Palaeogeography, Palaeoclimatology, Palaeoecology 655 (2024) 112532

Contents lists available at ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeo

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

Ángel C. Domínguez-García [a,b,*], Juan Manuel López-García [c,d], Carmen Núñez-Lahuerta [a,c,d,e], Julia Galán [a,f], Gloria Cuenca-Bescós [a]

[a] Aragosaurus-IUCA, Departamento de Ciencias de la Tierra, Facultad de Ciencias, Universidad de Zaragoza, c/ Pedro Cerbuna 12, 50009 Zaragoza, Spain
[b] Departamento de Geodinámica, Estratigrafía y Paleontología, Facultad de Ciencias Geológicas, Universidad Complutense de Madrid, c/ José Antonio Novais 12, 28040 Madrid, Spain
[c] IPHES-CERCA, Institut Català de Paleoecologia Humana i Evolució Social, Zona Educacional 4, Campus Sescelades URV, Edifici W3, 43007, Tarragona, Spain
[d] Universitat Rovira i Virgili, Departament d'Història i Història de l'Art, Avinguda de Catalunya 35, 43002 Tarragona, Spain
[e] Departamento de Geología, Facultad de Ciencia y Tecnología, Universidad del País Vasco/Euskal Herriko Unibertsitatea UPV/EHU, Barrio Sarriena s/n, 48940 Leioa, Spain
[f] Senckenberg Forschungsinstitut und Naturmuseum, Abteilung Messelforschung und Mammalogie, Senckenberganlage 25, 60325 Frankfurt am Main, Germany

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 (TELRU, 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 (Behrensmeyer, 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

---

* Corresponding author at: Departamento de Geodinámica, Estratigrafía y Paleontología, Facultad de Ciencias Geológicas, Universidad Complutense de Madrid, c/ José Antonio Novais 12, 28040 Madrid, Spain.

E-mail addresses: acdomgar@unizar.es, angelcdo@ucm.es (Á.C. Domínguez-García), jmlopez@iphes.cat (J.M. López-García), cnunez@iphes.cat (C. Núñez-Lahuerta), julia.galan@senckenberg.de (J. Galán), cuencag@unizar.es (G. Cuenca-Bescós).

https://doi.org/10.1016/j.palaeo.2024.112532
Received 25 June 2024; Received in revised form 30 September 2024; Accepted 1 October 2024

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 Trinchera Elefante, TE), Gran Dolina (named as Trinchera Dolina, TD), Sima de los Huesos (abbreviated as SH), the Galería complex (named as Trinchera Galería-Trinchera 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).

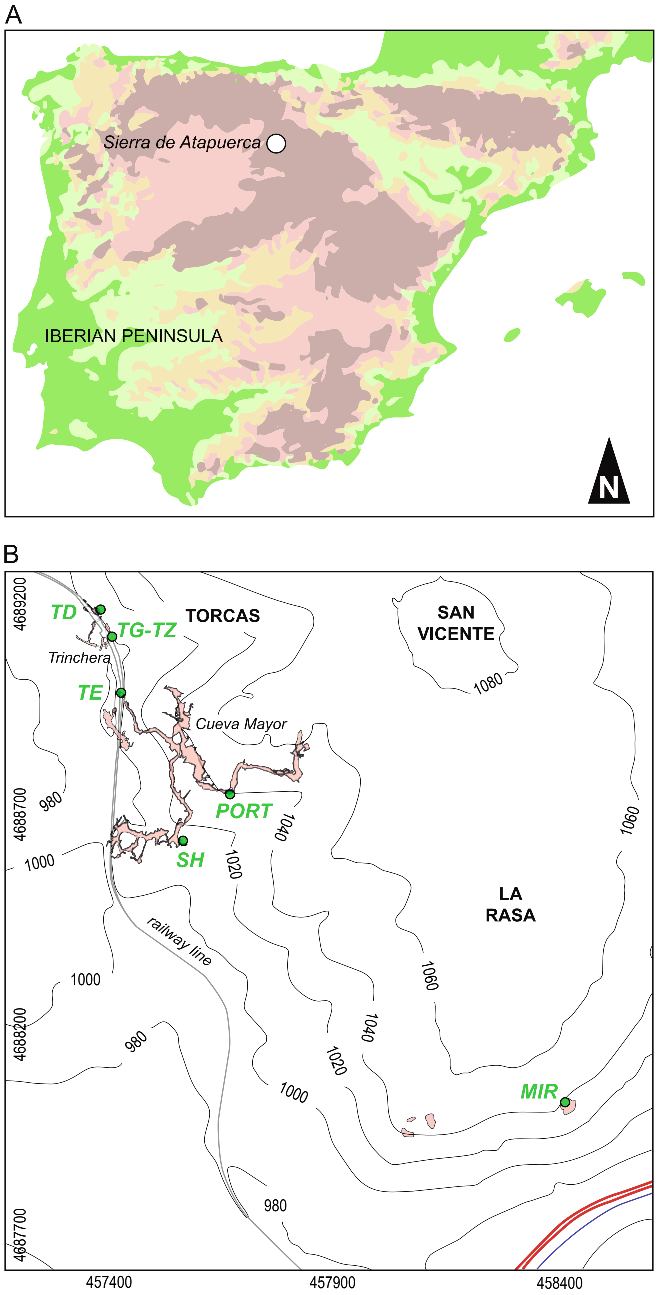

Fig. 1. A) General location of the study area in the Iberian Peninsula B) Location of the sites in the Sierra de Atapuerca. TD: Gran Dolina, TG-TZ: Galería complex, TE: Sima del Elefante, PORT: El Portalón, SH: Sima de los Huesos, MIR: El Mirador. Modified from Ortega et al. (2013).

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 ± 190 yr BP to 16,890 ± 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 Pellicena et al. (2011), Cuenca-Bescós et al. (2016), Bañuls-Cardona et al.

(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 ($BCi = (\Sigma\ CRIi)\ 100/S$, 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)
El Mirador	MIR9–6	6.9–5.4 cal kyr BP	Bañuls-Cardona et al. (2017)
	MIR17–16–10–11	6.7–5.9 cal kyr BP	
	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	
El Portalón	PORT1	21–20 cal kyr BP*	López-García et al. (2010) Cuenca-Bescós et al. (2016)
	PORT2		
	PORT4–3		
	PORT6–5		
	PORT7		
	PORT8		
	PORT9		
	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)
Galería-Zarpazos	TG-TZ-III	225 ± 18 ka 260 ± 20 ka	Galindo Pellicena et al. (2011) Cuenca-Bescós et al. (2016)
	TG-TZ-II	231 ± 20 ka 324 ± 42 ka	
Gran Dolina	TD10–11	372–337 ka	Cuenca-Bescós et al. (2016)
Sima de los Huesos	SH	440 ± 15 ka 455 ± 17 ka	Cuenca-Bescós et al. (2016)López-García et al. (2021)
Gran Dolina	TD8a	602 ± 52 ka	Cuenca-Bescós et al. (2016) Moya-Costa et al. (2023)
	TD7		
	TD6b	730 ± 63 ka	
	TD6a	856 ± 75 ka	
	TD5		
	TD3–4	902 ± 149 ka	
Sima del Elefante	TE14		Cuenca-Bescós et al. (2016)
	TE13		
	TE12		
	TE11		
	TE10		
	TE9	1.2 Ma	
	TE8		
	TE7		

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	Artic (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*, *Beremendia fissidens*, *Dolinasorex glyphodon*, *Sorex margaritodon*, and *Sorex rutonensis/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*MAT). 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://agroclimap.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 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

