



Palaeoclimatic analysis of Quaternary terrestrial small mammal assemblages from the Sierra de Atapuerca (Burgos, Spain)

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ARTICLE INFO

Editor: Dr. Paul Hesse

Keywords:

Bioclimatic Model
Rodentia
Eulipotyphla
Pleistocene
Holocene
Thermotype
Southwestern Europe

ABSTRACT

Understanding past climatic changes is one of the central challenges in palaeontological research. The Bioclimatic Model (BM) enables the reconstruction of qualitative and quantitative climatic conditions using the fossil record of rodents and eulipotyphlans. Here, we applied this model to the rich and well-documented fossil record from the localities of the Sierra de Atapuerca karst complex, including six archaeological and palaeontological sites spanning nearly continuously from the Early Pleistocene to the Late Holocene ~1.2 Ma - 3.1 ka. A typical temperate climate was inferred for most of the sequence, with variations between Mediterranean and temperate climates, and the influence of boreal climates during the Late Pleistocene cold climatic oscillations recorded in El Portalón and El Mirador assemblages. The record from the base of the sequence of Sima del Elefante (TELUR, TE7-TE14) indicates relatively warmer conditions than the current climate, and a trend of thermal increase was observed from the end of Calabrian and Chibanian based on the Gran Dolina levels TD6 and TD8. Additionally, we obtained a thermotype classification reflecting regional-scale climatic changes linked to shifts in altitudinal belts boundaries. This work constitutes the first, diachronic, bioclimatic analysis of the entire biostratigraphic sequence of the Atapuerca site complex, providing an updated synthesis of long-term climatic reconstruction over more than one million years.

1. Introduction

Paleoclimatology has been extensively developed as a relevant research field for studying past climatic and environmental changes and their impact on the evolutionary patterns of terrestrial ecosystems (Behrensmeier, 1992; Hernández Fernández and Vrba, 2005; Twitchett, 2006; Hernández Fernández et al., 2022). A diverse array of data sources, including geology, mineralogy, geochemistry, and faunal and floral assemblages' composition, are commonly employed in Quaternary palaeontological research within this field (Bradley, 1999; Martínez-Pillado et al., 2014; Fagoaga et al., 2019a; Fernández-García et al., 2019;

Ilvonen et al., 2022).

The abundant and well-documented fossil record of the Quaternary vertebrates, together with their sensitivity to changes in climate and habitat, make them reliable paleoenvironmental and paleoclimatic proxies (Andrews, 1995; Sommer and Nadachowski, 2006; Álvarez-Lao and García, 2011; Discamps and Royer, 2017). Among these, small mammals, especially rodents, stand out as the most informative mammals due to their vast diversity and high sensitivity to environmental and climatic conditions. Since their skeletal remains are commonly abundantly preserved in archaeological and palaeontological sites, small mammals are widely used for conducting palaeoecological

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<https://doi.org/10.1016/j.palaeo.2024.112532>

Received 25 June 2024; Received in revised form 30 September 2024; Accepted 1 October 2024

Available online 2 October 2024

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reconstructions (Nadachowski, 1989; Chaline et al., 1995; Montuire et al., 1997; Hernández Fernández et al., 2007; Cuenca-Bescós et al., 2009, 2011; Fagoaga et al., 2019b; Álvarez-Vena et al., 2021; García-Morato et al., 2021; López-García et al., 2021; Sala et al., 2021; Domínguez-García et al., 2023, among others).

The sites considered in this study are found in the Sierra de Atapuerca, a karstified hill of Upper Cretaceous limestones (Ortega et al., 2013) located in the northern central area of the Iberian Peninsula, at about 1080 m above sea level and 15 km from the city of Burgos (Spain) (Fig. 1). This cave-complex is known primarily for its key contributions to the understanding of human evolution. The palaeontological and archaeological record provided by the many sites that make it up proves the presence of the genus *Homo* in the area over a long period, ranging from the Early Pleistocene (including some of the earliest evidences of

human presence in Western Europe) to the Holocene (Arsuaga et al., 1993, 2014, 2015; Carbonell et al., 1995, 2008; Bermúdez de Castro et al., 1997, 2008). The localities considered in this study are: the Sima del Elefante (named as Trincheras Elefante, TE), Gran Dolina (named as Trincheras Dolina, TD), Sima de los Huesos (abbreviated as SH), the Galería complex (named as Trincheras Galería-Trincheras Zarpazos, TG-TZ), El Portalón (abbreviated as PORT) and El Mirador (abbreviated as MIR). Together, these sites have yielded an exceptional small vertebrate fossil record, the chronostratigraphical period represented by the assemblages spans nearly continuously from the Early Pleistocene to the Holocene (Cuenca-Bescós et al., 2016). Since 1990, extensive research works have been conducted, focusing on the rich and diverse fauna of all major groups of small vertebrates, including fishes, amphibians, reptiles, birds and small mammals (e.g., Cuenca-Bescós et al., 1997, 1999, 2001, 2013; Laplana and Cuenca-Bescós, 2000; Blain et al., 2009, 2013; López-García et al., 2010, López-García et al., 2011; Rofes and Cuenca-Bescós, 2013; Núñez-Lahuerta et al., 2016, 2021a, 2021b, 2022; Bañuls-Cardona et al., 2017; Galán et al., 2016, 2019a, 2019b, 2023; Bisbal-Chinesta et al., 2020; Blanco-Lapaz et al., 2021; Martínez-Monzón et al., 2021; Rofes et al., 2021; Moya-Costa et al., 2023).

The primary aim of this study is to provide a synthesis of the long-term Quaternary climatic evolution in the central-northern region of the Iberian Peninsula, using the published small mammal data obtained from the Atapuerca site complex. To achieve this objective, a bioclimatic analysis is applied to the update record of rodents and eulipotyphlans from the whole chronostratigraphical period represented at the Sierra de Atapuerca cave-sites. By comparing our findings together with other proxies (isotopes, herpetofauna, palaeobotany), we will be able to identify the main climatic patterns operating during this time-frame.

2. Materials and methods

2.1. The fossil assemblages included in the analysis

This work is based on the published data concerning the Rodentia and Eulipotyphla fossil assemblages from six archaeo-palaeontological sites at the Sierra de Atapuerca: Sima del Elefante TE (the basal section corresponds to the Lower Red Unit, TELRU, comprising levels TE7 to TE14, and was dated as 1.2 Ma, Carbonell et al., 2008; the upper section corresponds to the Upper Red Unit, TEURU, including small mammal record from levels TE18 and TE19, the top of level TE18 was dated to 307 ± 19 ka and 255 ± 12 ka, giving thus maximum ages for TE18 and a minimum age for TE19, Huguet et al., 2017); Gran Dolina, TD (level TD3–4 was dated as 902 ± 149 ka, Álvarez-Posada et al., 2018; level TD10 dated as 390 ± 59 ka, Falguères et al., 1999); Sima de los Huesos, SH (lithostratigraphic unit LU6 was dated as 455 ± 17 ka and 440 ± 15 ka, Demuro et al., 2019), Galería Complex, TG-TZ (unit GII was dated as 324 ± 42 ka and 231 ± 20 ka, and unit GIII was dated between 260 ± 20 ka and 225 ± 18 ka, Arnold et al., 2015), El Portalón, PORT (Pleistocene levels dated to $30,300 \pm 190$ yr BP to $16,890 \pm 80$ yr BP, López-García et al., 2010, and the Holocene level PORT79 was dated between 5294 and 4732 cal yr BP, Rofes et al., 2021) and El Mirador, MIR (level MIR51/3 was dated as 15,110–14,470 cal yr BP, the top of level MIR4 as 3390–3070 cal yr BP; Bañuls-Cardona et al., 2017). Thus, the set of fossil assemblages employed in this study constitute a composite sequence spanning more than one million years almost continuously, except for two main chronological hiatuses between MIS 16 and MIS 12 and between MIS 6 and MIS 3. For a more detailed description on the stratigraphy and chronology of the sites, abundant literature is available (Rosas et al., 2006; López-García et al., 2010; López-García et al., 2011; Demuro et al., 2019; Arnold et al., 2015; Vergès et al., 2016; Campaña et al., 2017; Galán et al., 2023).

