Implications of population changes among the Arvicolinae (Rodentia, Mammalia) in El Mirón Cave (Cantabria, Spain) for the climate of the last c. 50,000 years

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ABSTRACT

The El Mirón Cave site in Spain has one of the most complete archaeological and palaeontological records of the Late Pleistocene in the Iberian Peninsula, encompassing most of the last c. 50,000 years. Among other studies, the fossiliferous record has allowed the development of various interpretations of faunal and climatic changes during this period of time in the northern Atlantic region of the Iberian Peninsula. The addition of more radiocarbon dates from El Mirón Cave make it possible to revise some of the interpretations of the micromammal sequence carried out earlier for this major site. The record of small mammals is one of the most used tools to study the climate of the past, and among them the several Arvicolinae species are of great importance for the study of Quaternary climatic variations, due to their adaptations to a great diversity of habitats. New methodologies such as ancient DNA and geometric morphometric analyses now permit us to conduct a review of the Arvicolinae species previously described at this site and better to differentiate between species with similar morphologies, like *Microtus arvalis* and *M. agrestis*. We also identified the presence of a species not recorded before in El Mirón, *Terricola pyrenaicus*. With the study of the Arvicolinae species associations, we reaffirm the climate variations originally described in this deposit, indicating in detail how the successive changes in temperature and environment took place throughout the course of the late Last Glacial and early Postglacial periods (Marine Isotope Stages 3–1).

1. Introduction

The study of micromammals is one of the most widely used tools for making inferences about the climates and environments of the past (e.g., Cuenca-Bescós et al., 2011; Domínguez-García et al., 2022; Fagoaga et al., 2018; Galán et al., 2019; García-Morato et al., 2022; López-García et al., 2013; Rofes et al., 2015, 2016). The particular morphological, physiological and ethological characteristics of the species that inhabit an area are indicative of their levels of adaptation to different climatic and other environmental conditions. Specifically, rodents are among the main proxy indicators of changes in temperature and humidity, environmental stability, climatic fluctuations, and even human influences on

an area (e.g., Bañuls-Cardona et al., 2017; Bennàsar et al., 2016; Laplana et al., 2016; López-García et al., 2010, 2021). In addition, these small mammals are distributed in relation to specific soil and vegetation types, key factors that indicate landscape type (e.g., Cuenca-Bescós and Morcillo-Amo, 2022).

Among the large number of species included in the rodent group, the members of the subfamily Arvicolinae (Cricetidae, Rodentia, Mammalia) have proven to be essential for understanding the climate variations of the last many thousands of years, thus being one of the most important tools for climatic continental studies of the Quaternary (Pleistocene and Holocene). This is because these small mammals are adapted quite specifically to different types of habitats, as well as because they are

widespread in continental environments. Both factors, plus the high evolutionary rate of these species (e.g., Baca et al., 2020; Bañuls-Cardona et al., 2017; Chaline et al., 1999, Cuenca-Bescós et al., 2008; López-García et al., 2021) make the arvicolines one of the best proxies for climatic reconstruction. Within the Arvicolinae, a large number of species have been identified and well classified, both fossil and modern. In the Upper Pleistocene of the Iberian Peninsula, two species of the genus *Arvicola* have been identified: *A. sapidus* and *A. terrestris*(=*amphibius*). In addition, other identified taxa are *Pliomys* (*P. lenki*), *Clethrionomys* (*C. glareolus*), and the species traditionally grouped in *Microtus sensu lato (s.l.)*, The latter belong to the genera and subgenera *Microtus* (*M. arvalis* and *M. agrestis*), *Terricola* (*T. duodecimcostatus, T. pyrenaicus* and *T. lusitanicus*), *Iberomys* (*I. cabrerae*), *Chionomys* (*C. nivalis*), *Lasiopodomys* (*L. gregalis*), and *Alexandromys* (*A. oeconomus*).

In palaeontological systematics, the species of the Arvicolinae group of mammals are generally identified by the morphology of the occlusal surface of the first lower molar (m1), as it is the element displaying the greatest anatomical difference to discriminate between species and it underwent some of the most significant changes during the evolution of the group (van der Meulen, 1973). However, some of these species and genera present a great deal of morphological convergence in m1. This fact leads to great difficulty in their classification. Discussions of their systematics and taxonomy are made even more problematic by the high evolutionary rate of this group of small mammals (e.g., Jaarola et al., 2004; Abramson et al., 2021). The systematic and correct classification of the Arvicolinae species is important because the presence of one species instead of another, despite similarities in morphology, may indicate a different type of climate or habitat. There are many works about the correct differentiation among some of these species by morphological characteristics of the m1, as in the case of *M. arvalis* versus *M. agrestis* (Luzi, 2018), or between the different species of the genus *Terricola* (e.g., Brunet-Lecomte, 1990), but the systematics and taxonomy of these rodents is far from being resolved. In addition to the traditional methods and techniques, we can use innovative methodologies, either separately or in combination, namely geometric morphometric and ancient DNA (aDNA) analyses, to confirm the classification obtained by using more traditional methods.

The aim of this work is to propose a more detailed interpretation of the possible climatic variations during the last 50,000 years in the northern Atlantic region of the Iberian Peninsula. For this objective, we conducted a revision of the Arvicolinae faunas identified in El Mirón Cave (Cantabria, Spain), which has one of the most complete palaeontological records of the late Pleistocene and early Holocene of Iberia. The study of this site therefore can help to understand the climatic variations that took place during the Late Quaternary. In previous studies, the paleoenvironments were studied based on the general associations of identified small mammals (Cuenca-Bescós et al., 2008, 2009, 2012), as well as by other palaeobiological methods, including palynological studies (Iriarte-Chiapusso et al., 2015). However, there has not yet been a detailed study of variations among the species of Arvicolinae, and how these reflect climatic changes during formation of the deposit in El Mirón Cave. In addition, new radiocarbon dates and analysis of the whole corpus of dates from the site (Hopkins et al., 2021) make it necessary to revaluate the climatic conditions evidenced in this deposit, along with their relationships with global climatic fluctuations recorded during the past c. 50,000 years.

2. Study site

El Mirón Cave is located in massive limestone of the Urgonian facies that forms the karstic complex of Monte Pando in a northern foothill range of the Cantabrian Cordillera (North-Central Spain). The mouth of the cave is in the western cliff face of the Pando-Moro massif (43°14′44″ N, 3°27′9″ W, 260 m a.s.l., European Datum ETRS89), 100 above the valley of the Asón river, near the boundary between the provinces of Cantabria and Vizcaya, about 2 km to the south of the town of Ramales de la Victoria (Fig. 1).

The excavation and study of this site started in 1996, led by Straus and González-Morales, and the main field work lasted until 2013, although they continue to conduct short-term archaeological work in the cave along with analytical studies. A significant amount of work has been carried out to study and date (now with one hundred radiocarbon assays) the stratigraphic sequence, which, along with temporally diagnostic lithic and osseous artifacts, has made it possible to relate the many stratigraphic levels to specific cultural periods (e.g., Hopkins et al., 2021; Straus et al., 2001; Straus and González-Morales, 2012, 2019). The archaeological excavations were carried out in three different areas of the spacious vestibule: the outer vestibule (OV-"Cabin"), in an area of 9.25 m², which presents a record ranging from the Lower Magdalenian through the Bronze Age; the vestibule rear (VR), in an area of 15.5 m² that includes the area of the "Corral", the "Deep Sondage"), and "The Red Lady Burial Area", which together cover the time period from the Late Mousterian through the Middle Magdalenian; and an area of 9 × 0.5–1 m connecting both areas, the "Mid-Vestibule Trench" (MV), that records levels from the early Magdalenian through the Neolithic period (Fig. 2). By joining the records present in these three excavation areas, we obtain a virtually continuous record from >47,000 cal. BP (level 130) to the Bronze Age (level 3), with few hiati in the microvertebrate record (Table 1) (Iriarte-Chiapusso et al., 2015; Hopkins et al., 2021).

