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Palaeobiological study of the Holocene micromammal assemblage Cueva del Hueso (Castrillón, Asturias, NW Spain)

Estudio paleobiológico de la asociación de micromamíferos del Holoceno de Cueva del Hueso (Castrillón, Asturias, NO España)

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Abstract: Cueva del Hueso is located in Castrillón, Asturias. In this work, we carried out a taxonomic, palaeoecological and biochronological study of the micromammals that inhabited the cave environment during the genesis of its most recent level, Level 0. The recovered assemblage presents considerable diversity, yielding a minimum of 286 individuals belonging to 16 taxa. This species association indicates that the landscape would be dominated by open areas and forested patches, with cooler climatic conditions than the current. The presence of *Rattus* sp. and *Mus musculus*, along with the climatic inferences, have allowed estimating a relative chronology for Level 0 between 450 AD and 1850 AD.

Resumen: Cueva del Hueso se encuentra en Castrillón, Asturias. En este trabajo se realiza un estudio taxonómico, paleoecológico y biocronológico de micromamíferos que habitaron el entorno de la cueva durante la génesis de su nivel más reciente, el Nivel 0. El conjunto recuperado presenta una considerable diversidad, habiéndose identificado un número mínimo de 286 individuos que conforman un total de 16 taxones. Esta asociación de especies indica que el paisaje estaría dominado por áreas abiertas y parches boscosos, con unas condiciones climáticas más frías que las actuales. La presencia de *Rattus* sp. y *Mus musculus* junto a las inferencias climáticas, han permitido estimar una cronología relativa el Nivel 0 entre 450 AD y 1850 AD.

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INTRODUCTION

Micromammals form a group that includes four orders (Rodentia, Lagomorpha, Eulipotyphla, and Chiroptera), whose common feature is not only their small size but also their phylogeny. Its utility in palaeoecology is linked to the preference of each taxon for a specific type of habitat, sometimes even being restricted to one of them (López-García, 2008). Besides, they are highly sensitive to environmental changes (Cuenca-Bescós *et al*., 2009). They are also useful in biostratigraphy because of their quick evolution and high reproduction rate (Herráez & Sesé, 1993). These features, together with the large number of remains preserved in palaeontological sites compared to macromammals, make it possible to conduct highly accurate studies about the chronology and climate of specific levels in Quaternary fossil sites. Results can be compared with other palaeoclimatic proxies, such as the ice- and marine cores, or even absolute dating in the specimens with higher relevance. This allows for a better understanding of the environment they lived in, as well as obtaining a more accurate time frame for the micromammal association. This paper provides a study of the remains of micromammals present in Level 0 of Cueva del Hueso, focusing on the following main aims: (1) to carry out an anatomical and taxonomical study of the micromammal fauna recovered at this deposit, (2) according to the data obtained from the taxonomical study, to perform a palaeoenvironmental study that sheds light both on the climate and landscape in the surroundings of the cave, when it was inhabited by the identified species, (3) to conduct a study on the palaeobiogeography of each species separately, as well as the association as a whole, to estimate a chronological frame from the association of micromammals so that the environmental interpretation made can be set.

GEOLOGICAL SETTING

The archaeopalaeontological site

Cueva del Hueso, also known as Cueva de la Peña de Tante, is in San Cipriano de Pillarno (Castrillón, Asturias, NW Spain), at about 120 m asl (Fig. 1). The entrance of the cave is located on a promontory formed by Namurian limestones of the Barcaliente Formation (Merino-Tomé *et al*., 2021).