The review presented here includes data from 41 faunal assemblages grouped by the different sites described above; the stratigraphic layers and chronology follow López-García et al. (2010, 2011), Galindo Pelliscena et al. (2011), Cuenca-Bescós et al. (2016), Bañuls-Cardona et al.

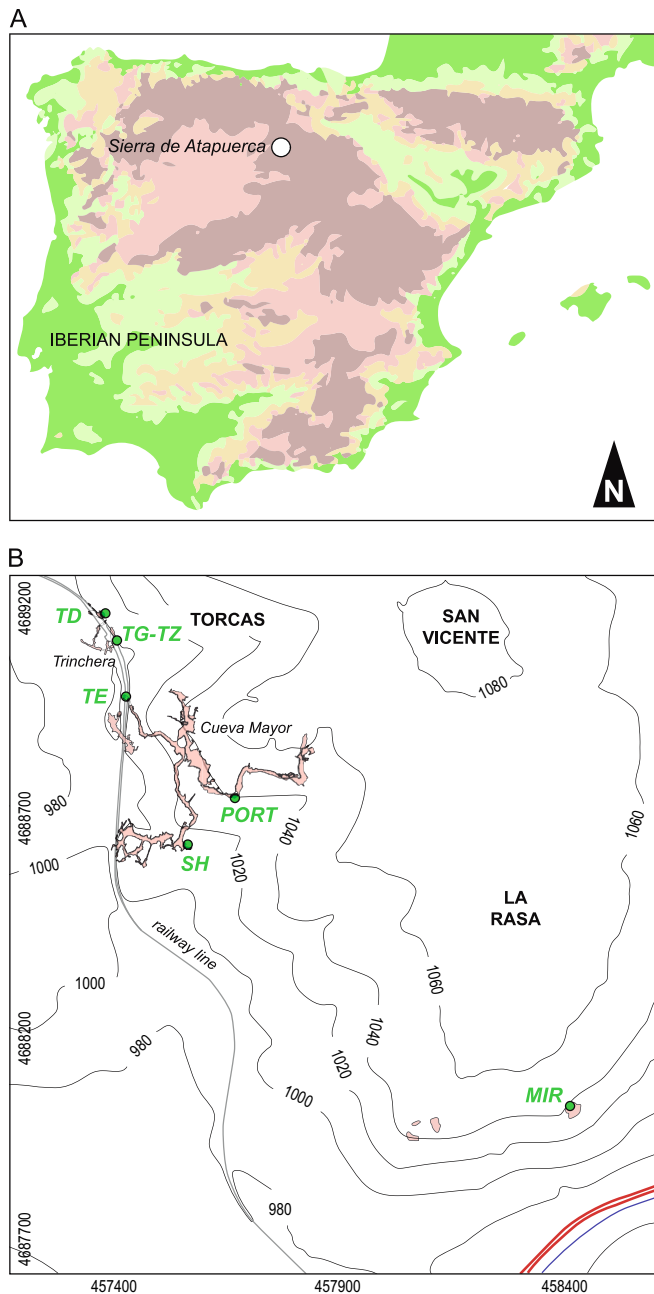


Fig. 1. A) General location of the study area in the Iberian Peninsula B) Location of the sites in the Sierra de Atapuerca. TD: Gran Dolina, TG-TZ: Galería complex, TE: Sima del Elefante, PORT: El Portalón, SH: Sima de los Huesos, MIR: El Mirador. Modified from Ortega et al. (2013).

(2017), Rofes et al. (2021), Moya-Costa et al. (2023), as shown in the Table 1 (Galán et al., 2023 was also followed for the chronological data on MIR49). Some radiocarbon uncalibrated ages provided in López-García et al. (2010) were here calibrated using OxCal 4.4 (Bronk Ramsey, 2009) and the calibration curve IntCal 20 (Reimer et al., 2020). Since an appropriate sample size is essential to avoid some methodological issues, following Berto et al. (2022b) only levels with more than 25 MNI were considered representative and therefore included in the analysis. For that reason, the data of some consecutive stratigraphic levels with similar chronology and lower MNI were unified in a single faunal assemblage. Faunal lists including representatives of the orders Rodentia and Eulipotyphla from these assemblages were used for conducting the Bioclimatic Analysis.

2.2. Bioclimatic analysis

To reconstruct the climatic conditions from small mammal assemblages at the Sierra de Atapuerca complex, the Bioclimatic Analysis proposed by Royer et al. (2020) was used. This method, originally developed by Hernández Fernández, 2001b and Hernández Fernández and Peláez-Campomanes (2003, 2005), relies on the correlation between climate and mammal communities.

Royer et al. (2020) proposed a new version of the Bioclimatic

Analysis focused on extant rodents and eulipotyphlans from the Palaearctic realm. The method enables the estimation of qualitative and quantitative climatic data from fossil assemblages based on present-day distribution of mammals across broad ecological and climatic zones. Specifically, the bioclimatic characterisation of the fauna is established on the assignment of a Climatic Restriction Index (CRI) to each species, according to their current geographical distribution in the ten global climate zones defined by Walter (1970), as summarised in Table 2. The CRI is assigned a value of 0 when the species is absent from a particular climate zone, or 1/n when it is present, with “n” representing the number of climate zones where the species occurs (Hernández Fernández, 2001a, 2001b). Subsequently, the Bioclimatic Component (BC) is calculated, representing each of the ten climate zones in a locality or fossil site based on its faunal assemblage ($BC_i = (\sum CRI_i) 100/S$, where “i” denotes the climatic zone, and “S” is the number of species identified in each locality or fossil assemblage). By combining all ten BC values for each climate zone in a given locality or fossil site, its bioclimatic spectrum is obtained. For a more detailed description of this method, see Hernández Fernández, 2001b and Hernández Fernández and Peláez-Campomanes (2003, 2005), as well as Royer et al. (2020).

Royer et al. (2020) developed algorithms enabling the calculation of bioclimatic spectra, as well as applied predictive equations to climate zone classification, and to calculate quantitative climatic variables.

Table 1

Fossil sites and small mammal assemblages analyzed in this work and references for faunal lists. * Calibration conducted in this work.