3. Methods

3.1. Excavation methodology

The archaeological excavation method used in this site are described in Straus and González-Morales (2012). The authors indicate that for the recovery of the microfauna or microvertebrate remains, fishes, amphibians, reptiles, birds, and small mammals, almost all the excavated sediment was washed and sieved by passing it through screens of different mesh sizes (2 - 1 mm) with water. One sample of microfauna is that which resulted from the sediment collected by an excavator from a spit (excavation layer within a natural level) in a quarter-meter square area within each 1 × 1 m excavation unit (for the sediment collection methodology for microvertebrates, see Cuenca-Bescós and Morcillo-Amo, 2022). The sediment, once washed and sieved, results in a concentrate that is treated in the laboratory, separating the remaining sediment from the bones and teeth using tweezers and stereoscopic magnifying glasses. Each sample is curated with indication of level, square, and depth of origin.

3.2. Geometric morphometry

As in most of the systematic works about fossil micromammals, the palaeontological study is carried out using the molars of the samples. Until now there had been ten different species identified in El Mirón Cave: *Arvicola terrestris* [=*amphibius* according to Corbet (1978), but we are going to use the nomenclature indicated by Palomo et al. (2007)], *A. sapidus, Microtus arvalis, M. agrestis, Terricola lusitanicus, Alexandromys oeconomus, Chionomys nivalis, Lasiopodomys gregalis, Clethrionomys glareolus* and *Pliomys lenki* (Cuenca-Bescós et al., 2008, 2012). In this work we have identified a total of 1925 teeth based on the m1 (lower first molar) morphology of 11 different species of Arvicolinae. For the morphological identification of the species, we have used the characteristics published in the relevant literature (e.g., Brunet-Lecomte, 1990; Chaline, 1972; Cuenca-Bescós and Morcillo-Amo, 2022; Luzi, 2018; van der Meulen, 1973).

Due to the similarities observed in the m1 of some of the species of the diverse *Microtus s.l.*, we carried out a morphometric geometric analysis. A maximum of five specimens for each species and for each level studied were selected, for a total of 686 specimens. The selection criteria consisted of choosing the specimen whose preservation
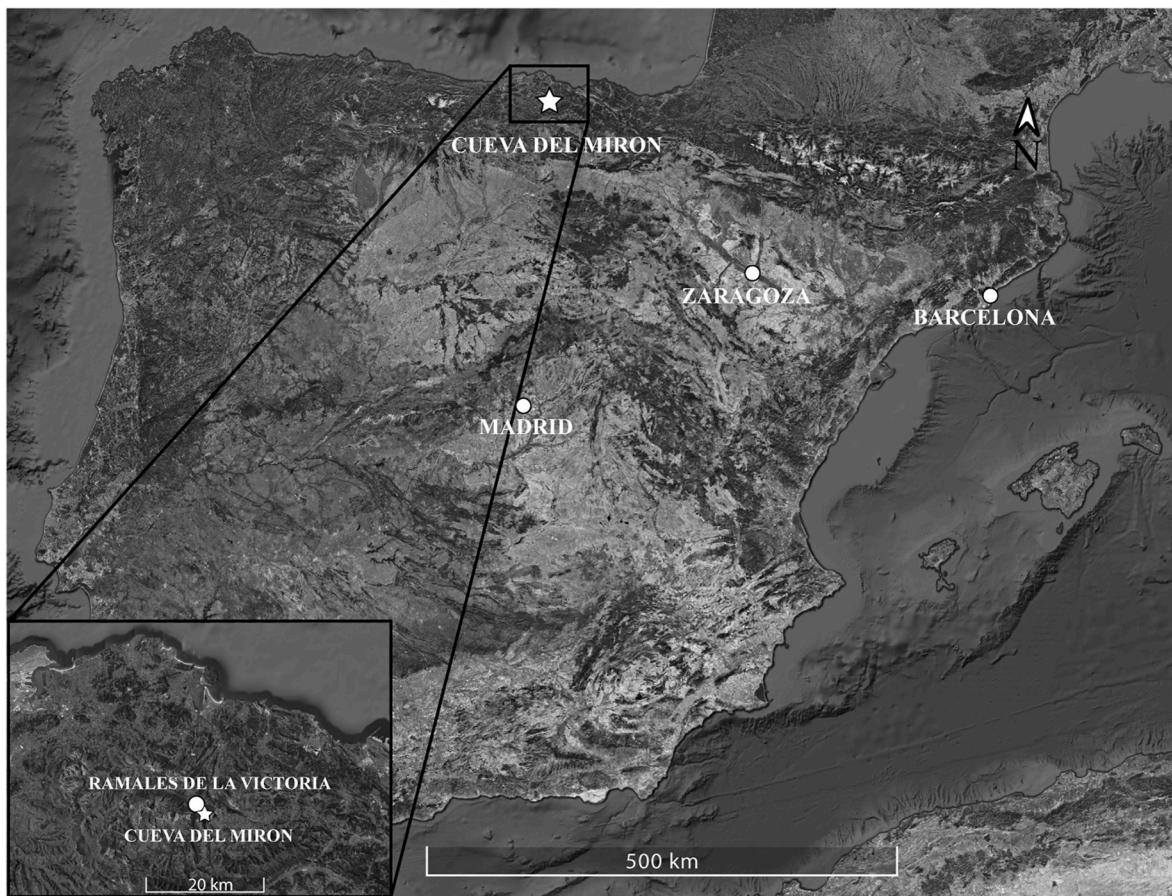
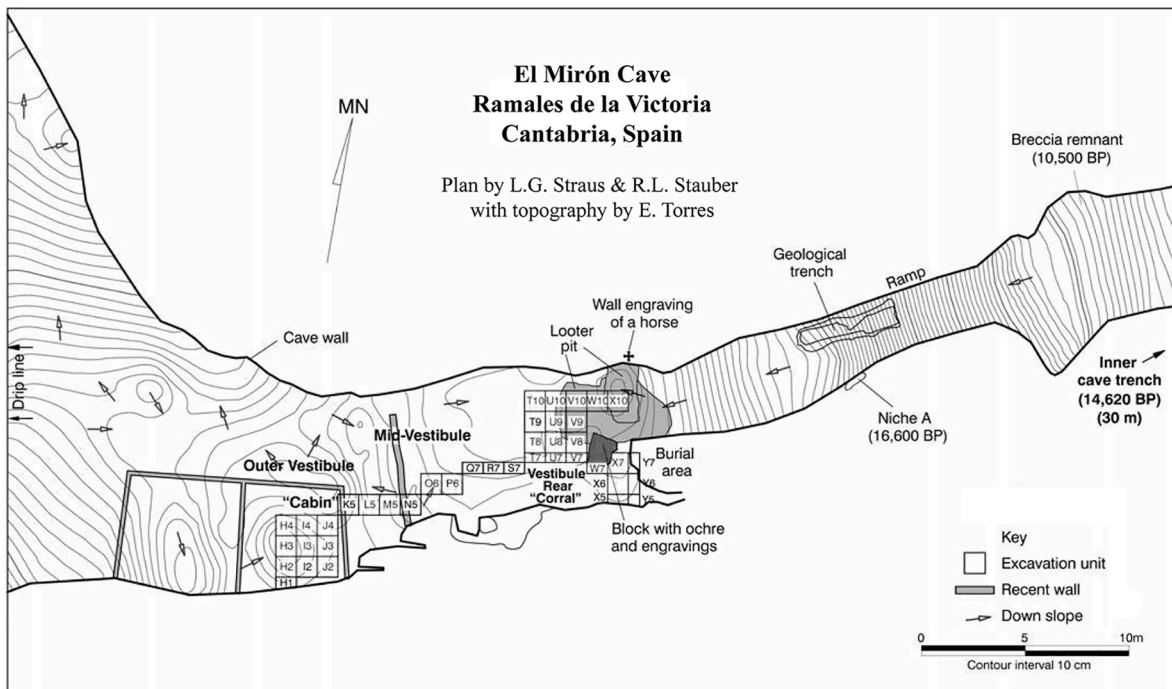**Fig. 1.** Geographical location of El Mirón Cave (star) in the Iberian Peninsula.