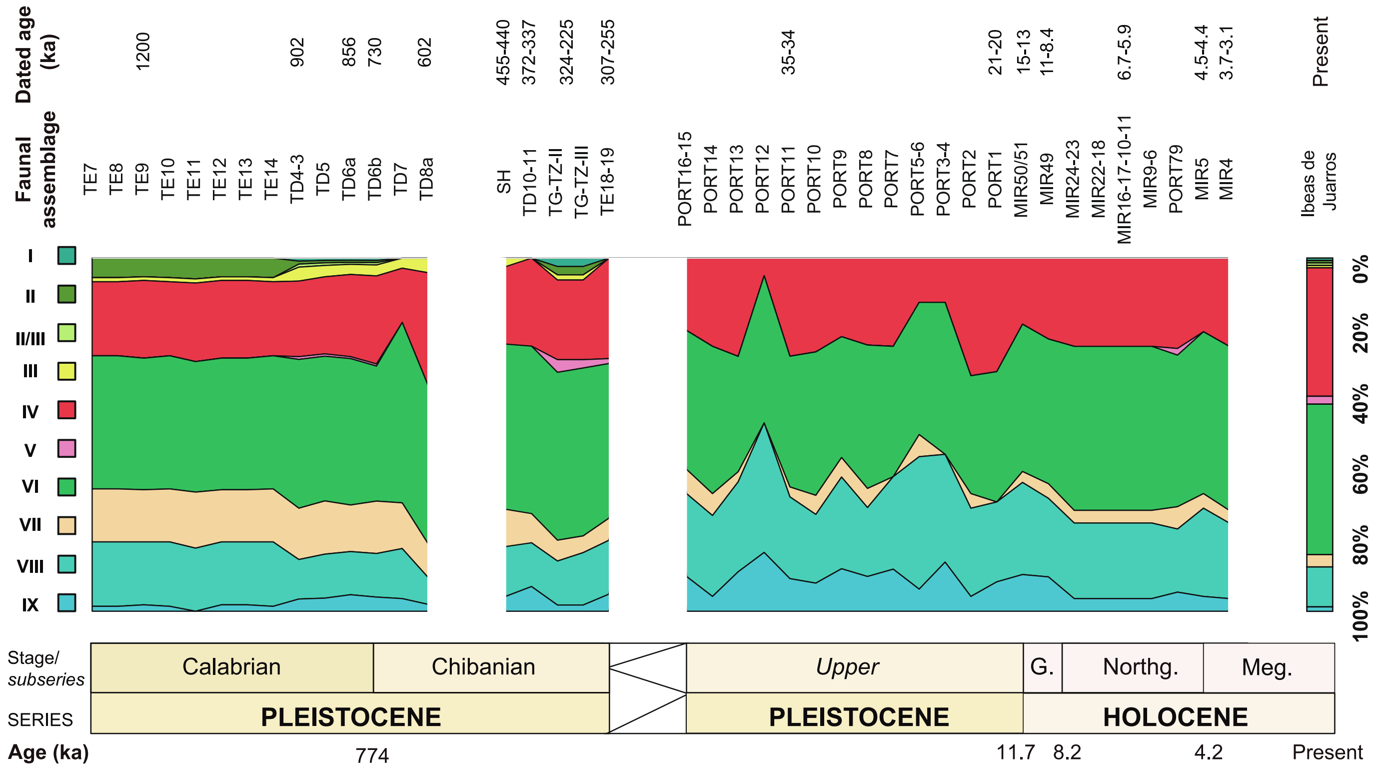

Fig. 2. Bioclimatic spectra of small mammal assemblages during the Quaternary in Sierra de Atapuerca sites. Climate zones: equatorial (I), tropical (II), transition tropical semiarid (II/III), subtropical arid (III), Mediterranean (IV), warm-temperate (V), typical temperate (VI), continental (VII), boreal (VIII), polar (IX). Abbreviations: G = Greenlandian, Norhg = Northgripian, 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 1, $p = 0.73$). 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 Northgrippian 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; p_1: probability of first predicted climate zone; 2nd CZ: second predicted climate zone; p_2: probability of second predicted climate zone. Thermotypes: Mte, Mesotemperate; Ste, supratemperate; Ote: Orotemperate; Mme, Mesomediterranean; Sme, Supramediterranean; Tbo, thermoboreal.

	Qualitative Bioclimatic Model				Quantitative Bioclimatic Model	
Assemblage	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 supratemperete, orotemperate 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 pussila*) 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

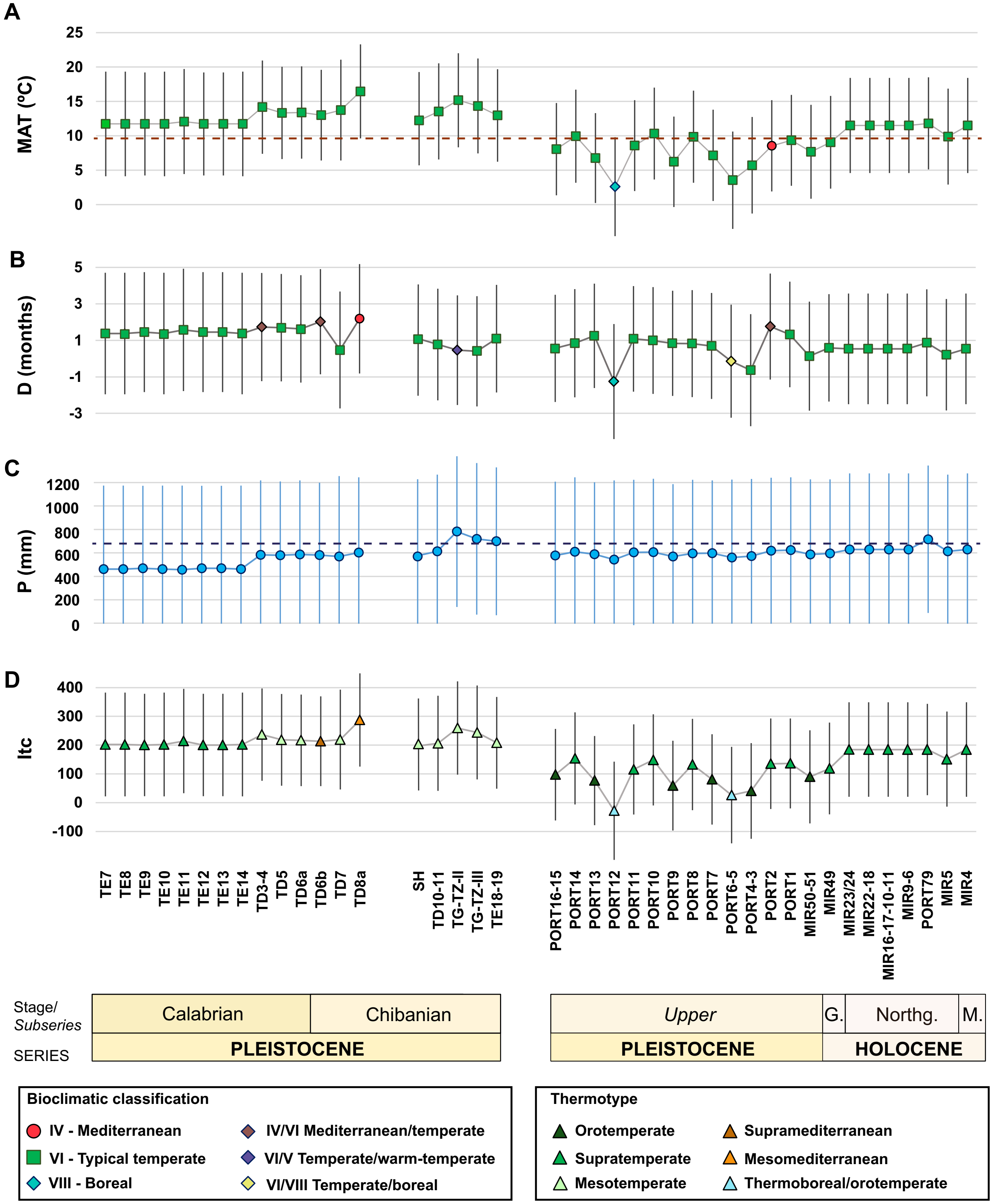

Fig. 3. Evolution of the climate along the Sierra de Atapuerca sequence. A) Mean annual temperature (MAT), symbols represent qualitative climatic classification; B) drought length (D), symbols represent quantitative climatic classification according to Walter (1970); C) annual total precipitation (P); 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, Norhg = Northgripian, 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 were 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 oeconomus* 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. oeconomus* 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 $\delta^{18}O$ 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 (Martinez-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 *Croylus* 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