Site	Assemblage	Published age	References
El Mirador	MIR4	3.7–3.1 cal kyr BP	Bañuls-Cardona et al. (2017)
	MIR5	4.5–4.4 cal kyr BP	
El Portalón	PORT79	5.3–4.7 cal kyr BP	Rofes et al. (2021)
	MIR9–6	6.9–5.4 cal kyr BP	
El Mirador	MIR17–16–10–11	6.7–5.9 cal kyr BP	Bañuls-Cardona et al. (2017)
	MIR22–18	7.4–6.8 cal kyr BP	
	MIR24–23	8–7.1 cal kyr BP	
	MIR49	11–8.4 cal kyr BP	
	MIR50–51	15–13 cal kyr BP	
	PORT1	21–20 cal kyr BP*	
	PORT2		
	PORT4–3		
	PORT6–5		
	PORT7		
	PORT8		
El Portalón	PORT9		López-García et al. (2010) Cuenca-Bescós et al. (2016)
	PORT10		
	PORT11	35–34 cal kyr BP*	
	PORT12		
	PORT13		
	PORT14		
	PORT16–15		
Sima del Elefante	TE18–19	255 ± 12 ka 307 ± 19 ka	López-García et al. (2011) Cuenca-Bescós et al. (2016)
	TG-TZ-III	225 ± 18 ka	
Galería-Zarpazos	TG-TZ-III	260 ± 20 ka	Galindo Pellicena et al. (2011) Cuenca-Bescós et al. (2016)
	TG-TZ-II	231 ± 20 ka	
Gran Dolina	TD10–11	324 ± 42 ka 372–337 ka	Cuenca-Bescós et al. (2016)
	SH	440 ± 15 ka 455 ± 17 ka 602 ± 52 ka	
Sima de los Huesos	TD8a		Cuenca-Bescós et al. (2016) López-García et al. (2021)
	TD7		
	TD6b	730 ± 63 ka	
	TD6a	856 ± 75 ka	
	TD5		
	TD3–4	902 ± 149 ka	
	TE14		
Gran Dolina	TE13		Cuenca-Bescós et al. (2016) Moya-Costa et al. (2023)
	TE12		
	TE11		
	TE10		
	TE9	1.2 Ma	
	TE8		
	TE7		
Sima del Elefante			Cuenca-Bescós et al. (2016)

Table 2

Climate zone (CZ) and zonobiome (ZB) typology used in this work following Hernández Fernández, 2001b - modified from Walter (1970). The colour code of the first column corresponds to Figure 2

CZ/ZB	Climate zone	Zonobiome (mainly vegetation type)
I	Equatorial	Evergreen tropical rainforest
II	Tropical with summer rains	Tropical deciduous woodland
II/III	Transition tropical semiarid	Savanna
III	Subtropical arid	Subtropical desert
IV	Winter rains and summer drought (Mediterranean)	Sclerophyllous woodland–shrubland
V	Warm-temperate	Temperate evergreen forest
VI	Typical temperate	Nemoral broadleaf-deciduous forest
VII	Arid-temperate (continental)	Steppe to cold desert
VIII	Cold-temperate (boreal)	Boreal coniferous forest (taiga)
IX	Arctic (polar)	Tundra

Furthermore, they provided both CRI and bioclimatic spectrum values for each extant species and modern localities of reference included in their study. However, as highlighted by Domínguez-García et al. (2023), the CRI values of *Arvicola sapidus*, *Microtus duodecimcostatus* and *Talpa occidentalis* did not align with their current geographic distribution. Consequently, these values were adjusted according to Wilson et al. (2017) and Wilson and Mittermeier (2018), along with the bioclimatic spectra of modern localities where these species are present (Supplementary material 1).

Additionally, a significant limitation of this method is the climatic characterisation of extinct species, which requires the identification of their living ecological analogues. For this purpose, the bioclimatic characterisation provided by Hernández Fernández (2001a) and Hernández Fernández et al. (2007) was used in this study. For additional extinct taxa (*Arvicola jacobaeus*, *Marmota* sp., *Crocidura kornfeldi*, *Beremedia fissidens*, *Dolinasorex glyphodon*, *Sorex margaritodon*, and *Sorex rutenensis/subaraneus*) the CRI values were processed similarly to the work conducted by Berto et al. (2022a, 2024). This processing was based on their past geographic ranges and the geographical distribution of the morphologically closest extant species (Rzebik-Kowalska, 1998; Hernández Fernández, 2001a; Rofes et al., 2016; Rofes and Cuenca-Bescós, 2009a, 2009b, 2011, 2013) (Supplementary material 1). Additionally, one extant species previously uncharacterized (*Galemys pyrenaicus*) was also included according to Quaglietta (2022). Moreover, when specific identifications were unavailable, such as pairs of similar species (e.g. *Apodemus sylvaticus-flavicollis*, *Sorex coronatus-araneus*) or a taxon assigned only to genus, “quimeric” species were employed for their climatic characterisation, averaging the climate zone occupation of all potential species, following the approach outlined by Royer et al. (2020).

The Bioclimatic Analysis was applied to Rodentia and Eulipotyphla using the 41 faunal assemblages spanning the extensive stratigraphic sequence of the Atapuerca site complex. For each fossil assemblage, the bioclimatic spectrum, climate zone classification, and nine climatic variables were calculated using the approach based on Rodentia and Eulipotyphla, facilitated by the R script provided by Royer et al. (2020) (Supplementary material 2). To analyse climatic trends and establish comparisons, four variables of palaeoclimatic relevance were selected: MAT (mean annual temperature), P (annual total precipitation), ITC (compensated thermicity index), D (drought length, defined as the period when P values are lower than 2*²MAT). The results were compared with present-day climate of the nearest locality to the Sierra de Atapuerca, Ibeas de Juarros, sourced from the Iberian Climate Atlas (Couto et al., 2011), and accessed via the online GIS application <http://a.groclimap.aemet.es/>. In addition, the Bioclimatic Analysis was applied to the locality of Sierra de Atapuerca (10 × 10 km UTM square

30TVM58) using current faunal data concerning rodents and eulipotyphlans (data from Asociación Española para la Conservación y Estudio de los Mamíferos, <https://secem.observation.org/>).

Furthermore, two climatic classifications were conducted using the quantitative results. Firstly, a climate zone was assigned to each studied assemblage according to the climatic typology of Walter (1970), using MAT and D following Hernández Fernández (2001a). Secondly, a classification was performed according to Rivas-Martínez et al. (2017), relying on various thermic parameters and indices: MAT, D, ITC, Ic (simple continentality index or annual thermic interval), and Tp (positive annual temperature). All parameters were obtained through the Bioclimatic Analysis (Royer et al., 2020), except Ic, which was computed as the mean temperature of the warmest month minus the mean temperature of the coldest month (Tmax - Tmin) in degrees Celsius. Consequently, the bioclimates and thermotypes derived from each faunal association were determined. For a more detailed description of the correspondence between parameter or index values and bioclimates and thermotypes, see Rivas-Martínez et al. (2017).

