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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

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ABSTRACT

La Güelga Cave (Asturias, NW Spain) contains a stratigraphic succession dating from 47.2 ± 2.2 to 38.6 ± 0.5 cal kyr BP. Evidence of Mousterian, Châtelperronian and Aurignacian occupations in the succession documents the transition from Neanderthals to Early Modern Humans. To better understand the palaeoenvironmental context of this transition, we analyzed a rich small-mammal assemblage, comprising a minimum number of 2227 individuals and 20 taxa, in a high-resolution stratigraphic context, using the Bioclimatic Model, the Habitat Weighting Method, and biodiversity measures. Results identify a climate-cooling phase at the end of the Mousterian occupations (~45 ka), which transformed a mosaic of patchy forest and humid meadows into a more arid open landscape. Another cooling event, matching Heinrich stadial 4 (H4), coincided with the arrival of the Aurignacians (~39 ka). Comparison with regional and global records shows that the alternating cool-wet and arid events documented at La Güelga Cave are coeval with the advance and retreat of the Picos de Europa glaciers, and with global climatic events recorded in marine and ice cores. The impact of these environmental changes on the human cultural and biologic transitions is discussed.

1. Introduction

During Marine Isotope Stage 3 (MIS 3), from 57 to 27.5 kyr BP (Andersen et al., 2006; Svensson et al., 2006; Rasmussen et al., 2014) global climate was characterized by rapid and abrupt oscillations between cold stadials and temperate interstadials, as registered in ice-core (Fig. 1A) and marine (Fig. 1B–C) records (Dansgaard et al., 1993; Barron and Pollard, 2002; Andersen et al., 2004; Van Meerbeeck et al., 2011). This climatic instability had a great impact on terrestrial ecosystems, driving the replacement of forests by herbaceous plants, as has been shown in the pollen assemblages of marine and terrestrial records (Sepulchre et al., 2007; Sánchez-Goñi et al., 2008; Fletcher et al., 2010). The extinction of the Neanderthals and the colonization of Europe by Early Modern Humans took place in this context of climatic stress (Higham et al., 2014; Hublin, 2015; Marín-Arroyo et al., 2018), and therefore a causality between these millennial-scale climate cycles and the replacement of human species has been suggested by several studies (e.g. d'Errico and Sánchez Goñi, 2003; Sepulchre et al., 2007; Staubwasser et al., 2018), without neglecting other causes such as genetic assimilation (Trinkaus, 2007), immunology (Houldcroft and Underdown, 2016), competition (Hortolà and Martínez-Navarro, 2013), and inbreeding (Ríos et al., 2019).

In the Iberian Peninsula, the Cantabrian region is a particularly important area for the study of this time interval and episode of human evolution. The bedrock of the Cantabrian region (Fig. 2A–B) comprises widespread karstified carbonate terrains, in which thousands of caves have developed (Rossi, 2004). The sedimentary infill of these caves is rich in archaeological and paleontological remains from MIS 3, including several Middle and Upper Paleolithic deposits (e.g. Wood, 2011; Maroto et al., 2012; Higham et al., 2014; Marín-Arroyo et al., 2018), making this region a key area for the study of the climatic conditions concerning the Neanderthal to Early Modern Human transition.

Contemporary large-mammal fossil assemblages from this region reveal the existence of intense cold episodes, involving the occurrence of

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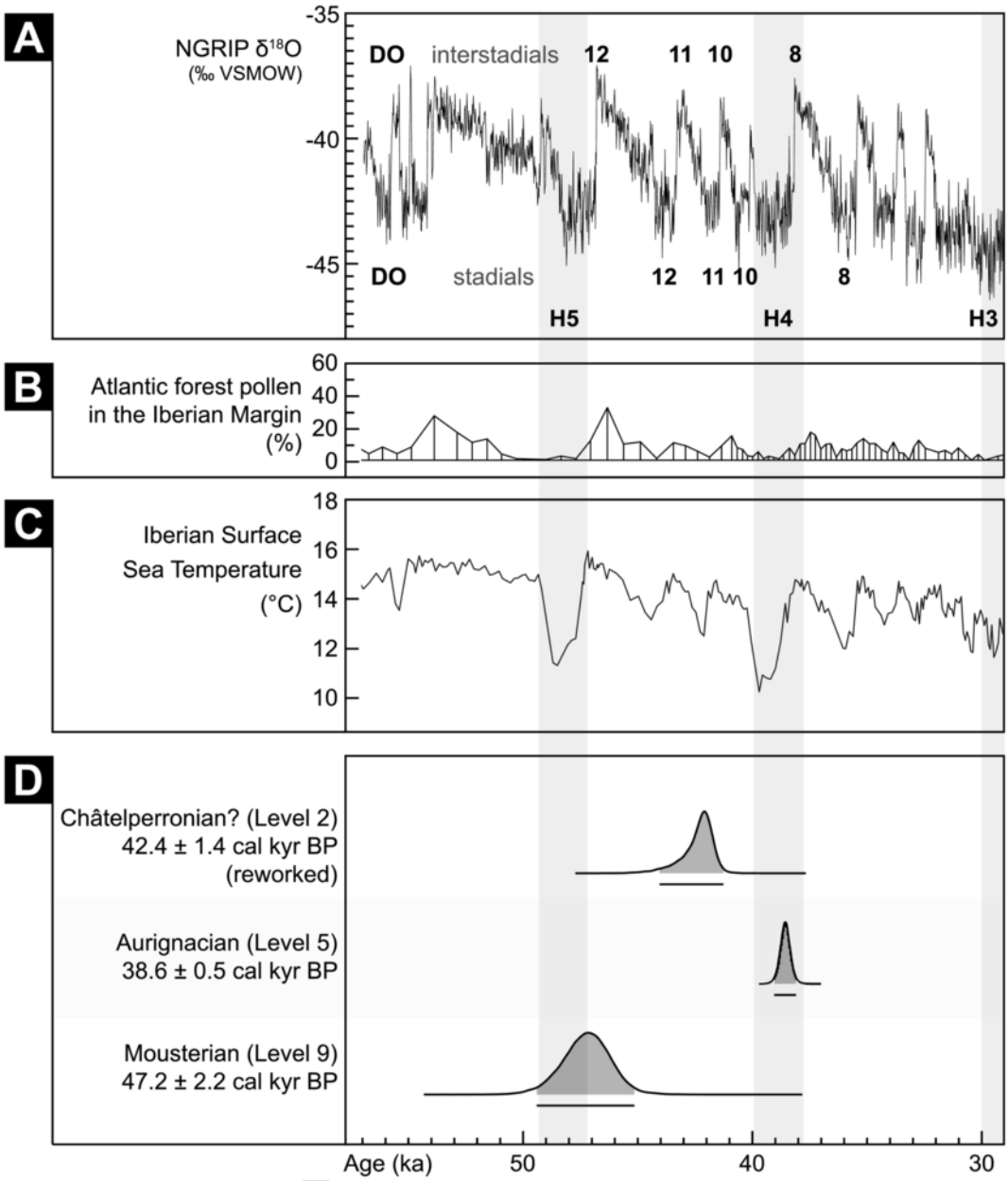
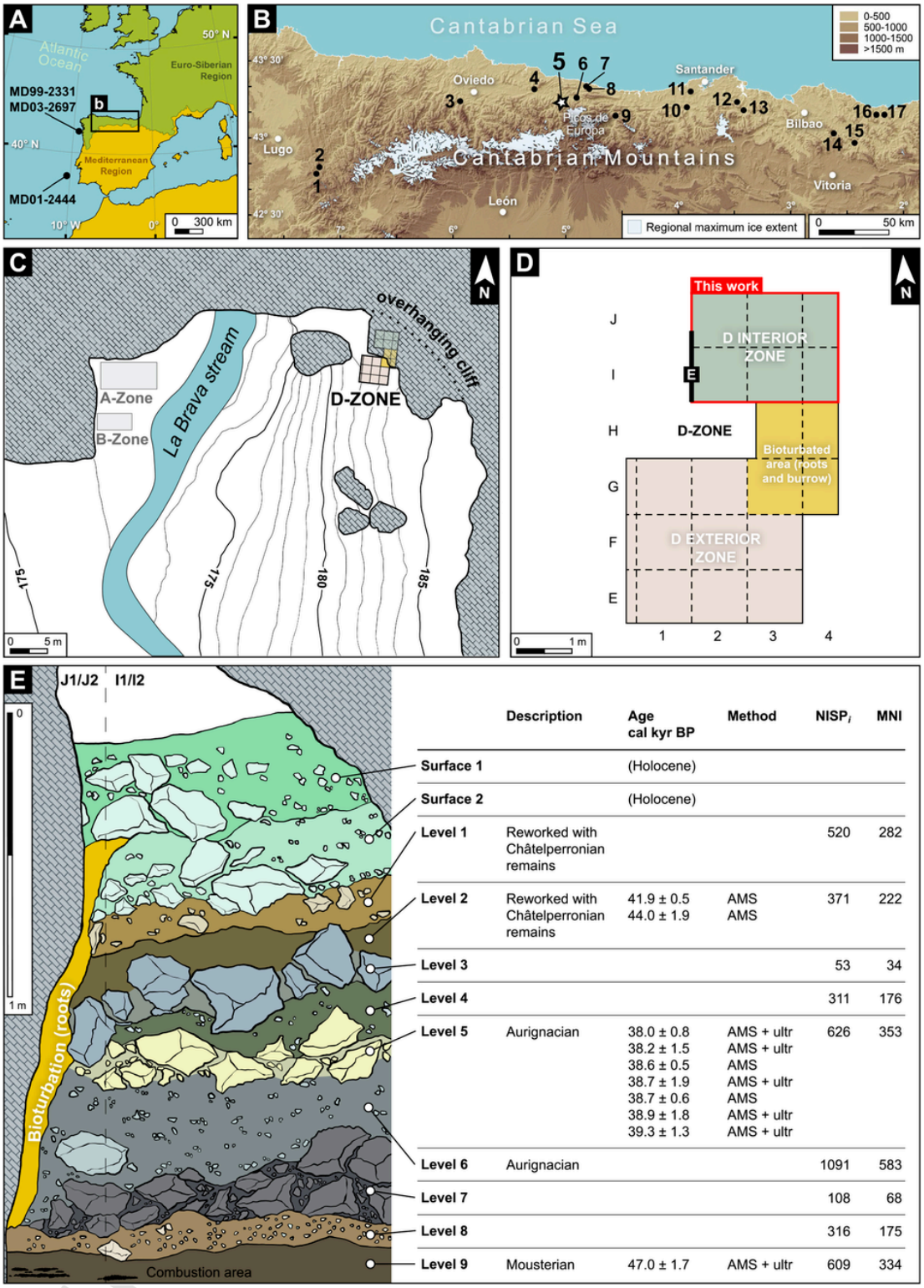


Fig. 1. Global and regional context for human evolution in Iberia during Marine Isotope Stage (MIS) 3. (A) NGRIP ∂18O (Andersen et al., 2004), DO: Dansgaard-Oeschger events; H: Heinrich stadial. Nomenclature suggested by Rasmussen et al. (2014). (B) Atlantic forest pollen percentage in Iberian margin cores MD03–2697 and MD99–2331 (42°N, 9°W) (Sánchez-Goñi et al., 2008). (C) Sea surface temperatures at the south-western Iberian margin: core MD01–2444 (37°33.68′N, 10°08.53′W, 2637 m below sea level) (Martrat et al., 2007). (D) Radiocarbon dates for Levels 2, 5, and 9 from La Güelga Cave showing the three archaeological assemblages (Menéndez et al., 2018). Modeled in ChronoModel 2.0.18 (Lanos and Dufresne, 2019) against IntCal13 (Reimer et al., 2013).

cold-adapted taxa such as woolly mammoth (*Mammuthus primigenius*), woolly rhinoceros (*Coelodonta antiquitatis*) and reindeer (*Rangifer tarandus*), in co-occurrence with other species such as red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*) and Iberian wild goat (*Capra pyrenaica*), among others (Álvarez-Lao, 2014; Álvarez-Lao et al., 2015), hosting a transitional faunal assemblage between the northern cold faunas and the southern predominantly temperate faunas (Álvarez-Lao and Méndez, 2016).