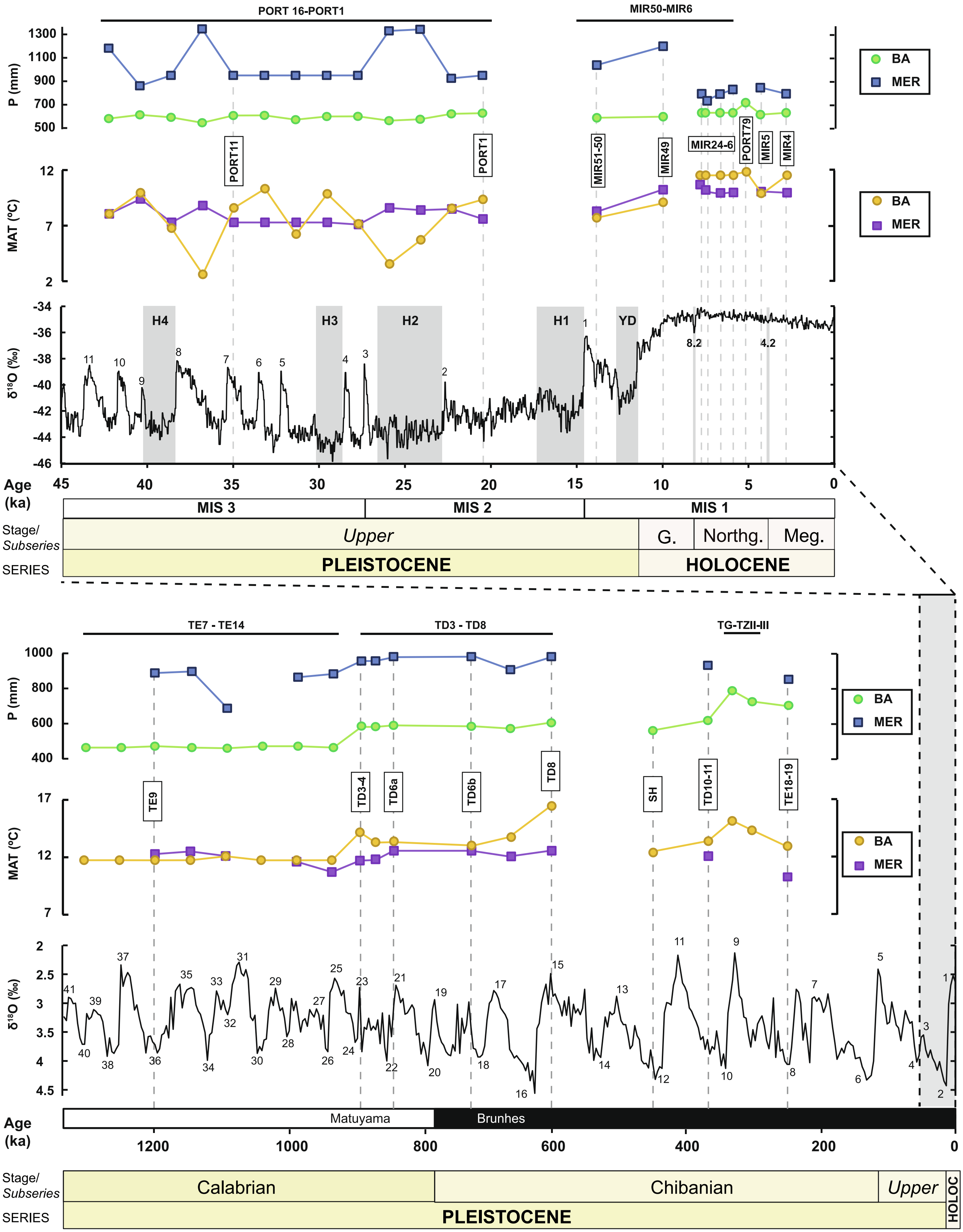

Fig. 4. Climatic evolution based on the microvertebrate record of Atapuerca site complex. Legend = BA: Bioclimatic Analysis (this work); MER: Mutual Ecogeographical Range (Blain et al., 2009, 2011, 2012, 2013; López-García et al., 2010; Bañuls-Cardona et al., 2017; Martínez-Monzón et al., 2021); δ18O curves (North GRIP Members, 2004; Lisiecki and Raymo, 2005). Abbreviations: G = Greenlandian, Norhg = Northgripian, 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 assignations 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 supratemperate, 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-100] 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.

References

Álvarez-Lao, D.J., García, N., 2011. Geographical distribution of Pleistocene cold-adapted large mammal faunas in the Iberian Peninsula. In: Quaternary International, Quaternary Floral and Faunal Assemblages: Ecological and Taphonomical Investigations, 233, pp. 159–170. https://doi.org/10.1016/j.quaint.2010.04.017.

Álvarez-Posada, C., Parés, J.M., Cuenca-Bescós, G., Van der Made, J., Rosell, J., Bermúdez de Castro, J.M., Carbonell, E., 2018. A post-Jaramillo age for the artefact-bearing layer TD4 (Gran Dolina, Atapuerca): New paleomagnetic evidence. Quat. Geochronol. 45, 1–8. https://doi.org/10.1016/j.quageo.2018.01.003.

Álvarez-Vena, A., Álvarez-Lao, D.J., Laplana, C., Quesada, J.M., Rojo, J., García-Sánchez, E., Menéndez, M., 2021. Environmental context for the Late Pleistocene (MIS 3) transition from Neanderthals to early Modern Humans: Analysis of small mammals from La Güelga Cave, Asturias, northern Spain. Palaeogeogr. Palaeoclimatol. Palaeoecol. 562, 110096. https://doi.org/10.1016/j.palaeo.2020.110096.

Andrews, P., 1995. Mammals as palaeoecological indicators. Acta Zool. Cracov. 38 (1), 59–72.

Arnold, L.J., Demuro, M., Parés, J.M., Pérez-González, A., Arsuaga, J.L., Bermúdez de Castro, J.M., Carbonell, E., 2015. Evaluating the suitability of extended-range luminescence dating techniques over early and Middle Pleistocene timescales: Published datasets and case studies from Atapuerca, Spain. Quat. Int. 389, 167–190. https://doi.org/10.1016/j.quaint.2014.08.010.

Arribas, O., 2004. Fauna y Paisaje de los Pirineos en la era glaciar. Lynx Edicions, Bellaterra, Barcelona.

Arsuaga, J.-L., Martínez, I., Gracia, A., Carretero, J.-M., Carbonell, E., 1993. Three new human skulls from the Sima de los Huesos Middle Pleistocene site in Sierra de Atapuerca, Spain. Nature 362, 534–537. https://doi.org/10.1038/362534a0.