3. Results

3.1. Bioclimatic spectra

The results obtained for the ten climate zones (CZ) representation in the Sierra de Atapuerca sequence are shown in Fig. 2 and supplementary material 2. Broadly speaking, the typical temperate climate zone (CZ VI) is dominant in the entire bioclimatic spectra, followed by the Mediterranean (CZ IV). The continental (CZ VII) and boreal (CZ VIII) climate zones are the next, more important components during the Calabrian and Chibanian, representing a similar proportion in the bioclimatic spectra. However, from the Upper Pleistocene and onwards, the boreal component (CZ VIII) increases at the expenses of the continental one, together with an increase in the proportion of the polar climate zone (CZ IX) representation. Later in the Megalayan, this trend is somehow reverted with the decrease of those zones related to colder conditions (CZ VIII and CZ IX) and the recovery of CZ IV.

The bioclimatic spectra show rather stable features during the Calabrian period and most of the Holocene, while several pronounced oscillations are observed along the Chibanian and, more pronouncedly, during the Upper Pleistocene. Regarding the Chibanian, what we first observe is that the proportion of the Mediterranean climate zone (CZ IV) decreases while the typical temperate (CZ VI) increases in TD7, then the proportion of CZ IV is recovered at the expense of CZ VII and CZ VIII in TD8a. Secondly, after the MIS 16-MIS 12 temporal hiatus, slight variations are related to an increase of CZ IX and reduction of CZ IV, showed by the SH and TD10–11 assemblages, whereas in the Galería

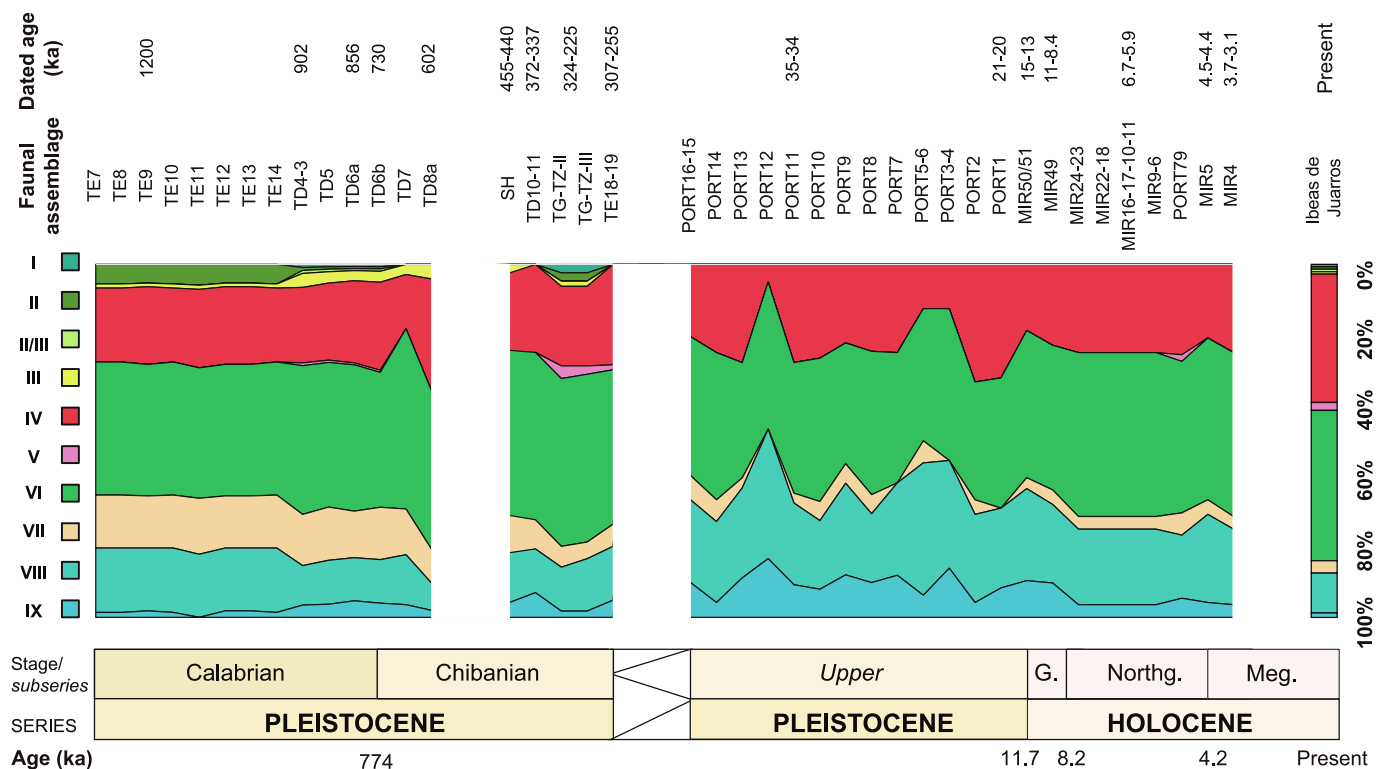


Fig. 2. Bioclimatic spectra of small mammal assemblages during the Quaternary in Sierra de Atapuerca sites. Climate zones: equatorial (I), tropical (II), transition tropical semiarid (II/III), subtropical arid (III), Mediterranean (IV), warm-temperate (V), typical temperate (VI), continental (VII), boreal (VIII), polar (IX). Abbreviations: G = Greenlandian, Northg = Northgripiian, Meg = Meghalayan.

assemblages TG/TZ, the climate zones I, II, II/III and V are represented; then, the climate zones related to colder conditions increase in TE 18–19. Regarding the Upper Pleistocene, represented at El Portalón and El Mirador sites, major variations are detected: peaks related to an increase of colder climate zones are observed in PORT12, PORT9, PORT5–6, PORT3–4 and MIR50–51, while, on the contrary, an increase of CZ IV and CZ VI is observed in PORT2 and PORT1.

3.2. Qualitative bioclimatic analysis

The qualitative bioclimatic results show that the typical temperate (CZ VI) is the first climate zone predicted for the majority of studied assemblages, showing high probabilities ($p_1 > 0.9$, Table 3), while the Mediterranean (CZ IV) is the second (Table 3; Fig. 3a). Some exceptions are observed in TD8a (CZ VI, $p_1 = 0.86$), P12 (CZ VIII, $p_1 = 0.53$), P2 (CZ IV, $p_1 = 0.99$) and P1 (CZ I, $p = 0.73$). These results indicate that climate was fairly stable along the entire sequence analyzed.

3.3. Quantitative bioclimatic analysis

The use of the Quantitative Bioclimatic Analysis based on rodent and “insectivore” species from the Atapuerca site complex allowed to infer numerical values for some climatic parameters, as well as to obtain two different bioclimatic classifications of each faunal assemblage (Table 3; Fig. 3b, d; Supplementary material 2). Overall, the results show a stable pattern similar to that of those of the bioclimatic spectra and the qualitative climatic classification exposed above, although variations are more pronounced in some cases.