Fig. 2. Map of the floor plan of the cave, showing the excavated squares and the different excavation zones (modified from Hopkins et al., 2021).

Table 1
Chronostratigraphic table of El Mirón Cave, based on data from Hopkins et al. (2021), relating the levels of each of the areas studied with the archeologically determined cultural periods and the corresponding to Marine Isotope Stage (MIS), indicating from which of these levels microfauna have been recovered. OV: Outer Vestibule, MV: Middle Vestibule; VR: Vestibule Rear.

| Cultural period | OV | | MV | | VR | | MIS | Microfauna |
	Level	Age (cal BP) (Hopkins et al., 2021)	Level	Age (cal BP) (Hopkins et al., 2021)	Level	Age (cal BP) (Hopkins et al., 2021)		
Bronze Age	3	4250-3720						X
Chalcolithic	4	4420-4020						X
	5	4600-4180						X
	5.1	4750-4380						X
	6	4950-4520						X
	7	5200-4650						X
Neolithic	8	5450-4820						X
	8.1	5950-5180						
	9	6190-5590					1	X
			302	6210-4960				
			303	6330-5810				X
	9.6	6350-6010						X
			303.1	6400-3180				X
			303.3	7360-6260				
	10	8000-6130						X
Mesolithic			304	11210-6500				X
	10.1	12610-6700						X
Azilian	11/11.1	14890-11730	305	13440-9150				X
Azilian/Final Magdalenian			306	14010-12390				X
Upper Magdalenian			307	14630-13530				X
								X
			308	16460-13870				
	12	17810-13930						X
Middle Magdalenian	13	18390-16370						X
					108-104	18490-15870	2	X
	14	18520-18160						X
Lower Magdalenian	15	18630-18310						X
	16	18760-18450						X
			311-309	18830-14900				X
					109	18950-18200		X
	17	19190-18610						X

				110	19420-18610		X
18	19890-18890			111	19910-19010		X
				113-112	20200-19470		X
				114	20340-19900		X
19	20370-19480			115	20500-20150		X
		312	20730-17120	116	20650-20300		X
Initial Magdalenian				117	20750-20480		X
				118	20830-20610		
				119	21100-20680		X
		313	21950-19320	119.2	21610-20830		
							X
Solutrean				121	21960-21320		X
				122	22270-21660		X
				124-123	22640-21950		X
				125	22980-22240		X
				126	23580-22510		X
				127	28380-22860		X
Gravettian				128	39010-24800		X
				129	46890-33160	3	X
Mousterien				130	50900-39280		X

conditions made it possible to identify all the anatomical features of the occlusal surface of the m1: entrant and salient angles, and posterior lobule and anteroconid complex (ACC). We have distributed a total of 16 landmarks (LM) and 80 semi-landmarks around the molar contour, with the semi-landmarks concentrating in the contour of the ACC, by the TPSDig2 (Rohlf, 2015) (Fig. 3, A). The landmarks have been located at the point of greater curvature, and at the enamel-dentine junction to avoid the effect of thickness variations due to attritional wear on the external face. The semi-landmarks were located in the ACC to obtain a better characterisation of this structure, because it is the area of the m1 that presents the most variations between the species of *Microtus s.l.* As

already indicated by van der Meulen (1973), the ACC is the anatomical region of the m1 that records most of the changes due to the evolution of Arvicolinae species, that may be related to adaptations to changes in diet. The biomechanics of mastication in the Arvicolinae subfamily indicates that increased entrant and salient angles increase the enamelled perimeter of the molar, without requiring an increase in occlusal surface area, and increased resistance to abrasion and wear during mastication.

We used the command package Geomorph v. 4.0.2 (Baken et al., 2021; Adams et al., 2021), by RStudio Team (2022) to analyse the data. The used Generalized Procrustes Superimposition (GPA) analysis consists in the processes of rotation, translation, and scaling on each of the
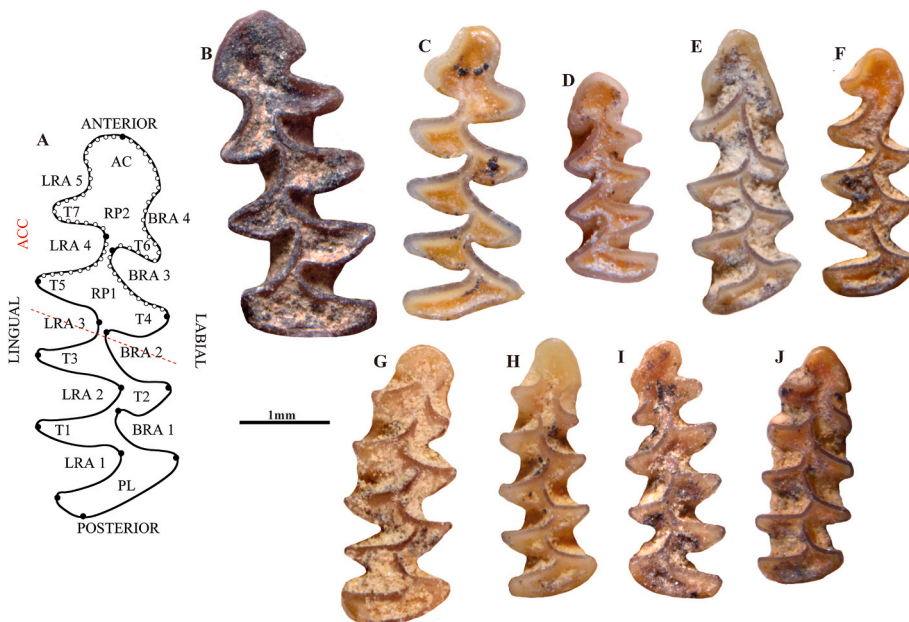

Fig. 3. Nomenclature and distribution of the landmarks (black circles) and semi-landmarks (white circles) in the contour of the molar (A). PL: posterior lobule; AC: anterior cusp; T: triangles; LRA: lingual re-entrant angles; BRA: buccal re-entrant angles; RP: pitimian rhombus. Lower first molars (m1) of the Arvicolinae species found in El Mirón Cave. B: *Arvicola terrestris* (level 12, spit 5, subsquare A, square V9); C: *Pliomys lenki* (level 130, spit 35, subsquare C, square W10); D: *Clethrionomys glareolus* (level 10, spit 18, subsquare C, square I3); E: *Chionomys nivalis* (level 130, spit 25, subsquare A, square X10); F: *Alexandromys oeconomus* (level 127, spit 15, subsquare D, square V10); G: *Microtus agrestis* (level 130, spit 2, subsquare B, square x10); H: *M. arvalis* (level 129, spit 22, subsquare A, square X10); I: *Terricola lusitanicus* (level 127, spit 15, subsquare D, square V10); J: *T. pyrenaicus* (level 128, spit 14, subsquare C, square X10). Scale: 1 mm.

images, eliminating the size factor, but maintaining the influence it has on shape. As a result, by means of the GPA we obtained the values of the centroid size and shape. This same analysis was also used for the process of sliding semi-landmarks, by the technique of bending energy (Bookstein, 1997). The principal component analysis (PCA) was performed with the same command package, which allowed us to study the grouping of the different specimens according to the variation in shape, as well as to help us taxonomically classify them.

3.3. Ancient DNA

In order to confirm the classification obtained by using more traditional methods, a *Terricola* right mandible with the incisor, m1 and m2 displaying morphological characteristics more similar to *T. pyrenaicus* than to *T. lusitanicus* (the only species of *Terricola* described so far in this deposit) was used for the palaeogenomic analysis. All ancient DNA work was carried out at the Paleogenomics laboratory in the University Institute for Research in Environmental Sciences of Aragon (IUCA) of the University of Zaragoza (Spain). The mandible (laboratory number 130), from square X10, subsquare D, level 130, spit 30, was wiped with 0.5% bleach, submerged in water and then in 80% ethanol, air-dried and irradiated with UV for 15 min on each side. Once dry, it was mechanically fragmented inside a 2 ml tube with tweezers, obtaining 65 mg of bone powder.