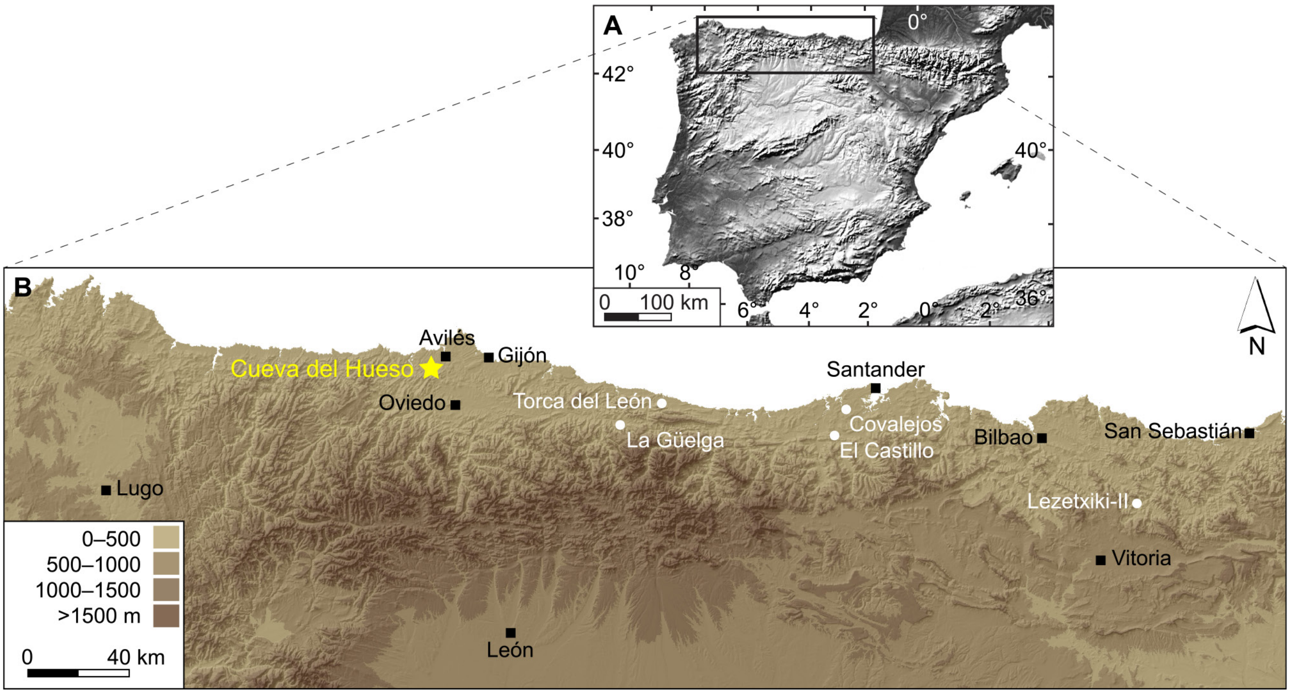

Figure 1. Geographic situation of Cueva del Hueso in the Cantabrian Region. Other sites mentioned in this work (white dots).

The cave (Fig. 2) is about 21 m long. It presents two different sectors (Fig. 2A): the Corridor (Fig. 2C), located near the entrance and formed by a straight gallery about 15 m long, developed mainly in a NW–SE orientation; and the Camarín (Fig. 2D), a chamber of 4 m long and 3 m wide, located at the bottom end of the cave. Excavations were conducted in both areas during April and May 2008 by a team of archaeologists and palaeontologists directed by Dr Gema Adán. These works provided the stratigraphic data of both sectors, published by Álvarez-Lao *et al*. (2008). Thus, according to these authors, a minimum of 3 levels, which were altered by pillages in some areas of the cave, were identified in the Corridor. From bottom to the top, these levels are:

Level 2 is the deepest the excavation reached, and it is apparently unaltered. This level is formed by orange to brown plastic clays. It has provided abundant remains of macromammals, which were assigned to 6 species: *Vulpes vulpes*, *Meles meles*, *Cervus elaphus*, *Capreolus capreolus*, *Capra pyrenaica* and *Equus caballus* (Álvarez-Lao *et al*., 2008). Along with these remains, evidence of human activity assigned to the early Late Palaeolithic has been found, consistent with the date of 34.8–33.9 cal ky BP for this level (Álvarez-Lao *et al*., 2008).

Level 1 is recognised stratigraphically above Level 2, with an irregular base and variable thickness (reaching 1.2 m). The alteration of Level 2 formed this level, so both present the same orange to brown plastic clays. It has a heterogeneous texture with abundant boulders. There is a noticeable mix of materials of different ages (some are modern), showing that this level belongs to the filling of materials caused by pillages. A rhinoceros molar was obtained among the recovered remains at this level, belonging to the *Stephanorhinus hemitoechus* species. This molar has been radiocarbon dated to >42,650 BP, evidencing the existence of older materials below Level 2, which were also altered during pillages (Álvarez-Lao *et al*., 2008).