Arsuaga, J.L., Martínez, I., Arnold, L.J., Aranburu, A., Gracia-Téllez, A., Sharp, W.D., Quam, R.M., Falguères, C., Pantoja-Pérez, A., Bischoff, J., Poza-Rey, E., Parés, J.M., Carretero, J.M., Demuro, M., Lorenzo, C., Sala, N., Martinón-Torres, M., García, N., Alcázar de Velasco, A., Cuenca-Bescós, G., Gómez-Olivencia, A., Moreno, D., Pablos, A., Shen, C.-C., Rodríguez, L., Ortega, A.I., García, R., Bonmatí, A., Bermúdez de Castro, J.M., Carbonell, E., 2014. Neandertal roots: Cranial and chronological evidence from Sima de los Huesos. Science 344, 1358–1363. https://doi.org/10.1126/science.1253958.

Arsuaga, J.L., Carretero, J.-M., Lorenzo, C., Gómez-Olivencia, A., Pablos, A., Rodríguez, L., García-González, R., Bonmatí, A., Quam, R.M., Pantoja-Pérez, A., Martínez, I., Aranburu, A., Gracia-Téllez, A., Poza-Rey, E., Sala, N., García, N., Alcázar de Velasco, A., Cuenca-Bescós, G., Bermúdez de Castro, J.M., Carbonell, E., 2015. Postcranial morphology of the middle Pleistocene humans from Sima de los Huesos, Spain. Proc. Natl. Acad. Sci. 112, 11524–11529. https://doi.org/10.1073/pnas.1514828112.

Bañuls-Cardona, S., López-García, J.M., Morales Hidalgo, J.I., Cuenca-Bescós, G., Vergès, J.M., 2017. Lateglacial to Late Holocene palaeoclimatic and palaeoenvironmental reconstruction of El Mirador cave (Sierra de Atapuerca, Burgos, Spain) using the small-mammal assemblages. Palaeogeogr. Palaeoclimatol. Palaeoecol. 471, 71–81. https://doi.org/10.1016/j.palaeo.2017.01.019.

Behrensmeyer, A.K., 1992. Terrestrial Ecosystems through Time: Evolutionary Paleoecology of Terrestrial Plants and Animals. University of Chicago Press.

Bermúdez de Castro, J.M., Arsuaga, J.L., Carbonell, E., Rosas, A., Martínez, I., Mosquera, M., 1997. A Hominid from the Lower Pleistocene of Atapuerca, Spain: Possible Ancestor to Neandertals and Modern Humans. Science 276, 1392–1395. https://doi.org/10.1126/science.276.5317.1392.

Bermúdez de Castro, J.M., Pérez-González, A., Martinón-Torres, M., Gómez-Robles, A., Rosell, J., Prado, L., Sarmiento, S., Carbonell, E., 2008. A new early Pleistocene hominin mandible from Atapuerca-TD6, Spain. J. Hum. Evol. 55, 729–735. https://doi.org/10.1016/j.jhevol.2008.03.006.

Berto, C., Luzi, E., Marchetti, M., Pereswiet-Soltan, A., Sala, B., 2022a. Faunal renewals during the Early Pleistocene on the northern Italian Peninsula: Climate and environment reconstructions inferred from the Rivoli Veronese small mammal assemblage (Adige River valley, Verona, Italy). Quat. Int. 633, 134–153. https://doi.org/10.1016/j.quaint.2021.11.025.

Berto, C., Szymanek, M., Blain, H.-A., Pereswiet-Soltan, A., Krajcarz, M., Kot, M., 2022b. Small vertebrate and mollusc community response to the latest Pleistocene-Holocene environment and climate changes in the Kraków-Częstochowa Upland (Poland, Central Europe). Quat. Int. 633, 6–25. https://doi.org/10.1016/j.quaint.2021.09.010.

Berto, C., Arnaud, J., López-García, J.M., Luzi, E., Arzarello, M., 2024. Analysis of the Early Pleistocene small mammals from Pirro Nord 13 (Apricena, southern Italy) and their implications for reconstructing the palaeoenvironment of the early human occupation in Europe. Palaeogeogr. Palaeoclimatol. Palaeoecol. 647, 112251. https://doi.org/10.1016/j.palaeo.2024.112251.

Bisbal-Chinesta, J.F., Bañuls-Cardona, S., Fernández-García, M., Cáceres, I., Blain, H.-A., Vergès, J.M., 2020. Elucidating anuran accumulations: massive taphocenosis of tree frog Hyla from the Chalcolithic of El Mirador cave (Sierra de Atapuerca, Spain). J. Archaeol. Sci. Rep. 30, 102277. https://doi.org/10.1016/j.jasrep.2020.102277.

Blain, H.-A., Bailon, S., Cuenca-Bescós, G., Arsuaga, J.L., Bermúdez de Castro, J.M., Carbonell, E., 2009. Long-term climate record inferred from early-middle Pleistocene amphibian and squamate reptile assemblages at the Gran Dolina Cave, Atapuerca, Spain. J. Hum. Evol. 56, 55–65. https://doi.org/10.1016/j.jhevol.2008.08.020.

Blain, H.A., López-García, J.M., Cuenca-Bescós, G., 2011. A very diverse amphibian and reptile assemblage from the late Middle Pleistocene of the Sierra de Atapuerca (Sima del Elefante, Burgos, Northwestern Spain). Geobios 44 (2–3), 157–172. https://doi.org/10.1016/j.geobios.2010.08.003.

Blain, H.A., Cuenca-Bescós, G., Lozano-Fernández, I., López-García, J.M., Ollé, A., Rosell, J., Rodríguez, J., 2012. Investigating the Mid-Brunhes Event in the Spanish terrestrial sequence. Geology 40 (11), 1051–1054. https://doi.org/10.1130/G33427.1.

Blain, H.-A., Cuenca-Bescós, G., Burjachs, F., López-García, J.M., Lozano-Fernández, I., Rosell, J., 2013. Early Pleistocene palaeoenvironments at the time of the Homo antecessor settlement in the Gran Dolina cave (Atapuerca, Spain). J. Quat. Sci. 28, 311–319. https://doi.org/10.1002/jqs.2622.

Blain, H.-A., Lozano-Fernández, I., Agustí, J., Bailón, S., Menéndez, L.G., Espigares, P.O. M., Ros-Montoya, S., Jiménez, J.M.A., Toro-Moyano, I., Martínez-Navarro, B., Sala, R., 2016. Redefining upon the climatic background of the early Pleistocene hominid settlement in western Europe: Barranco León and Fuente Nueva-3 (Guadix-Baza basin, SE Spain). Quat. Sci. Rev. 144, 132–144. https://doi.org/10.1016/j.quascirev.2016.05.02.

Blanco-Lapaz, A., Martínez-Monzón, A., Blain, H.-A., Cuenca-Bescós, G., 2021. Early-Middle Pleistocene freshwater ecosystems in the Sierra de Atapuerca (northern Iberia) based on the Gran Dolina fish record. Palaeogeogr. Palaeoclimatol. Palaeoecol. 574, 110444. https://doi.org/10.1016/j.palaeo.2021.110444.

Bradley, R.S., 1999. Paleoclimatology: Reconstructing Climates of the Quaternary. Elsevier.

Bronk Ramsey, C., 2009. Bayesian analysis of radiocarbon dates. Radiocarbon 51 (1), 337–360. https://doi.org/10.1017/S0033822200033865.

Campaña, I., Benito-Calvo, A., Pérez-González, A., Ortega, A.I., Bermúdez de Castro, J. M., Carbonell, E., 2017. Pleistocene sedimentary facies of the Gran Dolina archaeo-paleoanthropological site (Sierra de Atapuerca, Burgos, Spain). Quaternary International, What's happening now in Atapuerca?. In: Latest research at the Sierra de Atapuerca sites, 433, pp. 68–84. https://doi.org/10.1016/j.quaint.2015.04.023.