DNA was extracted following the silica-based method of Brotherton et al. (2013) and using a modified binding buffer (Bover et al., 2019), obtaining a final volume of 100 μL of DNA extract. A double-stranded library (DSL) was constructed from the extract using a protocol based on Meyer and Kircher (2010) with modifications described in Llamas et al. (2016), in which short P5 and P7 adapters (including 7-mer barcoder in each adapter) were ligated to temperates. Extraction and library negative controls were processed along the sample. Finally, the library was shotgun sequenced in an Illumina HiSeqX platform (Paired End, 2 × 150 bp).

Raw sequencing fastq files were barcode demultiplexed using Sabre v1.0 (http://github.com/najoshi/sabre), allowing one mismatch (option -m 1). The quality of demultiplexed reads was assessed using FastQC v0.11.9 (http://www.bioinformatics.babraham.ac.uk/projects/fastqc). Adapter sequences were trimmed with AdapterRemoval v2.3.0 (Schubert et al., 2016) collapsing (merging) into a single read those paired reads overlapping by at least 11 bp and reads shorter than 30 bp were discarded.

A total of 32,524,978 collapsed reads were iteratively mapped to the mitochondrial genome of *Terricola thomasi* (Genbank Accesion number NC_057558) using BWA v0.7.17 backtrack algorithm (Li and Durbin, 2009) (with options: l 1024, -n 0.01, -o 2), and mapped reads with quality lower than a Phred score 25 were removed using SAMtools v1.11 (Li et al., 2009). Duplicate reads were filtered using FilterUniqueSAMCons.py (Kircher, 2012). An intermediate consensus sequence for subsequent mapping rounds was generated using a 75% majority and calling reference in positions with coverage depth <3 in Geneious Prime 2022.0.2 (Biomatters, https://www.geneious.com, Kearse et al., 2012). This process was iterated until no additional reads were mapped. A final 75% majority consensus sequence was generated using Geneious retaining the reference nucleotide at positions with read depth ≥3 (other positions were called as N).

After eight rounds of mapping to the *T. thomasi* mitochondrial genome, up to 947 unique reads mapped to the reference covering 73.1% of it with a coverage depth of 2.9X and a mean mapped read length of 49.1 bp. The final consensus sequence generated for sample 130 displayed a final length of 16298 bp, from which 8223 were Ns and 114 other degenerate nucleotides (67 Y, 45R, 1 M and 1 K).

Ancient DNA damage patterns were assessed using mapDamage v2.2.1 (Jónsson et al., 2013), displaying the typical features for fragmentation and nucleotide misincorporation patterns aDNA damage (Fig. S1).

As the number of Arvicolinae complete mitochondrial genomes are limited (e.g., no complete mitochondrial genomes are available for *Terricola pyrenaicus*, *T. gerbei* or *T. lusitanicus*), we aligned the mitochondrial cytochrome B (*cytb*) of sample 130 (Genbank Accession Number TBA) to all available *cytb* sequences from European Arvicolinae (excepting hybrids). The reads mapping on the *cytb* gene for sample 130 covered the 78.4% of the reference at a coverage depth 3.1X (mean read length 45.3 bp), and of the total length of 1143 bp, 507 were Ns and 9 other degenerate nucleotides. For those species with a large number of sequences, identical sequences were removed and up to 50 sequences were randomly selected to generate a restricted alignment including 659 sequences and *Eliomys quercinus* (MN935777) and *Apodemus sylvaticus* (MN964126) as outgroups (see Table S.1 for details of sequenced used). The final dataset aligned using MUSCLE implemented in Geneious was used to build a maximum likelihood tree using IQ-TREE v2.2.0 (Nguyen et al., 2015). Node support was estimated by performing 1000 ultrafast bootstrap replicates (Minh et al., 2013) with HKY substitution model.

4. Results

4.1. Species identification

We have identified a total of 11 species of the Arvicolinae subfamily in El Mirón Cave, adding the species *Terricola pyrenaicus* to the list of the previously identified species from this site (Fig. 3, Table 2, Table S.2).

The species *T. pyrenaicus* has been identified thanks to the morphology of the neck "d", according to van der Meulen (1973), as being more closed than in *T. lusitanicus,* partially isolating the anterior cusp (AC) from the rest of the molar. This species has also been identified for the inclination of the m1, and by the more pronounced inclination of the molar towards the labial side, caused by the inclination of the T4 towards the posterior part of the tooth (López-García et al., 2013), and for the marked protuberance of the re-entrant angles BRA3 and LRA4. The phylogenetic analysis using the mitochondrial *cytb* sequence of the putative *T. pyrenaicus* individual (sample number 130) corroborates its attribution to this species (see Fig. 4 and S1).

In general, individuals belonging to the same species cluster together in well supported clades [Maximum Likelihood Bootstrap (MLB) value between 95 and 100], and individual 130 falls within a well-supported clade (MLB = 100) formed by *T. gerbei/pyrenaicus* individuals [*T. gerbei* and *T. pyrenaicus,* are considered synonyms by Wilson and Reeder (2005)].

Some specimens of the *Terricola* species show confusing morphological characteristics, which is why they have been identified as *T. lusitanicus-pyrenaicus*. Two other species that have a high morphological similarity are *M. arvalis* and *M. agrestis*. For this reason, the samples whose classification into one or another species was confusing, have been identified as *M. arvalis-agrestis*.

The morphological and systematic description of the species previously identified in this site are extensively described in other works (Cuenca-Bescós et al., 2008, 2010a, 2010b).

4.2. Geometric morphometry

The Principal Component Analysis (PCA) shows that the amount of variance among the first three components only reaches 68.33% of the total variance. Even so, a discrimination between the genera *Terricola* and *Microtus* from the species *C. nivalis*, *A. terrestris* and *A. oeconomus* can be observed (Fig. 5). The species *M. arvalis* and *M. agrestis* present a better separation comparing PC1 versus PC3 (Fig. 5, B). Both species present similar values of PC1 and PC2 in the PCA graph (Fig. 5, A), but *M. agrestis* present more negative values of PC3 than *M. arvalis*. Those individuals that could not be classified into one or the other species due to the similarity in the morphology of the occlusal surface of the m1, are located in the PCA in the area of contact of both species, showing a closer proximity with the morphologies identified as *M. arvalis*.

Table 2
Table by levels of presence/absence of the Arvicolinae species identified in this site, indicating the number of species corresponding to each level. We have represented the different MIS (Marine Isotopic Stage) that this deposit includes, and the levels corresponding to each one. The mean temperatures were calculated following the method proposed by Montuire et al. (1997).

Levels	Cultural period	Age (cal BP) (Hopkins et al., 2021)	Microtus arvalis	Microtus agrestis	Terricola lusitanicus	Terricola pyrenaicus	Chionomys nivalis	Alexandromys oeconomus	Lasiopodomys gregalis	Arvicola terrestris	Arvicola sapidus	Pliomys lenki	Clethrionomys glareolus	N° species	Nª of samples	MIS	Mean temperatures (°C) (Montuire et al., 1997)
3	Bronze Age	4250-3720	X	X	X		X	X		X			X	7	33		
4	Chalcolitic	4420-4020	X							X				2	19		
5		4600-4180	X					X		X			X	4	30		
5,1		4750-4380	X	X	X		X			X				5	7		
6		4950-4520		X			X			X			X	4	29		
7		5200-4650		X	X		X							3	29		
8	Neolithic	5450-4820	X	X	X		X			X			X	6	17		
8,1		5950-5180												0	0		
9		6190-5590	X	X	X		X			X			X	6	19		
302		6210-4960												0	0	1	
303		6330-5810						X		X				2	5		
9,6		6350-6010	X	X	X		X	X					X	6	17		
303,1		6400-3180												0	0		
303,3		7360-6260												0	0		
10		8000-6130	X	X	X		X			X	X		X	7	31		
304	Mesolithic	11210-6500		X			X			X			X	4	4		
10,1		12610-6700		X	X	X	X	X		X			X	7	15		
305	Azilian	13440-9150					X			X				2	6		
11/11.1		14890-11730	X	X	X		X			X			X	6	23		
306	Azilian/Final Magdalenian	14010-12390	X	X			X			X				4	7		
307	Upper Magdalenian	14630-13530	X	X			X	X		X				5	5		
308		16460-13870												0	0		
12		17810-13930	X	X	X		X	X		X				6	16		
13	Middle Magdalenian	18390-16370	X	X	X		X	X		X				6	42		
108-104		18490-15870	X	X	X	X	X	X		X		X	X	9	128	2	
14		18520-18160	X	X	X		X	X		X				6	22		
15	Lower Magdalenian	18630-18310	X	X			X	X		X				5	17		
16		18760-18450	X	X	X		X	X		X				6	26		
311-309		18830-14900	X	X	X	X	X	X		X				7	10		
109		18950-18200	X	X	X	X	X	X		X		X		8	11		