Level 0 has been found in the cave areas where there has been no pillaging (therefore, the original stratigraphy is preserved); stratigraphically above Level 2, it is formed by a clay and silt brown to grey sediment, lightly compacted. Although this level lacks absolute dating, it is the most recent of the cave according to stratigraphy. The small mammal remains studied in this paper were recovered from this level.

Concerning the Camarín sector, five levels have been identified. From the bottom, Level 3, formed by brown plastic clays, stands out among them due to its thickness and richness in faunal remains. In this level, remains of macromammals belonging to six different taxa have been recovered: *Vulpes vulpes*, *Canis lupus*, *Cervus elaphus*, *Capreolus capreolus*, Bovinae indet. and *Equus caballus* (Álvarez-Lao *et al*., 2008). This

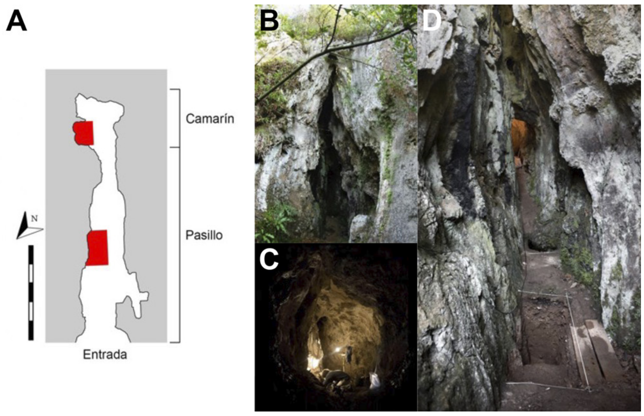

Figure 2. Cueva del Hueso. **A,** Top view of the cave system (excavation areas highlighted in red); **B,** entrance of the cavity; **C,** Camarín sector; **D,** Corridor sector; scale bar = 5 m.

level has been dated to 34.7–34.9 cal ky BP, making it almost contemporary to the Level 2 of the Corridor sector (Álvarez-Lao *et al*., 2008).

MATERIAL AND METHODS

Processing and taxonomic identification

The sediment samples processed for this work come from Level 0 of the main corridor in the cave, which is the most recent level found. For this work, we have studied 6,240 elements, comprising both postcranial material and, mostly, dental elements.

During the campaigns carried out in 2008, sediment samples were collected and stored in plastic bags. Part of the material was sifted with water by the excavation team back then. To prepare the material for this study, the remaining sediment was processed by water screening with superimposed sieves with mesh sizes of 2 mm and 0.5 mm. Due to the difficulty of removing some clay particles, a second wash of the material was carried out after drying it out. The skeletal remains of interest were collected using a binocular microscope Nikon SMZ 800 with a 10x magnification. The teeth and mandibles of the rodents were fixed with their occlusal side up so that the tooth morphology could be studied using a binocular microscope.

Measuring and counting the anatomical features with diagnostic value was done using the IC Measure software on the image recorded by a Nikon SMZ 800N binocular microscope equipped with a 5 MP digital camera. The most representative specimens for each species were photographed by a camera Olympus Air A01 and a Nikon Plan Apo 0.5x WD objective mounted on the same microscope.

For taxonomic identification of the subfamily Arvicolinae, the first lower molars (M_1) were mainly used. The third and second upper molars (M^3 y M^2) were used as well (Fig. 3) for those species of the subgenus *Terricola* (little voles of the *Microtus* genus, characterised by their subterraneous way of life) and for the *Microtus* ex gr. *agrestis-arvalis* group, respectively. Material belonging to the subfamily Murinae was identified by studying the first and second upper molars (M^1 and M^2).

The diagnostic anatomical elements employed for the identification of the Eulipotyphla order were: mandibles for the subfamily Soricinae; the lower second molars (M_2) and the upper fourth premolars (P^4) for the subfamily Crocidurinae Wagler, 1832, and the humeri for the subfamily Talpinae.

For the general identifications of rodents and eulipotyphlans, the works of Román (2019) and Chaline (1974) were followed, respectively. Morphometric detailed studies were based on Pasquier (1974), Nores (1988) and Knitlová and Horácek (2017) for the mice belonging to the genus *Apodemus*; Nores (1989) for the genus *Crocidura*; Barti (2006) and Pemán (1983) for the genus *Neomys*; and Niethammer (1990) for the genus *Talpa*. Regarding the taxonomical classification, we followed the systematics proposed by Wilson *et al*. (2016, 2017) and Chevret *et al*. (2020) for voles, rats and mice, and Wilson and Mittermeier (2018) for shrews and moles.

