; Godinho et al., 1999), divided into 10 x 10 km UTM squares. Climatic parameters have been estimated for each UTM square using climatic maps of the Iberian Peninsula (Font Tullot, 2000, based on 1961-1990 values; Ninyerola et al., 2005, based on 1951-1999 values). The use of a modern distributional dataset "restricted" to the Iberian Peninsula is supported by the fact that most of the species represented today in the Iberian Peninsula correspond to Iberian endemic species (for example *Discoglossus jeanneae*, *Pelophylax perezi*, *Chalcides bedriagai*), French-Iberian species (*Pelobates cultripes*, *Bufo* gr. *bufo-spinosus*, *Timon lepidus* or *Rhinechis scalaris*) or Ibero-Maghrebian species (*Mauremys leprosa*).

When searching for analogous assemblages, careful attention has been paid to ensure that the actual current distribution corresponds to the potential ecological/climatic distribution and has not been strongly affected by other limiting or perturbing parameters, such as urbanism, landscape anthropogenic impacts, predation, or competition with another species. For example tortoises (*Testudo* sp.) are usually excluded from the analyses because their actual distribution is too different from their potential distribution. In addition, for Cueva Victoria (Murcia), *Bufotes* sp. (*viridis* group) has been excluded from the analysis not only because it is currently absent from the Iberian Peninsula but also because it may represent an extinct taxon and the imprecision of its systematic attribution hampered comparison with extant taxa (Blain et al., 2010a, 2016b).

For the present synthesis we only used four climatic parameters: mean annual temperature (MAT), mean temperature of the coldest month (MTC), mean temperature of the warmest month (MTW), and mean annual precipitation (MAP). For an accurate comparison between the different sites, sometimes located in different climatic areas within the Iberian Peninsula, the difference from current values (Δ) was calculated, thus allowing us to correct disparities in the estimated climate values between northern/southern and/or inland/littoral sites.

2.3. Habitat Weighting

In addition to the climatic parameters, the representation of forested habitats (%wood; Table 2) estimated from the composition of the amphibian and reptile assemblage using the Habitat Weighting method (see Blain et al., 2008b for its application to herpetofauna) has been compiled for each site. Even if not representing true environmental successions (because of the geographical and topographical disparities between sites), %wood will be interpreted here in comparison with the different climatic parameters to explore potential correlations with temperature and precipitation, in order to discuss and compare with the palynological reconstructions for southern Europe.

2.4. Chronological uncertainty

One of the main challenges of such a synthesis is to place the results into a wider, ideally global, stratigraphic context such as that provided by the marine isotope stratigraphy (e.g. Lisiecki and Raymo 2005). In the source papers, the correlation between a particular archaeological context and the marine isotope stratigraphy has usually been done using the range given by absolute (e.g. radiometric) dating at the site informed by the local palaeoclimatic reconstruction. For sites where the source papers provide a detailed discussion of geo- and biochronology, palaeomagnetic data and numeric dates, the age uncertainties have been reported as ellipses in Figure 2. Otherwise, no uncertainty is shown in the figure.

2.5. Statistics

For the statistical analyses, any repeated result has been deleted from the same stratigraphic level in order to avoid redundancy. Linear regressions have been used with the main goals of (1) evaluating patterns, if they exist, between pairs of climatic and ecological variables and (2) establishing the nature and strength of their relationships from the samples used in our analyses . Linear regression is an approach that permits modeling of the relationship between a dependent variable (y) and, in the case of simple linear regression, an independent or explanatory variable (x). In order to model such relationships we use linear predictor functions (linear models):

$$y = a\,x^{b}$$

where a represents the Y-intercept and b the slope value calculated from two given sets of data.

Although linear regression has been widely used for prediction, in this paper we mainly use it for evaluating the null hypothesis [H_0 ($b = 0$)] that is, if the slope obtained for each linear regression is equal to 0. If the p-value is <0.05 we can reject the H_0. In addition, we evaluate the strength of the relationships, denoted by the coefficient of determination (R^2).

The adjustment technique used in this study is Ordinary Least Squares (OLS) which aims to minimize the sum of the squares of the difference between the observed values of a given dataset and the predicted ones by the linear function (that is, the sum of the squares of the residuals). Regression functions were estimated using the statistical package JMP 13.

3. Results

3.1. Climatic and environmental synthesis

Table 2 presents the climatic and environmental parameters compiled for this synthesis. The number of observations is 52 corresponding to 10 archaeo-palaeontological sites, some of them represented by different stratigraphic levels and/or different samples. Despite the number of sites/levels represented in this synthesis, it is obvious from Fig. 2 that the records do not span the entire interval. It is the case particularly for the period between MIS 16 and MIS 12 (i.e. from 650 ka to 450 ka). Correlation with the MIS stages for the latest Early Pleistocene and early Middle Pleistocene (MIS 22 to MIS 17) are hampered by quite large chronological uncertainties. And finally even for the period between MIS 11 and MIS 6 (i.e. between 400 ka and 140 ka) where there are a larger number of studied localities, many stages and substages are still entirely undocumented, for example MIS 11e, 11d, the whole of MIS 10, and probably also MIS 7d to MIS 6b.

Despite the incomplete record, this synthesis allows comparison between sites and between periods. ΔMAT estimates range between -3.9ºC and +4.0ºC relative to current local temperature. ΔMTC ranges between -4.5ºC and +3.1ºC; ΔMTW between -4.1ºC and +2.6ºC; and ΔMAP values are always positive (i.e. higher than current values) reaching up to +518 mm in Cal Guardiola during MIS 22.

When comparing our results with the lettered marine isotope record (Railsback et al. 2015) (Fig. 2), it seems that negative peaks in the climate reconstructions, indicating cold conditions, fit well with the isotopic changes taking place in MIS 22 (at Cal Guardiola) and MIS 6 (at Estanque de Tormentas de Butarque H-02) while positive peaks in our climatic reconstructions, indicating warmer conditions, fit well with the isotopic patterns of MIS 11c (Gran Dolina T17) and MIS 9e (Gran Dolina T9). Also, the apparently long-lasting "warmer than present" climatic conditions registered in level TD6 from the Gran Dolina (T55 to T32) seems to fit with the isotopic pattern of MIS 21.

The environmental parameter for forest and shrub land cover (%wood) ranges between a maximum value of 41.5% in Gran Dolina TD6 (T47 = MIS 21) and a minimum value of 11.2% for Cueva Victoria (MIS 22) (Table 2, Fig. 2). In this context, %wood does not represent any palaeoenvironmental temporal evolution as the representation of woodlands also depends on the topography and soils around the different archaeological sites that are not taken into account in this study. For an effective palaeoenvironmental reconstruction, a sort of "Δ%wood" must be evaluated in order to be able to compare how different from the present the woodland cover was for each of the sites. Nevertheless due to the modern human impact on the Iberian landscape such approximations would have been problematic and highly controversial.

3.2. Comparison between parameters

Table 3 summarizes the results obtained in the regression analyses. When the dependent/independent variable pairs are mean annual temperature (MAT)/mean temperature of the coldest month (MTC) and MAT/mean temperature of the warmest month (MTW) both regressions give slopes that are significantly different from zero. In addition, the coefficients of determination are high, especially that of MTC on MAT. These results are expected because MAT depends on both MTC and MTW. The distribution of the data in the parameter space defined by MTC on MAT (Fig. 3A) is very homogeneous. Nevertheless, the Gran Dolina TD6 sample T47 falls under the lower limit of the confidence interval indicating the lowest MTC value as a function of the MAT value. On the other hand, ETB (H-02) exhibits a high MTW value in relation to MAT (Fig. 3B).

When the independent variables are those related to temperature and the dependent is the MAP, all regressions provide slopes significantly different from 0 (Fig. 4).

Nevertheless, it is noteworthy that MAP on MTW supplies the highest coefficient of determination and the lowest *p*-value indicating that the MAP is better predicted by the MTW (Fig. 4C). Interestingly, all the slopes present negative values indicating that higher annual precipitations are associated with lower annual and seasonal temperatures. The bivariate plot shows that Cal Guardiola presents a very high rain regime in relation to temperature variables (Fig. 4A, B, C). On the other hand, Ambrona and ETB (H-02) present a low MAP value when plotted against MAT and MTC (Fig. 4A, B). In addition, Ambrona and TE-URU display the lowest values when MTW is the independent variable (Fig. 3C).

Consistent with expectation, ΔMTC and ΔMTW are strongly correlated with ΔMAT (Fig. 5). In the first case, Cal Guardiola falls on the lower limit of the confidence interval and Áridos-1 well beyond the upper one (Fig. 5A). In the second case, Cal Guardiola and Valdocarros II (level 4) are located under the lower limit of the confidence interval while Ambrona is above the upper limit (Fig. 5B). No ΔMT variable (i.e. MAT, MTC and MTW) is significantly correlated with ΔMAP. This last fact is quite suprising however most glacial modeling shows that increase in ice cover is linked with an increase in winter rainfall (e.g. Vigne and Bailon, 2000; Nesje et al., 2008; Hodell et al., 2008), demonstrating that temperature is not necessarily directly correlated with precipitation. This lack of correlation between ΔMAP and ΔMT raises issues for palaeoprecipitation reconstructions based on vertebrate proxy, especially on amphibians that are strongly related with such parameters (Blain et al., 2008b, 2009).

Considering %wood as the independent variable, the only two regressions that provide slopes significantly different from zero are MTW and MAP (Fig. 6A, B), the second one supplying a higher coefficient of correlation and a lower *p*-value. Interestingly, the MTW gives a negative slope (Fig. 6A) while the MAP provides a positive one (Fig. 6B) indicating that as a general rule the forest cover (%wood) is higher when summers are colder and the amount of rainfall is larger. In both cases, the variance in the data is high. A particular note is the low value of the tree cover estimated for Ambrona and CDLB (CB3) with respect to the MTW (Fig. 6A).

Lastly, when the differences between Early-Middle Pleistocene estimates and modern climatic values (Δ) are used as independent variables and the %wood as the dependent one, the low value of the coefficients of determination indicates a weak relationship among these pairs of variables (Fig. 7). The only two regressions that provide slopes statistically different from zero are ΔMAT and ΔMAP. When the independent variable is ΔMAT, Cal Guardiola displays the highest %wood value and Ambrona the lowest one (Fig. 7A). When the independent variable is ΔMAP, Cueva Victoria 2 shows the lowest %wood and Gran Dolina-TD10 (T16) the highest one, although not exceeding the upper limit of the interval of confidence (Fig. 7B).

4. Discussion

Interglacials (and glacials) are phenomena that can be considered widespread (probably of global extent), even if their regional expression is neither globally uniform or synchronous (PAGES, 2016). Numerous records are used as temperature proxies (like % arboreal pollen or alkenone-based sea surface temperature estimates in marine records) but most of them do not propose temperature estimates comparable with modern climate values. Even after a decade of herpetofauna-based palaeoclimatic quantitative estimates on the Iberian Peninsula, the reconstructed record is still highly fragmentary compared with that resulting from lake and marine pollen or isotopic sequences (see Fig. 2). However, they remain important and interesting because (a) they provide a range of temperature and precipitation estimates that are understandable in comparison with present climate; (b) they allow the testing of predicted temperature changes under scenarios of future climate change (between 1 and 3ºC worldwide for next 100 years but up to 6ºC for other scenari; e.g. Proistosescu and Huybers, 2017); and (c) quantitative temperature and precipitation estimates for past glacials and interglacials for specific regions/latitudes can help to understand their effects on flora, fauna and hominids.

4.1. How cold were the glacial complexes?

The uplands of the Mediterranean are thought to have been particularly important centers of biotic refuge. The mountainous peninsulas of southern Europe provided refuge for temperate biota during Quaternary cold stages when northern Europe and the Alps were covered by ice sheets and permafrost, and the lowland areas of the Mediterranean were characterized by cold and dry steppe (Hewitt, 1999). This is thought to be responsible for genetic diversity with a richness of endemic species (Blondel and Aronson, 1999). Pollen records from long lacustrine sequences confirm that the mid-altitudes of this region were a refugial area (wet enough but not too cold) for temperate tree taxa through multiple glacial cycles (Bennett et al., 1991; Tzedakis, 1993).

Among the climatic reconstructions, two localities are particularly interesting for documenting cold periods: Cal Guardiola (tentatively correlated with MIS 22; Agustí et al., 2009) and Estanque de Tormentas de Butarque H-02 (tentatively correlated with MIS6a by Blain et al., 2017b).

4.1.1 Marine Isotope Stage 22

The palaeontological locality from the latest Early Pleistocene of Cal Guardiola (Barcelona, NE Spain) has yielded fossil remains of the following amphibians and reptiles: *Bufo* gr. *bufo-spinosus* and *Epidalea calamita*, *Rana* cf. *temporaria*, cf. *Testudo* s.l., cf. *Lacerta* s.l. and small sized lacertids and *Natrix* cf. gr. *natrix-astreptophora* (Blain, 2005, 2009). This herpetofauna, as a whole, could be indicative of colder and especially more humid climatic Mediterranean conditions than those which currently occur in this area. Today in the Iberian Peninsula, *B. spinosus*, *E. calamita*, *R. temporaria* and *N.* gr. *natrix-astreptophora* are found together in an area included within the Eurosiberian bioclimatic domain. The resulting overlap of their current distribution suggests a MAT = 11.6 ± 1.9°C and a MAP = 1168 ± 430 mm: i.e. much colder (-3.9ºC) and wetter (+ 518 mm) by comparison with modern values for the area. MTC was estimated as 4.5 ± 2.2°C and MTW 18.9 ± 1.7°C (Agustí et al., 2009). Summers were then much colder than today (-6.7°C relative to present values) and winter slightly colder (-2.7°C). However this reconstruction must be nuanced by the occurrence of tortoises (cf. *Testudo* s.l.), that would suggest warmer and dryer conditions, even if as said before modern potential distribution for tortoises in the Iberian Peninsula is largely unkown. Landscape reconstruction based on herpetofauna shows the prevalence of a humid environment comprising both open herbaceous areas and wooded areas (37.0 %).