The results of the mean annual temperature (MAT) have provided higher values for the Calabrian and Chibanian (MAT = 11.7–16.5 °C) and they also show a slight warming trend towards the Chibanian (Fig. 3a). During the Upper Pleistocene a clear cooling was inferred compared to the previous ages, showing MAT values between 2.6 °C and 10.3 °C, followed by a later warming in the Holocene (MAT =

9.9–11.8 °C). Temperate temperatures were obtained by all assemblages, except for sublevels 12 and 5–6 of Portalón (PORT12, PORT5–6) which have yielded the lowest MAT values. In addition, certain less pronounced cooling events were recognized: 1) during Chibanian from SH and TD 10–11; 2) in the Upper Pleistocene from P9; 3) in the end of the Pleistocene from MIR 50/51 and MIR 49; 4) a small drop in temperature in the end of Northgripiian to Meghalayan from MIR 5.

The drought period (D) values follow a similar pattern than MAT (Fig. 3b). Some differences are observed, since an increase in MAT at the TD7 and TG/TZ-II layers correspond to a decrease in D. The inferred D values are below the threshold of 2 months in almost the entire sequence, except to TD6b, TD8a and TGII during the Chibanian, whereas the minimum values obtained correspond to the lowest MAT in the Upper Pleistocene.

The inferred annual precipitation (P) values expose greater stability than the rest of parameters, ranging from 463 mm to 784 mm (Fig. 3c). Lower precipitation values under 500 mm are recorded for the Calabrian assemblages from TE, whereas P increased during the Chibanian, reaching the maximum in TGII. Upper Pleistocene and Holocene P values are fairly stable between 544 mm and 718 mm showing some slight variations.

Concerning the compensated thermal index (Itc), the result shows a very similar and parallel pattern to that of MAT and D (Fig. 3d), except for TG/TZ-II, which show opposite patterns of Itc and D. Along the sequence, the Itc estimated values range from –28 in PORT12 to 287 in TD8a. Overall, higher values were found during the end of Calabrian and Chibanian, while lower ones were recorded during the Upper Pleistocene showing relevant variations.

The climatic assignments according to the climatic typology of Walter (1970) based on quantitative results are in general agreement with the qualitative analysis. Thus, the typical temperate climate (CZ VI) predominates through the sequence (Table 3, Fig. 3b). Some discrepancies were found between the qualitative and quantitative models, as in TD3–4, TD6b and PORT2 which were classified by the qualitative

Table 3

Qualitative and quantitative bioclimatic classifications. Climate assignment based on the Quantitative Bioclimatic Model results was performed following Walter (1970), Hernández Fernández (2001) and Rivas-Martínez et al. (2011, 2017). Abbreviations: 1st CZ: first predicted climate zone; p₁: probability of first predicted climate zone; 2nd CZ: second predicted climate zone; p₂: probability of second predicted climate zone. Thermotypes: Mte, Mesotemperate; Ste, supratemperate; Ote: Orottemperate; Mme, Mesomediterranean; Sme, Supramediterranean; Tbo, thermoboreal.

Assemblage	Qualitative Bioclimatic Model				Quantitative Bioclimatic Model	
	1st CZ	p ₁	2nd CZ	p ₂	Walter	Thermotype
MIR4	VI	1	IV	< 0.001	VI	Ste
MIR5	VI	1	IV	< 0.001	VI	Ste
Ste/mte	VI	0.999	IV	0.001	VI	Supratemperate/mesotemperate
MIR9-6	VI	1	IV	< 0.001	VI	Ste
MIR17-16-10-11	VI	1	IV	< 0.001	VI	Ste
MIR22-18	VI	1	IV	< 0.001	VI	Ste
MIR24/23	VI	1	IV	< 0.001	VI	Ste
MIR49	VI	1	IV	< 0.001	VI	Ste
MIR50-51	VI	1	VIII	< 0.001	VI	Ote
PORT1	VI	0.734	IV	0.266	VI	Ste
PORT2	IV	0.99	VI	0.01	VI/IV	Ste
PORT4-3	VI	0.999	VIII	0.001	VI	Ote
PORT6-5	VI	0.962	VIII	0.038	VI/VIII	Tbo/ote
PORT7	VI	1	IV	< 0.001	VI	Ote
PORT8	VI	1	IV	< 0.001	VI	Ste
PORT9	VI	0.997	VIII	0.003	VI	Ote
PORT10	VI	1	IV	< 0.001	VI	Ste
PORT11	VI	0.998	IV	0.002	VI	Ste
PORT12	VIII	0.525	VI	0.475	VIII	Tbo/ote
PORT13	VI	0.991	IV	0.009	VI	Ote
PORT14	VI	1	IV	< 0.001	VI	Ste
PORT16-15	VI	1	VIII	< 0.001	VI	Ote
TE18-19	VI	0.99	IV	0.01	VI	Mte
TG-TZ-III	VI	1	IV	< 0.001	VI	Mte
TG-TZ-II	VI	1	IV	< 0.001	VI/V	Mte
TD10-11	VI	1	IV	< 0.001	VI	Mte
SH	VI	1	IV	< 0.001	VI	Mte
TD8a	VI	0.864	IV	0.136	IV	Mme
TD7	VI	1	IV	< 0.001	VI	Mte
TD6b	VI	0.993	IV	0.007	VI/IV	Sme
TD6a	VI	1	IV	< 0.001	VI	Mte
TD5	VI	1	IV	< 0.001	VI	Mte
TD3-4	VI	1	IV	< 0.001	VI/IV	Mte
TE14	VI	1	IV	< 0.001	VI	Ste
TE13	VI	1	IV	< 0.001	VI	Ste
TE12	VI	1	IV	< 0.001	VI	Ste
TE11	VI	1	IV	< 0.001	VI	Ste
TE10	VI	1	IV	< 0.001	VI	Ste
TE9	VI	1	IV	< 0.001	VI	Ste
TE8	VI	1	IV	< 0.001	VI	Ste
TE7	VI	1	IV	< 0.001	VI	Ste

analysis as climate zone VI, while the quantitative results assigned them in an ecotone between VI and IV. Even a more striking case was found in TG/TZ-II, which was assigned in an ecotone between VI and warm-temperate climate (CZ V) using quantitative results. In addition, PORT12 was classified as boreal climate (CZ VIII) with both quantitative and qualitative analysis, and PORT5-6 is placed in an ecotone between CZ VI and CZ VIII by the quantitative results, while it was classified as CZ VI using the qualitative model.

Concerning the climatic classification following Rivas-Martínez et al. (2017), the Temperate macrobioclimate was inferred for most of the analyzed assemblages, except some cases assigned to the Mediterranean and boreal macrobioclimates (Table 3; Fig. 3d). Interesting variations are observed along the sequence in thermotypes inferred. The results indicate that the supratemperate thermotype was represented in the Sierra de Atapuerca during the Calabrian, while at the end of that Stage and during the Chibanian, the mesotemperate and the supra- and mesomediterranean alternated. For the Upper Pleistocene and Holocene were reordered fluctuations between supratemperate, orottemperate and thermoboreal thermotypes.

4. Discussion

The bioclimatic analysis of the rodents and eulipotyphlans record has provided valuable and detailed results, enabling us to reconstruct the long-term bioclimatic history of the paleoanthropological localities of the Sierra de Atapuerca from 1200 ka to 3.1 ka. By integrating the findings with various models, we can interpret the bioclimatic evolution in this region over the represented timeframe.