Remains were quantified using the Minimum Number of Individuals (**MNI**) and the Number of Identified Specimens (**NISP**) numbers. NISP accounts for the number of taxonomically-identified remains, in which every tooth and mandible are counted individually. The MNI is calculated using the abundance of the most frequent diagnostic element, considering its laterality. The relative abundance of each taxon is based on the MNI.

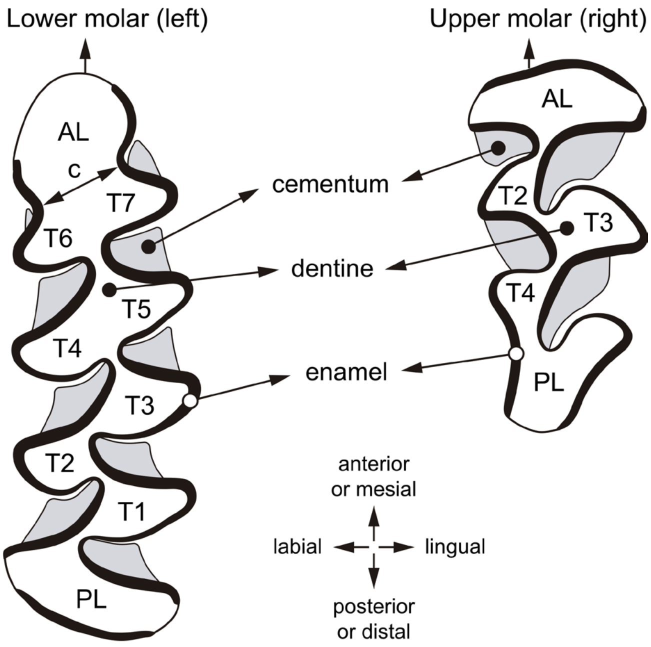

Figure 3. Nomenclature utilised in the description of the occlusal surface of the arvicoline molars. **AL,** Anterior loop; **PL,** posterior loop; **T,** triangle; **c,** constriction between triangles 6–7 and the anterior loop.

Environmental and climatic reconstructions

An estimation of the type of habitats present in the surroundings of the cave was inferred using the Habitat Weighing Method (Evans *et al*., 1981; Andrews, 2006; Cuenca-Bescós *et al*., 2009; López-García *et al*., 2014). This method is based on the relative abundances of the different species and their preference for different types of habitats, which were divided into the following (López-García *et al*., 2014): Open Dry (**OD**), referring to grasslands under seasonal dryness; Open Humid (**OH**), humid meadows with a dense herbaceous cover; Open Woodland (**OW**), arboreal vegetation patches alternating with bushy or herbaceous sectors irregularly distributed; Woodland (**Wo**), referring to mature forests; Rocky (**Ro**), areas with a suitable rocky or stony substratum; and Water (**Wa**), areas nearby watercourses or freshwater bodies. The preferences of each species for one or more types of habitats are taken from López García (2008), Cuenca-Bescós *et al*. (2009), López-García *et al*. (2010, 2014), Álvarez-Lao *et al*. (2020) and Álvarez-Vena *et al*. (2021).

In order to estimate the climatic conditions of the site during the formation of Level 0, the Mutual Ecogeographic Range (Blain *et al*., 2009, 2016) was utilised. This method is based on the mutual climatic requirements of a given species association (Martínez-Solano & Sanchiz, 2005; Agustí *et al*., 2009). A mutual distribution area is obtained by overlapping the current geographic distribution of each species (in UTM coordinates of 10 × 10 km; Palomo *et al*., 2007). After that, the Iberian Climatic Atlas was used through the online Geographic Information System (**GIS**) application (agroclimap.aemet.es) to gather the following present-day climatic parameters for the joint distribution area: Mean Annual Temperature (**MAT**), Mean Temperature of the Warmest month (**MTW**), Mean Temperature of the Coldest month (**MTC**) and Mean Annual Precipitation (**MAP**). Therefore, quantitative climatic data is obtained and extrapolated to Cueva del Hueso during the time this zone was inhabited by species association of Level 0. In the case of open nomenclature, the distribution of all the species belonging to the group has been utilised for the Mutual Ecogeographic Range. The UTM grids were obtained from Martínez-Solano and Sanchiz (2005). Since the assemblage contains Iberian endemisms, data on the current distribution of each species comes from the Atlas and red list of the terrestrial mammals of Spain (Palomo *et al*., 2007).