Carbonell, E., Bermúdez de Castro, J.M., Arsuaga, J.L., Díez, J.C., Rosas, A., Cuenca-Bescós, G., Sala, R., Mosquera, M., Rodriguez, X.P., 1995. Lower Pleistocene Hominids and Artifacts from Atapuerca-TD6 (Spain). Science 269, 826–830. https://doi.org/10.1126/science.7638598.

Carbonell, E., Bermúdez de Castro, J.M., Parés, J.M., Pérez-González, A., Cuenca-Bescós, G., Ollé, A., Mosquera, M., Huguet, R., van der Made, J., Rosas, A., Sala, R., Vallverdú, J., García, N., Granger, D.E., Martinón-Torres, M., Rodríguez, X.P., Stock, G.M., Vergès, J.M., Allué, E., Burjachs, F., Cáceres, I., Canals, A., Benito, A., Díez, C., Lozano, M., Mateos, A., Navazo, M., Rodríguez, J., Rosell, J., Arsuaga, J.L., 2008. The first hominin of Europe. Nature 452, 465–469. https://doi.org/10.1038/nature06815.

Chaline, J., Brunet-Lecomte, P., Campy, M., 1995. The last glacial/interglacial record of rodent remains from the Gigny karst sequence in the French Jura used for palaeoclimatic and palaeoecological reconstructions. Palaeogeogr. Palaeoclimatol. Palaeoecol. 117, 229–252. https://doi.org/10.1016/0031-0182(94)00137-W.

Couto, M.A., Sánchez, G., Tavares, C.D., Barceló, A.M., Nunes, L.F., Herráez, C.F., Pires, V., Marques, J., Mendes, L., Chazarra, A., Cunha, S., Mendes, M., Neto, J., Silva, A., 2011. Atlas climático Ibérico-Iberian Climate Atlas. Instituto de Meteorologia de Portugal and Agencia Estatal de Meteorología, Ministerio de Medio Ambiente y Medio Rural y Marino, p. 80 (Eds.).

Cuenca-Bescós, G., Laplana Conesa, C., Canudo, J.I., Arsuaga, J.L., 1997. Small mammals from Sima de los Huesos. J. Hum. Evol. 33, 175–190. https://doi.org/10.1006/jhev.1997.0153.

Cuenca-Bescós, G., Laplana, C., Canudo, J.I., 1999. Biochronological implications of the Arvicolidae (Rodentia, Mammalia) from the Lower Pleistocene hominid-bearing level of Trinchera Dolina 6 (TD6, Atapuerca, Spain). J. Hum. Evol. 37, 353–373. https://doi.org/10.1006/jhev.1999.0306.

Cuenca-Bescós, G., Canudo, J.I., Laplana, C., 2001. La séquence des rongeurs (Mammalia) des sites du Pléistocene inférieur et moyen d'Atapuerca (Burgos, Espagne). L'Antrhopologie 105, 115–130. https://doi.org/10.1016/S0003-5521(01)80009-1.

Cuenca-Bescós, G., Straus, L.G., Morales, M.R.G., Pimienta, J.C.G., 2009. The reconstruction of past environments through small mammals: from the Mousterian to the Bronze Age in El Mirón Cave (Cantabria, Spain). J. Archaeol. Sci. 36, 947–955. https://doi.org/10.1016/j.jas.2008.09.025.

Cuenca-Bescós, G., Straus, L.G., García-Pimienta, J.C., González Morales, M., López-García, J.M., 2010. Faunal turnover in the Late Pleistocene in Cantabria. The extinction of *Pliomys lenki* (Rodentia Mammalia). Quat. Int. 212, 129–136. https://doi.org/10.1016/j.quaint.2009.06.006.

Cuenca-Bescós, G., Melero-Rubio, M., Martínez, I., Blain, H.-A., López-García, J.M., Rofes, J., Arsuaga, J.L., Bermúdez de Castro, J.M., Carbonell, E., 2011. The Early-Middle Pleistocene environmental and climatic change and the human expansion in Western Europe: A case study with small vertebrates (Gran Dolina, Atapuerca Spain). J. Hum. Evol. 60, 481–491. https://doi.org/10.1016/j.jhevol.2010.04.002.

Cuenca-Bescós, G., Rofes, J., López-García, J.M., Blain, H.-A., Rabal-Garcés, R., Sauqué, V., Arsuaga, J.L., Bermúdez de Castro, J.M., Carbonell, E., 2013. The small mammals of Sima del Elefante (Atapuerca, Spain) and the first entrance of *Homo* in Western Europe. Quat. Int. 295, 28–35. https://doi.org/10.1016/j.quaint.2011.12.012.

Cuenca-Bescós, G., Blain, H.-A., Rofes, J., López-García, J.M., Lozano-Fernández, I., Galán, J., Núñez-Lahuerta, C., 2016. Updated Atapuerca biostratigraphy: Small-mammal distribution and its implications for the biochronology of the Quaternary in Spain. Compt. Rend. Palevol. 15, 621–634. https://doi.org/10.1016/j.crpv.2015.09.006.

Demuro, M., Arnold, L.J., Aranburu, A., Sala, N., Arsuaga, J.-L., 2019. New bracketing luminescence ages constrain the Sima de los Huesos hominin fossils (Atapuerca, Spain) to MIS 12. J. Hum. Evol. 131, 76–95. https://doi.org/10.1016/j.jhevol.2018.12.003.

Discamps, E., Royer, A., 2017. Reconstructing palaeoenvironmental conditions faced by Mousterian hunters during MIS 5 to 3 in southwestern France: A multi-scale approach using data from large and small mammal communities. In: Quaternary International, Cleaning up a Messy Mousterian: How to describe and interpret Late Middle Palaeolithic chrono-cultural variability in Atlantic Europe, 433, pp. 64–87. https://doi.org/10.1016/j.quaint.2016.02.067.

Domínguez-García, Á.C., Laplana, C., Sevilla, P., Álvarez-Vena, A., Collado Giraldo, H., 2023. Small mammals of the Holocene sequence of Postes Cave (SW Spain): biogeographic and palaeoenvironmental implications for southwestern Iberia. Hist. Biol. 35, 483–497. https://doi.org/10.1080/08912963.2022.2045981.

Expósito, I., Burjachs, F., Verges, J.M., 2017. Human trace on the landscape during the Holocene at El Mirador Cave (Sierra de Atapuerca, Spain): The palynological evidence. The Holocene 27 (8), 1201–1213. https://doi.org/10.1177/0959683616683253.

Fagoaga, A., Blain, H.-A., Marquina-Blasco, R., Laplana, C., Sillero, N., Hernández, C.M., Mallol, C., Galván, B., Ruiz-Sánchez, F.J., 2019a. Improving the accuracy of small vertebrate-based palaeoclimatic reconstructions derived from the Mutual Ecogeographic Range. A case study using geographic information systems and UDA-ODA discrimination methodology. Quat. Sci. Rev. 223. https://doi.org/10.1016/j.quascirev.2019.105969, 105969.

Fagoaga, A., Laplana, C., Marquina-Blasco, R., Machado, J., Marin-Monfort, M.D., Crespo, V.D., Hernández, C.M., Mallol, C., Galván, B., Ruiz-Sánchez, F.J., 2019b. Palaeoecological context for the extinction of the Neanderthals: A small mammal study of Stratigraphic Unit V of the El Salt site, Alcoi, eastern Spain. Palaeogeogr. Palaeoclimatol. Palaeoecol. 530, 163–175. https://doi.org/10.1016/j.palaeo.2019.05.007.