Small mammals (rodents, bats, shrews, hedgehogs and hares) represent around 80% of all mammal species richness (Fernández-Jalvo et al., 2016), and their geographical distribution is strongly conditioned by climatic factors. For these reasons, the small-mammal record has been frequently used to reconstruct the environmental conditions in archaeological and paleontological sites (e.g. Sesé, 2005; Cuenca-Bescós et al., 2008, 2009; López-García et al., 2011a, 2011b; Rofes et al., 2015; Álvarez-Lao et al., 2020a). The MIS 3 small-mammal record of the Cantabrian Region has been widely studied by different authors (Zabala, 1984; Pemán, 1990, 2000; Cuenca-Bescós et al., 2008, 2009, 2010; López-García et al., 2011b; Rofes et al., 2015; Sesé, 2005, 2017; Sesé et al., 2018; Álvarez-Lao et al., 2020a). However, in the surroundings of the Picos de Europa Mountains, where some of the last Mousterian occupations of the northwest Iberian Peninsula are located (e.g., the sites of Sopeña, El Esquilleu and La Güelga; Maroto et al., 2012; Higham et al., 2014; Marín-Arroyo et al., 2018), the small-mammal paleoecology and paleobiogeography remain poorly known.

Excavations at La Güelga (Fig. 1D; Fig. 2C–E) have allowed the recovery of a rich sample of small mammals throughout its MIS 3 se-



	Description	Age cal kyr BP	Method	NISP$_i$	MNI
Surface 1		(Holocene)			
Surface 2		(Holocene)			
Level 1	Reworked with Châtelperronian remains			520	282
Level 2	Reworked with Châtelperronian remains	41.9 ± 0.5 44.0 ± 1.9	AMS AMS	371	222
Level 3				53	34
Level 4				311	176
Level 5	Aurignacian	38.0 ± 0.8 38.2 ± 1.5 38.6 ± 0.5 38.7 ± 1.9 38.7 ± 0.6 38.9 ± 1.8 39.3 ± 1.3	AMS + ultr AMS + ultr AMS AMS + ultr AMS AMS + ultr AMS + ultr	626	353
Level 6	Aurignacian			1091	583
Level 7				108	68
Level 8				316	175
Level 9	Mousterian	47.0 ± 1.7	AMS + ultr	609	334

Fig. 2. Geographical and geological context for La Güelga Cave. (A–B) Location of La Güelga Cave in the Cantabrian Region (NW of the Iberian Peninsula). Digital Elevation Model from the National Geographical Institute of Spain. Postion of marine cores shown in Fig. 1B, C from Martrat et al. (2007) and Sánchez-Goñi et al. (2008). (B) MIS 3 sites mentioned in this paper: 1 Valdavara; 2 Cova Eirós; 3 El Conde; 4 El Sidrón; 5 La Güelga; 6 Sopeña; 7 Cueto la Mina; 8 Torca del León; 9 El Esquilleu; 10 El Castillo; 11 Covalejos; 12 Cobrante; 13 El Mirón; 14 Askondo; 15 Labeko Koba; 16 Ekain; 17 Amalda. Regional maximum extent of glaciers from Rodríguez-Rodríguez et al. (2015). (C) Plan of La Güelga Cave in which the excavated zones are indicated (Quesada and Menéndez, 2009). (D) Ground plan of the excavation of Zone D (Quesada and Menéndez, 2009). The small-mammals assemblage studied in this work comes from Zone D-Interior. (E) Stratigraphic profile of the interior sector of zone D (Menéndez et al., 2018).

quence, significantly more abundant in the number of remains and species than other nearby sites previously studied such as El Esquilleu (Sesé, 2005; Uzquiano et al., 2012) and Sopeña (Pinto-Llona et al., 2012). Taking this context into account, the objectives of this work are: a) to the study of the small mammal record from La Güelga from a paleontological and paleoecological perspective; b) to more precise char-

acterize the environmental conditions in which Neanderthals and Early Modern Humans lived; c) to understand the relationship between the environmental evolution of La Güelga sequence and the glaciers of the nearby Picos de Europa mountain range; d) to improve the paleobiogeography of some uncommon small mammal genera (e.g., *Neomys*, *Talpa* and *Crocidura*) from the MIS 3 record of the Cantabrian Region.

2. The La Güelga site

The Cantabrian Region forms a strip of land of rugged topography, about 500 km long and 30–50 km wide, in which short fluvial valleys run perpendicular to the coast. It is located in the southwestern end of the Euro-Siberian biogeographic region, while the rest of the Iberian Peninsula is part of the Mediterranean region (Fig. 2A). Both biogeographic regions are separated by the Cantabrian Mountain Range (Fig. 2B), which reaches heights of more than 2.000 m a.s.l. and recorded several episodes of glacier development (Fig. 2B) throughout the Pleistocene (Serrano et al., 2016; Rodríguez-Rodríguez et al., 2015, 2016, 2018; Oliva et al., 2019).

La Güelga Cave (43°20′11.99"N - 5°6′2.48"O) (Fig. 2C–E) is located in the vicinity of Narciandi (Cangas de Onís, Asturias, northern Spain), 182 m a.s.l. and ~ 15 km south of the current coastline. The entrance of the cave system is located at the base of a limestone scarp, at the northern end of a small valley excavated by the La Brava stream. This complex developed within Carboniferous limestone of the Bondón-Ponga Unit (Alonso et al., 2009).

The site is currently located in an Atlantic climatic domain, characterized by temperate summers and absence of a dry season (type *Cfb* according to the Köppen-Geiger classification; Beck et al., 2018). Precipitation is distributed throughout the year reaching an annual mean of ~1300 mm, while the mean annual temperature (MAT) is 12.2 °C, with maximum and minimum month-mean temperatures of 18.4 and 6.7 °C, respectively.

2.1. Excavation zones

La Güelga Cave houses a set of archaeological sites formed during the Late Pleistocene, all of them located in rock shelters and cavities filled by fluvial terrace deposits overlying the current riverbed. This set of occupations has been divided into different sectors (or zones) for archaeological research (Fig. 2C). The excavations at La Güelga started in the Solutrean and Magdalenian occupations of Zones A and B, located in the lower terrace of the system, around the current cave entrance (Fig. 2C). These two areas were excavated from 1989 to 2000 (García et al., 2004; Menéndez and Martinez-Villa, 1992; Menéndez et al., 2004, 2006b).

Zone D (Fig. 2C–E), whose small-mammal record is studied in this paper, is located 11 m above the current river level, in what was an ancient opening of the cave, occupied during the Mousterian, Châtelperronian, and Aurignacian cultures (Menéndez et al., 2005, 2006a, 2006b; Quesada and Menéndez, 2009; Menéndez et al., 2018). This zone is divided into two adjacent spaces (D-interior and D-exterior zones) with different stratigraphic sequences, separated by a bioturbation-affected area (Fig. 2D) that has interrupted the stratigraphic continuity between the levels of both sequences. In this work, we present the study of the interior sequence (D-interior zone) (Fig. 2D–E), which comprises the richest record of this area.

2.2. Stratigraphic succession

Stratigraphic levels are numbered 9 to 1, from oldest to youngest. The first Mousterian lithic remains appear at Level 9, dated in 47 ± 1.7 cal kyr BP (Menéndez et al., 2013; Menéndez et al., 2014, 2018; Quesada and Menéndez, 2009). The large mammals identified in Level 9 include *Cervus elaphus* (red deer), *Rupicapra pyrenaica* (Pyrenean chamois) and, in smaller quantities, *Capreolus capreolus* (roe deer) and *Equus* sp. (horse) (Menéndez et al., 2018). Evidences of combustion (rubefaction and dispersed ashes) were also found at this level (Jordá et al., 2013), indicating the most intense occupations of the sequence. Most of the faunal remains show anthropic marks, among which are the alterations produced by fire (Menéndez et al., 2018). The micromorphological analysis of Level 9 shows signs of compaction, internal layering, and a horizontal orientation of elongated fragments, which are indicative features of well-preserved undisturbed sedimentation (Kehl et al., 2018).

Level 8 comprises clays with very few anthropic remains, consisting on some lithic manufacture residues of Middle Paleolithic technology (Menéndez et al., 2018). Above is Level 7, which represents the infill of a set of blocks detached from the ceiling of the cave.

Levels 6 and 5 are of Aurignacian cultural attribution (Menéndez et al., 2005, 2006a, 2006b, 2018; Quesada and Menéndez, 2009; Menéndez et al., 2018). The micromorphological analysis and sedimentological and stratigraphic studies corroborate that these levels are undisturbed (Jordá et al., 2013; Kehl et al., 2018). The large mammal record at Level 6 it includes mainly *Cervus elaphus* and *Rupicapra pyrenaica*, and, at a lesser abundance, *Equus* sp. and *Sus scrofa* (wild boar), while level 5 comprises *Rupicapra pyrenaica*, an undetermined large-bovid (aurochs or bison) and *Cervus elaphus* (Menéndez et al., 2018). The archaeological content is poorer in Level 6 and increases towards the top of Level 5, presenting, in any case, signs of low-intensity and occasional occupations (Menéndez et al., 2018). In addition, carnivore activity is virtually absent in level 5 and higher at the base of level 6 (Menéndez et al., 2018). Radiocarbon dating on bone remains from Level 5 yielded a range from 40.8 to 36.6 cal kyr BP (Menéndez et al., 2018).

Level 4, a sand silt level, and Level 3, formed by a layer of limestone blocks generated by gravitational collapse of the cave shelter, are both of insecure cultural ascription (Jordá et al., 2013; Kehl et al., 2018; Menéndez et al., 2018).

The upper Levels 2 and 1, which are 15 to 30 cm thick, appear below a surface layer ~70 cm thick (Surface Levels 1 and 2). The lithic industry in these levels is characterized by the presence of two Châtelperronian points, which allow its assignment to this technocomplex (Menéndez et al., 2005, 2006a, 2006b; Quesada and Menéndez, 2009; Menéndez et al., 2018). The large mammals recovered at these levels comprise remains of *Cervus elaphus*, *Rupicapra pyrenaica*, *Bos/Bison*, *Capreolus capreolus* and *Sus scrofa* (Menéndez et al., 2018). Radiocarbon dating on bones with cut marks from level 2 yielded a chronological range of 45.9–41.4 cal kyr BP (Menéndez et al., 2018), which is consistent with its archaeological content. However, micromorphological characteristics include features of slope deposits, indicating that the sediments of this level are not in their original position (Kehl et al., 2018), and therefore not in temporal sequence.