Palaeobiogeography

A bibliographic review was conducted on the distribution of some of the most relevant species from a paleobiogeographic standpoint since some of the studied taxa have undergone relevant range shifts throughout the Late Pleistocene and the Holocene. This means that the presence or absence of this species may help us precisely approximate the chronology of the site.

SYSTEMATIC PALAEONTOLOGY

The material studied herein is housed in the Department of Geology of the Universidad de Oviedo. It has been classified as the following taxa:

Order RODENTIA Bowdich, 1821
Family CRICETIDAE Fischer, 1817
Subfamily ARVICOLINAE Gray, 1821

Genus *Arvicola* Lacépède, 1799

Type-species. *Mus amphibius* Linnaeus, 1758. Nowadays, it can be found from the North of the Iberian Peninsula to Ukraine, missing in France's western and southwestern regions. Its northern limit is in North Germany, and the southern boundary is in the Alps and the Balkans.

Arvicola sapidus Miller, 1908
Figure 4A

Material. This species appears in the site represented by a single left mandible containing a complete molar series (M_1–M_3) (Fig. 4A).

Remarks. The genus *Arvicola* presents a larger size than the genus *Microtus*. Its M_1 is formed by five triangles, in contrast to the seven triangles in the M_1 of the genus *Microtus* (Fig. 4C, 4D, 4F; Román, 2019). The M_1 of *Ar. sapidus* (Fig. 4A) also presents a narrower neck and a lingual salient in the anterior loop, unlike *Ar. amphibius*, whose M_1 does not present such a pronounced lingual salient angle (Fig. 4B; Román, 2019). The enamel of the lower molar series in *Ar. sapidus* is thicker on the posterior side of the triangles, a primitive character shown in the specimens of Cueva del Hueso. In comparison, *Ar. amphibius* presents a thicker enamel on the anterior side, constituting a derived character (Heinrich, 1978).

Biogeography and ecology. It often inhabits riverbanks with arboreal or scrub-like vegetation and a soft terrain which allows it to dig burrows, although it can occasionally live in other environments such as humid meadows or peat zones (Palomo *et al*., 2007; Wilson *et al*., 2017). Its distribution comprises the Iberian Peninsula, except for some northern and eastern regions (Palomo *et al*., 2007). Its older record in the Cantabrian Region dates to MIS 7, in Lezetxiki-II (Level K), Basque Country (García-Ibaibarriaga *et al*., 2018).

Arvicola amphibius (Linnaeus, 1758)
Figure 4B

Material. This species is represented in the site by one left mandible with an M_2–M_3 and an isolated left M_1 (Fig. 4B).

Remarks. The M_1 of *Ar. amphibius* present a similar aspect to those of *Ar. sapidus*, but with a broader neck at the anterior loop (Fig. 4B; Román, 2019). As an additional criterion, the already mentioned difference in enamel thickness for the lower molar series has been used since the anterior loop morphology is a criterion depending on ontogeny (Román, 2019).

Biogeography and ecology. In populations from Central Europe, this species occupies an ecological niche like that of *Ar. sapidus*. However, in the Iberian Peninsula, it has subterraneous habits, living in burrows excavated in natural meadows in quite a wide range of altitudes, ranging from coastal zones to alpine prairies (Palomo *et al*., 2007; Wilson *et al*., 2017). In the Iberian Peninsula, it can currently be found in a northern stripe to the north of the Pyrenees mountain ranges, the Cantabrian Range or the Ancares Mountain Range, with some geographically isolated populations (Palomo *et al*., 2007; Wilson *et al*., 2017). Its first occurrence in the Cantabrian Region dates from MIS 7, at level K of Lezetxiki-II (García-Ibaibarriaga *et al*., 2018).

Genus *Microtus* Schrank, 1798

Type-species. *Microtus terrestris* Schrank, 1797. Previously *Mus arvalis* Pallas, 1778. It extends from the centre of Russia, through central Europe, to the Atlantic coast of France and the Iberian Peninsula. It is absent from Northern Europe, the Mediterranean Region, and the British Islands.