Falguères, C., Bahain, J.-J., Yokoyama, Y., Arsuaga, J.L., Bermúdez de Castro, J.M., Carbonell, E., Bischoff, J.L., Dolo, J.-M., 1999. Earliest humans in Europe: the age of TD6 Gran Dolina, Atapuerca, Spain. J. Hum. Evol. 37, 343–352.

Fernández-García, M., Royer, A., López-García, J.M., Bennàsar, M., Goedert, J., Fourel, F., Julien, M.-A., Bañuls-Cardona, S., Rodríguez-Hidalgo, A., Vallverdú, J., Lécuyer, C., 2019. Unravelling the oxygen isotope signal (δ18O) of rodent teeth from northeastern Iberia, and implications for past climate reconstructions. Quat. Sci. Rev. 218, 107–121. https://doi.org/10.1016/j.quascirev.2019.04.035.

Galán, J., Cuenca-Bescós, G., López-García, J.M., 2016. The fossil bat assemblage of Sima del Elefante Lower Red Unit (Atapuerca, Spain): First results and contribution to the palaeoenvironmental approach to the site. Compt. Rend. Palevol. 15 (6), 647–657.

Galán, J., Núñez-Lahuerta, C., Moya-Costa, R., López-García, J.M., Cuenca-Bescós, G., 2019a. Fossil bat assemblages as palaeoenvironmental and palaeoclimatic indicators: A case study in the Lower to Middle Pleistocene Gran Dolina sequence of Sierra de Atapuerca, Northern Spain. Palaeogeogr. Palaeoclimatol. Palaeoecol. 535, 109365.

Galán, J., Núñez-Lahuerta, C., López-García, J.M., Cuenca-Bescós, G., 2019b. Did humans disturb bats? Exploring the hominin-chiropter interactions in the Sierra de Atapuerca sites (early to Middle Pleistocene, Spain). Quat. Sci. Rev. 226, 106018. https://doi.org/10.1016/j.quascirev.2019.106018.

Galán, J., Bañuls-Cardona, S., Cuenca-Bescós, G., Vergès, J.M., 2023. Understanding the biogeography of Western European bats: the latest Pleistocene to Middle Holocene assemblage of El Mirador site (Sierra de Atapuerca, Spain). Hist. Biol. 35, 1686–1700. https://doi.org/10.1080/08912963.2022.2107430.

Galindo Pellicena, M.Á., Cuenca Bescós, G., Arsuaga, J.L., 2011. Los micromamíferos (Rodentia, Soricomorpha, Erinaceomorfa, Lagomorpha y Chiroptera) del Pleistoceno Medio de la Covacha de los Zarpazos (Sierra de Atapuerca, Burgos, España). In: Boletín de la Real Sociedad Española de Historial Natural: Seccion Geología 105 (1-4), pp. 87–97.

García, N., Arsuaga, J.L., 2011. The Sima de los Huesos (Burgos, northern Spain): palaeoenvironment and habitats of *Homo heidelbergensis* during the Middle Pleistocene. Quat. Sci. Rev. 30 (11−12), 1413–1419. https://doi.org/10.1016/j.quascirev.2010.11.008.

García-Morato, S., Fernández-Jalvo, Y., Montalvo, C.I., Andrews, P., Marin-Monfort, M. D., Fagoaga, A., Domínguez García, Á.C., Alberdi, M.T., Bonini, R., Cerdeño, E., Denys, C., Domingo, L., Domingo, S., Gutiérrez, M.A., López-Cantalapiedra, J., Pesquero, M.D., Prado, J.L., Sevilla, P., Stoetzel, E., Tomassini, R.L., Fernández, F.J., 2021. New palaeoecological approaches to interpret climatic fluctuations in Holocenic sites of the Pampean Region of Argentina. Quat. Sci. Rev. 255, 106816. https://doi.org/10.1016/j.quascirev.2021.106816.

Hernández Fernández, M., 2001a. Análisis paleoecológico y paleoclimático de las sucesiones de mamíferos del Plio-Pleistoceno ibérico (PhD Thesis). Universidad Complutense de Madrid Madrid.

Hernández Fernández, M., 2001b. Bioclimatic discriminant capacity of terrestrial mammal faunas. Glob. Ecol. Biogeogr. 10, 189–204. https://doi.org/10.1046/j.1466-822x.2001.00218.x.

Hernández Fernández, M., Peláez-Campomanes, P., 2003. The Bioclimatic Model: A Method of Palaeoclimatic Qualitative Inference based on Mammal Associations. Glob. Ecol. Biogeogr. 12, 507–517.

Hernández Fernández, M., Peláez-Campomanes, P., 2005. Quantitative palaeoclimatic inference based on terrestrial mammal faunas. Glob. Ecol. Biogeogr. 14, 39–56.

Hernández Fernández, M., Vrba, E.S., 2005. Macroevolutionary Processes and Biomic Specialization: Testing the Resource-use Hypothesis. Evol. Ecol. 19, 199–219. https://doi.org/10.1007/s10682-004-8152-7.

Hernández Fernández, M., Álvarez Sierra, M.Á., Peláez-Campomanes, P., 2007. Bioclimatic analysis of rodent palaeofaunas reveals severe climatic changes in Southwestern Europe during the Plio-Pleistocene. Palaeogeogr. Palaeoclimatol. Palaeoecol. 251, 500–526. https://doi.org/10.1016/j.palaeo.2007.04.015.

Hernández Fernández, M., Pelegrin, J.S., Gómez Cano, A.R., García Yelo, B.A., Moreno-Bofarull, A., Sánchez-Fontela, N., Rodríguez-Ruiz, C., Ramiro Camacho, A., Domingo, L., Menéndez, I., Martín-Perea, D.M., Bazán, C.M., Alcalde, G.M., Domingo, M.S., Luna, B., Cortés, Peinado, Del M, Arias, A., González Couturier, G., Márquez Villena, A., Anaya, N., Blanco, F., Galli, E., Gamboa, S., Quesada, Á., Sanz-Pérez, D., Varela, S., Cantalapiedra, J.L., 2022. Macroevolution and climate changes: a global multi-family test supports the resource-use hypothesis in terrestrial mammals. Hist. Biol. 34, 1471–1479. https://doi.org/10.1080/08912963.2022.2042807.

Hewitt, G.M., 1999. Post-glacial re-colonization of European biota. Biol. J. Linn. Soc. 68 (1163), 87–112.

Huguet, R., Vallverdú, J., Rodríguez-Álvarez, X.P., Terradillos-Bernal, M., Bargalló, A., Lombera-Hermida, A., Menéndez, L., Modesto-Mata, M., Van der Made, J., Soto, M., Blain, H.-A., García, N., Cuenca-Bescós, G., Gómez-Merino, G., Pérez-Martínez, R., Expósito, I., Allué, R., Rofes, J., Burjachs, F., Canals, A., Bennàsar, M., Núñez-Lahuerta, C., Bermúdez de Castro, J.M., Carbonell, E., 2017. Level TE9c of Sima del Elefante (Sierra de Atapuerca, Spain): A comprehensive approach. Quat. Int. 433, 278–295. https://doi.org/10.1016/j.quaint.2015.11.030.

Ilvonen, L., López-Sáez, J.A., Holmström, L., Alba-Sánchez, F., Pérez-Díaz, S., Carrión, J. S., Ramos-Román, M.J., Camuera, J., Jiménez-Moreno, G., Ruha, L., Seppä, H., 2022. Spatial and temporal patterns of Holocene precipitation change in the Iberian Peninsula. Boreas 51, 776–792. https://doi.org/10.1111/bor.12586.

Laplana, C., Cuenca-bescós, G., 2000. Una nueva especie de *Microtus* (*Allophaiomys*) (Arvicolidae, Rodentia, Mammalia) en el Pleistoceno Inferior de la Sierra de Atapuerca (Burgos, España). Spanish J. Palaeontol. 15, 77–87. https://doi.org/10.7203/sjp.15.1.22088.