3. Materials and methods

3.1. Collecting and sorting

The small-mammal assemblage studied in this work comes from the excavations carried out in the D-interior zone (Fig. 2D–E) between 2000 and 2008. It comprises 4005 taxonomically identified remains, belonging to a minimum number of 2227 individuals, and corresponding to 20 taxa (Table 1). All the sediment was water-screened using superimposed sieves, the lower one with a 1 mm mesh size. The material was sorted in the field laboratory and later revised with a binocular microscope under 10× magnification at the archaeology laboratory housed in the Madrid facilities of the National Distance Education Uni-

Table 1
Small mammal species[a] from La Güelga and its weighted habitat-preferences[b].

	L-9	L-8	L-7	L-6	L-5	L-4	L-3	L-2	L-1	Wa	OH	OD	Ro	OW	Wo
Arvicola amphibius	15.0	32.0	20.6	20.6	22.7	25.0	11.8	21.6	24.5		1				
Arvicola sapidus	5.4	13.7	10.3	6.0	7.1	7.4	5.9	12.6	8.5	1					1
Microtus agrestis	25.7	26.9	25.0	20.1	16.1	11.9	8.8	16.2	10.3		0.5			0.5	
Microtus arvalis		0.6	2.9	2.1	3.4	7.4	17.6	3.6	4.6			0.75		0.25	
Microtus lusitanicus	19.8	9.7	10.3	5.7	3.4	3.4	8.8	9.9	3.2		0.5			0.5	
Alexandromys oeconomus				0.2		1.1		0.5	0.7		0.5			0.5	
Chionomys nivalis				0.2	0.8	0.6	2.9	0.5	0.4				1		
Pliomys coronensis	4.2	7.4	11.8	16.0	17.6	13.6	5.9	12.2	9.9				1		
Apodemus cf. *sylvaticus*	6.3	1.1	2.9	4.3	5.1	1.7	8.8	5.9	7.8					1	
Eliomys quercinus									0.4				0.25	0.75	
Sorex minutus	5.7			0.2	0.6	0.6	2.9	0.5	0.7		0.25				0.75
Sorex ex gr. *coronatus-araneus*	12.6	1.7		4.5	3.1	1.1		5.0	2.1		0.75				0.25
Crocidura russula				0.3	0.3	0.6	2.9	0.9	2.8			0.75		0.25	
Crocidura gueldenstaedtii						0.6			0.7		0.5			0.5	
N. f. fodiens	1.2			1.9	1.1	0.6		0.5	0.4	0.75	0.25				
N. f. niethammeri						0.6			0.7	0.75	0.25				
Neomys anomalus				0.3	0.3					0.25	0.75				
Talpa occidentalis	1.5	4.0	4.4	12.3	11.6	16.5	8.8	6.3	16.0		0.75			0.25	
Talpa ex gr. *europaea-aquitania*	2.1	2.3	5.9	5.0	5.9	5.1	8.8	2.7	5.7		0.75			0.25	
Galemys pyrenaicus	0.6	0.6	5.9	0.5	0.8	2.3	2.9	1.4	0.7	1					
MNI	**334**	**175**	**68**	**583**	**353**	**176**	**34**	**222**	**282**						
NISP*i*	**609**	**316**	**108**	**1091**	**626**	**311**	**53**	**371**	**520**						

[a] The relative abundance (%) per level (L) of each taxon is based on the MNI (Appendix 1).
[b] Habitat-preferences: Wa, water; OH, open humid; OD, open dry; Ro, rocky; OW, open woodland; Wo, woodland.

versity (UNED, Spain). The small-mammal remains were classified and studied at the Geology Department of the University of Oviedo (Spain).

3.2. Taxonomy and quantification

Taxonomic identifications were carried out by means of a parallel-optics type stereomicroscope Nikon SMZ800N, equipped with a 5 Mpx digital camera and a drawing tube. Measurements, which are expressed in millimeters (mm), were taken on the microscope photographs using Adobe Photoshop CC software, which allows us to obtain the correct orientation of the images and the use of guides for a better adjustment of the measurements.

The anatomical elements selected for taxonomic identifications were the following: isolated teeth (except incisors) for murids and glirids; m1 for arvicolines (considering also the M3 for *Microtus lusitanicus*); mandibles and maxillae for soricids; and humeri for talpids. For comparison, small-mammal remains obtained from recent *Tyto alba* pellets, collected in the vicinity of the site, as well as the small-mammal collection of the Faculty of Biology (University of Oviedo) were used.

The general identification of rodent and shrew followed Chaline (1972, 1974), Nadachowski (1982), Nores (1989) and Román (2019). Detailed taxonomical and morphological analyses were based on: Nadachowski (1984) and Luzi and López-García (2019) for *Microtus agrestis* and *M. arvalis* lower dentition; Nores et al. (1982), Pemán (1983) and Barti (2006) for *Neomys* mandibles; Pasquier (1974) and Nores (1988) for *Apodemus* dentition; and Niethammer (1990) for *Talpa* humeri. The taxonomic classification followed the systematics proposed by Wilson et al. (2016, 2017) and Chevret et al. (2020) for rodents, and Wilson and Mittermeier (2018) for shrews and moles.

The number of identified specimens (NISP) was obtained by counting the most frequent taxonomically identifiable element per species (NISP*i*), following Lyman (1984). The minimum number of individuals (MNI) was calculated according to the most frequent diagnostic element, considering its laterality. The relative abundance of each small-mammal species was based on the MNI.

3.3. Predator identification

For a preliminary identification of the accumulating agent, the enamel of arvicoline molars and incisors was analyzed in search of alterations caused by digestion, following Andrews (1990) and Fernández-Jalvo et al. (2016). The observed digestion signals were counted and classified according to the following categories: absent, light, moderate, heavy and extreme (Andrews, 1990; Fernández-Jalvo et al., 2016). 95% confidence intervals (CI) of the digestion degree were calculated by means of the Clopper-Pearson method (Clopper and Pearson, 1934), applied using the PAST 4.0 software (Hammer et al., 2001) following Suchéras-Marx et al. (2019).

3.4. Paleoenvironment

The landscape that surrounded La Güelga Cave was inferred by means of the Habitat Weighting Method (Cuenca-Bescós et al., 2009; López-García et al., 2014), which is based on the habitat-type preferences of each small-mammal taxon (Evans et al., 1981). The habitat types are detailed in López-García et al. (2014) as follows: open dry (OD) denotes meadows under seasonal climate change; open humid (OH) corresponds to evergreen meadows with dense pastures and suitable topsoil; open woodland (OW) represents woodland margins and forest patches with moderate ground cover; woodland (Wo) indicates mature forest; water (Wa) corresponds to areas along streams, lakes and ponds; and rocky (Ro) denotes areas with a suitable rocky or stony substratum. The environmental preferences of each species were obtained from Nores (1989), Cuenca-Bescós et al. (2010), Wilson et al. (2016, 2017) and Wilson and Mittermeier (2018).

In order to determine if there were significant differences concerning the landscape inferred by the small-mammals assemblage of each level, a statistical analysis was carried out: the Clopper-Pearson Method (Clopper and Pearson, 1934) was applied using the PAST 4.0 software (Hammer et al., 2001) to calculate multiple proportion 95% confidence intervals (CI) for the relative abundance of each type of landscape. Following Suchéras-Marx et al. (2019) the differences were considered statistically significant when CI values for a particular type of landscape did not overlap among levels.

3.5. Paleoclimate

The climatic conditions under which the deposit was formed were inferred by means of the Bioclimatic Model. This method is based on quantitative climate estimates inferred from the rodent associations present in a given location (Hernández-Fernández, 2001, 2001b).

A value is assigned to each of the species in a climate zone (called Climate Restriction Index, CRI: Hernández-Fernández, 2001). Values are 0 when the species is absent from that climatic zone, or $1/n$ when the species does inhabit that climatic zone, where n is the number of climatic zones in which the species is present. The CRI of the extinct species *Pliomys coronensis* was obtained from Hernández-Fernández et al. (2007). The Bioclimatic Component (BC) (Hernández-Fernández, 2001) is the representation in a specific locality or, in this case, at a specific archaeological level, of each of the climatic zones. The BC of each level was calculated according to the formula: $BC_i = (\Sigma\ CRI_i)\ 100/S$, where i is the climatic zone and S is the number of species identified in each level. Based on the bioclimatic components of rodents (Hernández-Fernández and Peláez-Campomanes, 2005), we calculated the following parameters using a multiple linear regression for each of them: the mean temperature of the warmest month (MTW), the mean annual temperature (MAT), the mean temperature of the coldest month (MTC), and the mean annual precipitation (MAP). The results were compared with present day data for the location of La Güelga: MTW = 18.4 °C; MAT = 12.2 °C; MTC = 6.7 °C and MAP = 1321 mm, according to the Iberian Climate Atlas (Couto et al., 2011), consulted in the online GIS application agroclimap.aemet.es.

3.6. Paleodiversity

Climate has been found to be one of the main factors affecting microvertebrate biodiversity (e.g. Araújo et al., 2008; Blois and Hadly, 2009; Cuenca-Bescós et al., 2009; Blois et al., 2010; López-García et al., 2013). The environmental stress produced by abrupt climatic changes can be perceived through the decrease in parameters such as evenness and diversity (e.g. Blois et al., 2010; López-García et al., 2013). The evenness (E: how equal is the relative abundance among species) and diversity (D: a combination of richness and evenness) (Maurer and McGill, 2011) of the small mammal assemblage from La Güelga have been measured by means of the Simpson evenness ($1/D/S$: $E_{Simpson}$) and diversity ($1/D$: $D_{Simpson}$) indices respectively.

The formula $D = \Sigma(n_i/N)^2$, where n_i is the number of individuals of taxon i, and N is the total number of individuals in the sample, represents the probability that two individuals selected at random from the sample belong to the same species. Since D represents the homogeneity of the sample, the most common way of converting this homogeneity into diversity is $D_{Simpson} = 1/D$ (Maurer and McGill, 2011). The highest values of the Simpson diversity index ($1/D$) indicate the highest diversity.

To obtain the Simpson evenness index, species richness (S = count of species regardless of their relative abundance) was removed from the Simpson diversity index ($E_{Simpson} = D_{Simpson}/S$) following Maurer and McGill (2011). Results range from 0 (maximally uneven) to 1 (perfectly even). Both indices ($1/D$ and $1/D/S$) were obtained using the PAST 4.0 software (Hammer et al., 2001).