By comparison, large mammals from Cal Guardiola have suggested temperate climatic conditions with the occurrence of primates (*Macaca sylvanus* cf. *florentina*; Alba et al., 2008) and hyenas (*Pachycrocuta brevirostris*; Madurell-Malapeira et al., 2009), large expanses of water (indicated by the abundance of hippos) and woodlands (indicated by the large representation of cervids and fallow-deer).

In the same way, palaeobotanical analyses (pollen and macroremains) suggested warm-temperate and humid conditions and a vegetal cover composed of a mixed deciduous forest with significant numbers of oaks (*Quercetum mixtum* formations). Thermophilous, mesohygrothermophilous and river forest species are also present, including some taxa rarely recorded for the Pleistocene, e.g., the mesocratic group of species represented by *Juglans*, *Carya* and *Platanus* (Postigo Mijarra et al., 2007). In addition, statistical analysis of herpetofaunal estimates shows that Cal Guardiola displays high rainfall regime and tree coverage in relation to temperature (Fig. 4A, B, C; Fig. 7A).

As a result, MER estimates for Cal Guardiola are clearly colder, whereas other proxies suggest warm and humid conditions. However, close comparison between proxies is hampered by the fact that the context of the herpetofaunal remains within the Cal Guardiola stratigraphical sequence is not yet well understood and consequently we have no way to determine whether the studied amphibian and reptile remains are exactly contemporaneous with the recovered large mammals and palaeobotanical remains. In addition, taphonomic studies (Madurell-Malapeira et al., 2012) suggested that the whole assemblage may have been dragged down by a flood event in a mountain spring. Such a flood could have transported cold-tolerant species (like *Rana temporaria*) downstream from higher altitudes, thus lowering temperature estimates for Cal Guardiola. Nonetheless, attribution of the cold period represented by the herpetofaunal assemblage to MIS 22 agrees with the chronological range given by palaeomagnetism, biochronology and absolute dating (ESR-US) for the sequence of the nearby, stratigraphically correlated with Cal Guardiola, site of Vallparadis which is dated between 1.0 and 0.83 Ma (Madurell-Malapeira et al., 2010; Martinez et al., 2010; Lozano-Fernández et al., 2015).

Consequently, if the Cal Guardiola cold herpetofaunal assemblage corresponds to MIS 22 and is not affected by transport, it represents an interesting data point as it documents how cold was the climate during this MIS (centred on 0.87 Ma) representing the first Quaternary ice sheet expansion associated with a sea-level drop of over 100 m (Maslin and Ridgwell, 2005; Muttoni et al., 2007).

Cueva Victoria is another Iberian palaeontological site recently attributed to MIS 22 (Gibert et al., 2016). It is a karstic cavity located near the city of Cartagena (Murcia, SE Spain), first excavated in 1976. Its abundant and well preserved large mammal fauna date from the late Early Pleistocene (1.6 to 0.8 Ma). It is worth mentioning that this site has provided the only specimens of the African cercopithecid *Theropithecus oswaldi* recovered from Europe. It has also yielded five teeth (Gibert et al., 1995; Ferràndez-Cañadell et al., 2014) and a phalanx (Martínez-Navarro et al., 2005) whose attribution to the genus *Homo* (Gibert and Pons-Moyá, 1984; Ribot Trafi et al., 2012-14) greatly contributed to the media coverage of the site. Earlier analysis of the fauna, based on the stage of evolutionary development of *Stephanorhinus etruscus*, placed the site at 1.6 Ma (Agustí et al., 1987), and Blain et al. (2008a) proposed that the normal chron at the top of Cueva Victoria can best be assigned to the base of the Jaramillo event, with an estimated age of 1.072 ± 0.2 Ma (MIS 31). Gibert et al. (2016) constrain the age of the vertebrate remains from Cueva Victoria by palaeomagnetism, vertebrate biostratigraphy and ^{230}Th/U dating and interpret the lower reversal (N-R) to be the end of the Jaramillo magnetochron (0.99 Ma). These ages bracket the chronology of the fossiliferous breccia between 0.99 and 0.78 Ma, suggesting that the capping flowstone was formed during the wet MIS 19. Consequently, according to these authors, the age of the breccia in the upper part of Cueva Victoria is ~0.9-0.85 Ma (i.e. MIS 22).

Two palaeoclimatic reconstructions based on herpetofaunal remains have been carried out for Cueva Victoria: the first one using the collections from the first field campaigns of the Museu de Geologia de Barcelona (Blain, 2005, 2009; Blain et al., 2008a; Agustí et al., 2009) and then the collections from the 1984-2009 field campaigns of the Museo Arqueológico Municipal de Cartagena, Murcia (Blain, 2012-2014). No information associated with the material from these two collections permits a more precise stratigraphical localization within the fossiliferous breccia (only the name of the chambers was given on the original labels).

The first reconstruction (Blain et al., 2008a) is based on the following recovered fauna of anurans and squamate reptiles: cf. *Pelodytes* sp., *Bufo* gr. *bufo-spinosus*, *Blanus cinereus*, *Tarentola* sp., *Chalcides* cf. *bedriagai*, *Timon* cf. *lepidus* and indeterminate small lacertids, *Natrix maura*, *Coronella girondica*, *Rhinechis scalaris* and *Malpolon* cf. *monspessulanus* (Blain, 2005, 2009; Blain et al., 2008a). In Cueva Victoria, the overlap resulting from such an assemblage suggested a MAT slightly cooler than present (-1.0°C lower than at present in the area), with cooler winters but warmer summers and above all higher MAP (+ 387 mm). The reconstructed landscape may correspond to an open woodland environment (21.0%). These results match well with the presence in Cueva Victoria of the Hermann's tortoise (*Testudo hermanni*; García-Porta, 2001), whose current distribution in the Iberian Peninsula (restricted to Catalonia) is characterized by MAT above 14°C and MAP below 700 mm (Cheylan, 1981; Llorente et al., 2004).

The second reconstruction (Blain, 2012-2014) gives more temperate results. It is worth noting that from a statistical point to view, it deviates more strongly from the general trends. The faunal list of the material hosted in the Museo Arqueológico Municipal de Cartagena is composed of 6 anurans (*Pelobates cultripes*, *Pelodytes* sp., *Bufo* gr. *bufo-spinosus, Epidalea* cf. *calamita, Bufotes viridis* s.l. and *Pelophylax perezi*), 5 lizards (*Tarentola mauritanica*, *Chalcides bedriagai*, *Acanthodactylus erythrurus*, *Timon lepidus* and a small indeterminate lacertid) and 3 snakes (*Malpolon monspessulanus*, *Rhinechis scalaris* and *Vipera latastei*). This study completed previous faunal lists of Blain et al. (2008a), adding *P. cultripes*, *B. calamita*, *B. viridis* s.l., *P. perezi*, *A. erythrurus* and *V. latastei*. The large abundance of green toads (*B. viridis* s.l.), Montpellier snakes (*M. monspessulanus*) and ladder snakes (*Rh. scalaris*) is indicative of dry conditions, with well developed steppe and rocky environments. Evidence for woody areas is rather scarce (11.2%). This reconstruction is consistent with the presence of *Theropithecus*, a taxon that displayed a diet more based on C_4 plants than *Homo* in Africa (Cerling et al., 2013). Reconstructed climatic parameters suggested a MAT = 17.2 ± 1.6°C, slightly lower (-0.5ºC) than modern values, and MAP = 611 ± 160 mm, thus higher (+282 mm) than current values.

These results seem to indicate that Cueva Victoria was formed during a cold-temperate and wetter period than today but temperature estimates are far warmer than those obtained for the northern Iberian site of Cal Guardiola. Consequently two hypotheses can be made: 1) there was a stronger latitudinal temperature gradient than today, or 2) the chronology of the Cueva Victoria upper breccia should be correlated with early MIS 21 and thus, as said by Gibert et al. (2016), would correspond to the first entrance of *Theropithecus* into Europe during or just after MIS 22 (when climate improved but sea-level was not yet high). In this second hypothesis, the second more temperate climate reconstruction based on the herpetofaunal assemblage comprising green toads (*Bufotes viridis* s.l.), and representing the last appearance of this anuran group in the Iberian Peninsula (Blain et al., 2010a, 2016b), would be correlated with MIS 23. This could also suggest that the diseappearance of *Bufotes viridis* s.l. from the Iberian Penisula at that time would have been linked with the harsher conditions of MIS 22.

4.1.2 Marine Isotope Stage 8

According to the deep sea oxygen isotope records, MIS 8 does not seem to have been a particularly cold glacial, at least in its early part. This means that it can be difficult to securely correlate sites clearly with either MIS 8 or the end of MIS 9. The Cuesta de la Bajada (Teruel, eastern Spain) herpetofaunal assemblage has recently been suggested as representing cold climatic conditions during part of MIS 8 (Blain et al., 2017a). Cuesta de la Bajada is a Middle Pleistocene site at which some of the earliest evidence of Middle Palaeolithic stone tool traditions and primary access to fleshed cervid and equid carcasses by hominins have been documented (Santonja et al., 2014, 2016), (Domínguez-Rodrigo et al., 2015). The numerical ages derived from the combination of

ESR and OSL dating methods indicate that the lowermost level CB3 is between 317 and 240 ka, which encompasses MIS 8 and most of MIS 9 (Santonja et al., 2014; Arnold et al., 2016; Duval et al., 2017). These dates are corroborated by the small-mammal study, in particular the morphological state of *Cricetulus* (*A.*) *bursae*, *Arvicola* aff. *sapidus* and *Microtus* (*I.*) *brecciensis*. This makes it possible to place the site of Cuesta de la Bajada (levels CB3 and CB2) in the advanced, but not final, Middle Pleistocene (Sesé et al., 2016). The large mammal assemblage composed of *Canis lupus*, *Elephas* (*Palaeoloxodon*) *antiquus*, *Stephanorhinus* cf. *hoemitoechus*, *Equus chosaricus*, *Cervus elaphus*, *Bos primigenius*, *Rupicapra rupicapra* and *Capra* sp., is also characteristic of the Middle Pleistocene (Santonja et al., 2014).

The herpetofaunal assemblage from Cuesta de la Bajada is composed of at least 9 taxa, including 6 anurans (*Alytes obstetricans*, *Pelodytes punctatus*, *Bufo* gr. *bufo-spinosus*, *Epidalea calamita*, *Hyla* gr. *arborea-molleri*, and *Pelophylax perezi*), a small-sized lacertid lizard (Lacertidae indet.), and 2 snakes (*Coronella* cf. *girondica* and *Vipera* sp.). *Hyla* gr. *arborea-molleri* is the only species represented in Cuesta de la Bajada that is currently absent in the area (the species is present today in the northwestern Iberian Peninsula) and whose presence would suggest cool and moist climatic conditions. The palaeoclimatic parameters suggest for CB2 and CB3 that MAT was much colder (-2.2ºC and -2.5°C, respectively) and MAP much higher (+ 291.9 and +282.3 mm) than today in the Teruel area. The summer was temperate and the winter was cold, with three months of mean temperatures below 6°C. Rainfall was low but its distribution was regular, occurring throughout the year but with the highest levels during winter and spring and lowest levels occurring in the summer (July and August) (Blain et al., 2017a). Summer and winter temperatures are similarly depressed (January and July

1.2°C lower than today). The palaeoenvironmental reconstruction based on the herpetofaunal assemblage suggests a sparsely wooded (15-20%) patchy landscape with a large representation of dry herbaceous areas, and scrubland habitats together with aquatic habitats. These reconstructions are consistent with other proxies recovered from Cuesta de la Bajada (pollen, small and large mammals) and other European MIS 8-9 palaeoclimatic records (see Blain et al., 2017a), enabling correlation of levels CB2 and CB3 (which are also constrained by the OSL and ESR dates), with the later part of MIS 8 (265-257 ka) or MIS 9b (303-290 ka).

Such a cold climate and minor woodland cover (15 to 20% of the total landscape) described above are similar to that observed in level 2 of the Valdocarros II archaeological site (Madrid, Spain), which is correlated to the latest part of MIS 8 just before Termination III (Blain et al., 2012b). This would suggest that rather similar climatic and environmental conditions were in place during these cold periods over large areas of the inner Iberian Peninsula.

The archaeological site of Valdocarros II is located in an abandoned meander of the Valdocarros unit. Amino-Acid Racemization provided ages of 254 ± 47 ka BP (made on ostracods *Herpetocypris reptans*) and 262 ± 0.7 ka BP (made on herbivore teeth) corresponding to the end of MIS 8 and the beginning of MIS 7 (Panera et al., 2011). The site consists of four layers (1, 2, 3 and 4), fining upwards from silt to silty-clay, each one 30-50 cm thick and several tens of meters wide. For level 2, the occurrence of *Hyla* gr. *arborea-molleri* again, which is currently absent from large areas in the south of the Iberian Peninsula, suggest cool and moist climatic conditions, whereas levels 3 and 4 show warmer conditions. The reconstructed climate for level 2 is relatively cold with MAT 1.8ºC lower than today. These cooler climatic conditions are mainly linked to a greater decrease in the summer (-2.9ºC) (Fig. 5B) than in the winter (-1.0ºC) temperatures. Even if rather low, the total amount of rainfall is higher than the current level in Madrid. Environmental reconstructions based on the herpetofaunal assemblages suggest that riverine woodlands are somewhat poorly represented in level 2 (less than 15% of the total) unlike in more temperate-warm levels 4 and 3 (with woodlands reaching 34%), where the presence of *Bufo* gr. *bufo-spinosus* may indicate more stable climatic conditions than in level 2.