The bioclimatic spectra results display low representation of tropical (CZ II), subtropical (CZ III) and continental (CZ VII) biozones in the earlier phases, which progressively disappeared or reduced their proportion in the Upper Pleistocene and Holocene (Fig. 2) in concordance with the Iberian rodent faunas (Hernández Fernández et al., 2007). The fluctuations between the representation of typical temperate (CZ VI), boreal (CZ VII) and polar (CZ IX) biomes observed in the spectra correlate with biogeographic dynamics associated to the irruption and the expansion of distribution ranges of cold-related species (*Alexandromys oeconomus*, *Chionomys nivalis*, *Stenocranius anglicus*, *Sicista belutina*, *Ochotona pusilla*) in the Iberian communities along the Upper Pleistocene glacial events (Arribas, 2004; Sesé, 2005; Cuenca-Bescós et al., 2010; López-García, 2011; Rofes et al., 2012; Laplana et al., 2015), thus reinforcing the notion that southern Mediterranean peninsulas

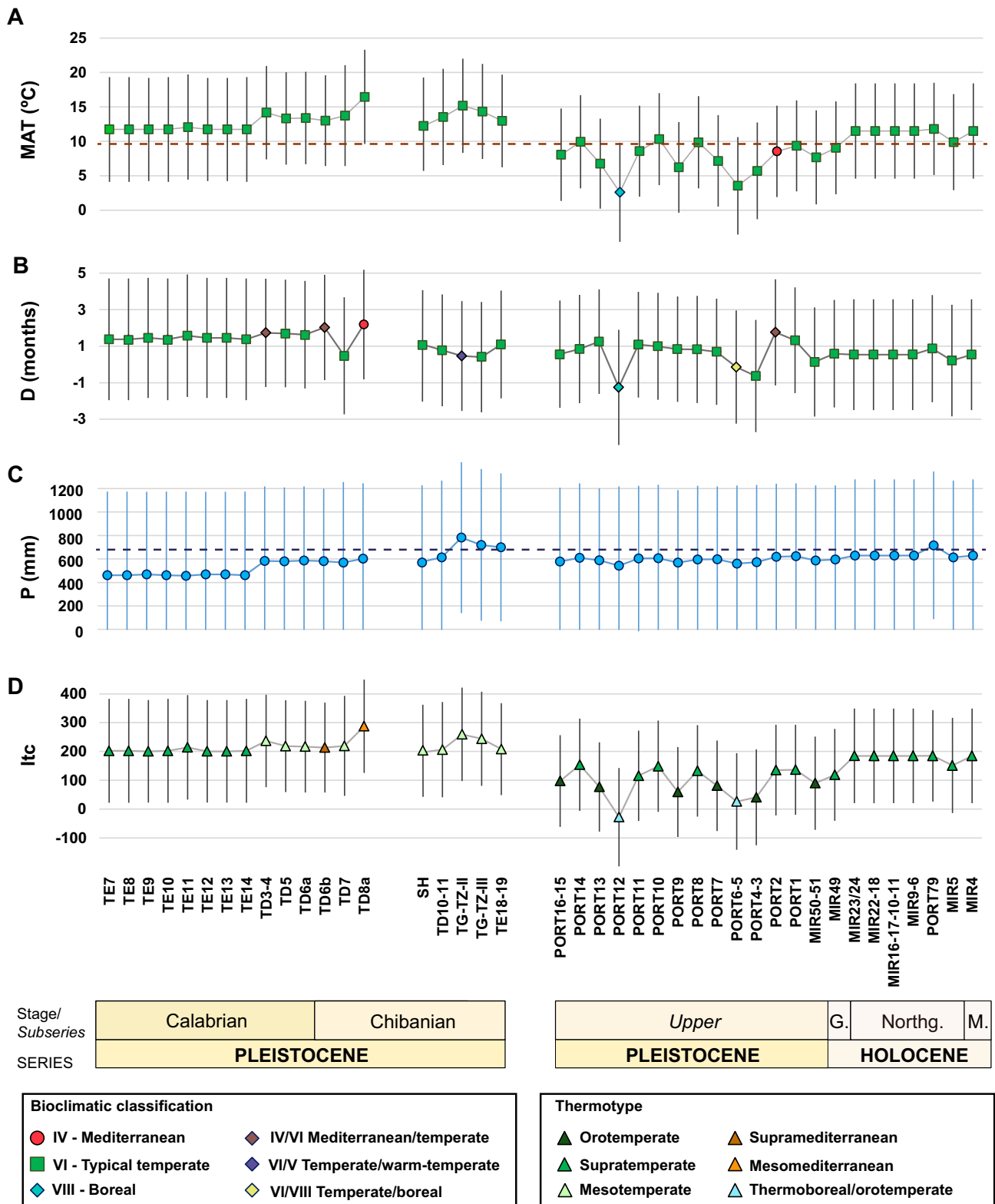


Fig. 3. Evolution of the climate along the Sierra de Atapuerca sequence. A) Mean annual temperature (MAT), symbols represent qualitative climatic classification; B) drought length (D), symbols represent quantitative climatic classification according to Walter (1970); C) annual total precipitation (P); D) compensated thermicity index (Itc), symbols represent thermotype classification according to Rivas-Martínez et al. (2017). Fit values for each parameter are provided together to the confidence intervals for the estimation shown as vertical lines. Abbreviations: G = Greenlandian, Northg = Northgripan, Meg = Meghalayan.

constitute biotic refuges during Quaternary cold phases (Hewitt, 1999; Sommer and Nadachowski, 2006; O'Regan, 2008).

Climate assignments for the Atapuerca small mammal faunas were typical temperate (CZ VI) for most of the time period analyzed using both quantitative and qualitative models (Table 3, Fig. 3), in concordance with previous works suggesting that during most of the Pleistocene the glaciations had not a drastic influence in the Iberian ecosystems (Hernández Fernández et al., 2007).

Before comparing the quantitative results obtained with other proxies and palaeoclimatic methods, it is important to note that the inferred quantitative values should not be taken as absolutes. Instead, they should be viewed as indicators of general trends, given the statistical uncertainty inherent in all climate estimation (Hernández Fernández and Peláez-Campomanes, 2005). Certain methodological issues might be also considered. The Upper Pleistocene and Holocene assemblages provide more detailed temporal resolution than those from earlier stages, thus resulting in higher climatic resolution for these chronologies. Additionally, most of the taxa represented in these later assemblages correspond to extant species with well-known distributions and bioclimatic characterizations. Therefore, the inferences resulting from those assemblages are likely more accurate than those from older deposits.

The record from TE7 to TE14 indicates a stable temperate climate around 1.2 Ma since few changes were recognized in the small mammal composition (Cuenca-Bescós et al., 2016). Afterwards, a warming trend was observed from the end of Calabrian and Chibanian, suggesting the existence of an ecotone between Mediterranean-temperate or Mediterranean climate, linked to a change from supratemperate to mesotemperate thermotypes, and supra- and mesomediterranean in TD6b and TD8, (Fig. 3).

Major variations have been found linked to the record from Portalón during the Upper Pleistocene. Overall, these assemblages indicated colder climatic conditions, associated to boreal and transitional boreal climates in PORT12 and PORT6–5 and variations between supra- and orotemperate thermotypes until the end of the Pleistocene from El Mirador (MIR50–51).