4. Results

4.1. Small-mammal record

The small-mammal assemblage of the La Güelga D-interior zone yielded a minimum (MNI) of 2227 individuals belonging to 20 taxa (Table 1; Fig. 3; Appendix 1) were identified. Arvicolines are dominant (Fig. 3a–i): genera *Arvicola* (*A. amphibius* and *A. sapidus*: 29.7%) and *Microtus* (*M. agrestis*, *M. lusitanicus* and *M. arvalis*: 29.4%) are the best represented, followed by *Pliomys coronensis* (12.2%), *Chionomys nivalis* (0.4%) and *Alexandromys oeconomus* (0.3%). Murids include only *Apodemus sylvaticus* (Fig. 3j) and glirids are represented by a single specimen of *Eliomys quercinus*. Soricids comprise 7 taxa belonging to genera *Neomys* (*N. anomalus, N. fodiens fodiens* and *N. fodiens niethammeri*, Fig. 3k–m"), *Sorex* (*S.* ex gr. *coronatus-araneus* and *S. minutus*, Fig. 3n–o"), and *Crocidura* (*C. russula* and *C. gueldenstaedtii*, Fig. 3p–q"). Talpids are the second family in relative abundance (15.3%), represented by genera *Galemys* (*G. pyrenaicus*, Fig. 3r–r') and *Talpa* (*T. occidentalis* and *T.* ex gr. *europaea-aquitania*, Fig. 3s–t').

4.2. Predator identification

A sample of 2136 arvicoline lower first molars from levels 9–1, which represents 69% of the arvicoline NISP*i* of these levels, was analyzed (Table 2; Appendix 5, Table S1). The percentage of teeth with signs of digestion ranges from 4.2% in level 8 to 19.8% in level 9, indicating that the accumulation of small-mammal remains was caused by the action of predators.

4.3. Paleoenvironment

The relative abundances of the species identified in La Güelga (Table 1, Fig. 8) represent, for most of the stratigraphic sequence, a landscape dominated by open and humid grasslands (OH: 35.3–56.3%) with poor forest development (OW: 17.9–33.1; Wo: 0–4.3%), abundant rocky areas (Ro: 4.2–18.4%), and continuous-flow water bodies (Wa: 6.9–16.2%) which vary in depth and slope (Table 3, Fig. 9B).

4.4. Paleoclimate

The temperatures estimated by means of the Bioclimatic Model (Table 4; Fig. 9C; Appendix 5, Table S2) are, overall, colder than the present-day data, except for the mean temperatures of the warmest month for Levels 9–7 and 5, which are slightly warmer. The greatest differences are observed in the mean temperatures of coldest month (MTC), which are between 4.8 °C (Level 7) and 8.3 °C (Levels 6 and 4) lower than the present-day MTC, but also the mean annual temperatures (MAT) are between 2 °C (Level 7) and 4.8 °C (Levels 6 and 4) colder than the present-day MAT.

4.5. Paleodiversity

Species richness decreases from Level 9 (12 taxa) to Level 7 (10 taxa), increasing again at Levels 6, 5 and 4, with 17, 16 and 18 taxa respectively (Table 1; Fig. 8; Appendix 6). Due to this rise in the species richness, diversity values, measured through Simpson diversity (1/D) index (Fig. 9; Appendix 6), also increase from bottom (Level 9D: 6.4) to top (Level 3: 10.6) of the sequence, excepting for Level 8 (4.7), which yielded the lowest diversity of the sample. Conversely, evenness, represented by Simpson evenness (1/D/S) index (Fig. 9D; Appendix 6), is higher in Levels 9 and 7 (0.53 and 0.66) than in Levels 8, 6 and 5 (0.43, 0.43 and 0.46).

5. Discussion

5.1. Paleobiogeography and paleoecology

The small-mammal assemblage of the La Güelga D-interior zone is of special interest because of its great abundance and species richness.

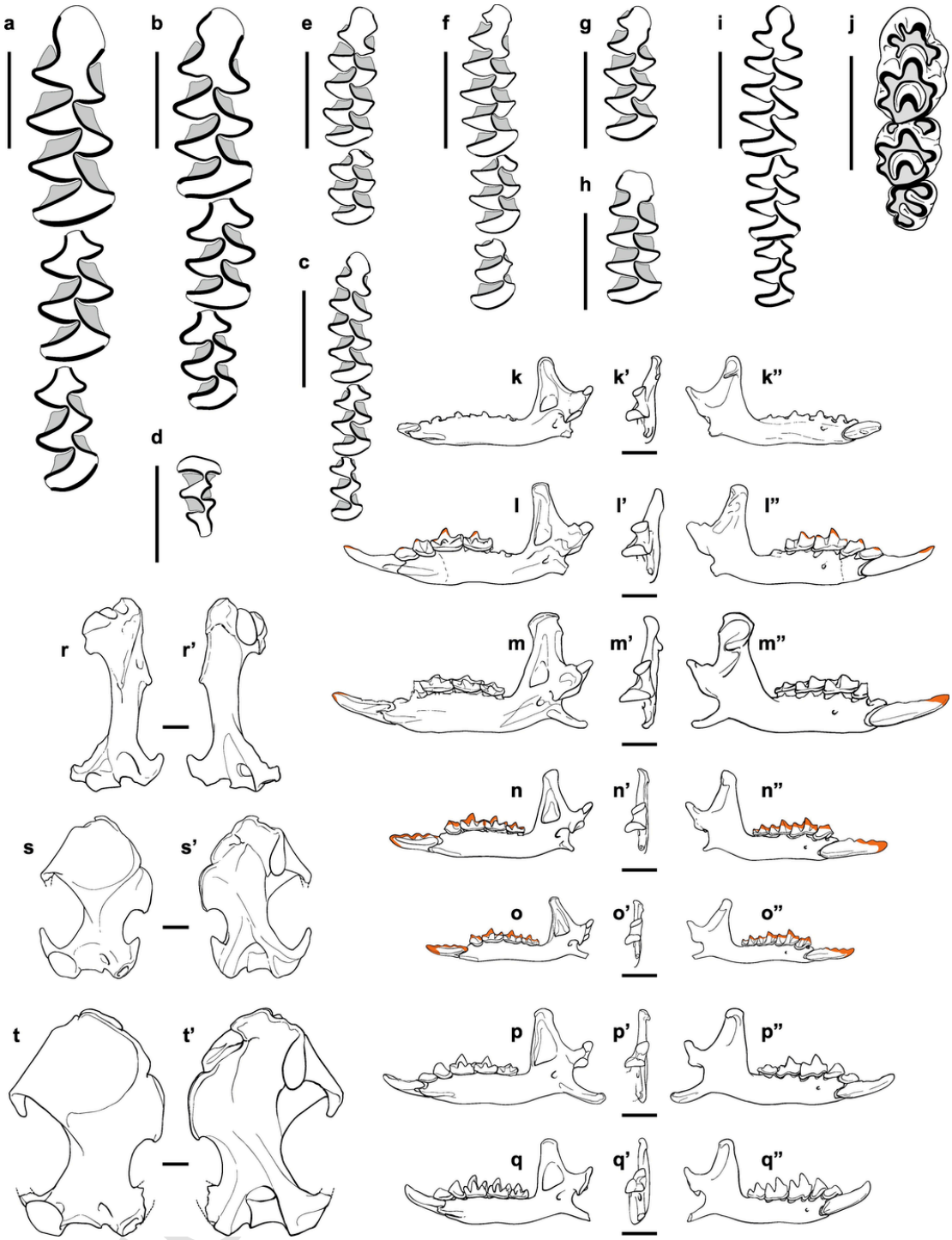


Fig. 3. Selected small mammal specimens from La Güelga. *Arvicola sapidus*: right m1–m3 from level 2 in occlusal (a) view. *Arvicola amphibius*: right m1–m3 from level 2 in occlusal (b) view. *Microtus lusitanicus*: right m1–m3 from level 2 in occlusal (c) view, and left M3 from level 9 in occlusal (d) view. *Microtus arvalis*: right m1–m2 from level 5 in occlusal (e) view. *Microtus agrestis*: right m1–m3 from level 2 in occlusal (f) view. *Alexandromys oeconomus*: right m1 from level 6 in occlusal (g) view. *Chionomys nivalis*: right m1 from level 5 in occlusal (h) view. *Pliomys coronensis*: right m1–m3 from level 2 in occlusal (i) view. *Apodemus sylvaticus*: right M1–M3 from level 1 in occlusal (j) view. *Neomys anomalus*: right mandible from level 5 in lingual (k), posterior (k') and labial (k") views. *Neomys fodiens fodiens*: right mandible from level 6 in lingual (l), posterior (l') and labial (l") views. *Neomys fodiens niethammeri*: right mandible from level 1 in lingual (m), posterior (m') and labial (m") views. *Sorex* ex gr. *coronatus-araneus*: right mandible from level 2 in lingual (n), posterior (n') and labial (n") views. *Sorex minutus*: right mandible from level 2 in lingual (o), posterior (o') and labial (o") views. *Crocidura russula*: right mandible from level 2 in lingual (p), posterior (p') and labial (p") views. *Crocidura gueldenstaedtii*: right mandible from level 1 in lingual (q), posterior (q') and labial (q") views. *Galemys pyrenaicus*: right humerus from level 7 in anterior (r) and posterior (r') views. *Talpa occidentalis*: right humerus from level 6 in anterior (s) and posterior (s') views. *Talpa* ex gr. *europaea-aquitania*: right humerus from level 6 in anterior (t) and posterior (t') views. Scale bars 2 mm.

This represents a mixture of endemic Iberian taxa such as *M. lusitanicus, T. occidentalis* and *G. pyrenaicus* along with other species whose distribution is virtually limited to the Euro-Siberian region, such as *M. agrestis*, *A. amphibius*, *S.* ex gr. *coronatus-araneus*, *S. minutus*, and *N. fodiens*. Other species present at La Güelga which are currently extant in the region, such as *Ch. nivalis*, characteristic of the mountainous regions of central

Table 2
Digestion degree shown by the lower first molars of arvicolines from La Güelga and proportion (%) of digested molars with 95% confidence intervals.

	N	Absent	Light	Moderate	Heavy	Extreme	Total digested	95% CI
Level 1	199	88.44	10.05	1.51			11.56	7.47–16.84
Level 2	217	94.01	5.53	0.46			5.99	3.23–10.03
Level 3	34	94.12	5.88				5.88	0.72–19.68
Level 4	223	87.89	9.42	1.79	0.90		12.11	8.13–17.13
Level 5	431	80.74	15.78	3.48			19.26	15.64–23.30
Level 6	528	88.45	8.33	2.84	0.19	0.19	11.55	8.95–14.59
Level 7	87	87.36	9.20	1.15	2.30		12.65	6.48–21.50
Level 8	144	95.83	4.17				4.17	1.54–8.85
Level 9	273	80.22	12.82	4.76	2.20		19.78	15.22–25.01

Table 3
Weighted (%) habitat-preferences[a] with 95% confidence intervals of the small mammal assemblage from each level of La Güelga.