Finally, among the Pleistocene localities of the Sierra de Atapuerca, the site called Sima del Elefante in its upper part (TE-URU) has fossiliferous levels pertaining to the late Middle Pleistocene (350-250 ka). Two travertine samples from the upper part of TE18 Unit were dated using U/Th series, giving 254.727 +13.121/-11.773 ka BP, and 307.175 +22.579/-18.868 ka BP (Lombera-Hermida et al., 2015). Such ages were already suggested by the small-mammal biochronological studies that provided an age between ca. 250-350 ka for levels TE18 and TE19, i.e. slightly younger than Atapuerca-TD10 and quite similar to Atapuerca-Galería (López-García et al., 2011d). At that time the amphibians and reptiles from the two upper levels TE18 and TE19 were analyzed and have proved to be one of the richest assemblages of all the localities of the Sierra de Atapuerca (Blain et al., 2011b). The faunal list is composed of 18 taxa made up of urodeles (*Salamandra salamandra* and *Lissotriton helveticus*), anurans (*Discoglossus* sp., *Alytes* sp. *Pelobates cultripes*, *Pelodytes punctatus*, *Bufo* gr. *bufo-spinosus*, *Epidalea calamita*, *Hyla* gr. *arborea-molleri* and cf. *Rana* sp.), a terrestrial tortoise (*Testudo* s.l.), lizards (*Lacerta* s.l., *Podarcis* sp. and *Anguis fragilis*) and snakes (*Natrix* gr. *natrix-astreptophora*, *N. maura*, *Coronella* cf. *girondica* and *Vipera latastei*). The

TE19 assemblage suggested a slightly warmer (+0.4ºC) and moister (+95 mm) climate than the current one (Blain et al., 2011b). However, the MAP was low given the estimated temperatures, specifically those for the MTW (Fig. 4C). The landscape was probably composed of a gallery forest (20.0%) along a quiet water river within a Mediterranean environment alternating laterally between dry meadows, rocky or stony areas and open scrubland.

The presence of charcoal pieces of *Pinus silvestris/nigra* in TE19 together with the abundance of horses has been interpreted as an indicator of cold, dry climatic conditions, with the development of open landscapes (Rosas et al., 2006). However, López-García et al. (2011d) suggested that the presence of horses together with other herbivores such as *Stephanorhinus hemithoecus*, *Cervus elaphus*, *Dama dama* and *Bos* sp. is indicative of open forests, and the occurrence of taxa representative of temperate Europe, such as *C. elaphus* and *D. dama*, could be associated with mild climatic conditions. Moreover, the small mammal assemblage is dominated by temperate-Mediterranean taxa such as *Iberomys brecciensis*, *Terricola atapuerquensis*, *Oryctolagus* sp., *Crocidura* sp., *Miniopterus schreibersii* and *Rhinolophus euryale-mehelyi* (López-García et al., 2011d). Ongoing studies of the sublevels within TE19 suggest some disparities between them and TE19f may have been much colder than TE19c (Blain, unpublished data). Waiting for a new contextualization of these remains and MER estimates, TE19 may correspond, taking into account dating of the underlying level TE18, to the MIS 10a/9e, the MIS 9b/9a or the MIS 8a/7e transitions.

4.1.3 Marine Isotope Stage 6

In southwestern Mediterranean Europe, only a very few archaeo-palaeontological sites document the terrestrial faunas of the penultimate glacial. Recently the minimum age of the archaeological site of Estanque de Tormentas de Butarque H-02 (Madrid, Central Spain) has been estimated as MIS 6, based on the occurrence of the proboscidean *Palaeoloxodon antiquus* together with the rodents *Microtus brecciensis* and *M. arvalis* (Laplana et al., 2015; Blain et al., 2017b). TL samples taken from the overlying level yield ages of 84.6 (+12.6/-11.2), 74.9 (+10.2/-9.2) and 56.8 ± 4 ka, respectively (Domínguez Alonso et al., 2009). Although this site is not directly dated, i.e. in the same layer as the fossil assemblage, the ages of the overlying level provides a minimum age of MIS 5 and rodent biochronology suggests a late Middle Pleistocene age between MIS 8 and MIS 6 (Laplana et al., 2015).

The herpetofaunal assemblage from H-02 (ETB) is composed of at least 10 amphibians and reptiles (Blain et al., 2017b): six anurans (*Discoglossus* sp., *Pelobates cultripes*, cf. *Pelodytes* sp., *Bufo* gr. *bufo-spinosus*, *Epidalea calamita* and *Pelophylax perezi*), one turtle (*Emys* or *Mauremys*), one or two indeterminate lizards (Lacertidae indet.) and two snakes (*Natrix* gr. *natrix-astreptophora* and *Coronella girondica*). Quantitative climate reconstruction applied to the herpetofaunal assemblage suggested a colder (-3.0ºC) and slightly wetter (+122.8 mm) climate than present. The temperature difference is greater for winter (ΔMTC = -3.1ºC) than for summer (ΔMTW = -1.6ºC), which remains reasonably temperate. A relevant aspect is the low relative amount of rain in relation to annual and winter temperatures (Fig. 4A, B). Palaeoenvironmental reconstruction suggests a large representation of dry environments on the overlying plateau, together with a probable corridor of humid meadows and woodlands (16.9%) along the river where the site is located (Blain et al., 2017b).

Even if the chronology of the site has still to be constrained, it can be correlated with part of the penultimate glacial (~ 185–135 ka) corresponding to the late Saalian glaciation in Europe. Global sea-level reconstructions (Thompson and Goldstein, 2006; Elderfield et al., 2012; Bintanja et al., 2005) indicate a sea-level drop of more than 100 m towards the end of MIS 6 (after 150 ka). Sea surface temperatures were 5ºC lower than present as the climate approached a stable maximum glacial state, culminating in one of the largest Quaternary glaciations (Margari et al., 2014). With regard to temperature and precipitation quantification, several different reconstructions have concluded that the climate of at least some intervals in early MIS 6 must have been characterized by temperature depressions (summer and annual) of 8–9°C below modern values and annual precipitation of >2000 mm (and possibly >3000 mm) in the highest mountains in order to form glaciers (Hughes et al., 2007; Hughes and Braithwaite, 2008). Modeled atmospheric temperatures for the Northern Hemisphere suggest that extremes were 17 ± 2.7ºC below present (Bintanja et al., 2005). Long pollen sequences from France have also yielded estimates for MAT and MAP (Guiot et al., 1989, 1993). At La Grande Pile (Vosges), the annual temperature was 4 to 8°C lower and precipitation 200 to 800 mm lower than at present in the area. In south-central France, reconstructions for the Les Echets area suggest an MAT 8 to 12°C lower and precipitation 400 to 600 mm less than today. Such results have also been corroborated by the coleopteran assemblage studies in La Grande Pile, with a cold and continental climate reconstructed for the later part of MIS 6 (Ponel, 1995). At a more global scale, modeled temperature reconstructions for the EPICA Dome C record (Masson-Delmotte et al., 2010), for equatorial Pacific Sea Surface Temperature (Medina-Elizalde and Lea, 2005) and deep ocean temperature (Zachos et al., 2001; Bintanja et al., 2005) suggest a maximum difference during glacial and interglacial periods for the last 800 ka around -4.0ºC or -5.0ºC (see Masson-Delmotte et al., 2010 fig. 7).

Consequently, the ETB (H-02) climate reconstruction may suggest that 1) temperature variations were not extreme and precipitation was sufficient in southern Mediterranean Europe during MIS 6 for the persistence of temperate trees (Blain et al., 2017b) or 2) that the site better matches a cold period of MIS 7 (i.e. MIS 7d) or early MIS 6 and does not correspond with the lowest temperatures.

4.2. How warm were the interglacial complexes?

Interglacials refer to warm periods, with low ice extent (high sea level); end-members of the glacial cycles (PAGES, 2016). They are often defined as the most prominent peak(s) within each odd-numbered marine isotopic complex and "as warm or warmer than the Holocene". In this synthesis numerous climate reconstructions show temperatures warmer than present. However, because of dating uncertainties, it is often difficult to correlate archaeological sites to the marine isotope stratigraphy. The highest temperature within the same locality has been thus referred to be the best approximation to the interglacial maximum within general positive temperatures that belong to the interglacial complex as a whole. According to this synthesis, temperature reconstructions higher than present levels seem to be better represented in the Middle Pleistocene Spanish record than colder ones. This could be explained by the fact that interglacial assemblages usually show a higher faunal diversity and are usually associated with a higher intensity or duration of archaeological occupations more susceptible to interest the archaeologists or to be detected.

4.2.1 Marine Isotope Stage 21

Among the very latest Early Pleistocene sites, the Gran Dolina (or Trinchera Dolina, abbreviated as TD) TD6 level (Burgos, northern Spain) is certainly the best studied archaeological site in Spain that documents a warm-temperate interglacial complex before the Mid-Brunhes Event (Blain et al., 2013a). Here the compiled data are based on the material from partial excavations of the TD sequence during a preliminary evaluation of its archaeological and palaeontological significance known as ’Trinchera Dolina Sondeo Sur’ which lasted from 1993 to 1999. Hominin remains were first unearthed in 1994 and 1995 from level TD6. They were dated to slightly more than 780 ka on the basis of palaeomagnetic and microfaunal evidence making these, at the time, the oldest known hominins in Europe, and they were described as a new species, *Homo antecessor* (Carbonell et al., 1995; Bermúdez de Castro et al., 1997). TD6 has a pre-Matuyama negative polarity (>0.78 Ma) (Parés and Pérez-González, 1995, 1999). Biostratigraphy confirms an Early Pleistocene age (Cuenca-Bescós et al., 1999, 2010, 2015, 2016; Cuenca-Bescós and García, 2007). Radiometric dating by ESR dating of optically bleached quartz and U-series methods has provided an age for TD6 of between 800 and 880 ka (Falguères et al., 1999; Moreno García, 2011) and consequently TD6 has been associated with MIS 21 (Cuenca-Bescós and García, 2007; Cuenca-Bescós et al., 2011; Blain et al., 2012a, 2013a).

MER estimates gave positive temperatures (between +0.8 and +2.7ºC) and higher rainfall (between +308 and +477 mm) for the whole TD6 sequence (Table 2). One of the characteristics of such detailed climate reconstructions is that the highest value is obtained for numerous spits (T50, T48, T45, T44, T43, T41, T40, T37, T36, T35, and T33), and gives the impression of a long-lasting interglacial, something that is also observed in marine isotope records (see Fig. 2). The reconstructed climate is temperate, with a temperate summer and a cold winter (Fig. 3A, B). Rainfall is abundant and its distribution is regular, occurring throughout the year, with the highest levels during spring (Blain et al., 2013a). In comparison with current climatic data, the "interglacial optimum values" can be estimated to be 2.7°C higher, well out of the range of the standard deviation, with a quite similar increase in temperature during summer (+1.9°C) and winter (+1.2°C). MAP is higher (+409 mm) than the current level and occurred principally, as today, during the spring. The duration of the dry period during summer (estimated for level TD6-2, i.e. T38-41; Blain et al., 2013a) is reduced with no dry months, whereas today there are two dry months (July and August). This was also clearly suggested by the values of the De Martonne aridity index, which is higher than 30 (humid climate) in TD6-2, whereas for the Burgos weather station the value is lower than 30 (semi-humid climate), suggesting that today conditions are more arid than those occurring during the formation of TD6-2 (Blain et al., 2013a). In conclusion, the overall climate pattern in TD6 is concordant with a Mediterranean climate, with temperate summers and cold winters and rainfall maximums corresponding to spring and autumn.

Reconstruction from the amphibian and reptile assemblages suggests that during the formation of TD6 level there was a patchy landscape with humid meadows and woody habitats. Some taxa, such as *Alytes obstetricans*, *Bufo* gr. *bufo-spinosus*, *Rana* sp., *Coronella austriaca* and *Vipera aspis*, preferentially live in open woodlands and/or humid meadows. *Pelobates cultripes* and to a lesser extent *Epidalea calamita* and *Pelodytes punctatus* are inhabitants of drier, open environments with poor and short plant cover and with loose or stony soils, which must have been well represented in the Sierra de Atapuerca calcareous substrate in the vicinity of the cave. Woodlands are reasonably well represented, totalling between 26.2 and 41.5% of the landscape (Table 2).