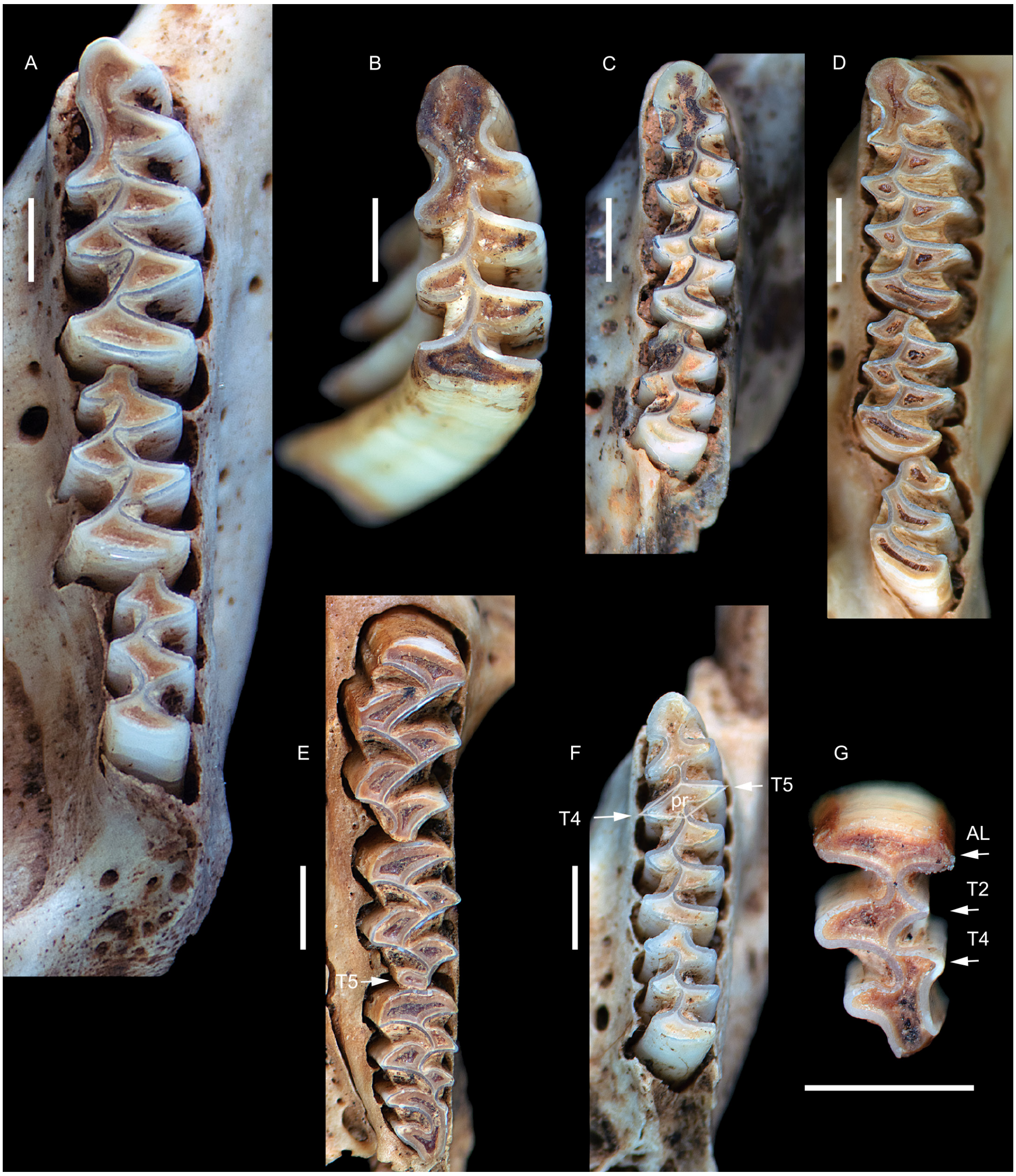

Figure 4. Arvicolines of Cueva del Hueso. **A,** Lower left molar series (M_1–M_3) of *Arvicola sapidus*, in occlusal view; **B,** left M_1 of *Arvicola amphibius*, in occlusal view; **C,** left M_1–M_2 of *Microtus arvalis* in occlusal view; **D,** lower left molar series (M_1–M_3) of *Microtus lavernedii* in occlusal view; **E,** complete upper left molar series (M^1–M^3) of *Microtus lavernedii* in occlusal view; **F,** left M_1–M_2 of *Microtus (Terricola) lusitanicus* in occlusal view; **G,** left M^3 of *Microtus (Terricola) lusitanicus* in occlusal view. **AL,** Anterior loop; **T,** triangles; **pr**, "Pitymyan rhombus"; scale bars = 1 mm.