	MNI	Wa	OH	OD	Ro	C
Level 1	282	10.02	50.18	5.59	10.37	2
95% CI		6.75–14.13	44.35–56.36	3.30–9.11	7.05–14.54	1
Level 2	222	14.30	45.61	3.38	12.61	2
95% CI		10.07–19.74	38.82–52.29	1.57–6.98	8.55–17.71	1
Level 3	34	11.03	35.29	15.44	8.82	2
95% CI		3.30–27.45	19.75–53.51	4.95–31.06	1.86–23.68	1
Level 4	176	10.51	50.99	5.97	14.20	1
95% CI		6.21–15.77	43.21–58.48	2.77–10.26	9.46–20.36	1
Level 5	353	8.85	48.58	2.76	18.41	2
95% CI		6.04–12.23	43.12–53.79	1.37–5.15	14.51–22.86	1
Level 6	583	8.02	50.64	1.80	16.12	2
95% CI		5.98–10.58	46.46–54.73	0.83–3.13	13.23–19.36	1
Level 7	68	16.18	45.96	2.21	11.76	2
95% CI		8.36–27.10	33.45–58.12	0.36–10.22	5.22–21.87	1
Level 8	175	14.29	56.29	0.43	7.43	2
95% CI		9.46–20.36	48.88–64.03	0.01–3.14	4.01–12.37	1
Level 9	334	6.89	51.57	0.00	4.19	3
95% CI		4.42–10.15	45.99–56.97	0.00–1.10	2.31–6.93	2

[a] Wa, water; OH, open humid; OD, open dry; Ro, rocky; OW, open woodland; Wo, woodland.

and southern Europe, and *N. anomalus*, with a similar but more extensive distribution, have also been registered although at lower abundances. The occurrence of *Alexandromys oeconomus*, whose current distribution ranges from central Europe, through North Eurasia, to the northwest of North America, is of great paleoclimatic interest, since it indicates colder climatic affinities than the other taxa. *Pliomys coronensis*, the single extinct species in the La Güelga sequence, provided the largest record of the species (NISP*i*) in the Cantabrian Region.

Several species identified in La Güelga have a limited or poorly known chronologic and geographic distribution during MIS 3 in the Cantabrian Region. Additionally, some of them are almost unknown in this region prior to MIS 3, probably due to a lack of suitable sedimentary record, since Pleistocene fossil deposits older than MIS 3 are very scarce in the Cantabrian Region (Álvarez-Lao and García, 2010). The most probable cause of this lack of sedimentary record is cave sediment removal related to a lowering of the water table and other processes occurred from ca. 125 to 45 ka (MIS 5–3; Ballesteros et al., 2017, 2019).

One of these poorly-represented species is the south-western water vole (*Arvicola sapidus*), whose oldest records in the Cantabrian Region are documented at Valdavara-3, in Galicia, dated to MIS 5 (Vaquero et al., 2018), and at Lezetxiki II, in the Basque Country, dated to MIS 7–6 (García-Ibaibarriaga, 2012; García-Ibaibarriaga et al., 2018). Further occurrences of this species in the Cantabrian Region are reported in MIS 3 at three sites: Cova Eirós, Galicia (dated to 41.3 to 38.4 cal kyr BP, Rey-Rodríguez et al., 2016); Cueva del Conde, Asturias (at 43.9 to 41.4 cal kyr BP, López-García et al., 2011b); and Bolinkoba, Basque Country (García-Ibaibarriaga et al., 2015b). At La Güelga, *A. sapidus* has been found throughout all the sequence, with a continuous presence from 47.2 ± 2.2 cal kyr BP to $< 38.6 \pm 0.5$ cal kyr BP, suggesting that the area probably acted as a refuge for the populations of the region during MIS 3. A larger dispersion of *A. sapidus* in this region is subsequently documented during MIS 2 (e.g. Altuna, 1981, 1986; Cuenca-Bescós et al., 2009; Laplana et al., 2017).

Other species of paleobiogeographic and paleoecological importance is the common vole (*Microtus arvalis*) (e.g. Luzi and López-García, 2019; Baca et al., 2020), whose absence at the base of the sequence (level 9), and progressive abundance increase towards the top of the sequence (level 3), is of special interest, since it is a species of continental affinities (Dienske, 1979; Nores, 1989; Paupério et al., 2012). Based on high genomic divergence, the subspecies *M. agrestis lavernedii*, *M. a. rozianus* and *M. a. agrestis* have been found to be cryptic species (Paupério et al., 2012; Wilson et al., 2017), suggesting that northern and southen lineages separated at around the Last Glacial Maximum (Paupério et al., 2012), matching the intraspecific changes observed in the dental-pattern shape by Luzi and López-García (2019) throughout the Late Pleistocene fossil record. Since *M. lavernedii* lineage split occurred later than the La Güelga sequence formed, we assigned the material from La Güelga to the species *Microtus agrestis*. Some authors, based on the morphological similarity between *Microtus arvalis* and the species of the *Microtus agrestis* group (field voles), unify the remains of these species into *Microtus agrestis-arvalis* (e.g. Sesé, 2005, 2017), which makes it difficult to specify their geographical and chronological distribution.

Except for a few isolated populations in the northern slope of the Cantabrian Range, *M. arvalis* is nowadays mostly distributed in the southern slope of these mountains, while *M. lavernedii*, which is the current representative of the *M. agrestis* group in most of the region, is spread throughout the Cantabrian Region (Nores, 1989). Conversely, *M. arvalis* is the dominant species in MIS 2 records of this region such as Las Caldas (Laplana et al., 2017), El Mirón (Cuenca-Bescós et al., 2009), Kiputz IX (Garcia-Ibaibarriaga et al., 2012), or Praileaitz I (García-Ibaibarriaga et al., 2017). Ancient DNA analyses performed on *M. arvalis* remains of MIS 2–1 age from Northern Spain suggest that the

Table 4
Temperature and precipitation values[a] estimated for the La Güelga Cave sequence by means of the Bioclimatic Model.

	Current values	Level 9	Level 8	Level 7	Level 6	Level 5	Level 4	Level 3	Level 2	Level 1
MTW (°C)	18.40	20.35	19.15	19.39	17.32	18.54	17.32	18.54	17.32	17.67
SE	–	4.75	4.75	4.75	4.75	4.75	4.75	4.75	4.75	4.75
Δ		1.95	0.75	0.99	−1.08	0.14	−1.08	0.14	−1.08	0.14
MAT (°C)	12.20	9.92	9.41	10.20	7.39	8.98	7.39	8.98	7.39	8.15
SE	–	3.63	3.63	3.63	3.63	3.63	3.63	3.63	3.63	3.63
Δ		−2.28	−2.79	−2.00	−4.81	−3.22	−4.81	−3.22	−4.81	−3.22
MTC (°C)	6.7	0.14	0.42	1.89	−1.65	0.31	−1.65	0.31	−1.65	−0.41
SE	–	5.08	5.08	5.08	5.08	5.08	5.08	5.08	5.08	5.08
Δ		−6.56	−6.28	−4.81	−8.35	−6.39	−8.35	−6.39	−8.35	−6.39
MAP (mm)	1321	716	946	979	935	936	935	936	935	959
SE	–	471	471	471	471	471	471	471	471	471
Δ		−605	−375	−342	−386	−385	−386	−385	−386	−385

[a] Mean temperature of the warmest month (°C) (MTW); mean annual temperature (°C) (MAT); mean temperature of the coldest month (°C) (MTC); mean annual precipitation (mm) (MAP); standard error of the predicted values (SE); and difference (Δ) between the obtained values for each level and modern data.

highest population size of this species in the region occurred around the end of the Last Glacial Maximum, and subsequently declined towards the Holocene (Baca et al., 2020).

In the MIS 3 context, the small-mammal assemblages from El Mirón (level 130, >47.8 cal kyr BP, Cuenca-Bescós et al., 2009; Straus and González Morales, 2016) and La Güelga (level 9, 47.2 ± 2.2 cal kyr BP, Menéndez et al., 2018; this work), which, due to their chronology and environmental affinities, can be tentatively assigned to Greenland Interstadials 14 and 12 respectively, stand out by the absence of *M. arvalis* and the high abundance of *M. agrestis*. At other coeval records from the West of the Cantabrian Region, such as Cova Eirós (level 3, 41.3–38.4 cal kyr BP, Rey-Rodríguez et al., 2016), *Microtus arvalis* is the most abundant species, probably because this is the most continental site of those reviewed in this work. At El Conde (e.g. level 20a, dated to 42.9–41.4 cal kyr BP, López-García et al., 2011b), both species are present, *M. agrestis* being more abundant than *M. arvalis*. The same applies to other coeval sites from the eastern side of the Cantabrian Region (e.g. Askondo, >41.4 kyr BP, García-Ibaibarriaga et al., 2015a; Bolinkoba, García-Ibaibarriaga et al., 2015b), whose *M. arvalis/M. agrestis* abundance ratio is similar to that from El Conde. To summarize, the *M. arvalis/M. agrestis* ratio throughout MIS 3 is more similar to that of the present than to that of MIS 2, because during MIS 3 the abundance of *M. arvalis* increases in more continental environments and in the cold stadials while, conversely, *M. agrestis* dominates in areas of Atlantic influence and during the temperate interstadials.

Two species of the genus *Apodemus* have been identified in the MIS 3 record of the region: the long-tailed field mouse (*Ap. sylvaticus*) and the yellow-necked field mouse (*Ap. flavicollis*) (Álvarez-Lao et al., 2020a). All diagnostic upper molar series of *Apodemus* recovered from La Güelga matched the morphology of *Ap. sylvaticus* (Fig. 3j). To assess if this was the only species of the genus at the site, upper and lower second molars were measured and compared to other populations of *Ap. sylvaticus* and *Ap. flavicollis* (Fig. 4; Appendix 2). The frequent presence of a well-developed t9 in the M2, and the more squared morphology of these teeth, grouped the sample from La Güelga with modern populations of *Ap. sylvaticus*. This is relevant from a paleoecological perspective, since *Ap. sylvaticus* has less strict habitat requirements, inhabiting the edges of forests and shrublands, while *Ap. flavicollis* needs denser forests (Wilson et al., 2017).

Among the soricomorphs, species of the genus *Talpa* have not been conclusively identified in most Cantabrian deposits. Specimens of this genus in the fossil record of the region are normally ascribed to two different species depending on their size: the Iberian mole (*Talpa occidentalis*) and the European mole (*Talpa europaea*). Recently, a new species of the genus has been recognized in the Iberian Peninsula and south of France, where the modern populations of *Talpa europaea* have been ascribed to *Talpa aquitania* (Aquitanian mole) (Nicolas et al., 2015; Nicolas et al., 2017; Wilson et al., 2017). The smaller size morphotype recognized in the Cantabrian Region corresponds to *Talpa occidentalis* and has been identified in Cova Eirós (Rey-Rodríguez et al., 2016); the bigger morphotype, which has been ascribed to *Talpa europaea*, has been reported at Cueva del Conde (López-García et al., 2011b), El Castillo (Sesé, 2017), and El Mirón (Cuenca-Bescós et al., 2009). In the central area of the Cantabrian Region, the co-occurrence of both species has been documented at the sites of Cueto de la Mina (Castro-Bernárdez, 1986), El Castillo (Sánchez, 1983) and Torca del León (Álvarez-Lao et al., 2020a), where the bigger morphotype (considering the new species *T. aquitania*) has been ascribed to *Talpa europaea–aquitania*. Abundant and well-preserved mole postcranial material from La Güelga (Fig. 3s–t') allowed a confident identification of both morphotypes, obtaining a normal distribution for the measurements of each species (Fig. 5; Appendix 3), but, due to the lack of complete upper molar-series, a discrimination between *T. europaea* and *T. aquitania* was not possible.