The results obtained here overall agree with previous paleoclimatic studies developed using microvertebrates. An alternative method applied is the Mutual Ecogeographical Range (MER – Blain et al., 2009, 2016), which was applied to the microvertebrate record of the Sierra de Atapuerca sequence (Blain et al., 2009, 2011, 2012, 2013; López-García et al., 2010; Bañuls-Cardona et al., 2017; Martínez-Monzón et al., 2021). This approach is based on the overlapping area of the current geographic distribution of Iberian species represented in a given fossil assemblage. Thus, MER has been applied to the herpetofaunal record for earlier assemblages obtained in the sections of Early and Middle Pleistocene age, as the species represented currently inhabit the Iberian Peninsula (Blain et al., 2009, 2011, 2012, 2013). The MER method using small mammal record was also applied to the Upper Pleistocene and Holocene assemblages, although certain taxa were excluded of the analysis (López-García et al., 2010; Bañuls-Cardona et al., 2017). Particularly, the exclusion of the cold-adapted species which shows a northernmost distribution today such as *Alexandromys oconomus* is remarkable. Although its climatic requirements were considered in the interpretation of results (López-García et al., 2010; Bañuls-Cardona et al., 2017), its absence strongly influenced the obtained paleoclimatic results. Overall, the Bioclimatic Analysis has provided higher MAT than those obtained using the MER, except those correlated to cold stadials within the Upper Pleistocene, which showed significantly lower temperature values when BA was applied (Fig. 4). This can be related to the greater proportion of cold biomes associated with the presence of cold adapted taxa such as *A. oconomus* and *Chionomys nivalis* in less diverse assemblages (PORT12, POTR9, PORT6–3). However, the BA has provided lower precipitation values compared to those obtained using the MER (Fig. 4). P shows a relative low coefficient of determination value ($R^2 = 0.73$) in the predictive equations developed by Royer et al. (2020) for the BA, providing

wider confidence intervals (Fig. 3). Therefore, the results of this variable should be taken with caution, suggesting that the BA tends to underestimate the inferred P and results obtained using the MER method seem to be more accurate.

The available ages for certain assemblages (Álvarez-Posada et al., 2018; Arnold et al., 2015; Bañuls-Cardona et al., 2017; Campaña et al., 2017; Demuro et al., 2019; Galán et al., 2023; López-García et al., 2011; López-García et al., 2010; Rosas et al., 2006; Vergès et al., 2016) enable us to correlate our climatic results with different Marine Isotopic Stages (MIS) following the isotopic benthic $\delta^{18}\text{O}$ global curve (Lisiecki and Raymo, 2005) and from the NGRIP ice core (North Greenland Ice Core Project members, 2004). Certain levels of the first part of the section can be correlated with interstadials of the Early and Middle Pleistocene (Fig. 4). Particularly TD 3–4, TD6a, TD8 and TG-TZII-II correlate with MIS 23, MIS 21, MIS 15 and MIS 9 respectively, whereas SH, TD10–11 and TE 18–19 are associated with stadial phases of MIS 12, MIS 10 and MIS 8, showing general agreement with other proxies (Martínez-Monzón et al. 2021, Núñez-Lahuerta et al., 2022) For the cold stadials, the climatic parameters inferred suggest slightly lower temperatures and precipitation values than in previous phases, although the climate type remains stable as typical temperate. Climatic variations of the Upper Pleistocene are clearly recorded in the Portalón sequence (PORT16-PORT1) together with the older level of El Mirador site (MIR 50/51). The temporal position of each assemblage from each level of El Portalón in the Fig. 4 is approximate since only two radiocarbon ages are available (PORT1, PORT11 - López-García et al., 2010). Nevertheless, this section clearly shows the climatic variation linked to glacial and interglacial cycles of the Upper Pleistocene. Cold episodes reached boreal or boreal-temperate transitional climates in PORT12 and PORT6–5. Since radiocarbon dates were calibrated in this work, the ages obtained here are older than previously considered by López-García et al. (2010). Therefore, the cold episode recorded from PORT7 to PORT4–3 fit better to the Henrich event 2 (LGM), whereas the older ones from PORT9 and PORT13-PORT12 seem to be related to Henrich events 3 and 4 respectively.

The environmental evolution also suggests stability both on the basis of macrovertebrate faunas and palaeobotany along to the Early and Middle Pleistocene, in agreement with our results. Pollen and carpological content found at the sedimentological deposits composing the Early-Middle Pleistocene sequence are not abundant and therefore only provided an approximate view for reconstructing the habitat evolution. Palaeobotanical analyses have exposed a continuous tree component including conifers, mesic trees and Mediterranean trees and shrubs, together with Poaceae and open dry species in fluctuating proportions. These results spectra together with the macromammal record suggest a savanna-like open woodland landscape surrounding the Sierra de Atapuerca sites through the entire Early-Mid Pleistocene sequence showing slight variations (Rodríguez et al., 2011; García and Arsuaga, 2011; Huguet et al., 2017), which correlate with the dominant temperate and transitional temperate/ mediterranean climates inferred in this work.

Concerning the Upper Pleistocene, a dominance of non-arboreal pollen in almost the entire sequence at El Portalón site (López-García et al., 2010; Ruiz Zapata et al., 2006, 2008) including mainly *Pinus* and sporadic appearance of deciduous *Quercus* and *Crotylus* as arboreal taxa, and Ericaceae and Asteraceae as the most abundant open taxa. The landscape inferred was characterized by temperate open woodlands. The cold pulses observed in our analysis associated with PORT12 are correlated to the minimum arboreal pollen proportion of the sequence, whereas unfortunately PORT5-PORT3 resulted in a sterile pollen phase because of lithology (Ruiz Zapata et al., 2006, 2008). Regarding the Holocene environment, the sedimentary sequence of El Mirador has provided palynological evidence to identify a landscape of mixed forest with evergreen and deciduous oaks and pinewood, as well as a reduction in the tree cover related to the increasing human transformation of the landscape (Expósito et al., 2017).