Level	Cultural period	Date													Count	NISP		Graph
17	Lower Magdalenian	19190-18610	X	X	X	X	X	X		X				7	23		
110		19420-18610	X	X	X	X	X	X		X		X		8	37		
18		19890-18890												0	0		
111		19910-19010	X	X	X		X	X		X				6	27		
113-112		20200-19470	X	X	X		X	X	X	X				7	10		
114		20340-19900	X		X			X		X				4	6		
19		20370-19480												0	0		
115		20500-20150	X		X		X	X		X				5	4		
116		20650-20300	X	X	X		X	X		X				6	13		
312		20730-17120												0	0		
117	Initial Magdalenian	20750-20480	X							X				2	2		
118		20830-20610												0	0		
119		21100-20680			X			X						2	2		
119,2		21610-20830												0	0		
313		21950-19320												0	0		
121	Solutrean	21960-21320	X	X	X	X	X	X		X		X		8	7		
122		22270-21660	X	X	X	X	X	X		X				7	10		
124-123		22640-21950	X	X	X		X	X		X		X		7	17		
125		22980-22240	X	X	X		X	X		X				6	8		
126		23580-22510	X	X	X		X	X		X				6	14		
127		28380-22860	X	X	X	X	X	X		X				7	9		
128	Gravettian	39010-24800	X	X	X	X	X	X		X				7	12		
129		46890-33160	X	X	X	X	X	X		X		X		8	11	3	
130	Mousterien	50900-39280		X	X	X	X			X		X		6	13		-10 -5 0 5 10 15 20

The species of *Terricola* are mainly separated by PC1, which is indicative to size variation associated with the shape. Although individuals classified as *T. pyrenaicus* are fewer than those identified as *T. lusitanicus*, the separation between both species is clearly shown in Fig. 5, A. In this case, there are also some individuals whose characteristics did not allow them to be classified with certainty into one or the other species, but in general it is observed that they most likely correspond to *T. pyrenaicus*.

4.3. Climatic analysis: environmental characteristics indicated by Arvicolinae species

The studied Arvicolinae species are well distributed throughout the sequence of El Mirón Cave. This fact helps to reconstruct the climatic conditions during the successive times of deposition (Tables 1 and 2). In the levels pertaining to the Solutrean (Levels 127-126-125-124-121 and possibly 313) and Initial Magdalenian (Levels 119.2-119-118-117) cultural periods, there is a reduction in the number of Arvicolinae species that could be associated with the worst climatic and environmental conditions of the Last Glacial Maximum [LGM: 26 - 16 cal Ka, as defined in the global chronostratigraphical correlation table for the last 50Ka published by Cohen and Gibbard (2019)]. However, in those levels with sufficient samples from these cultural periods, the maximum number of species of Arvicolinae is eight. *Microtus arvalis* and *M. agrestis* are two species that are currently found in a wide variety of habitats, displaying opportunistic behaviour. In general, they are characteristic for open and humid environments, with an Atlantic or mid-European type of climate, with the presence of ubiquitous herbaceous cover. However, both species have been observed in the proximity of young forest areas, and *M. agrestis* has even been observed in heaths and dunes. The species of *Terricola* are found in open and humid meadows with Mediterranean climate, but *T. lusitanicus* is a species typical of climatic zones with a certain degree of Atlantic climate influence. Generally, the *Terricola* species are indicators of more temperate climate conditions, more stable and warmer than are indicated by *M. arvalis* and *M. agrestis*. The presence of *T. pyrenaicus*, currently living in mountainous areas where the average annual temperature does not usually exceed 15-16 °C, thus being generally an indicator of a colder climate at certain times in the record. A colder climate is also indicated by the presence of *Chionomys nivalis*, a species characteristic of cold climates in high mountain areas, with the presence of rocky areas. *Lasiopodomys gregalis* is a very rare species in El Mirón, present in only one level of the whole sequence (Level 113, c. 20,000 cal BP). Currently this species can be observed in subarctic regions, under tundra or semi-desert conditions. Species that live in the vicinity of water bodies (lakes, rivers, streams, marshes) have also been identified: *Clethrionomys glareolus* (also present in forested areas)*, Arvicola terrestris, A. sapidus* and *Alexandromys oeconomus*. This last species is also observed in tundra and taiga regions, with abundant ground cover (Palomo et al., 2007; IUCN, 2022).

In addition to the species already mentioned, *Pliomys lenki* is the only Arvicolinae present in the record of El Mirón Cave without extant representatives. The last record of this rodent in El Mirón is detected in Level 106 (imprecisely dated between 18,490–15,870 cal BP [Hopkins et al., 2021]). According to Cuenca-Bescós et al. (2010b) there is a correlation between the progressive disappearance of *P. lenki* and the increase in the numbers of *C. nivalis*, so it is likely that both species shared the same habitat. *P. lenki* also presents a strong morphological similarity with the extant species *Dinaromys bogdanovi*. For this reason, both species could have had a similar habitat, which also coincides with high mountain rocky areas and great environmental stability (Kryštufek, 2018). In addition, it has been proven that the presence of *P. lenki* decreases drastically with forested areas, ultimately disappearing completely from the record (Marquet, 1988; Cuenca-Bescós et al., 2006).