Species of the genus *Neomys* (water shrews) occur at almost all the studied sites from the Cantabrian Region, but normally in low abundances. Most of their MIS 3 occurrences correspond to the Eurasian water shrew (*N. fodiens*) (e.g. Cuenca-Bescós et al., 2009; Sesé, 2017); however, at the nearby site of Torca del León, Asturias, a morphometric analysis allowed the identification of two subspecies: *N. fodiens fodiens* and *N. fodiens niethammeri* (Álvarez-Lao et al., 2020a). The Mediterranean water shrew (*Neomys anomalus*) has been reported from two sites in the Cantabrian Region: El Castillo (Sánchez, 1983) and Cueto de la Mina (Castro-Bernárdez, 1986); nevertheless, based on the published criteria, these ascriptions have been discussed in Álvarez-Lao et al. (2020a), considering that they correspond most likely to *N. fodiens fodiens*.

Based on the coronoid height (Fig. 6; Appendix 4) and the position of the mental foramen (Fig. 3k", l", m"), the abundant and well-preserved *Neomys* sample from La Güelga allowed the identification of *N. anomalus* (Fig. 3k–k") and of both *N. fodiens* subspecies (Fig. 3l–m"). In addition, specimens from levels 5 (dated to 38.6 ± 0.5 cal kyr BP) and 6 (undated, but older than 5) of this site represent the earliest occurrences of *N. anomalus* in the Cantabrian Region.

Regarding *N. fodiens*, the nominal subspecies is represented throughout all the sequence of La Güelga, while *N. f. niethammeri* first occurs at level 4. This suggests an initial presence of *N. f. fodiens* in the area, being later replaced by *N. f. niethammeri*, which is the subspecies that still inhabits the region nowadays. The oldest records of *N. f. niethammeri* correspond to the large specimens of El Castillo, Cantabria (>43 cal kyr BP, Sánchez, 1983; Wood et al., 2018; Álvarez-Lao et al., 2020a) and Torca del León, Asturias (43 ± 0.5 cal kyr BP, Álvarez-Lao et al.,

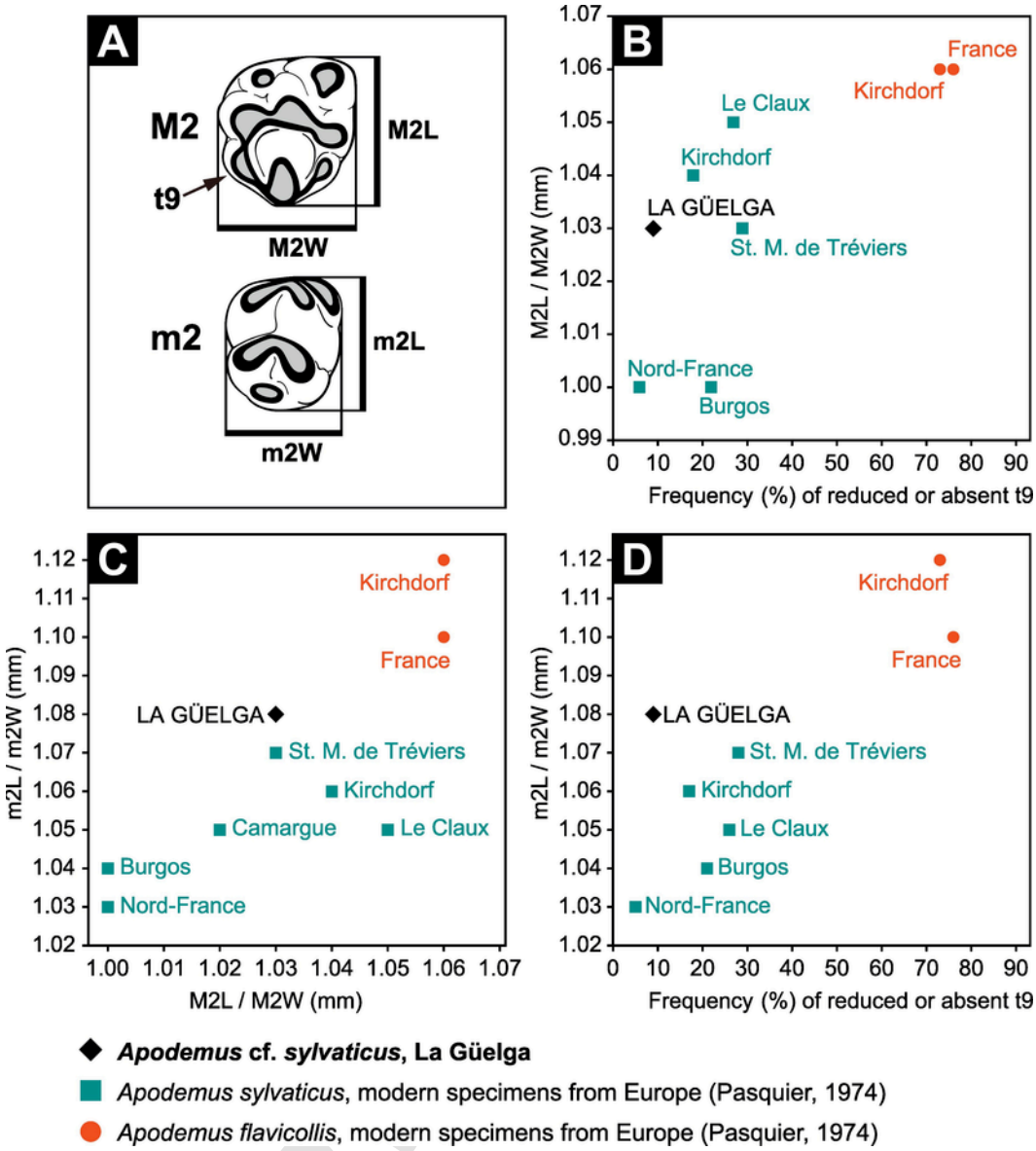


Fig. 4. Characterization of the *Apodemus* sample from La Güelga Cave (Levels 4 to 9; Appendix 2) based on the second molars. Comparison data obtained from Pasquier (1974). (A) Measurement of molars according to Pasquier (1974). (B) Bivariate plot comparing the percentage of M2 with reduced or absent t9 and the length/width ratio of the M2. (C) Bivariate plot comparing the length/width ratio of the m2 and the length/width ratio of the M2. (D) Bivariate plot comparing the percentage of M2 with reduced or absent t9 and the length/width ratio of the m2.

2020a). This suggests the following timing for the colonization of *N. f. niethammeri* in the Cantabrian Region: the subspecies first occurs at the littoral area of Cantabria, later spreading westward and eastward, to the Asturian and Basque regions, respectively. Due to the lack of genetic divergence between both *N. fodiens* subspecies, the taxonomic validity of *N. f. niethammeri* has been recently questioned by Balmori-de la Puente et al. (2019), who suggest that the size variation could represent an adaptation to local environmental conditions. However, according to the indicated arguments, we consider the *N. f. niethammeri* morphotype of significant biogeographic value.

The *Crocidura* genus (white-toothed shrews) is scarcely represented in the MIS 3 record of the Cantabrian Region, where almost all the published specimens are ascribed to the greater white-toothed shrew (*C. russula*) (e.g. Sesé, 2005, 2017), with the exception of Torca del León, Asturias, where remains of the Güeldenstädt's white-toothed shrew (*C. gueldenstaedtii*) have also been identified (Álvarez-Lao et al., 2020a). A total of 26 *Crocidura* mandibles have been recovered at La Güelga, 22 of which show an undulated shape of the m2 cingulum in labial view (Fig. 3p–p''), which allows to ascribe these specimens to the species *C. russula*; the m2 cingula of the remaining 4 mandibles show a convex shape, which is a diagnostic feature of *C. gueldenstaedtii* (Fig. 3q–q'').

5.2. Predator identification

According to Andrews (1990) such percentages of digested molars (4.2–19.8%) are typical of nocturnal raptors (Fig. 7A), belonging to digestion categories 2 and 3 (Fig. 7B). The size of the preys, which ranges from the pygmy shrew (*Sorex minutus*) to the south-western water vole (*Arvicola sapidus*), as well as the high species richness (10–19 species per level), suggest large opportunistic Strigiformes such as the great grey owl (*Strix nebulosa*), which is absent from the fossil record of the region, the European eagle owl (*Bubo bubo*) and the tawny owl (*Strix aluco*), although the sporadic contributions of other predators

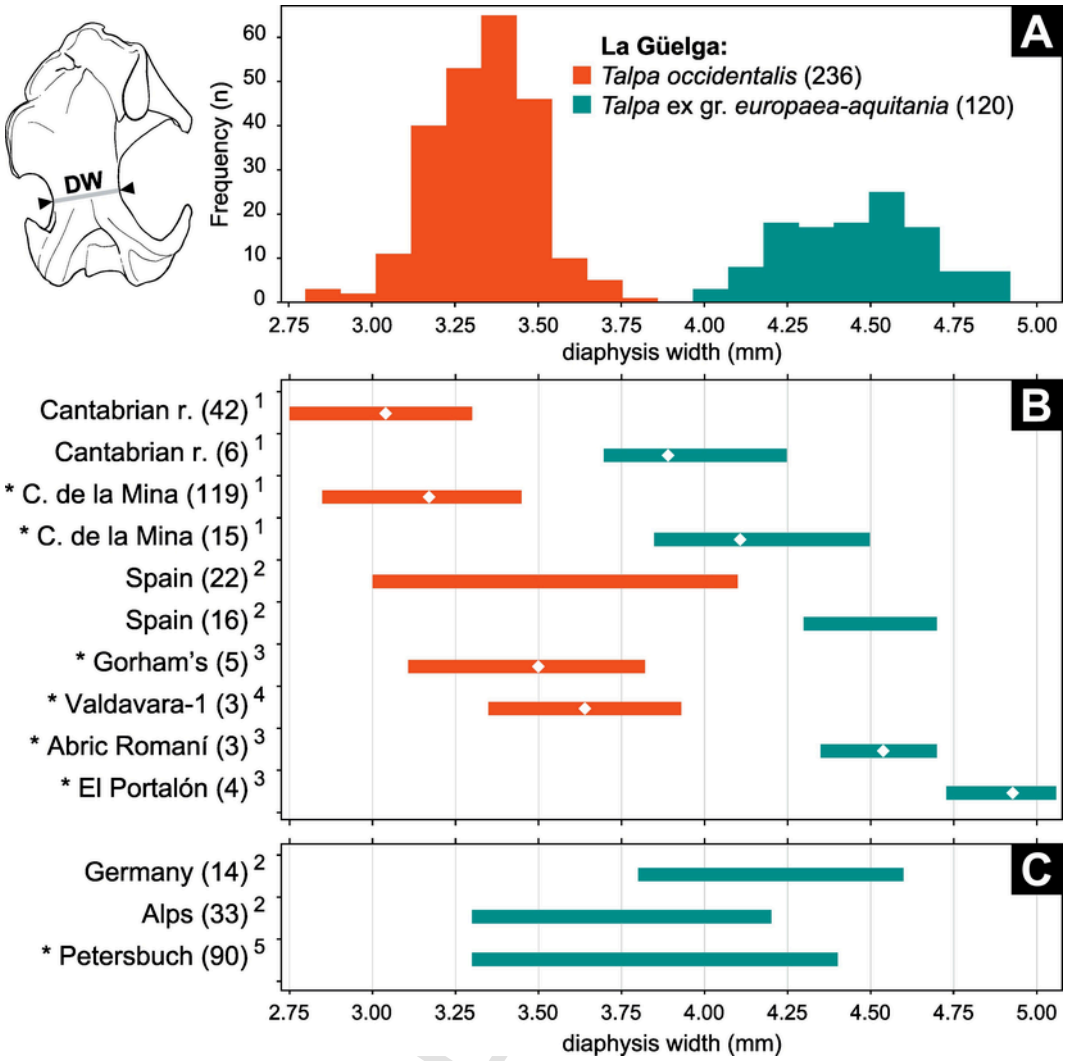


Fig. 5. Characterization of the *Talpa* sample from La Güelga Cave based on the diaphysis width (DW) of the humeri. (A) Frequency diagram of metric variation in the sample from La Güelga (Appendix 3). (B) Range bar chart comparing *T. occidentalis* and *T.* ex gr. *europaea-aquitania* samples from Iberian modern localities and archaeological sites. (C) Range bar chart comparing European modern and fossil samples of *Talpa europaea*. Sources: 1, Castro-Bernárdez (1986); 2, Niethammer (1990); 3, López-García (2008); 4, López-García et al. (2011a); 5, von Koenigswald (1970). (*) Fossil specimens. The numbers in brackets are sample sizes.