Compared to the current climate at Ibeas de Juarros, the oldest

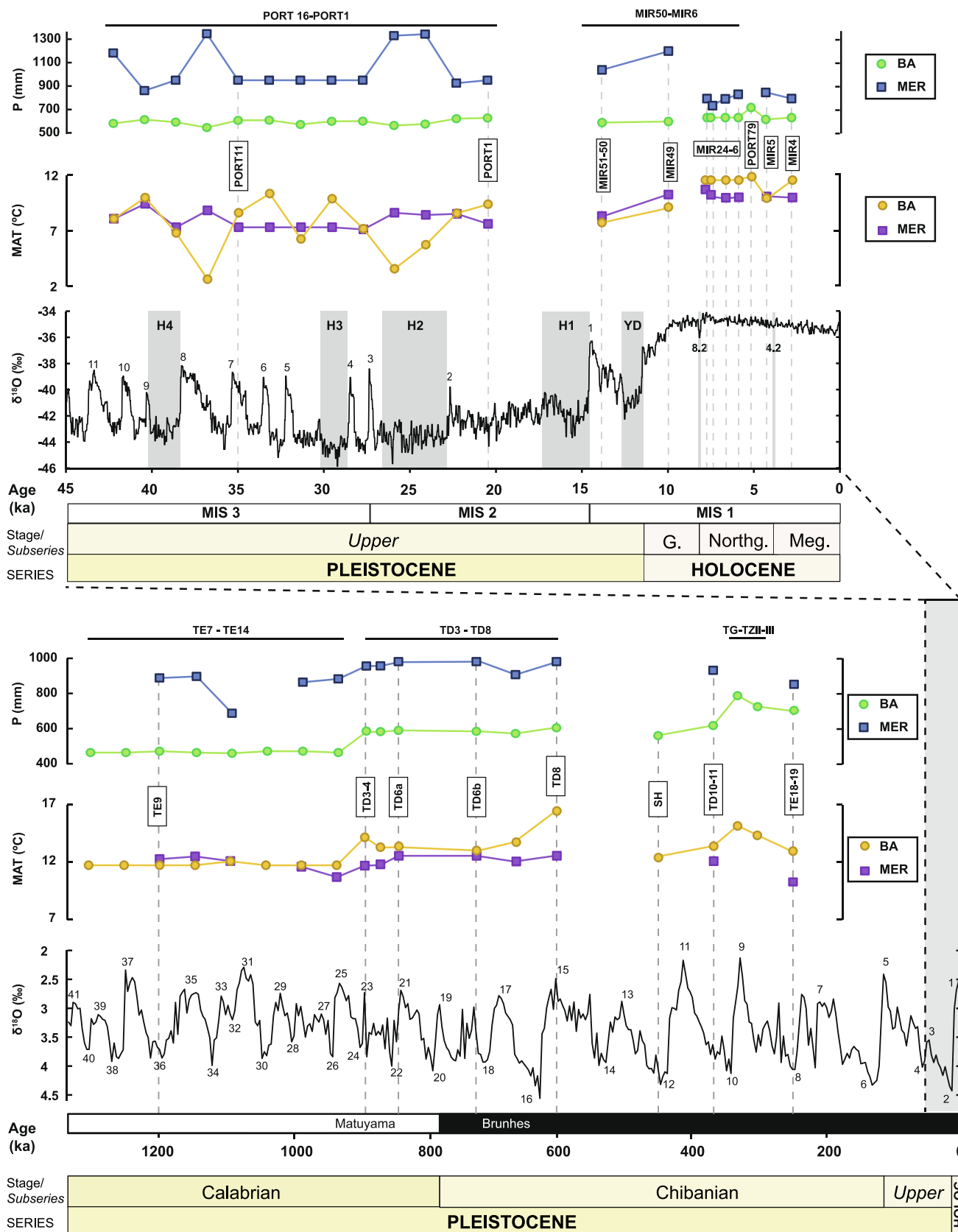


Fig. 4. Climatic evolution based on the microvertebrate record of Atapuerca site complex. Legend = BA: Bioclimatic Analysis (this work); MER: Mutual Ecogeographical Range (Blain et al., 2009, 2011, 2012, 2013; López-García et al., 2010; Bañuls-Cardona et al., 2017; Martínez-Monzón et al., 2021); $\delta^{18}O$ curves (North GRIP Members, 2004; Lisiecki and Raymo, 2005). Abbreviations: G = Greenlandian, Northg = Northgripiian, Meg = Meghalayan.

assemblages of the sequence from Calabrian and Chibanian indicate relatively warmer conditions than today (Fig. 3a), while the Upper Pleistocene and Early Holocene assemblages show oscillations between colder temperatures and those similar than today. Precipitation shows lower values, except at the youngest levels (Fig. 3c). At present-day this locality can be considered representative of the submediterranean bioclimatic variant within the temperate Macrobioclimate, as transitional variant between temperate and Mediterranean (Rivas-Martínez et al., 2017). In the same sense, the Sierra de Atapuerca is characterized as an ecotone and a natural corridor between the Eurosiberian and Mediterranean biogeographic regions (Martínez-Monzón et al., 2021), which coincides with the boundary between typical temperate (CZ VI) and Mediterranean (CZ IV) climates according to Walter (1970). Therefore, this character is reflected in the past climatic evolution of this area, since our results show different climatic classifications using the qualitative or the quantitative models and transitional bioclimatic assignments in several assemblages (TD3–4, TD6b, TD8a, TG-TZ-II, PORT12, PORT6–5, PORT2). This suggests that the area was affected by small latitudinal shifts of the Mediterranean and temperate climate zone boundary, such a northward shift in warm periods and a southward shift in cold episodes, even under the influence of boreal climates during the coldest pulses recorded in the Upper Pleistocene. Similarly, the thermotype classification achieved across the sequence shows a similar pattern of transition between temperate, mediterranean and transitional thermotypes associated to an altitudinal shift of their boundaries, including orotemperate and thermoboreal in cold pulses. The Holocene assemblages indicate climatic stability associated with the supra-temperate, which changed to the mesotemperate thermotype found today (Rivas-Martínez et al., 2017).

5. Conclusions

The palaeo-archaeological cave-sites of the Sierra de Atapuerca complex have provided one of the most complete, composite biostratigraphic sequence in the Quaternary continental sedimentary record of Europe. The application of the new bioclimatic models to the fossil record of Rodentia and Eulipotyphla from six of the cave-sites of this complex, comprising 41 assemblages from the entire geochronological span of the sequence, has provided an updated synthesis on the palaeoclimate of the interior-northern region of the Iberian Peninsula during more than 1 Ma.

The obtained results exposed that mild temperate conditions prevailed along the time span represented, showing variations between temperate and Mediterranean climates and thermotypes, with the influence of the colder boreal climate during the glacial pulses of the Upper Pleistocene. Our results reinforced the ecotone character of the area, as well as the status of glacial refugia for hominins and temperate faunas during glacial periods.

CRedit authorship contribution statement

Ángel C. Domínguez-García: Visualization, Investigation, Formal analysis, Data curation, Conceptualization, Writing – review & editing, Writing – original draft. **Juan Manuel López-García:** Funding acquisition, Formal analysis, Writing – review & editing. **Carmen Núñez-Lahuerta:** Formal analysis, Writing – review & editing. **Julia Galán:** Formal analysis, Writing – review & editing. **Gloria Cuenca-Bescós:** Validation, Supervision, Resources, Formal analysis, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data is provided in Supplementary Materials

Acknowledgements

ACD-G is supported by a postdoctoral Margarita Salas contract (CT18/22) funded by the European Union “NextGenerationEU/PRTR”. JG is the beneficiary of a Postdoctoral Fellowship from the Alexander von Humboldt Foundation (ESP - 1235332 - HFST-P). This is a contribution of the Research Group UNIZAR E18-23R Aragosaurus: Recursos geológicos y Paleoambientes. This work is a part of the Spanish Ministry of Science and Innovation (MCIN/AEI/10.13039/501100011033/FEDER ‘Una manera de hacer Europa’) [grant number: PID2021-122533NB-I00] and AGAUR-Generalitat de Catalunya [grant number 2021SGR-01238 and 2023PFR-URV-01238]. We thank the Atapuerca team for conducting the fieldwork and research on small mammals over the years.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.palaeo.2024.112532>.

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