Such warm and humid conditions are well supported by other proxies, such as palynological studies at Gran Dolina that have documented little pollen preserved for TD6 but documenting more or less open forest cover (around 45–60% arboreal pollen), in which Mediterranean taxa such as *Quercus* type *ilex–coccifera*, *Olea*, *Celtis*, *Pistacia* and *Coriaria* are dominant. Mesophilous taxa such as deciduous *Quercus*, *Acer*, *Tilia*, *Prunus*, *Carpinus* and *Corylus* are also well represented, suggesting a temperate climate, with no intensely cold conditions and rainfall sufficient to maintain deciduous trees (Burjachs, 2001). The high abundance of *Celtis* seeds at TD6 is also a notable proof of Mediterranean conditions (Rodríguez et al., 2011). Large mammals, represented in TD6 by *Canis mosbachensis*, *Mustela palerminea* and *Lynx* sp., also suggest a warm and relatively wooded landscape (Cuenca-Bescós and García, 2007). Nevertheless, the presence of *Mammuthus* sp. shows that open country was also significant at this time. The presence of Mediterranean taxa towards the top of TD6 suggests a temperate climate, coinciding with the Mediterranean character of the large porcupine *Hystrix refossa* (Laplana and Cuenca-Bescós, 1996; Cuenca-Bescós et al., 2005). In addition, the presence of *Castor fiber*, the giant shrew *Dolinasorex glyphodon* and *Mimomys savini* is notable (Cuenca-Bescós et al., 2005, 2017; Rofes and Cuenca-Bescós, 2009; Lozano-Fernández et al., 2013), indicating the existence of a permanent water stream in the vicinity of the site. Similarly, the birds are predominantly species of open-country and bushland habitats, while the presence of waterfowl (*Anas* sp.) and waders (*Limosa limosa*, *Scolopax rusticola*) constitutes additional evidence supporting the existence of a large body of water (Sánchez-Marco, 1999).

4.2.2 Marine Isotope Stage 19

Again in the Sierra de Atapuerca, level TD8 of the Gran Dolina is considered the first Middle Pleistocene fossiliferous level of this sequence. The TD8 level is formed by a succession of brecciated flows of red lutites with gravels and boulders (Parés and Pérez-González, 1999). The Matuyama-Brunhes Boundary has been identified between the TD7 and TD8 levels (Parés and Pérez-González, 1999). In order to date this deposit, several samples were analyzed with different methods. An average age of 600 ka was obtained by ESR and U-series from samples collected from the middle part of the sedimentary deposit (602 ± 52 kyr) (Falguères et al., 1999), thus, it correlates with MIS 15. On the other hand, the range of error of one TL date from the base of TD8 overlapped the Matuyama-Brunhes Boundary (820 ± 140 kyr) (Berger et al., 2008). Faunal remains were recovered from the middle to lower part of TD8 (the upper part is sterile). The small-mammal assemblage from TD8 corresponds to an older assemblage called TD8a by Cuenca-Bescós et al. (1999) and is characteristic of Atapuerca Faunal Unit 5 (local faunal zones), which corresponds to changes between the Early and Middle Pleistocene (Cuenca-Bescós et al., 2010, 2011, 2016). Sublevel TD8b is characterized by the disappearance of *Mimomys savini* and is now considered to be a different stratigraphic unit called TD8/9. In addition TD8 is peculiar in retaining a species of the giant deer genus *Eucladoceros* and a small rhinoceros. Such a small rhinoceros is common in the late Early Pleistocene. The persistence of these forms suggests that TD8 belongs to the oldest Middle Pleistocene (Blasco et al., 2011) consistent with an attribution to MIS 19.

The studied amphibians and reptiles derive from the same test pit of ‘Dolina Sondeo Sur’ dug in TD8 during the 1994 field season. The herpetofaunal assemblage is composed of 8 anurans (*Alytes obstetricans*, *Pelobates cultripes*, *Pelodytes punctatus*, *Bufo* gr. *bufo-spinosus*, *Epidalea calamita*, *Hyla* gr. *arborea-molleri*, *Rana* sp., and *Pelophylax* sp., 2 lizards (*Blanus cinereus* and Lacertidae indet.), and 5 snakes (*Natrix* cf. gr. *natrix-astreptophora*, *Natrix* cf. *maura*, *Coronella austriaca*, *Rhinechis scalaris*, and *Vipera* cf. *aspis*). Reconstructed climate is warmer (+1.7ºC) and wetter (+409 mm) (Blain et al., 2009) in a similar way to that previously described for MIS 21. A warm climate is coherent with the presence of tortoise (*Testudo* sp.). Pollen studies show an association of temperate Mediterranean woodlands with several Atlantic taxa based on the presence of *Castanea* and *Quercus*, *Betula*, *Acer*, *Alnus*, *Hedera*, *Fagus* and *Salix* (García-Antón, 1989), also suggesting a temperate and humid climate during the formation of TD8.

4.2.3 Marine Isotope Stage 17

In the Iberian Peninsula, the site of Cúllar Baza 1 (Granada, southeastern Spain) has been correlated with MIS 17 with an age of 700-600 ka based on the recovered lithic industries (Vega Toscano, 1989), the evolutionary stage of arvicolines (Ruiz-Bustos and Michaux, 1976; Sesé, 1989; Sesé et al., 2016; Agustí et al., 2009, 2010) and the large mammal association that has been correlated with Ponte Galeria Faunal Unit (i.e. MIS 18-17; Florindo et al., 2007). It should be noted that some AAR datings yielded an age of 476 ± 24 ka (Ortiz et al., 2000) and 441 ± 27 ka (Torres et al., 1997) for the site, suggesting that it has to be correlated with MIS 11. However such estimates are not coherent with previous studies.

MER estimates for Cúllar Baza 1 rely on the squamate fauna studied by Barbadillo (1989): *Blanus cinereus*, *Chalcides* cf. *bedriagai*, *Acanthodactylus* cf. *erythrurus*, *Timon* cf. *lepidus*, *Podarcis* sp., cf. *Natrix* sp. and *Rhinechis scalaris*. No amphibians have ever been described from this site, perhaps because of the small size of the sample or taphonomic bias. The squamate assemblage suggests a warm and dry climate (drier than previous Early Pleistocene periods), with the development of dry meadows, rocky areas and Mediterranean open forest areas. The MER method estimates MAT to be 16.5 ± 2.2 ºC (i.e. +4.0 ºC in relation with present) and MAP to be 568 ± 204 mm (i.e. +268 mm in relation with present) (Agustí et al., 2009, 2010).

According to marine isotope records, MIS 17 does not seem to have been particularly warmer than other interglacials in the marine oxygen isotope record (see for example Fig. 2). The fact that reconstructed temperatures for Cúllar Baza 1 are the highest of all the herpetofauna-based reconstructions may signify that 1) the site is coeval with a particular warm maximum of MIS 17 (i.e. MIS 17c; Fig. 2) or 2) that interglacial warmth was more pronounced in southern Spain or in the continental Guadix-Baza basin than the global record.

4.2.4 Marine Isotope Stage 11

Three herpetofaunal assemblages in the Iberian Peninsula have been referred to MIS 11 (Blain et al., 2015): the base of level TD10 of Gran Dolina (TD10.3) correlated with MIS 11c, Áridos-1 correlated with MIS 11b and Ambrona (AS4 and AS3) correlated with MIS 11a. Compared with today, reconstructed mean annual temperature varies from +2.7 to +0.3°C and mean annual precipitation varies from +311.7 to +74.4 mm, suggesting a progressive decrease in temperature and rainfall from the fully interglacial conditions of MIS 11c to the end of MIS 11. The presence of woodland areas is also well substantiated throughout the duration of MIS 11, at least during the interglacial and interstadial periods (Blain et al., 2015).

T17 ('Talla 17', an artificial excavation layer within TD10.3) has been correlated with the MIS 11c interglacial on the basis of reconstructed mean annual temperatures which point to a much higher temperature for that archaeological sample than for the other samples from TD10.3 (Blain et al., 2012a). Attribution to MIS 11 relies on biochronological data (middle part of the Middle Pleistocene) and is corroborated by numeric datings, with a combined ESR/U-series age of around 430 ka for the base of level TD10.3 (Berger et al., 2008; Falguères et al., 2013). Higher temperatures obtained for this level are due to the presence of a typical Mediterranean species (*Pelobates cultripes*), but the assemblage also included some Eurosiberian taxa (*Rana* sp. and *Vipera aspis*) and the presence of *Hyla* gr. *arborea-molleri*, which is currently absent from large areas in the south of the Iberian Peninsula. The MAT was 12.9°C and the MAP was 867 mm. The reconstructed climate was found to be temperate with warm summers and cold winters, with the mean temperature of the coldest month equal to 5.2°C. The total amount of rainfall is higher (ΔMAP= +311.7 mm) than the current level in Burgos.

While there are numerous palaeoclimatic records of MIS 11 in northern and central Europe (UK, Germany, Czech Republic, France and Poland), such records are relatively scarce in southern Europe (Candy et al., 2014), with just a few marine cores from the western margin of the Iberian Peninsula (de Abreu et al., 2005; Desprat et al., 2005; Martrat et al., 2007; Voelker et al., 2010) and the classic lacustrine pollen records from Ioannina and Tenaghi Philippon in Greece (Tzedakis et al., 2001, 2006; Tzedakis, 2005). Moreover, most of these Iberian offshore records only document SSTs, while a single pollen-based analysis by Desprat et al. (2005) described the potential MIS 11 climate and environmental succession on the Iberian land mass (deep-sea core MD01-2447). In this analysis the warmest peak of MIS 11c is characterized by MTC and MTW similar to current values and lower MAP (-100 mm). However in many records, MIS 11c is characterized as one of the warmest interglacials of the last 800 ka (PAGES, 2016), even warmer than the Holocene. Temperature estimates vary from place to place, but range from similar to the present to warmer (1 or 2 °C above modern levels; Kukla, 2003; Rousseau, 2003), in accordance with the herpetofauna-based reconstructed temperatures presented here for the whole interglacial complex.

4.2.5 Marine Isotope Stage 9

Progressing up through the Gran Dolina TD10 sequence, the next temperature maximum has been found for spit T9 (Fig. 2). In accordance with the numeric datings (around 300 ka) this spit has been correlated with MIS 9 (Blain et al., 2012a). Reconstructed temperature is lower than for spit T17 (MIS 11c), yet a warmer (ΔMAT = +2.8ºC) and wetter (ΔMAP = 292 mm) climate than at present in the Burgos area is indicated. Such results are based on samples from the 1993 partial excavations of the TD sequence. Further contextualization of these temperature and precipitation estimates and correlation with the new stratigraphical separations of TD10 by sublevels will be complemented in the future by the ongoing studies on the mammal and herpetofaunal material recovered during the excavation campaigns since 2010 on the whole surface of the level TD10.

4.2.6 Marine Isotope Stage 7

MIS 7 is rather poorly known in the Iberian Peninsula. Besides the spit T1 (TD10) in the Gran Dolina stratigraphical sequence carefully correlated with MIS 7 by Blain et al. (2012a) (Figure 2), few sites have been attributed to MIS 7.

New excavations conducted between 2001 and 2005 at Mollet Cave (Serinyà, north-east Spain), led to a more precise characterization of the archaeological and palaeontological contents of level 5, recovery of small vertebrates, and collection of samples for radiometric dating (Maroto et al., 2012; López-García et al., 2014). The results obtained using U-series disequilibrium dating ascribed an age of ca. 215 ka to Level 5, which would correspond to MIS 7c. The faunal association suggests a landscape formed by an open and humid woodland characteristic of an interstadial phase. The herpetofaunal assemblage is represented by a few ubiquitous species as *Pelodytes punctatus*, *Bufo* gr. *bufo-spinosus* and *Vipera* sp. that unfortunately did not permit the application of the MER method.

Close to the Mediterranean coast another cave, the Cova del Rinoceront (Barcelona, northeastern Spain), has delivered a small vertebrate assemblage, in levels VII and VIII, that has been correlated with MIS 7/6. The exposed stratigraphy has a thickness of 11 m and a width of between 1.5 and 3 m. The sequence can be divided into three main units (Units 1, 2 and 3), comprising eight layers designated I to VIII (from top to bottom). The publication by Daura et al. (2015) and López-García et al. (2016) showed that the chronological range of the upper part of sequence (layers I to III), as determined by U-Th dating and microfaunal evidence, relates to MIS 5, in agreement with its faunal composition that indicates widespread temperate conditions (probably equivalent to MIS 5e), mainly illustrated by the presence of the Mediterranean tortoise.

Even if the maximum age indicated for layer VII by U-Th (~175 ka) implies that layer VII post-dates MIS 7, the lower part of the sequence’s mammal assemblage suggests warm climatic conditions that do not fit well with an attribution to MIS 6 but better with an attribution to MIS 7 as the layer VII assemblage is very similar to other small vertebrate associations from the Mediterranean zone, such as Bolomor level 5 (dated to ca. 228 ka; Guillem-Calatayud, 2000), Mollet cave (dated to ca. 215 ka; Maroto et al., 2012; López-García et al., 2014), Valdocarros II (MIS 8 to MIS 7; Sesé et al., 2011a; Blain et al., 2012b), la Baume Bonne (MIS 8/7; Hanquet, 2011) and Cèdres (MIS 7; Hanquet, 2011). Consequently further dating would be of interest for better constraining the age of the lower part of Cova Rinoceront (levels VII and VIII) as well as a detailed study of the herpetofaunal assemblage that already furnished a nice amphibian and reptile association with 3 anurans (*Pelobates cultripes*, *Bufo* gr. *bufo-spinosus*, *Pelophylax* sp.), one lizard (*Anguis fragilis*), and 3 snakes (*Natrix* gr. *natrix-astreptophora*, *Malpolon monspessulanus*, *Vipera* sp.) (Daura et al., 2015; López-García et al., 2016).