from categories 1 and 4 need to be considered. Some of the suggested predators, such as the European eagle owl, usually nest in cliff ledges and crevices (Andrews, 1990), so La Güelga presents an ideal location for this species. These Strigiformes present generalist habits, therefore, they represent quite accurately the environment in which they hunt (Andrews, 1990).

5.3. Paleoenvironment, paleoclimate, and paleodiversity

The results of the Habitat Weighting method show significant differences between levels (Fig. 9B; Table 3). From the bottom to the top of the sequence there is a decreasing trend in the relative abundance of the temperate and forest-affinity species (*Apodemus sylvaticus*, *Sorex minutus, Sorex* ex gr. *coronatus-araneus*, *Microtus agrestis* and *Microtus lusitanicus*), coinciding with the arrival and increase of other small-mammals with colder or more continental requirements (*Microtus arvalis*, *Alexandromys oeconomus*, *Crocidura russula* and *Neomys anomalus*) (Fig. 8). Aquatic affinity species (*Neomys fodiens*, *Arvicola sapidus* and *Galemys pyrenaicus*) suggest the presence of diverse types of river courses, ranging from shallow mountain streams (*G. pyrenaicus*), to quieter and deeper rivers (*A. sapidus*), which is consistent with the orographic characteristics of the landscape, currently furrowed by diverse rivers and streams.

The chronological range represented by La Güelga zone-D (Fig. 1D: 47.2 ± 2.2 to < 38.6 ± 0.5 cal kyr BP) matches that of a process of expansion of aridity indicated by the replacement of arboreal by herbaceous plants in northern latitudes of the Iberian Peninsula (Sepulchre et al., 2007; Sánchez-Goñi et al., 2008), also coincident with a period of reduced stalagmite grow in the area (Stoll et al., 2013) and a general retreating of the glacier fronts at Picos de Europa after 38 ka associated with the development of open, cold and dry conditions in mountain areas (Moreno et al., 2010, 2012). The glacier front at Enol lake was situated ~10 km from La Güelga during the glacial local maximum extension, which would have occurred at ca. 45 ka (Jiménez-Sánchez et al., 2013). Small-mammal samples from level 9, which indicate the most forested landscape of the sequence (OW + Wo = 37.4%), decrease in their proportion of forest species from bottom to top, reaching the minimum of the sequence at level 8 (OW = 21.6%). According to this forest-cover reduction and the chronological dating of level 9 (47.2 ± 2.2 cal kyr BP), level 8 could be coeval with this local maximum extent of the glaciers. The subsequent retreating of these glaciers could be related to the increase in the relative abundance of *Pliomys*

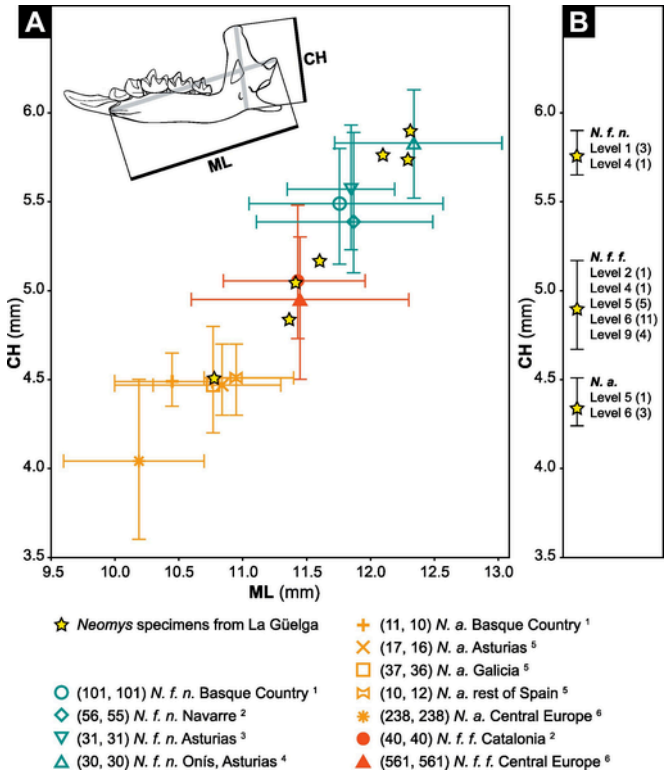


Fig. 6. Characterization of the *Neomys* sample from La Güelga Cave based on the mandible size. (A) Bivariate plot comparing the mandibular length (ML) and coronoid height (CH) of the *Neomys* specimens from La Güelga (Appendix 4) with samples from Spain and Central Europe. Sources: 1, Pemán (1983); 2, López-Fuster et al. (1990); 3, collection of the Department of Organisms and Systems Biology, University of Oviedo (Appendix 4); 4, personal comparative collection A.A.-V. (Appendix 4); 5, Nores et al. (1982); 6, Ruprecht (1971). (B) Range bar chart of coronoid height of all *Neomys* mandibles from La Güelga, including specimens whose mandibular length could not be measured (Appendix 4) grouped by species.

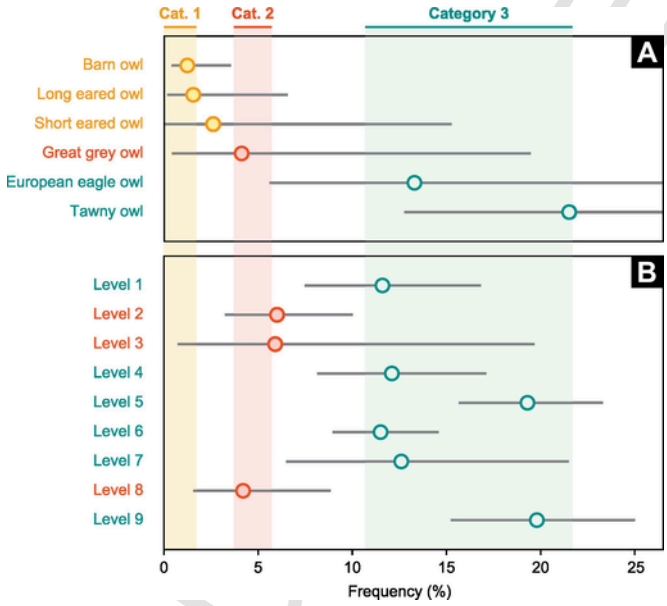


Fig. 7. Characterization of the digestion categories observed in the arvicoline molars of each level of the La Güelga sequence. (A) Proportion (%) of digested molars obtained from Strigiformes regurgitation pellets ordered by species. Predator data and digestion categories obtained from Andrews (1990), Fernández-Jalvo et al. (2016) and Royer et al. (2019). (B) Proportion (%) of digested molars observed in each level of the La Güelga sequence (Appendix 5, Table S1).

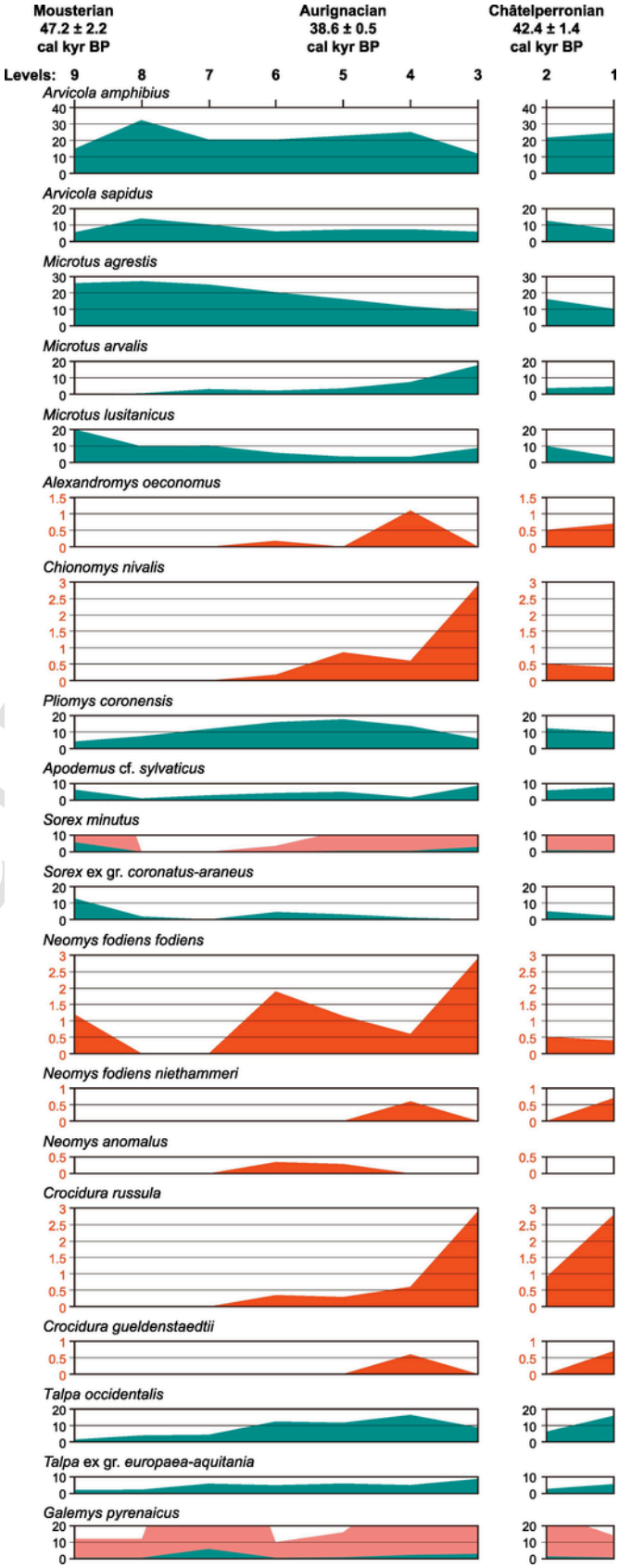


Fig. 8. Relative abundance (%MNI, minimum number of individuals) variations of each small mammal species (Appendix 1) throughout the La Güelga sequence. Red and light-red polygons are on a different scale than blue polygons. (For interpretation of the refer-

ences to colour in this figure legend, the reader is referred to the web version of this article.)

coronensis, as well as to the arrival of *Chionomys nivalis* (Fig. 8), two species typical of karstic areas from the Pleistocene of the Cantabrian Region (e.g. Cuenca-Bescós et al., 2009, 2010; Uzquiano et al., 2012; Álvarez-Lao et al., 2020b; Ballesteros et al., 2020), whose rising presence suggests the developing of extensive rocky areas in the vicinity of the cave.