The vast majority of the identified Arvicolinae species are characteristic of open grassland areas with a weak distribution of trees.
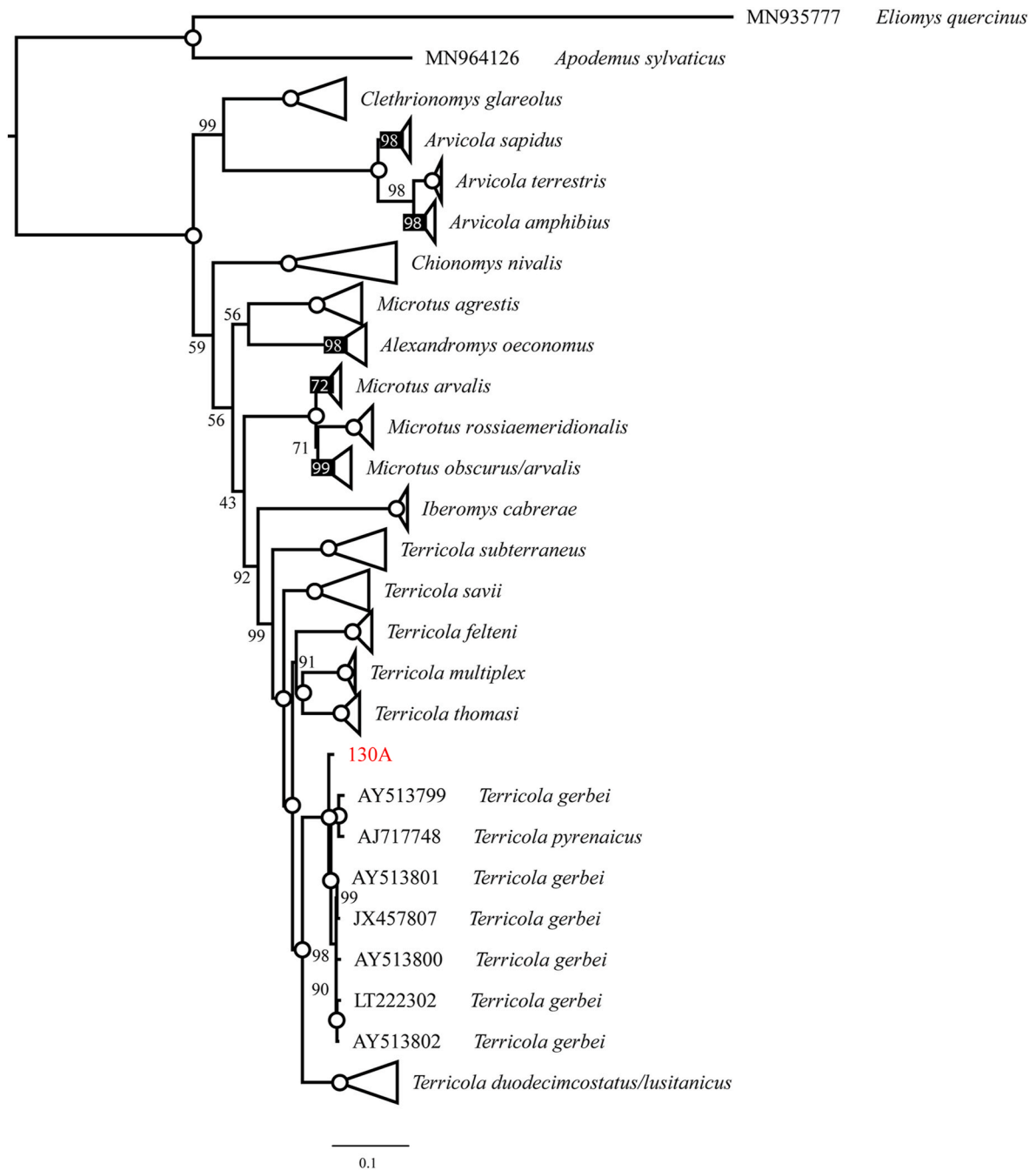
Fig. 4. Maximum Likelihood (ML) phylogenetic relationships of Arvicolinae individuals (see Table S1) including *Eliomys quercinus* and *Apodemus sylvaticus* as outgroups. Branches containing the same species have been collapsed (see Fig. S2 for full detailed tree) except the branches for *T. gerbei* and *T. pyrenaicus* to indicate the position of sample 130A. The analysis was performed in IQTREE2 using mitochondryal cytb sequences. ML Bootstrap (MLB) values are given on each node, and circles in nodes indicate MLB = 100. Sample 130A falls within the variability of *T. gerbei/pyrenaicus*.

5. Discussion

5.1. Climate variation along the stratigraphic sequence of the El Mirón Cave

In almost all the levels of the stratigraphic sequence of El Mirón Cave there are representatives of some of the species studied in this work. Thanks to this extensive species distribution, and their climatic specifications, interpretations can be made about the climatic and environmental variations that took place during the long period represented by this deposit. These climatic and environmental interpretations are in concordance with the presence of other small mammal species identified in other works (Cuenca-Bescós et al., 2008, 2009).

In general, a strong predominance of open landscapes is observed by the association of Arvicolinae species during most of the Palaeolithic sequence. There are also some moments of minor woodland development, with a constancy of humid meadow and/or water bodies (streams) in the surrounding area, with a practically uninterrupted presence of *A. terrestris* in the record. Cuenca-Bescós et al. (2009) already described a total of major seven changes in the paleoenvironment; it was only between 10 and 3 Ka BP when we can observe a major development of forest areas.
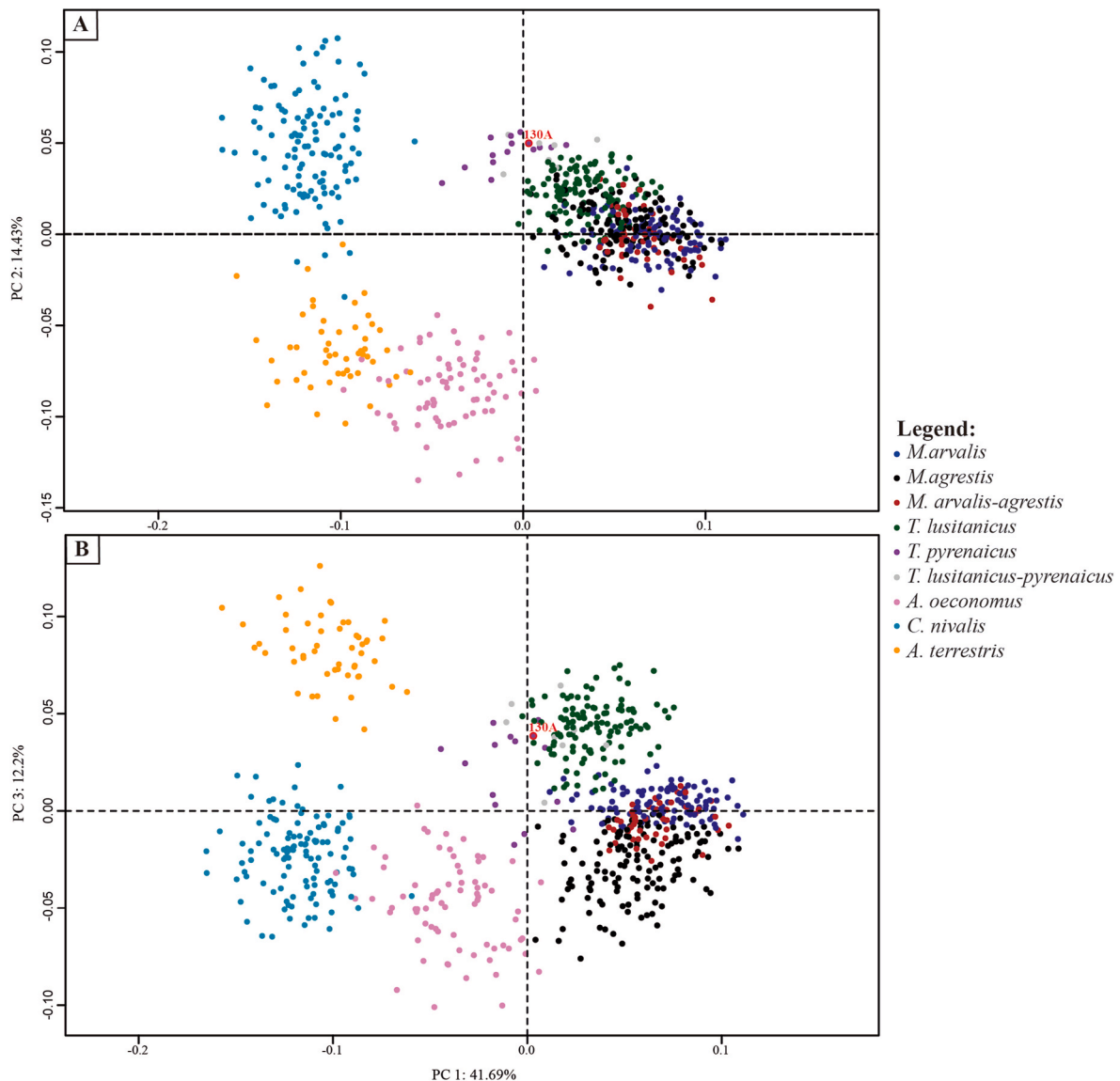
Fig. 5. Principal Component Analysis (PCA) of the species traditionally included in *Microtus s.l.* and *Arvicola terrestris*. A) Plot of PC1(41.69% of the variance)-PC2 (14.43% of the variance), showing the separation between *Terricola pyrenaicus* and *T. lusitanicus*. B) Plot of PC1(41.69% of the variance)-PC3(12.2% of the variance), where the separation between *Microtus arvalis* and *M. agrestis* is observed, predominating in the contact zone between both groups the more intermediate forms (*M. arvalis-agrestis*). Both plots include the sample of *T. pyrenaicus*, 130A.