Laplana, C., Sevilla, P., Arsuaga, J.L., Arriaza, M.C., Baquedano, E., Pérez-González, A., López-Martínez, N., 2015. How far into Europe did pikas (Lagomorpha: Ochotonidae) go during the Pleistocene? New evidence from Central Iberia. PLoS One 10, e01405.

Lisiecki, L.E., Raymo, M.E., 2005. A Pliocene-Pleistocene stack of 57 globally distributed benthic δ18O records. Paleoceanogra. Paleoclimatol. 20, 1–17.

López-García, J.M., 2011. Los micromamíferos del Pleistoceno superior de la Península Ibérica: Evolución de la diversidad taxonómica y cambios paleoambientales y paleoclimáticos. Editorial Académica Española, Saarbrücken.

López-García, J.M., Blain, H.-A., Cuenca-Bescós, G., Ruiz-Zapata, M.B., Dorado-Valiño, M., Gil-García, M.J., Valdeolmillos, A., Ortega, A.I., Carretero, J.M., Arsuaga, J.L., de Castro, J.M.B., Carbonell, E., 2010. Palaeoenvironmental and palaeoclimatic reconstruction of the latest Pleistocene of El Portalón Site, Sierra de Atapuerca, northwestern Spain. Palaeogeogr. Palaeoclimatol. Palaeoecol. 292, 453–464. https://doi.org/10.1016/j.palaeo.2010.04.006.

López-García, J.M., Blain, H.A., Taillefer, R.D.M.I., García, A., Martinell, J., Félix, M.L.B., Bescós, G.C., 2011. Small-mammals from the Middle Pleistocene layers of the Sima del Elefante (Sierra de Atapuerca, Burgos, northwestern Spain). Geol. Acta 9, 29–43. https://doi.org/10.1344/105.000001644.

López-García, J.M., Cuenca-Bescós, G., Galindo-Pellicena, M.Á., Luzi, E., Berto, C., Lebreton, L., Desclaux, E., 2021. Rodents as indicators of the climatic conditions during the Middle Pleistocene in the southwestern Mediterranean region: implications for the environment in which hominins lived. J. Hum. Evol. 150. https://doi.org/10.1016/j.jhevol.2020.102911Martínez-Monzón, 102911.

Martínez-Monzón, A., Cuenca-Bescós, G., Bisbal-Chinesta, J.-F., Blain, H.-A., 2021. One million years of diversity shifts in amphibians and reptiles in a Mediterranean landscape: resilience rules the Quaternary. Palaeontology 64, 673–686. https://doi.org/10.1111/pala.12547.

Martínez-Pillado, V., Aranburu, A., Arsuaga, J.L., Ruiz-Zapata, B., Gil-García, M.J., Stoll, H., Yusta, I., Iriarte, E., Carretero, J.M., Edwards, R.L., Cheng, H., 2014. Upper Pleistocene and Holocene palaeoenvironmental records in Cueva Mayor karst (Atapuerca, Spain) from different proxies: speleothem crystal fabrics, palynology and archaeology. Int. J. Speleol. 43. https://doi.org/10.5038/1827-806X.43.1.1.

Montuire, S., Michaux, J., Legendre, S., Aguilar, J.-P., 1997. Rodents and climate. 1. A model for estimating past temperatures using arvicolids (Mammalia: Rodentia). Palaeogeogr. Palaeoclimatol. Palaeoecol. 128, 187–206. https://doi.org/10.1016/S0031-0182(96)00038-7.

Moya-Costa, R., Cuenca-Bescós, G., Rofes, J., 2023. The shrews (Soricidae, Mammalia) of the Early and Middle Pleistocene of Gran Dolina (Atapuerca, Spain): reassessing their paleontological record in the Iberian Peninsula. Quat. Sci. Rev. 309, 108093. https://doi.org/10.1016/j.quascirev.2023.108093.

Nadachowski, A., 1989. Origin and history of the present rodent fauna in Poland based on fossil evidence. Acta Theriol. 34, 37–53. https://doi.org/10.4098/AT.arch.89-2.

North Greenland Ice Core Project members, 2004. High-resolution record of Northern Hemisphere climate extending into the last interglacial period. Nature 431, 147–151. https://doi.org/10.1038/nature02805.

Núñez-Lahuerta, C., Cuenca-Bescós, G., Huguet, R., 2016. First report on the birds (Aves) from level TE7 of Sima del Elefante (Early Pleistocene) of Atapuerca (Spain). Quat. Int. 421, 12–22. https://doi.org/10.1016/j.quaint.2015.08.016.

Núñez-Lahuerta, C., Galán, J., Cuenca-Bescós, G., Huguet, R., 2021a. Birds from Sima del Elefante, Atapuerca, Spain: palaeoecological implications in the oldest human bearing levels of the Iberian Peninsula. Riv. Ital. Paleontol. Stratigr. 127 (2), 453–484.

Núñez-Lahuerta, C., Moreno-Azanza, M., Cuenca-Bescós, G., 2021b. Avian eggshell remains in the human bearing level TD6 of the Gran Dolina site (Early Pleistocene, Atapuerca, Spain. Hist. Biol. 33 (5), 660–671. https://doi.org/10.1080/08912963.16550099.

Núñez-Lahuerta, C., Galán, J., Cuenca-Bescós, G., García-Medrano, P., Cáceres, I., 2022. A bird assemblage across the MIS9/8 boundary: the Middle Pleistocene of Galería (Atapuerca). Quat. Sci. Rev. 293. https://doi.org/10.1016/j.quascirev.2022.107708, 107708.

O'Regan, H.J., 2008. The Iberian Peninsula–corridor or cul-de-sac? Mammalian faunal change and possible routes of dispersal in the last 2 million years. Quat. Sci. Rev. 27 (23–24), 2136–2144.

Ortega, A.I., Benito-Calvo, A., Pérez-González, A., Martin-Merino, M.A., Pérez-Martínez, R., Pares, J.M., Aramburu, A., Arsuaga, J.L., Bermúdez de Castro, J.M., Carbonell, E., 2013. Evolution of multilevel caves in the Sierra de Atapuerca (Burgos, Spain) and its relation to human occupation. Geomorphology 196, 122–137.

Quaglietta, L., 2022. IUCN Red List of Threatened Species: *Galemys pyrenaicus*. IUCN Red List of Threatened Species 2022: e.T8826A214429993. https://doi.org/10.2305/IUCN.UK.2022-1.RLTS.T8826A214429993.en. Accessed on 31 May 2024.

Rivas-Martínez, S., Rivas-Sáenz, S., Penas, A.S., 2011. Worldwide bioclimatic classification system. Glob. Geobot. 1, 1–634.

Reimer, P, Austin, W, Bard, E, et al., 2020. The IntCal20 Northern Hemisphere radiocarbon age calibration curve (0–55 cal kBP). Radiocarbon 62 (4), 725–757. https://doi.org/10.1017/RDC.2020.41.

Rivas-Martínez, S., Penas, Á., del Río, S., Díaz González, T.E., Rivas-Sáenz, S., 2017. Bioclimatology of the Iberian Peninsula and the Balearic Islands. In: Loidi, J. (Ed.), The Vegetation of the Iberian Peninsula, vol. 1. Springer International Publishing, Cham, pp. 29–80. https://doi.org/10.1007/978-3-319-54784-8_2. Plant and Vegetation.