Recently new datings around 200 and 235 ka have been obtained for the site of Preresa (Manzanares valley, SE Madrid), formerly attributed to MIS 5a (Rubio-Jara, 2011; Sesé et al., 2011b; Blain et al., 2013c; Panera et al., 2014), and thus suggesting an age comprised between MIS 7 and early MIS 6 (Moreno et al., in press). MAT 0.3ºC higher than current values obtained for the Preresa herpetofaunal assemblage (Blain et al., 2013c, in press) may suggest that this site would better be placed, if referring to the new dating, within MIS 7 than MIS 6. Anyway new analyses must be done to confirm the MIS attribution of this site.

Finally, as already stated above, the herpetofaunal assemblage from Estanque de Tormentas de Butarque (H-02) correlated with MIS 6a could also potentially be correlated with MIS 7d (Blain et al., 2017b, in press). Similarly to MIS8/9, the differentiation between cold stages of MIS 7 and MIS 6 is far from easy due to the large chronological uncertainty of the sites under study.

4.3. Climate pattern, thermal amplitude and coherence of MER estimates

4.3.1 Climate pattern and vegetal cover

Independently of the values of MER estimates, the regression analyses (OLS: Ordinary Least Squares) raised on one hand that although MTW is strongly correlated with MAT, the parameter that best drives MAT is MTC. On the other hand, MAP is more correlated with MTW than with MAT or MTC. In addition, %wood is negatively correlated with MTW and positively with MAP. MTW and MAP thus seem to be the decisive climatic parameters for %wood in Mediterranean environments. It is not surprising as today one of the most limiting factors for fauna and flora in the Mediterranean climate area is the period of aridity (intensity and length) during summer months (e.g. Blondel and Aronson, 1999). However MTC has also been said to be, together with MAP, an important factor having a strong influence on the vegetation and on the formation of steppe landscape in the Iberian Peninsula (e.g. Suarez Cardona et al., 1992). In our case, it is probable that even if it fluctuates, MTC does not reach temperatures cold enough to have had a real impact on %wood. MAP in the MER reconstructions is always higher than present levels in the Iberian Peninsula. A weak correlation between MAP and temperature parameters has been found. This suggests that the relation between temperature and precipitation must have been more complex, and that further investigations must be done on the distribution of rainfall during the year (winter vs. summer precipitation) in relation to temperature related to increasing anticyclonic circulation over the region, causing a northward or southward shift of the mid-latitude storm track (i.e. Giorgi and Lionello, 2008).

As far as Habitat Weighting estimated local extensions of forest area (%wood) is concerned, based on the proportion of the amphibian and reptile assemblage with affinities for open woodland areas in a particular archaeological site, we show here that the forest cover seems to be higher when summers are colder and the amount of rainfall is larger. Even if such an assumption is biologically or ecologically coherent, woodland cover seems to be equally represented between glacial and interglacial intervals, with the exception of some particular low percentages during MIS 22 (Cueva Victoria) and MIS 6 (ETB-H02). During interglacial periods %wood reaches only 30-40%. This fact seems to be in disagreement with pollen studies that usually associate higher Arboreal

Pollen levels with interglacial periods, so higher MAT (and higher MAP, at least during certain portions of the interglacials). Consequently, amphibians and reptiles do not seem to register any strong differences in forest cover between glacials and interglacials. Two possible reasons for this: (a) there were no major changes in forest cover at the site scale; (b) there were changes in forest cover but the herpetofauna does not register them. In support of (a), perhaps the sites were situated within refugial areas for temperate trees. Unfortunately pollen reconstructions at these sites are not rich enough (particularly in Atapuerca) for documenting the real extent of the vegetal cover. In support of (b), amphibian and reptile assemblages represent time periods long-enough to encompass both warm and cold intervals. This last hypothesis regarding the refugia/stable environment argument might be related to the sedimentation in the cave or also, as argued for a site like Sima del Elefante TE-URU, to the stratigraphical precision used for the microvertebrate analysis.

4.3.2 Thermal amplitude

What about the thermal amplitude or intensity proposed by MER reconstructions? As we saw MER climate estimates oscillate roughly between +4ºC and -4ºC for the Mediterranean environments. Such intensities are coherent with global records like Epica Dome C (Masson-Delmotte et al., 2010) but far away from other continental climate reconstructions such as in central France or northern Germany pollen estimates (see for example the discussion about MIS 6, with ∆MAT up to -8ºC in comparison with current temperature in mountain areas of the Balkan Peninsula; Hughes et al., 2007), the reconstructed surface air temperature by Bintanja et al. (2005) suggesting an extreme of 17ºC below present for glacial periods during the last 800 ka or the land-based proxy surface air temperature anomalies in Eurasia for the Last Glacial Maximum of -12 to -20ºC (Guiot et al., 1993, 1999, 2000; Kageyama et al., 2001, 2006; Allen et al., 1999). Because of the lack of comparative terrestrial temperature estimates in the western Mediterranean, it is difficult to known whether our estimate is too warm or the climate in the Mediterranean area was different (milder or much warmer) in comparison with other places, altitudes or latitudes. In this context, in our opinion, one of the main questions is where to place the "0" when comparing with present day climate. Most climate records do not help in answering such a question as it is often difficult to known exactly if the reference period is taken for present or for the Holocene maximum; and how good are reconstructions for the Holocene maximum? Such a calibration of the palaeoclimate records would help in answering which periods were colder than present measurements (i.e. 1951-1999) and also to appreciate if interglacials were warmer (and how much) than today rather than the Holocene maximum. Such data thus would permit to compare directly vegetation belt distribution in the past or to understand the palaeobiogeography of some extant species at a precise moment of the Pleistocene.

For discussing such an issue, the comparison with the composite western Iberian Margin alkenone-based SST record published by Rodrigues et al. (2011) is very interesting (Fig. 8). This composite record covers the last 600 ka and comes from cores MD03-2699 (MIS 1-2 and MIS 9 to MIS15; Rodrigues et al., 2011) and MD01-2443 and MD01-2444 (from MIS 1 to MIS 11; Martrat et al., 2007). This is one of the few records where the comparison with modern temperature is explicitely done (grey areas on Fig. 8). When compared with the MER estimates it seems, even if such direct comparison is again hampered by the chronological uncertainties, that MER estimates are coherent with SST values of the western Iberian Margin. Such a pattern may be completed in the future by the inclusion of the Late Pleistocene in the comparison.

4.3.3 Early and Mid-Brunhes Events

The Mid-Brunhes Event (MBE) corresponds to a climatic transition between MIS 13 and 11 that separates two climatic modes (Fig. 2): (1) Early-Middle Pleistocene interglacials (780–450 ka), which are characterized by only moderate warmth, and (2) Middle and Late Pleistocene interglacials (occurring after 450 ka), which are characterized by greater warmth consistent with, or warmer than, the Holocene. This event has been observed in a variety of long-term climate records such as the Mapping Spectral Variability in Global Climate Project (SPECMAP) and the European Project for Ice Coring in Antarctica (EPICA), many records of sea-surface temperature, and some long-term speleothem records, but its effect on terrestrial systems is still poorly understood due to the absence of detailed long-term records of environmental change (Tzedakis et al., 2006, 2009; Candy et al., 2010). Through their examination of the British terrestrial sequence, Candy et al. (2010) showed that interglacial climates during the early Middle Pleistocene were as warm as those that occurred during the late Middle and Late Pleistocene, suggesting that the MBE was not a global climatic transition, but was restricted to specific regions, in particular to higher latitudes of the Southern Hemisphere.

The longest small-vertebrate bearing section in the Iberian Peninsula is represented by the site of Gran Dolina (Atapuerca), with sediments that document from 1 Ma to approximately 200 ka years ago (with an important hiatus at the beginning of the

Middle Pleistocene). To date ~40,000 amphibian and squamate bone fragments have been studied, representing at least 20 taxa, including newts, toads and frogs, amphisbaenians, lacertids, anguids, and snakes. Such an assemblage permitted the application of climatic and environmental reconstruction methods to the whole sequence. The analysis of the differences between the successive interglacial peaks revealed that (Blain et al., 2012a): 1. Post-MBE interglacials were warmer than pre-MBE interglacials in accordance with the MBE climate transition as documented by ice (EPICA and SPECMAP) and sea-surface temperature records; 2. Pre-MBE interglacials were warmer than present day; 3. The reconstructed MIS 11 mean annual temperature is slightly warmer than MIS 9, and much warmer than MIS 7 in northern Spain (MIS 5 being absent from the Gran Dolina record); and 4. Post-MBE interglacials had lower rainfalls than pre-MBE interglacials, resulting in the increasing development of open dry environments on the Iberian Peninsula. However reappraisal of the conclusion by Blain et al. (2012a) through the present compilation of data shows that MIS 17 seems to have been much warmer than any post-MBE interglacials. Such a high temperature level reconstructed for Cúllar-Baza 1 would be consistent with the observation of Candy et al. (2010) for the British terrestrial sequence that MBE is not observable in Western Europe. However conclusions are hampered by the fact that we still lack data for most of the pre-MBE interglacials like for MISs 13a and 15a and 15e.

Another climate event, the Early Brunhes Event (EBE) suggests a shift to more extreme glacials between MIS 18 and 16 that separates two climatic modes (Fig. 2): (1) Early-Middle Pleistocene glacials (780–660 ka), which are characterized by only moderate cold, and (2) Middle and Late Pleistocene glacials (occurring after 660 ka), which are characterized by harsher cold maxima consistent with, or colder than, the Last Glacial

Maximum (MIS 2). According to the estimates presented here, MIS 22 seems to have been as cold as MIS 6 and MIS 8 estimates. In a same way as for MBE, the EBE is difficult to be appreciated in our reconstructions because of the lack of data for many glacial periods (i.e. MIS 10a, 12a, 14a, 14c, 16a, 18a, 18e, 20a and 20c) and also mainly because of the large chronological uncertainty for sites that document cold climate making difficult to know if they correspond to the glacial maximum or to a less cold stadial period.

5. Conclusions

A decade of amphibian- and reptile-based climate reconstructions carried out for the Iberian Peninsula using the Mutual Ecogeographic Range method is reviewed in order to present a regional synthesis from MIS 22 to MIS 6. Conclusions are as follows:

1. Despite the number of sites/levels represented in this synthesis, the records do not cover the entire interval. It is the case particularly for the period between MIS 16 and MIS 12 (i.e. from 650 ka to 450 ka). Correlation with the MIS stages for the latest Early Pleistocene and early Middle Pleistocene (MIS 22 to MIS 17) are hampered by quite large chronological uncertainties. And finally even for the period between MIS 11 and MIS 6 (i.e. between 400 ka and 140 ka) where there are a larger number of studied localities, many stages and substages are still entirely undocumented, for example MIS 11e, 11d, the whole of MIS 10, and MIS 7d to MIS 6b.

2. This synthesis allows comparison between sites and between periods. ΔMAT estimates range between -3.9ºC and +4.0ºC relative to current local temperature.

3. Independently of the amplitude and intensity of MER estimates, the statistical analyses highlighted that although MTW is correlated with MAT, the parameter that best drives MAT is MTC. MAP is more correlated with MTW than with MAT and MTC. %wood is negatively correlated with MTW and positively with MAP. MTW and MAP (i.e. summer aridity) thus seem to be the most important climatic parameters for %wood in Mediterranean environments.

4. As far as Habitat Weighting estimated local extensions of forest area (%wood) is concerned, amphibians and reptiles do not seem to register any strong differences in forest cover, such as those documented by pollen records, between glacials and interglacials. Either there were no major changes in forest cover at the site scale, or changes in forest cover were not recorded by the herpetofauna. Further studies are needed to document if, perhaps the sites were situated within refugial areas for temperate trees or if amphibian and reptile assemblages represent time periods long-enough to encompass both warm and cold intervals.

5. The Mid-Brunhes Event (MBE) previously documented in the sequence of Gran Dolina (Atapuerca; Blain et al., 2012a), is challenged by the climate reconstructions of the site of Cúllar-Baza 1 (Granada, SE Spain). MIS 17 seems to have been much warmer than any post-MBE interglacials and thus would suggest in accordance with observations by Candy et al. (2010) for the British terrestrial sequence that MBE is not observable in Western Europe. However conclusions are hampered by the fact that we still lack data for most of the pre-MBE interglacials like for MISs 13a and 15a and 15e.

6. In a same way as for MBE, the Early Brunhes Event (EBE) is difficult to be appreciated in our reconstructions because of the lack of data for many glacial periods and also mainly because of the large chronological uncertainty for sites that document cold climate in terms of knowing if they correspond to the glacial maximum or to a less cold stadial period. However MIS 22 (Cal Guardiola) seems to have been as cold as MIS 6 (ETB-H-02).

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Captions

Figure 1. Geographical location within the Iberian Peninsula of the Early-Middle Pleistocene (from MIS 22 to MIS 6) sites used in this study. Abbreviations: AMB: Ambrona (Soria), AR1: Áridos-1 (Madrid), CB1: Cúllar-Baza 1 (Granada), CDLB: Cuesta de la Bajada (Teruel), CG: Cal Guardiola (Barcelona), CV: Cueva Victoria (Murcia), ETB (H-02): Estanque de Tormentas de Butarque (Madrid), TD: Trinchera Dolina (Burgos), TEURU: Trinchera Elefante Upper Red Unit (Burgos), VALD: Valdocarros II (Madrid).