5.1.1. Mousterian - level 130 (VR): >47.000 cal BP or 50.900–39.280 cal BP modeled age

From this oldest archaeological level in El Mirón Cave, excavated in the 2 m² Deep Sondage of the vestibule rear (VR), with the exception of *M. arvalis* and *A. oeconomus,* all species studied had been identified previously. The strong presence of *P. lenki* and *M. agrestis* is indicative of a predominance of open landscapes opposed to wooded areas. In addition, the presence of *C. nivalis, T. pyrenaicus* and *T. lusitanicus* indicate a generally temperate-cold climate, of Atlantic type (this is also indicated by the presence of *M. agrestis*) (Table 2). A cold-temperate climate with predominance of open environments has been also described for the Cantabrian region of Northern Spain during this period in other papers (e.g., Álvarez-Lao et al., 2015; Fernandéz-García et al., 2023).

5.1.2. Level 129 (VR): 46.890–33.160 cal BP modeled age

This level, which corresponds in age to the Early Upper Paleolithic, has not been assigned to a cultural period because it contains very little evidence of human presence; it lies between the levels of Mousterian and Gravettian age both in turn culturally very poor. In comparison with the

Mousterian level, we observe the appearance of the species *M. arvalis* and *A. oeconomus* which indicate a predominantly open landscape. *A. oeconomus* would be indicative of an increase in humidity in the area, which continues to be observed in later levels. The increase in the number of Arvicolinae species could indicate a decrease of the average temperature for this period (<5 °C) (Table S.2).

5.1.3. Gravettian - level 128 (VR): 39010-24800 cal BP modeled age

During this cultural period, the species *P. lenki* is absent (Table 2), although the rest of the species observed in the underlying levels are still present in the record. The climate would be similar to that of Level 129, with temperate-cold temperatures, but probably with a slight increase in wooded areas, and also an increase in the humidity. This also coincides with recent interpretations of the general climate of Cantabria during this cultural period (Fernandéz-García et al., 2023).

5.1.4. Solutrean - levels 127 to 121 (VR) and possibly 313(MV): 28,380–21,320 cal BP modeled age

During the Solutrean, weather conditions worsened at the time of

formation of the first levels (from 127 to 125), with a reduction in the number of individuals of species living in areas close to watercourses (*A. terrestris* and *A. oeconomus*) with respect to the Gravettian (Table S.2). The disappearance of *T. pyrenaicus* together with the continued presence of *C. nivalis* could be an indicator of a decrease in temperature in this mountainous area, with lower temperatures providing the optimum habitat for *T. pyrenaicus*. The species *M. arvalis*, *M. agrestis* and *T. lusitanicus* are still present, but their numbers of individuals decrease in Levels 126 and 125, which could be related either to the decrease in temperature or to further development of woodland. Toward the end of the Solutrean (Levels 124–122) there was an increase in environmental stability, with a general increase in the numbers of individuals per species, and notably an increase in representatives of the species *A. terrestris* and *A. oeconomus*, and the re-appearance of *T. pyrenaicus* in this cultural period (Table S.2, Table 2). A similar evolution of the climatic conditions of the Solutrean cultural period, until these levels, is also observed in other sites on the northern of Spain (e.g., Garcia-Ibaibarriaga et al., 2015). In the last Solutrean level (Level 121), a change in the environment is again observed, and although none of the mentioned species disappears, a reduction in the numbers of individuals per species is again recorded (Table S.2). The number of the studied Arvicolinae species in Level 121, the highest layer of the Solutrean sequence in El Mirón Cave, reaching eight species, a fact that indicates cold conditions, with average temperatures not above the 5 °C according to Montuire et al. (1997) (Table 2). This climatic observation could be the reflection of the Last Glacial Maximum *sensu lato*.

5.1.5. Initial Magdalenian - levels 119 to 117 (VR) and alternatively possibly 313 (MV) which lacks temporally diagnostic artifacts: 20,370–18,890 cal BP modeled age

The microvertebrate record from these levels is practically non-existent. We have only identified one individual each of *T. lusitanicus* and *A. oeconomus* in Level 119, and one each of *A. terrestris* and *M. arvalis* in Level 117 (Table 2). This scarcity of microvertebrate material may be a consequence of the poor environmental stability of the LGM. The poor record does not provide us enough information to determine the climate during this period of time, beyond the fact that there was an Atlantic type of climate, with a certain degree ambient humidity.

5.1.6. Lower Magdalenian - levels 116 to 109 (VR), 19 to 15 (OV) and 312–308 (MV): 20.650–18,610 cal BP modeled age

During the first levels of the Lower Magdalenian (Levels 116–114 and Level 19) we observed an increase in the fossil record of Arvicolinae remains, which may indicate a slight improvement in the environmental conditions in comparison with the Initial Magdalenian. However, El Mirón Lower Magdalenian seems to initiate with cold climatic conditions (*C. nivalis* and *L. gregalis*), and relatively low ambient humidity (a few individuals of *A. terrestris* and *A. oeconomus*), but not as cold as during the Solutrean cultural sequence with a smaller number of Arvicolinae species (Table 2). In Levels 110 and 109 (post-LGM) we observe an increase in humidity, with higher numbers of *A. terrestris* and *A. oeconomus* (but less predominant in Level 109) (Table S.2). There is also the presence of *T. pyrenaicus* and *C. nivalis* in these two levels, with again an increase in the number of Arvicolinae species to eight, which would indicate a cold climate (<5 °C) (Table 2), and therefore a cold pulse just after the LGM. The increase in individuals of *M. arvalis, M. agrestis* and *T. lusitanicus* indicates the predominance of open areas with an Atlantic type of climate. In the massive horizon of Level 17, the last layer, which by its modeled age range (Hopkins et al., 2021) could be included within the LGM *sensu lato*, and apparently dating between the two cold levels 109 and 110, we observe a slight decrease of ambient stability, with a decrease in humidity, indicating a cold and drier climate during formation of this level. Conditions marked by cold temperatures and humid meadows during the Lower Magdalenian have also been observed in other palaeontological sites in the North of the Iberian Peninsula (e.g., Rofes et al., 2014).

In the rest of the Lower Magdalenian sequence of El Mirón, there is evidence for a more humid environment, marked by a progressive increase in temperature, as could be observed in the progressive decrease in the number of Arvicolinae species, as well as by the decrease of *C. nivalis* and the disappearance of *T. pyrenaicus* (Table 2, Table S.2). The disappearance of *T. lusitanicus* in Level 15 at the end of the Lower Magdalenian, with a decrease of the number of individuals of the *Microtus* species, may represent a development of wooded areas, as also noted by other authors in the Cantabrian Region (e.g., Rofes et al., 2015).

5.1.7. Middle Magdalenian - levels 14 and 13 (OV) and 108 to 104 (VR): 18.950–16,370 cal BP modeled age

In the Middle Magdalenian, there is still a predominance of species that prefer open landscapes, with constant presence of herbaceous cover over time, as shown by the abundant presence of the studied Arvicolinae species. However, the presence of wooded areas is also observed, as indicated by the species *C. glareolus* (Table 2). The climate would have been of Atlantic type, with environmental stability and high humidity, and with cold-temperate temperatures. In general, the environmental conditions would have been similar to those of the end of the Lower Magdalenian, but during Levels 108–104 we identified nine different species of Arvicolinae (Table 2). This large number of species may be an indicator of a decrease in temperatures at a given point in time during the deposition of the sequence (Montuire et al., 1997). This could have been a consequence of one cold pulse before the end of MIS2.

5.1.8. Upper Magdalenian and Azilian - levels 12 (OV) and from 308 to 307 (MV): 17,810–13,530 cal BP modeled age

In this period, the climatic conditions observed were practically the same as during the Middle Magdalenian, with the presence of the same Arvicolinae species (Table 2). A temperate-cold climate, but with a decrease in open meadows and environmental humidity, without being a dry climate. The average temperatures would be gradually warming, presenting an average temperature at the end of this period approaching the temperatures of MIS1, i.e., the Holocene (relatively warm), up to 13 °C (Montuire et al., 1997).