Rodríguez, J., Burjachs, F., Cuenca-Bescós, G., García, N., van der Made, J., Pérez González, A., Blain, H.-A., Expósito, I., López-García, J.M., García Antón, M., Allué, E., Cáceres, I., Huguet, R., Mosquera, M., Ollé, A., Rosell, J., Parés, J.M., Rodríguez, X.P., Díez, C., Rofes, J., Sala, R., Saladié, P., Vallverdú, J., Bennasar, M.L., Blasco, R., Bermúdez de Castro, J.M., Carbonell, E., 2011. One million years of cultural evolution in a stable environment at Atapuerca (Burgos, Spain). Quat. Sci. Rev. 30, 1396–1412. https://doi.org/10.1016/j.quascirev.2010.02.021.

Rofes, J., Cuenca-Bescós, G., 2009a. A new genus of red-toothed shrew (Mammalia, Soricidae) from the Early Pleistocene of Gran Dolina (Atapuerca, Burgos, Spain), and a phylogenetic approach to the Eurasiatic Soricinae. Zool. J. Linnean Soc. 155, 904–925. https://doi.org/10.1111/j.1096-3642.2008.00470.x.

Rofes, J., Cuenca-Bescós, G., 2009b. First record of *Beremendia fissidens* (Mammalia, Soricidae) in the Pleistocene of the Iberian Peninsula, with a review of the biostratigraphy, biogeography and palaeoecology of the species. Compt. Rend. Palevol. 8, 21–37. https://doi.org/10.1016/j.crpv.2008.08.004.

Rofes, J., Cuenca-Bescós, G., 2011. Evolutionary history and biogeography of the genus *Crocidura* (Mammalia, Soricidae) in Europe, with emphasis on *Crocidura kornfeldi*. Mamm. Biol. 76, 64–78. https://doi.org/10.1016/j.mambio.2009.12.001.

Rofes, J., Cuenca-Bescós, G., 2013. First record of *Sorex* (*Drepanosorex*) *margaritodon* (Mammalia, Soricidae) in Western Europe: biostratigraphy, biogeography and evolution of the species. Paläontol. Z. 87, 529–541. https://doi.org/10.1007/s12542-013-0172-6.

Rofes, J., García-Ibaibarriaga, N., Murelaga, X., Arrizabalaga, A., Iriarte, M.-J., Cuenca-Bescós, G., Villaluenga, A., 2012. The southwesternmost record of *Sicista* (Mammalia: Dipodidae) in Eurasia, with a review of the palaeogeography of the genus in Europe. Palaeogeogr. Palaeoclimatol. Palaeoecol. 348–349, 67–73. https://doi.org/10.1016/j.palaeo.2012.06.016.

Rofes, J., Moya-Costa, R., Bennàsar, M., Blain, H.-A., Cuenca-Bescós, G., 2016. Biostratigraphy, palaeogeography and palaeoenvironmental significance of *Sorex runtonensis* Hinton, 1911 (Mammalia, Soricidae): first record from the Iberian Peninsula. Palaeogeogr. Palaeoclimatol. Palaeoecol. 459, 508–517. https://doi.org/10.1016/j.palaeo.2016.07.021.

Rofes, J., Ordiales, A., Iriarte, E., Cuenca-Bescós, G., Galindo-Pellicena, M.Á., Pérez-Romero, A., Carretero, J.M., Arsuaga, J.L., 2021. Human Activities, Biostratigraphy and Past Environment Revealed by Small-Mammal Associations at the Chalcolithic

Levels of El Portalón de Cueva Mayor (Atapuerca, Spain). Quaternary 4, 16. https://doi.org/10.3390/quat4020016.

Rosas, A., Huguet, R., Pérez-González, A., Carbonell, E., de Castro, J.M.B., Vallverdú, J., van der Made, J., Allué, E., García, N., Martínez-Pérez, R., Rodríguez, J., Sala, R., Saladie, P., Benito, A., Martínez-Maza, C., Bastir, M., Sánchez, A., Parés, J.M., 2006. The "Sima del Elefante" cave site at Atapuerca (Spain). Estud. Geol. 62, 327–348. https://doi.org/10.3989/egeol.0662129.

Royer, A., Yelo, B.A.G., Laffont, R., Fernández, M.H., 2020. New bioclimatic models for the quaternary palaearctic based on insectivore and rodent communities. Palaeogeogr. Palaeoclimatol. Palaeoecol. 560. https://doi.org/10.1016/j.palaeo.2020.110040, 110040.

Ruiz Zapata, M.B., Ortega, A.I., Dorado, M., Valdeolmillos, A., Carretero, J.M., Gil García, M.J., Pérez González, A., Arsuaga, J.L., 2006. Vegetación y clima durante el Pleistoceno Superior en Atapuerca: análisis polínico del perfil ATP-05 (Portalón de CuevaMayor). In: Fernández-Martínez, E. (Ed.), XXII Jornadas de la Sociedad Española de Paleontología. Libro de Resúmenes. Universidad de León, León, pp. 80–81.

Ruiz Zapata, M.B., Ortega, A.I., Dorado, M., Valdeolmillos, A., Gil García, M.J., Carretero, J., Pérez-González, A., Arsuaga, J.L., 2008. Clima y vegetación durante el Pleistoceno Superior y Holoceno en el yacimiento del Portalón de Cueva Mayor (sierra de Atapuerca, Burgos). In: Ruiz-Omeñaca, J.I., Piñuela, L., García-Ramos, J.C. (Eds.), XXIV Jornadas de la Sociedad Española de Paleontología. Libro de Resúmenes, Museo Jurásico de Asturias, Colunga, p. 193.

Rzebik-Kowalska, B., 1998. Fossil history of shrews in Europe. Evol. Shrews 23–92.

Sala, N., Pablos, A., Rodríguez-Hidalgo, A., Arriolabengoa, M., Alcaraz-Castaño, M., Cubas, M., Posth, C., Nägele, K., Pantoja-Pérez, A., Arlegi, M., Rodríguez-Almagro, M., Conde-Valverde, M., Cuenca-Bescós, G., Arribas, A., Gómez-Olivencia, A., 2021. Cueva de los Torrejones revisited. New insights on the paleoecology inland Iberia during the Late Pleistocene. Quat. Sci. Rev. 253 (1). https://doi.org/10.1016/j.quascirev.2020.106765, 106765.

Sesé, C., 2005. Aportación de los micromamíferos al conocimiento paleoambiental del Pleistoceno Superior en la Región Cantábrica: Nuevos datos y síntesis. Museo y Centro de Investigación de Altamira. Monografías 20, 167–200.

Sommer, R.S., Nadachowski, A., 2006. Glacial refugia of mammals in Europe: evidence from fossil records. Mammal Rev. 36, 251–265. https://doi.org/10.1111/j.1365-2907.2006.00093.x.

Twitchett, R.J., 2006. The palaeoclimatology, palaeoecology and palaeoenvironmental analysis of mass extinction events. Palaeogeogr. Palaeoclimatol. Palaeoecol. 232, 190–213. https://doi.org/10.1016/j.palaeo.2005.05.019.

Vergès, J.M., Allué, E., Fontanals, M., Morales, J.I., Martín, P., Carrancho, Á., Expósito, I., Guardiola, M., Lozano, M., Marsal, R., Oms, X., Euba, I., Rodríguez, A., 2016. El Mirador cave (Sierra de Atapuerca, Burgos, Spain): A whole perspective. Quat. Int. 414, 236–243. https://doi.org/10.1016/j.quaint.2016.01.044.

Walter, H., 1970. Vegetationszonen und Klima. Eugen Ulmer, Stuttgart.

Wilson, D.E., Mittermeier, R.A. (Eds.), 2018. Handbook of the Mammals of the World. Insectivores, Sloths and Colugos.

Wilson, D.E., Lacher, T.E.J., Mittermeier, R.A. (Eds.), 2017. Handbook of the Mammals of the World, Rodents II. Lynx Edicions, Barcelona, Spain.