Figure 2. Chronological correlation of the Early-Middle Pleistocene (from MIS 22 to MIS 6) sites used in this study along the Marine Isotope Stage record and Difference with modern values for estimated Mean Annual Temperature (ΔMAT) and Mean Annual Precipitation (ΔMAP) and representation (%wood) in forest cover. Isotopic oxygen record and optimized scheme of lettered marine isotope substages from Railsback et al. (2015). Abbreviations: AMB: Ambrona (Soria), AR1: Áridos-1 (Madrid), CB1: Cúllar-Baza 1 (Granada), CDLB: Cuesta de la Bajada (Teruel), CG: Cal Guardiola (Barcelona), CV: Cueva Victoria (Murcia), ETB (H-02): Estanque de Tormentas de Butarque (Madrid), TD: Trinchera Dolina (Burgos), VALD: Valdocarros

II (Madrid). Red ellipses represent chronological uncertainty and vertical black lines represent the temperature standard deviation.

Figure 3. Biavariate plot using as independent variable MAT. A: MTC on MAT; B: MTW on MAT.

Figure 4. Bivariate plot using as dependent variable MAP. A: MAP on MAT; B: MAP on MTC; C: MAP on MTW.

Figure 5. Bivariate plot using as dependent variable ΔMAT. A: ΔMAT on ΔMTC; B: ΔMAT on ΔMTW.

Figure 6. Bivariate plots using as dependent variable %wood. A: %wood on MTW; B: %wood on MAP.

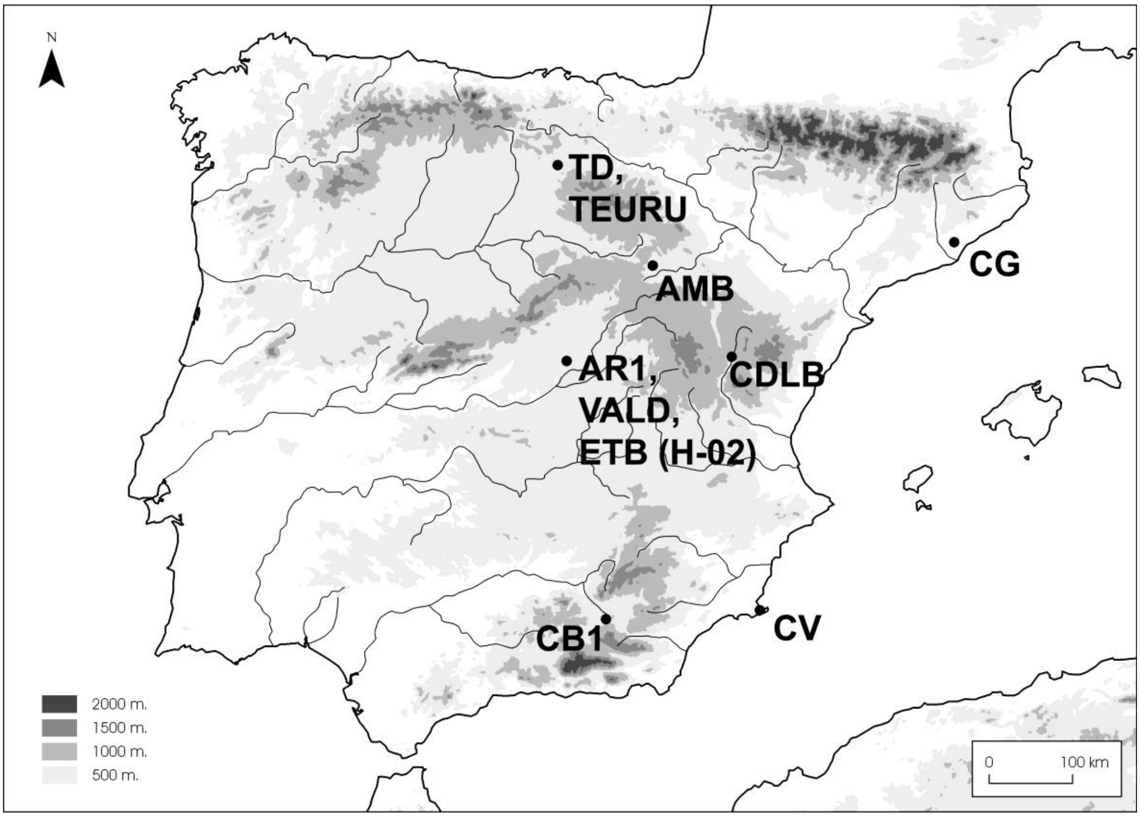
Figure 7. Bivariate plots using independent variables those defined by the difference between recent values and Middle Pleistocene estimations (Δ) and as dependent one, %wood. A: %wood on ΔMAT B: %wood on ΔMAP.

Figure 8. Comparison between MER estimates (if positive or negative ΔMAT) and Iberian Margin composite alkenone-based Sea Surface Temperature for the last 600 ka: MD03-2699 (Rodrigues et al., 2011) and MD01-2443 and MD01-2444 (Martrat et al., 2007). Grey areas represent SST higher than current level.

Table 1. Short summary of the different methods used for the paleoclimatical reconstruction with vertebrates as proxy, periods and regions that include climatic inferences, inferred parameters, validation of the method with other proxies. Climatic parameters: mean annual temperature (MAT), mean temperature of the coldest month (MTC), mean temperature of the warmest month (MTW), yearly positive temperature (Tp), mean annual precipitation (MAP), precipitation of the wettest month (Pwm), precipitation of the driest month (MINP), mean winter precipitation (MWP), mean summer precipitation (MSP), mean autumn precipitation (MAuP), mean spring precipitation (MSpP) and percentage of winter rainfall. Other values have been also obtained such as aridity indexes, humidity, seasonality of precipitation, average annual thermal amplitude (MATA), thermal index (IT), compensated thermal index (ITC), vegetative activity period (VAP) and drought length (D). References: [1]Brattstrom (1956), [2]Markwick (1994, 1998); [3]Böhme (2008), [4]Denny et al. (2009), [5]Makarieva et al. (2009), [6]Sniderman (2009), [7]Head et al. (2009a, 2009b, 2013), [8]Böhme (2002, 2003, 2004, 2008, 2010), [9]Böhme et al. (2006, 2012), [10]Klembara et al. (2010), [11]Hernández-Fernández and Peláez-Campomanes (2005), [12]Hernández-Fernández (2006), [13]Hernández-Fernández and Vrba (2006), [14]Hernández-Fernández et al. (2007), [15]Kay and Maden (1996), [16]Montuire et al. (1997, 2006), [17]Montuire (1999), [18]Aguilar et al. (1999), [19]Damuth et al. (2002), [20]Legendre et al. (2005), [21]van Dam (2006), [22]Escudé et al. (2013), [23]Fortelius et al. (2002, 2006), [24]Cruz et al. (2016), [25]Eronen and Rook (2004), [26]Eronen et al. (2010a, b, 2011), [27]Blain et al. (2007, 2008a, 2009, 2010b, 2011a, b, 2012a, b, 2013a, b, c, 2014a, b, 2015, 2016a), [28]López-García et al. (2008, 2010b, 2011a, b, c, d, 2013a, b), [29]Polly and Eronen (2011), [30]Bañuls-Cardona et al. (2012), [31]Smith and Polly (2013), [32]Motuzco and Ivanov (1996), [33]Avery (1999), [34] Jeannet (2009, 2010), [35] Manzano (2015), [36]Vieites et al (2009), [37]Holden et al. (2013).

Table 2. Herpetofauna-based Early-Middle Pleistocene Iberian climate and environmental reconstructions. Abbreviations: Marine Isotope Stage (MIS), mean annual temperature (MAT), mean temperature of the coldest month (MTC), mean temperature of the warmest month (MTW), mean annual precipitation (MAP), representation of woodland and woodland margins in the reconstructed environment (%wood), standart deviation (SD), difference with current value (Δ). References: [1]Agustí et al. (2009), [2]Blain et al. (2008a), [3]Blain (2012-2014), [4]Blain et al. (2008b), [5]Blain et al. (2009), [6]Blain et al. (2012a), [7]Blain et al. (2013a), [8]Blain et al. (2015), [9]Blain et al. (2014b), [10]Blain et al. (2017a), [11]Blain et al. (2011b), [12]Blain et al. (2012b), [13]Blain et al. (2017b). Grey bands represent the sample that corresponds to the warmest temperature and consequently have been correlated with the interglacial peak (Blain et al., 2012a).

Table 3. Descriptive statistics of regression analyses (OLS: Ordinary Least Squares); N: sample size; R^2: coefficient of correlation; *a*: Y–intercept; *b*: slope; H_0 (b=0): null hypothesis for slope zero.



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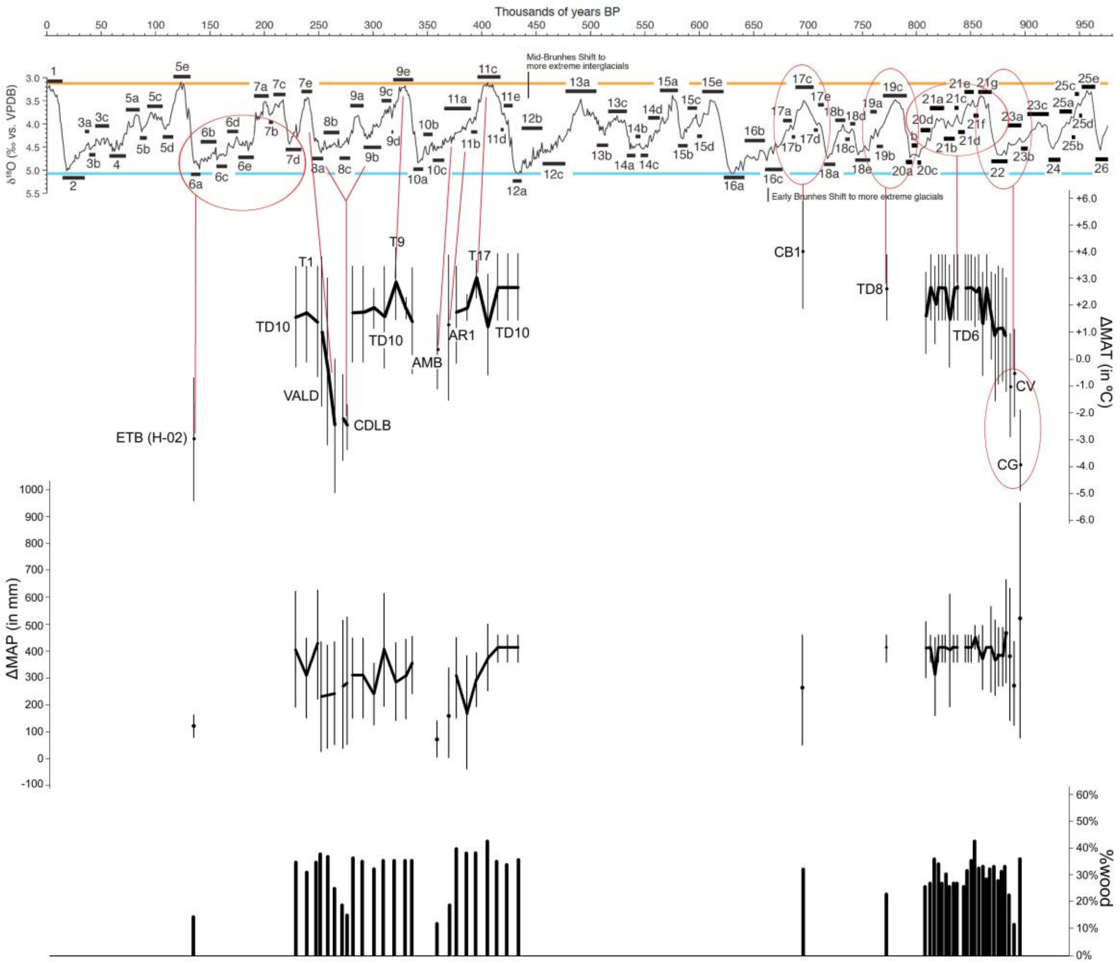

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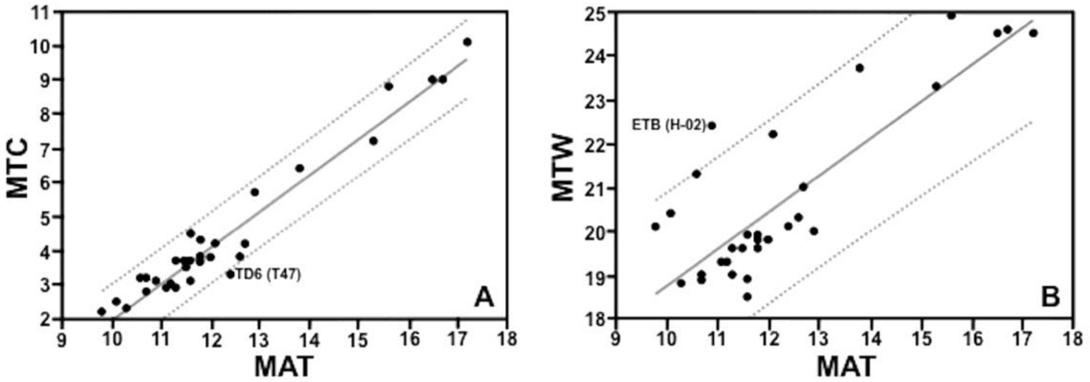