5.1.9. Azilian/final Magdalenian - level 306 (MV): 14.010–12.390 cal BP modeled age

The record of this period is very scarce in El Mirón Cave, with only one level with small mammal record (Table 1). In this level we observe the presence of the following species: *M. arvalis, M. agrestis, C. nivalis, A. oeconomus* and *A. terrestris* (Table 2). This species indicates an Atlantic type of climate with humid conditions, and temperate-cold temperatures.

5.1.10. Azilian - level 305 (MV) and 11/11.1 (OV): 13440-9150 cal BP modeled age

During the Azilian period, a total of six Arvicolinae species have been identified (Table 2), which could indicate an average temperature not exceeding 11 °C (Montuire et al., 1997). The presence of *C. nivalis* and *T. lusitanicus* also accentuates the temperate-cold character of this period, which includes the Youngest Dryas. *A. terrestris* is the most abundant species during this period, showing an increase in humidity, which, together with the reduced number of *M. arvalis* and *M. agrestis*, shows a decrease in open meadows, and the development of young forest areas and probably riverine vegetation.

5.1.11. Mesolithic - levels 10.1 (OV) and 304(MV): 12.610–6.700 cal BP modeled age

The Mesolithic Arvicolinae record is much more abundant in Level 10.1. The identified species represent a relatively cold climate with the presence of species such as *C. nivalis, T. pyrenaicus, T. lusitanicus* and *M. agrestis,* the last two being the most abundant ones in this culturally poor level (Table 2, Table S.2). Open meadows would be the

predominant type of habitat, with constant herbaceous cover and probably some young forest areas. The presence of *C. glareolus,* apart from being indicative of forest areas, together with *A. oeconomus* and *A. terrestris* in this period, also suggests higher ambient humidity and a greater presence of water areas (ponding, marshy areas). In addition, the number of species of Arvicolinae in this level indicate a decrease of the average temperature, between −8 to 7 °C.

5.1.12. Neolithic - levels 303.3 to 302(MV) and 10 to 8 (OV): 8.000–4.820 cal BP modeled age

The Neolithic in El Mirón Cave, although it includes many levels, has only five with micromammal records (Table 1). Most species and individuals are observed in the first level of this period in the Outer Vestibule (Level 10) (Table 2, Table S.2). The number of species indicates similar climatic conditions to those of Mesolithic age in the early Holocene, a cold-temperate climate, with the predominance of open landscapes (*M. agrestis* and *M. arvalis*). However, the absence of *T. pyrenaicus* and the large number of *T. lusitanicus* individuals indicate warmer temperatures and more humid climate conditions. There is also a continued presence of *C. nivalis* during this cultural period, and, although this could be indicative of cold climates, the abundant presence of *T. lusitanicus* does not indicate that this was the case, and therefore the lower climate temperature may only have affected high mountain zones or could have corresponded to only brief moments in the formation of this segment of the cave deposit. In the rest of the record, the climate conditions were similar, with a slight decrease in the number of Arvicolinae species that indicates warmer temperatures and in the number of individuals that indicates open landscapes, with the presence of *A. oeconomus* at some times during formation of the layers in question. This rodent, together with the presence of *A. terrestris* and *C. glareolus,* could indicate an increase in humidity and/or water areas, with the presence of forest areas.

5.1.13. Chalcolithic - levels 7 to 4 (OV): 5200-4020 cal BP modeled age

The start of the Chalcolithic is represented by a climate similar to that of the end of the Neolithic (humid and temperate). However, at the end of this period there is no evidence of *C. nivalis*, and almost all the species characteristic of open landscapes are absent in the last two levels; only *M. arvalis* and *A. terrestris* remain. The climate would have been warmer at the end of the Chalcolithic, with a marked Atlantic or mid-European climatic character. The open meadows would have decreased notably, remaining less extensive than during the Neolithic, with the presence of some wooded areas as indicated by *C. glareolus* (Table 2).

5.1.14. Bronze Age - level 3 (OV): 4250-3720 cal BP modeled age

Level 3 of the Outer Vestibule is the only level with a record of small mammals corresponding to the Bronze Age, being the most recent level of the prehistoric site (Table 1). Compared to the Chalcolithic period, there is a marked change in the identified Arvicolinae species. The species typical of open meadows reappear (*M. agrestis*), along with species typical of temperate and humid climate conditions (*T. lusitanicus, A. oeconomus*), with the presence of some forest areas (*C. glareolus*). The species already observed during the end of the Chalcolithic period increase their representation (*M. arvalis* and *A. terrestris*) (Table S.2). In addition, *C. nivalis* reappears in this period, which indicates that the general temperatures from this period were cold-temperate, with average temperatures not higher than 8 °C, based on the number of Arvicolinae species (Table 2). In general, the climate during the Bronze Age in El Mirón Cave was humid, with cold-temperate temperatures in an Atlantic-type climate, and an environment dominated by open meadows with the presence of some wooded patches, perhaps due to anthropic (farming-related) deforestation, contrary to other areas of the Northern of the Iberia Peninsula which present a major development of wooded areas during the Bronze Age (e.g., Garcia- Ibaibarriaga et al., 2015).

6. Conclusions

The fossil record of mammals from El Mirón Cave provides important information about the climatic changes that occurred during the late Upper Pleistocene and early Holocene history of the northern Atlantic fringe of the Iberian Peninsula. In this study we have carried out a detailed description of climatic and environmental variations through the proxy indicators of the Arvicolinae species found in El Mirón Cave. We observe that, during the period of time recorded in the sequence of this site, numerous climatic variations took place in the Cantabrian region, with changes in the extent of grasslands, with varying presence of more or less developed forested areas. In addition, the description of *T. pyrenaicus*, previously not identified in this site, has helped to gain a better understanding of the variation between warmer and colder temperatures.

During formation of the pre- LGM levels, there was an Atlantic type of climate, with temperate-cold temperatures and a progressive increase in humidity, until the start of the LGM. This pleniglacial period, with very adverse climate conditions at some times, had an important impact on the record of small mammal faunas, as is observed by the almost complete disappearance of Arvicolinae species in the record. However, in the LGM levels there are episodes for which we identified a total of eight different species of Arvicolinae, a fact that indicates cold temperatures, not above an annual mean of 5 °C. It is worth mentioning that the effects on these small mammals are not seen until the Initial Magdalenian or the end of the Solutrean, although the LGM encompasses all of the latter period. A partial faunal recovery began during the Lower Magdalenian, with an environmental improvement during the end of the LGM, but with a regression of these conditions in the last levels corresponding to this pleniglacial stage. During formation of massive Lower Magdalenian Level 17, there is again a decrease in the number of individuals identified, which, in relation even to the cold levels above and below Level 17, may indicate a slight worsening of environmental conditions during the deposition of this level. It is not until the end of the Lower Magdalenian, and especially during the Middle Magdalenian, well after the LGM, that the more temperate fauna fully recovered. A minor cold pulse is seen again towards the end of the MIS2 (Levels 108–104), presenting, according to the number of Arvicolinae species, an average temperature equal to or even lower than during the LGM. This could possibly correspond to the last part of Greenland Stadial 2. In the rest of the sequence, there are again several climatic changes: drier during the Upper Magdalenian than during the later cultural periods corresponding to MIS1 (Holocene—Neolithic and Chalcolithic), in which the climate was warmer and more humid. However, at the end of all the sequence, in Level 3 corresponding to the Bronze Age, an average temperature not higher than 8 °C is observed, making it the layer with the lowest average temperature since the early Neolithic in El Mirón Cave.

CRediT authorship contribution statement

M.P. Alfaro-Ibáñez: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Data curation, Writing, Visualization, Project administration. **G. Cuenca-Bescós:** Conceptualization, Investigation, Resources, Writing – review & editing, Supervision. **P. Bover:** Methodology, Formal analysis, Investigation, Resources, Writing – review & editing, Visualization, Supervision. **M. González Morales:** Resources, Writing – review & editing. **L.G. Straus:** Resources, 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

Mitochondrial aDNA data from Terricola pyrenaicus (130A) will be available at Genbank.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.quascirev.2023.108234.

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