The inferred climatic variations among levels are consistent with the evolution of the landscape (Fig. 9B): in those levels (8, 6 and 4) in which a decrease in temperatures with respect to their underlying levels (9, 7 and 5 respectively) is observed, the small-mammals assemblage also infers a more open landscape. The cooling events of levels 8 and 6–4 can be perceived also by a shift in the evenness of the small-mammal sample (Fig. 9D), which is also accompanied by a decrease in diversity in the case of level 8 (Fig. 9D). Conversely, diversity rises in Level 7 and continues to increase slightly towards the top of the sequence (Fig. 9D). Like diversity, species richness reaches its maximum at the top of the sequence, but evenness is greater in Levels 9 and 7, showing very low values at levels 8 and 6. According to previous works (e.g. Blois et al., 2010; López-García et al., 2013), high evenness could be related to greater environmental stability, which is consistent with the data from level 9, which would have been formed during Dansgaard-Oeschger event 12 (DO-12), at the beginning of which one of the largest increases in the Atlantic forest of MIS 3 is detected in the marine pollen records (Fig. 1B, Sánchez-Goñi et al., 2008).

The Level 7 sample is mainly composed of open-landscape species but, unlike Level 8, it presents high diversity and evenness, and also warmer estimated temperatures than those inferred for the other levels. This suggests that this level would have been formed during an interstadial, tentatively DO-11 or DO-10. The high diversity and the low evenness observed in levels 6 and 5 could be related to increasing species richness due to the occurrence of new taxa (*M. arvalis*, *Al. oeconomus*, *N. anomalus*, *Ch. nivalis* and *C. russula*), although in very low relative abundances, along with other species already present in levels 9, 8 and 7. In level 6, where the lowest mean temperatures were estimated, the increasing diversity could be related to the fact that this level was deposited during a long period, making it an average of different climatic oscillations including cold stadials. Although radiocarbon dating places level 5 within the H4 event (Fig. 1), all indicators show a slight climatic and environmental improvement with respect to level 6. Naughton et al. (2009) identify two differentiated stages within this Heinrich stadial: a cold and wet phase followed by a slightly warmer and more arid one, so the variation detected along both levels could be the reflection of these stages or, albeit less likely, the reflection of interstadial 8 in the sequence, since after this slight warming event, level 4 reflects a new cooling event (stadial 8 or later).

The features of slope deposits (Kehl et al., 2018) and the radiocarbon dating of level 2 (42.4 ± 1.4 cal kyr BP), which is older than level 5 (38.6 ± 0.5 cal kyr BP), indicate that the paleontological content of this level is probably reworked, and thus the paleoenvironmental analysis of levels 2 and 1 (Fig. 9) is given only for comparative and informative purposes.

Due to taphonomic issues, some of the best-dated small-mammal records from the MIS 3 of the Cantabrian Region, such as El Esquilleu, did not provide a small-mammal sample abundant enough to perform reliable paleoenvironmental interpretations (Sesé, 2005; Uzquiano et al., 2012). On the other hand, sites such as El Castillo (Sánchez, 1983; Sesé, 2017) require, in our opinion, a greater effort in the taxonomic discrimination between *Microtus agrestis* (of Atlantic affinity) and *Microtus arvalis* (of continental affinity). Regarding those sites where taxonomic criteria similar to ours are used, such as El Conde (López-García et al., 2011b) and El Mirón (Cuenca-Bescós et al., 2008, 2009), the first

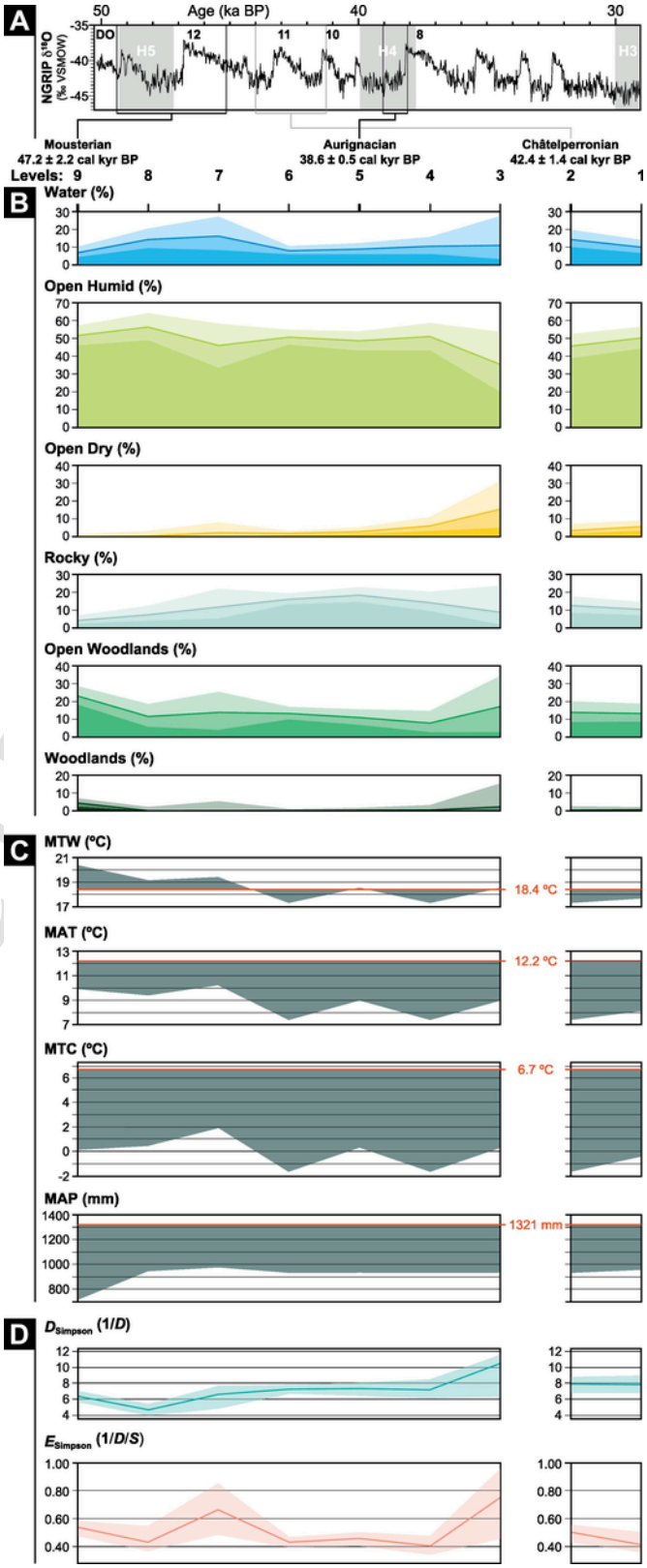


Fig. 9. Paleoenvironmental reconstruction of the La Güelga sequence compared with the NGRIP ∂18O curve. (A) NGRIP ∂18O (Andersen et al., 2004), DO: Dansgaard-Oeschger events; H: Heinrich stadial. Nomenclature suggested by Rasmussen et al. (2014). (B) Type of landscape inferred through the Habitat Weighting method for the surroundings of La Güelga at each level. Dark lines represent the habitat proportion and light-colored areas correspond to the maximum and minimum values of the 95% Confidence Intervals. (C)

Bioclimatic Model estimations: mean temperature of the warmest month (MTW), mean annual temperature (MAT), mean temperature of the coldest month (MTC), mean annual precipitation (MAP). Grey polygons: difference between present-day values (red numbers) and Bioclimatic Model estimations for La Güelga. (D) Simpson diversity index (1/*D*) and Simpson evenness index (1/*D*/*S*) (Appendix 6). Light colored areas correspond to 95% Confidence Intervals. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

yielded a much smaller sample than El Castillo or La Güelga, which entails a lower resolution. With regard to El Mirón, it only presents one level coeval with La Güelga, whose dates are outside the calibration range, but whose taxonomic content is coherent with the contemporary levels (9–8) of La Güelga. In the Sopeña rockshelter, a preliminary faunal list and a taphonomic study (Pinto-Llona et al., 2012) show an evolution of the relative-abundance of the different groups (voles, shrews and mice) through the sequence which is consistent with the data from La Güelga. At the eastern end of the Cantabrian Region, the small-mammal samples collected at sites such as Amalda (Pemán, 1990), Labeko Koba (Pemán, 2000) or Askondo (García-Ibaibarriaga et al., 2015a) provided a low number of specimens for the MIS 3 period, lacking, thus, the resolution from La Güelga.

Although the small-mammal record from MIS 3 from the Cantabrian Region is fragmentary and unequal, it can be seen that, in general, all the deposits mentioned above suggest very similar climatic and environmental conditions to those obtained at La Güelga: colder temperatures than at present, in a patchy landscape with low forest-development and open-grasslands predomination.

6. Conclusions

The small-mammal assemblage from La Güelga was mainly accumulated by the predation of nocturnal birds of prey and provided a minimum of 2227 individuals ascribed to 20 different taxa. The earliest record of *N. anomalus* for the Cantabrian Region is here reported, but also a timing for the replacement of the *N. f. fodiens* by the *N. f. niethammeri* morphotype is suggested.

The Habitat Weighting method allowed the reconstruction of a mosaic landscape in which humid grasslands with sparse forest patches predominated during the lower part of the sequence (corresponding to the last Neanderthal occupations), while rocky areas and dry grasslands increased towards the upper levels (concurrent with the first evidences of modern human cultures). Mean temperature values inferred by the Bioclimatic Model throughout the sequence, as well as the diversity and evenness indexes, suggest an overall cooler and dryer climate than the current one. The relatively mild climatic conditions of level 9, which probably took place during DO-12, ended in a cold event tentatively related to the local maximum glacier extension (~45 ka). At the arrival of AMH another environmental cooling is recorded in an episode including Heinrich stadial 4 (H4), inferred by the appearance at level 6 of cold adapted taxa such as *Alexandromys oeconomus*, and the increase in the relative abundance of continental-affinity species such as *Microtus arvalis*. The landscape and climate reconstructions are consistent with data reported from coeval deposits from the Cantabrian Region. The alternating events of cool-wet and arid environments documented by the La Güelga sequence, which are coeval with other local and global climatic events, should be considered when discussing the context in which the Middle to Upper Paleolithic transition occurred.

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Uncited references

Bronk Ramsey, 2017
Nicolas et al., 2015

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.

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