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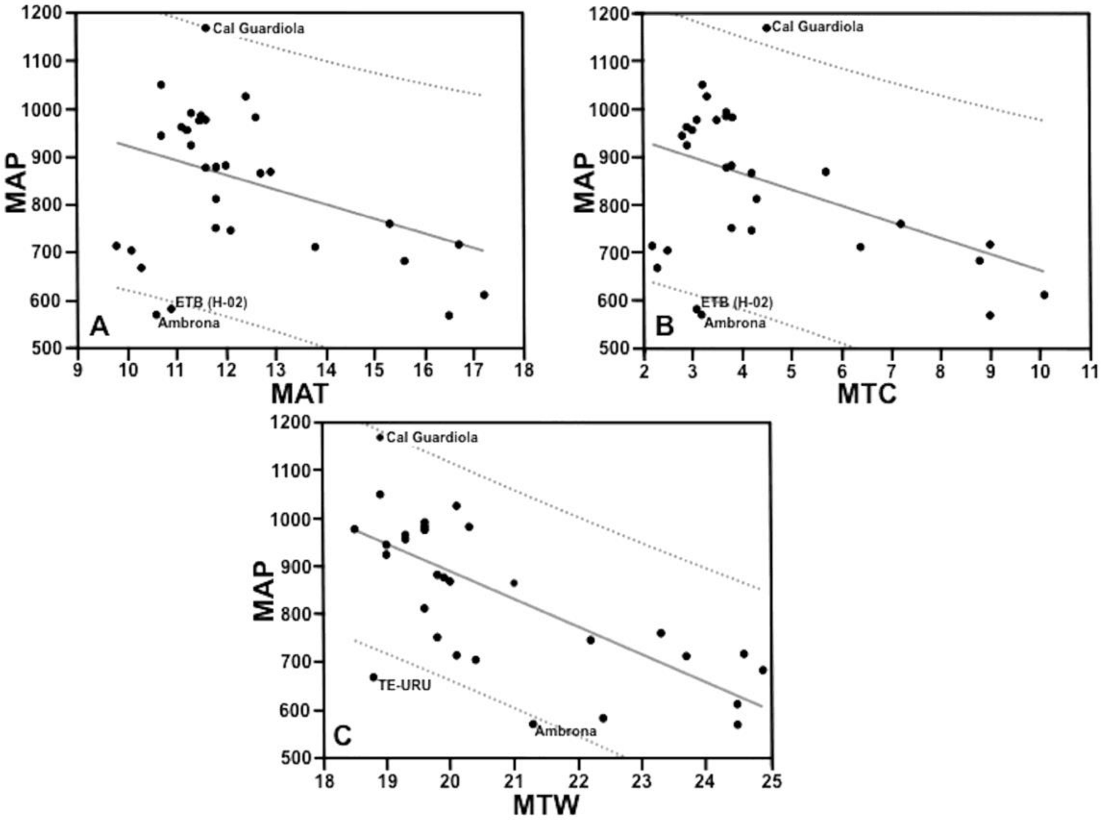

Figure 4. Bivariate plot using as dependent variable MAP. A: MAP on MAT; B: MAP on MTC; C: MAP on MTW.

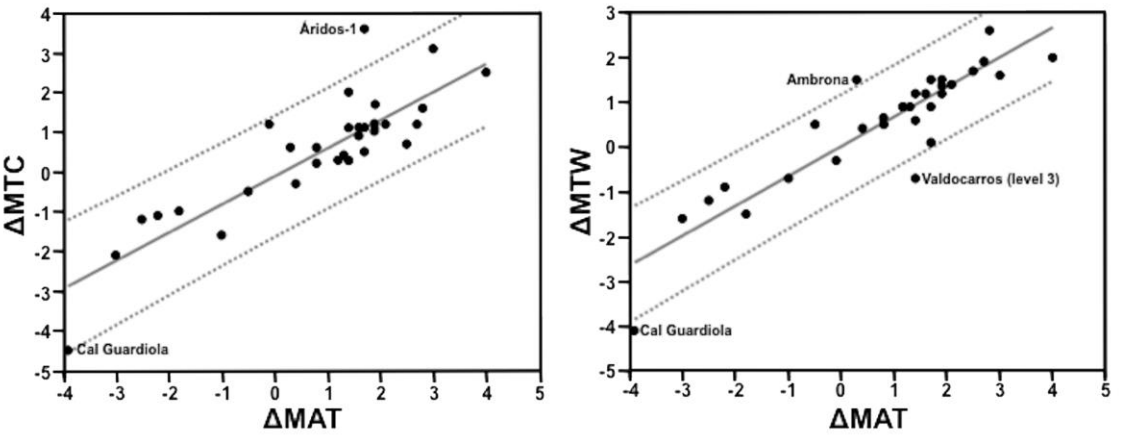

Figure 5. Bivariate plot using as dependent variable ΔMAT. A: ΔMAT on ΔMTC; B: ΔMAT on ΔMTW.

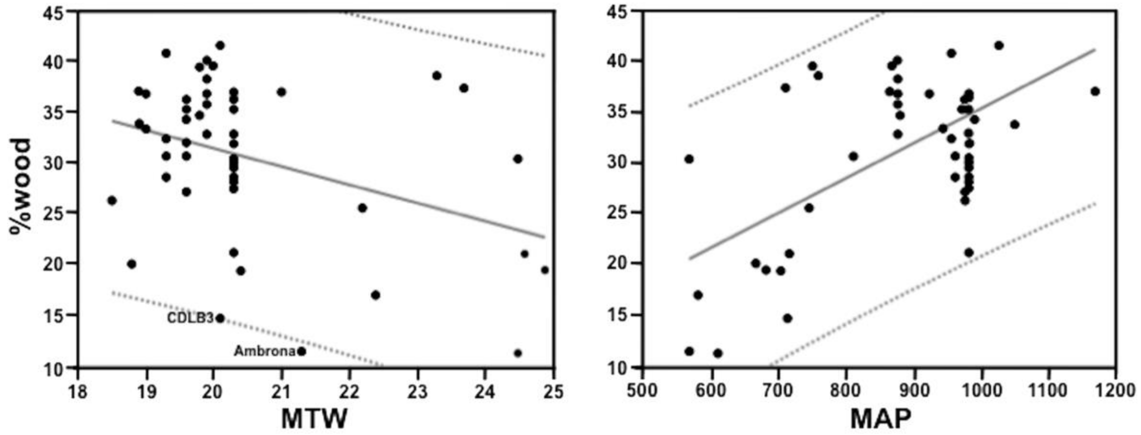

Figure 6. Bivariate plots using as dependent variable %wood. A: %wood on MTW; B: %wood on MAP.

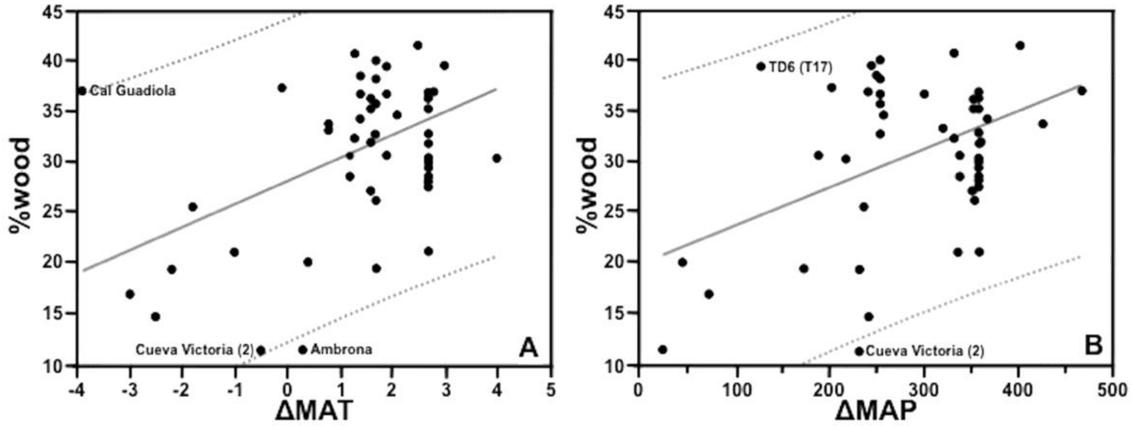

Figure 7. Bivariate plots using independent variables those defined by the difference between recent values and Middle Pleistocene estimations (Δ) and as dependent one, %wood. A: %wood on ΔMAT B: %wood on ΔMAP.

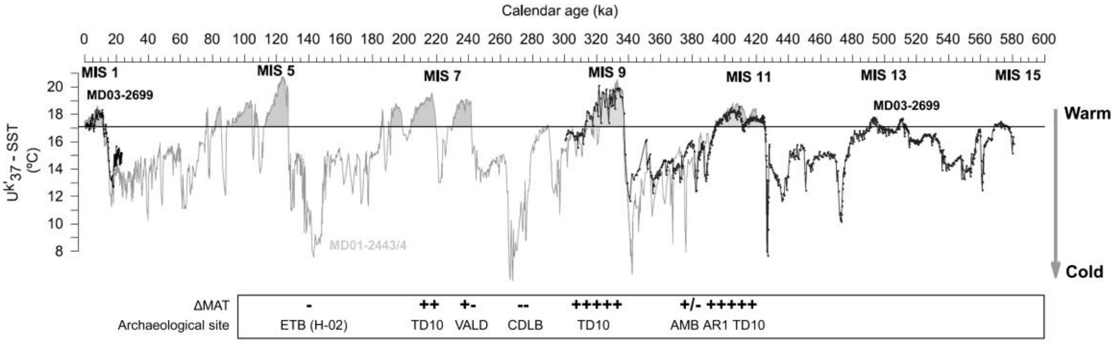

Figure 8. Comparison between MER estimates (if positive or negative ΔMAT) and Iberian Margin composite alkenone-based Sea Surface Temperature for the last 600 ka: MD03-2699 (Rodrigues et al., 2011) and MD01-2443 and MD01-2444 (Martrat et al., 2007). Grey areas represent SST higher than current level.

Table 1. Short summary of the different methods used for the paleoclimatical reconstruction with vertebrates as proxy, periods and regions that include climatic inferences, inferred parameters, validation of the method with other proxies. Climatic parameters: mean annual temperature (MAT), mean temperature of the coldest month (MTC), mean temperature of the warmest month (MTW), yearly positive temperature (Tp), mean annual precipitation (MAP), precipitation of the wettest month (Pwm), precipitation of the driest month (MINP), mean winter precipitation (MWP), mean summer precipitation (MSP), mean autumn precipitation (MAuP), mean spring precipitation (MSpP) and percentage of winter rainfall. Other values have been also obtained such as aridity indexes, humidity, seasonality of precipitation, average annual thermal amplitude (MATA), thermal index (IT), compensated thermal index (ITC), vegetative activity period (VAP) and drought length (D). References: [1]Brattstrom (1956), [2]Markwick (1994, 1998); [3]Böhme (2008), [4]Denny et al. (2009), [5]Makarieva et al. (2009), [6]Sniderman (2009), [7]Head et al. (2009a, 2009b, 2013), [8]Böhme (2002, 2003, 2004, 2008, 2010), [9]Böhme et al. (2006, 2012), [10]Klembara et al. (2010), [11]Hernández-Fernández and Peláez-Campomanes (2005), [12]Hernández-Fernández (2006), [13]Hernández-Fernández and Vrba (2006), [14]Hernández-Fernández et al. (2007), [15]Kay and Maden (1996), [16]Montuire et al. (1997, 2006), [17]Montuire (1999), [18]Aguilar et al. (1999), [19]Damuth et al. (2002), [20]Legendre et al. (2005), [21]van Dam (2006), [22]Escudé et al. (2013), [23]Fortelius et al. (2002, 2006), [24]Cruz et al. (2016), [25]Eronen and Rook (2004), [26]Eronen et al. (2010a, b, 2011), [27]Blain et al. (2007, 2008a, 2009, 2010b, 2011a, b, 2012a, b, 2013a, b, c, 2014a, b, 2015, 2016a), [28]López-García et al. (2008, 2010b, 2011a, b, c, d, 2013a, b), [29]Polly and Eronen (2011), [30]Bañuls-Cardona et al. (2012), [31]Smith and Polly (2013), [32]Motuzco and Ivanov (1996), [33]Avery (1999), [34] Jeannet (2009, 2010), [35] Manzano (2015), [36]Vieites et al (2009), [37]Holden et al. (2013).

Method	Proxy	Epoch	Region	Temperature	Precipitation	Others	Comparison with other proxies	Refs.
Thermal ecology	Anurans, Squamates, Crocodiles	Cretaceous to Holocene	North-America, Global	MAT, MTC	-	-	Pollen and paleoflora	1, 2, 3
Size-temperature-metabolic rate	Anurans, Squamates	Cretaceous, Paleocene, Eocene, Pleistocene	Africa, Asia, South´-America, Australia	MAT	-	-	Sea surface temperature, oxygen isotopes, paleoflora	4, 5, 6, 7
Ecophysiological groups	Fishes, Anurans, Caudates, Allocaudates, Testudines, Squamates	Paleocene to Pleistocene	Europe, Asia, Africa	MAT, MTC, MTW	MAP, Pwm	-	Small-mammals, paleoflora, pollen, oxygen isotopes	8, 9, 10
Transfer functions	Large and small mammals	Pliocene to Holocene	Europe, Asia, Africa	MAT, MTW,MTC, Tp	MAP	MATA, IT, ITC, VAP, D	Paleosoils, pollen, paleoflora, oxygen isotopes	11, 12, 13, 14
Diversity and abundance	Large and small mammals	Miocene to Holocene	Europe, South-America	MAT, MTC, MTW	MAP, MINP	Rainfall seasonality	Paleoflora, hypsodonty, oxygen isotopes	15, 16, 17, 18, 19, 20, 21, 22
Hypsodonty	Large mammals	Miocene, Pliocene	Europe, Asia	-	MAP	-	Paleoflora	19, 23, 25, 26
Mutual Climatic Range and Mutual Ecogeographic Range	Anurans, Caudates, Squamates, Testudines, Large and small mammals	Pleistocene, Holocene	Europe	MAT, MTC, MTW	MAP, MWP, MSP, MSpP, MAuP	Aridity indexes	Pollen, charcoal, mammals, oxygen isotopes	24, 26, 27, 28, 29, 30, 31
Arealogical method of climatograms	Small mammals	Holocene	Europe, Asia	MTC, MTW	MAP	-	-	32
Modern analogues	Small mammals	Pliocene, Pleistocene	Africa	MTW, MTC, maximum interval of monthly temperature	MAP, % of winter rainfall	Aridity index in summer	-	33
Climato-ecological Aptitudes	Small mammals, Amphibians, Reptiles	Pleistocene, Holocene	Europe	MAT, MTC, MTW	MAP			34, 35
Phylogeny and ENM	Caudates	Cretaceous to Present	Global	MAT	MAP	-	-	36
Insect-damage on vertebrate remains	Large mammals, birds	Pleistocene	North-America	MAT	-	Humidity	Oxygen isotopes	37

Table 2. Herpetofauna-based Early-Middle Pleistocene Iberian climate and environmental reconstructions. Abbreviations: Marine Isotope Stage (MIS), mean annual temperature (MAT), mean temperature of the coldest month (MTC), mean temperature of the warmest month (MTW), mean annual precipitation (MAP), representation of woodland and woodland margins in the reconstructed environment (%wood), standart deviation (SD), difference with current value (Δ). References: [1]Agustí et al. (2009), [2]Blain et al. (2008a), [3]Blain (2012-2014), [4]Blain et al. (2008b), [5]Blain et al. (2009), [6]Blain et al. (2012a), [7]Blain et al. (2013a), [8]Blain et al. (2015), [9]Blain et al. (2014b), [10]Blain et al. (2017a), [11]Blain et al. (2011b), [12]Blain et al. (2012b), [13]Blain et al. (2017b). Grey bands represent the sample that corresponds to the warmest temperature and consequently have been correlated with the interglacial peak (Blain et al., 2012a).

Site	**sample**	**MIS**	**MAT**		**MTC**		**MTW**		**MAP**		**%wood**	**Refs.**
			mean ± SD	Δ	mean ± SD	Δ	mean ± SD	Δ	mean ± SD	Δ		
Cal Guardiola		MIS 22	11.6 ± 1.9	-3.9	4.5 ± 2.2	-4,5	18.9 ± 1.7	-4,1	1168 ± 430	+518	37.0	1
Cueva Victoria		MIS 22	16.7 ± 1.9	-1.0	9.0 ± 2.3	-1,6	24.6 ± 1.4	-0,7	716 ± 241	+387	21.0	2
		MIS 22	17.2 ± 1.6	-0.5	10.1 ± 1.7	-0,5	24.5 ± 0.8	+0.5	611 ± 160	+282	11.2	3
Gran Dolina, TD6	T55	MIS 21	10.7 ± 2.1	+0.8	3.2 ± 2.0	+0.6	18.9 ± 1.6	+0.5	1049 ± 193	+477	33.7	4, 5, 6, 7
	T54		11.1 ± 2.1	+1.2	2.9 ± 2.2	+0.3	19.3 ± 1.7	+0.9	961 ± 102	+389	30.6	
	T53		11.1 ± 2.2	+1.2	2.9 ± 2.3	+0.3	19.3 ± 1.7	+0.9	961 ± 102	+389	28.5	
	T52		10.7 ± 2.3	+0.8	2.8 ± 2.3	+0.2	19.0 ± 1.8	+0.6	943 ± 137	+371	33.3	
	T51		11.5 ± 1.6	+1.6	3.7 ± 1.7	+1.1	19.6 ± 1.3	+1.2	983 ± 162	+411	31.9	
	T50		12.6 ± 1.2	+2.7	3.8 ± 1.9	+1.2	20.3 ± 1.2	+1.9	981 ± 46	+409	29.4	
	T49		11.2 ± 1.9	+1.3	3.0 ± 1.9	+0.4	19.3 ± 1.5	+0.9	955 ± 116	+383	32.3	
	T48		12.6 ± 1.2	+2.7	3.8 ± 1.9	+1.2	20.3 ± 1.2	+1.9	981 ± 46	+409	31.8	
	T47		12.4 ± 1.3	+2.5	3.3 ± 2.2	+0.7	20.1 ± 1.2	+1.7	1025 ± 46	+453	41.5	
	T45		12.6 ± 1.2	+2.7	3.8 ± 1.9	+1.2	20.3 ± 1.2	+1.9	981 ± 46	+409	36.3	
	T44		12.6 ± 1.2	+2.7	3.8 ± 1.9	+1.2	20.3 ± 1.2	+1.9	981 ± 46	+409	30.3	
	T43		12.6 ± 1.2	+2.7	3.8 ± 1.9	+1.2	20.3 ± 1.2	+1.9	981 ± 46	+409	27.5	
	T41		12.6 ± 1.2	+2.7	3.8 ± 1.9	+1.2	20.3 ± 1.2	+1.9	981 ± 46	+409	28.6	
	T40		12.6 ± 1.2	+2.7	3.8 ± 1.9	+1.2	20.3 ± 1.2	+1.9	981 ± 46	+409	28.6	

	T38		11.5 ± 1.9	+1.6	3.5 ± 2.0	+0.9	19.6 ± 1.7	+1.2	975 ± 206	+403	27.1	
	T37		12.6 ± 1.2	+2.7	3.8 ± 1.9	+1.2	20.3 ± 1.2	+1.9	981 ± 46	+409	29.9	
	T36		12.6 ± 1.2	+2.7	3.8 ± 1.9	+1.2	20.3 ± 1.2	+1.9	981 ± 46	+409	28.1	
	T35		12.6 ± 1.2	+2.7	3.8 ± 1.9	+1.2	20.3 ± 1.2	+1.9	981 ± 46	+409	32.8	
	T34		12.0 ± 1.4	+2.1	3.8 ± 2.2	+1.2	19.8 ± 1.5	+1.4	880 ± 148	+308	34.6	
	T33		12.6 ± 1.2	+2.7	3.8 ± 1.9	+1.2	20.3 ± 1.2	+1.9	981 ± 46	+409	28.1	
	T32		11.6 ± 1.5	+1.7	3.1 ± 2.1	+0.5	18.5 ± 2.1	+0.1	976 ± 103	+404	26.2	
Gran Dolina, TD8	T28	MIS 19	12.6 ± 1.2	+2.7	3.8 ± 1.9	+1.2	20.3 ± 0.8	+1.9	981 ± 46	+409	21.1	4, 5, 6
Cúllar Baza 1		MIS 17	16.5 ± 2.2	+4.0	9.0 ± 2.8	+2.5	24.5 ± 1.3	+2.0	568 ± 204	+268	30.3	1
Gran Dolina, TD10	T21	MIS 13	12.6 ± 1.2	+2.7	3.8 ± 1.9	+1.2	20.3 ± 1.2	+1.9	981 ± 46	+409	36.8	4, 5, 6, 8
	T20		12.6 ± 1.2	+2.7	3.8 ± 1.9	+1.2	20.3 ± 1.2	+1.9	981 ± 46	+409	35.2	
	T19		12.6 ± 1.2	+2.7	3.8 ± 1.9	+1.2	20.3 ± 1.2	+1.9	981 ± 46	+409	36.3	
	T18		11.2 ± 1.9	+1.3	3.0 ± 1.9	+0.4	19.3 ± 1.5	+0.9	955 ± 116	+383	40.7	
	T17	MIS 11c	12.9 ± 0.7	+3.0	5.7 ± 1.4	+3.1	20.0 ± 1.4	+1.6	867 ± 101	+295	39.5	
	T16		11.8 ± 0.4	+1.9	3.8 ± 1.9	+1.2	19.8 ± 0.4	+1.4	750 ± 212	+178	39.4	
	T15		11.6 ± 1.8	+1.7	3.7 ± 2.0	+1.1	19.9 ± 1.4	+1.5	876 ± 153	+304	40.0	
	T12		11.3 ± 1.9	+1.4	2.9 ± 1.9	+0.3	19.0 ± 1.6	+0.6	923 ± 122	+351	36.7	
	T10		11.8 ± 0.4	+1.9	3.7 ± 2.0	+1.1	19.9 ± 1.4	+1.5	876 ± 153	+304	36.7	
	T9	MIS 9	12.7 ± 1.3	+2.8	4.2 ± 2.0	+1.6	21.0 ± 1.2	+2.6	864 ± 126	+292	36.9	
	T8		11.5 ± 1.9	+1.6	3.5 ± 2.0	+0.9	19.6 ± 1.7	+1.2	975 ± 206	+403	36.2	
	T6		11.8 ± 0.8	+1.9	4.3 ± 0.7	+1.7	19.6 ± 1.2	+1.2	811 ± 121	+239	30.6	
	T5		11.6 ± 1.8	+1.7	3.7 ± 2.0	+1.1	19.9 ± 1.4	+1.5	876 ± 153	+304	35.7	
	T4		11.6 ± 1.8	+1.7	3.7 ± 2.0	+1.1	19.9 ± 1.4	+1.5	876 ± 153	+304	38.2	
	T2		11.3 ± 2.1	+1.4	3.7 ± 2.1	+1.1	19.6 ± 1.5	+1.2	990 ± 202	+418	34.2	
	T1		11.6 ± 1.8	+1.7	3.7 ± 2.0	+1.1	19.9 ± 1.4	+1.5	876 ± 153	+304	32.7	
	T0		11.5 ± 1.9	+1.6	3.5 ± 2.0	+0.9	19.6 ± 1.7	+1.2	975 ± 206	+403	35.2	
Áridos-1		MIS 11b	15.1 ± 2.7	+1.2	3.2 ± 2.2	+1.6	24.1 ± 2.1	+0.1	624 ± 164	+166	19.4	8, 9
Ambrona	AS4 & AS3	MIS 11a	10.6 ± 1.4	+0.3	3.2 ± 1.3	+0.6	21.3 ± 1.2	+1.5	569 ± 70	+74	11.4	8
CDLB	CB3	MIS 9/8	9.8 ± 0.8	-2.5	2.2 ± 1.2	-1.2	20.1 ± 1.0	-1.2	713 ± 227	+292	14.6	10
	CB2	MIS 9/8	10.1 ± 1.6	-2.2	2.5 ± 1.5	-1.1	20.4 ± 1.6	-0.9	703 ± 225	+282	19.3	
TEURU	TE19	MIS 9/8	10.3 ± 0.8	+0.4	2.3 ± 0.6	-0.3	18.8 ± 1.0	+0.4	667 ± 153	+95	20.0	11
Valdocarros II	level 2	MIS8a	11.4 ± 2.5	-2.5	3.1 ± 2.2	-2.1	21.6 ± 2.2	-2.4	699 ± 185	+241	25.5	12
	level 3	MIS 8/7	13.8 ± 3.1	-0.1	5.7 ± 3.4	+0.5	22.5 ± 2.3	-1.5	692 ± 187	+234	37.3	
	level 4	MIS 8/7	14.9 ± 2.8	+1.0	6.9 ± 3.4	+1.7	23.5 ± 2.0	-0.5	689 ± 197	+231	38.5	
ETB (H-02)		MIS 6	10.9 ± 2.3	-3.0	3.1 ± 2.7	-2.1	22.4 ± 2.1	-1.6	581 ± 40	+123	16.9	13

Table 3. Descriptive statistics of regression analyses (OLS: Ordinary Least Squares); N: sample size; R^2: coefficient of correlation; *a*: Y–intercept; *b*: slope; H_0 (*b*=0): null hypothesis for slope zero.

	N	**R^2**	***a***	***b***	**H_0 (*b*=0)**
MTC on MAT	37	0.937	-8.724	1.066	**<0.0001**
MTW on MAT	37	0.703	10.271	0.845	**<0.0001**
	N	**R^2**	***a***	***b***	**H_0 (*b*=0)**
MAP on MAT	37	0.134	1227.059	-30.487	<0.05
MAP on MTC	37	0.198	999.161	-33.656	<0.01
MAP on MTW	37	0.488	2043.132	-57.725	**<0.0001**
	N	**R^2**	***a***	***b***	**H_0 (*b*=0)**
ΔMTC on ΔMAT	37	0.746	-0.118	0.708	**<0.0001**
ΔMTW on ΔMAT	37	0.820	0.013	0.666	**<0.0001**
	N	**R^2**	***a***	***b***	**H_0 (*b*=0)**
ΔMAP on ΔMAT	37	0.016	319.389	7.319	0.450
ΔMAP on ΔMTC	37	0.017	332.027	9.213	0.436
ΔMAP on ΔMTW	37	0.001	328.333	2.504	0.850
	N	**R^2**	***a***	***b***	**H_0 (*b*=0)**
%wood on MAT	37	0.009	35.904	-0.455	0.571
%wood on MTC	37	0.029	33.533	-0.743	0.307
%wood on MTW	37	0.145	67.166	-1.788	<0.05
%wood on MAP	37	0.365	0.994	0.034	**<0.0001**
	N	**R^2**	***a***	***b***	**H_0 (*b*=0)**
%wood on ΔMAT	37	0.219	28.085	2.277	<0.005
%wood on ΔMTC	37	0.067	29.284	1.814	0.665
%wood on ΔMTW	37	0.067	29.190	1.713	0.122
%wood on ΔMAP	37	0.197	17.996	0.038	<0.01