Microtus arvalis (Pallas, 1778)

Figure 4C

Material. This vole has yielded 6 remains, consisting of a left mandible with M_1–M_2 and 3 isolated molars (2 right M_1 and 1 left M_1).

Remarks. Individuals belonging to the *Microtus* genus present smaller M_1 than the genus *Arvicola*. In the genus *Microtus*, *Mi. arvalis* presents seven alternating triangles, same as *Mi.* ex gr. *agrestis*, but the M1 of *Mi. arvalis* has symmetric labial and lingual triangles (Fig. 4C), while in *Mi. agrestis* (Linnaeus, 1761) these are noticeably asymmetric (Fig. 4D; Nadachowski, 1984; Luzi & López-García, 2019; Román, 2019).

Biogeography and ecology. The common vole inhabits open environments that provide a dense herbaceous or shrubby cover when there is a low population density. However, when population density is larger, it occupies all the environments within its distribution area. Thirty years ago, its presence in the Iberian Peninsula was limited to the northern mountain ranges (Pyrenees, Cantabrian Range, Central System and Iberian System). However, due to a change in land use caused by the development of lucerne crops, this vole has come to colonise the totality of the Northern Plateau (Rey, 1973; Luque-Larena *et al.*, 2013; Jareño *et al.*, 2014). Although *Mi. arvalis* is not found at present in the studied zone, its presence has been registered during the Pleistocene and Holocene in geographic expansions linked to cold episodes, such as MIS 2 or Greenland and Heinrich Stadials (*e.g.*, Cuenca-Bescós *et al.*, 2009; García-Ibaibarriaga *et al.*, 2012, 2017; Laplana *et al.*, 2017; Álvarez-Vena *et al.*, 2021), alternating with regressions linked to warm periods, such as MIS 3 interstadials (Álvarez-Vena *et al.*, 2021), when the populations were restricted to sites with a more continental climate *(e.g.*, López-García *et al.*, 2011; García-Ibaibarriaga *et al.*, 2015a, 2015b; Rey-Rodríguez *et al.*, 2016; Navazo Ruiz *et al.*, 2021). As it is a species of continental affinities (Dienske, 1979; Nores, 1989; Paupério *et al.*, 2012; Álvarez-Vena *et al.*, 2021), its presence in a site with an oceanic climate where it is not found nowadays, suggests that Level 0 was accumulated under cooler conditions than the current. Its oldest record in the Cantabrian Region dates from MIS 7, at level K of Lezetxiki-II (García-Ibaibarriaga *et al.*, 2018).

Microtus lavernedii (Crespon, 1844)

Figure 4D–4E

Material. This field vole is represented by 4 right mandibles with a complete dental series (I_1–M_3); 1 left mandible with a complete dental series; 1 right mandible fragment with a complete dental series; 1 right mandible with I_1–M_1; 3 right mandibles with I_1–M_2; 1 right mandible fragment with I_1–M_2; 1 right mandible with M_1–M_2; 1 left mandible with M_1–M_2; 1 left mandible with I_1–M_2; 2 left mandible fragments with I_1–M_2; 2 right mandible fragments with I_1–M_1; 1 cranial fragment with a complete left molar series (M^1–M^3), 1 cranial fragment with both incisors, right M^2–M^3, and left M^3; 1 cranial fragment with both incisors and left and right M^2–M^3; 1 cranial fragment with right M^2 and left M^2–M^3; 1 cranial fragment with left M^2; and 61 isolated molars (10 right M_1, 5 left M_1, 7 right M^2, 6 left M^2, 17 right M^1 and 16 left M^1).

Remarks. The M_1 of the field voles (*Mi.* ex gr. *agrestis*) shows a noticeable asymmetry between the labial and lingual triangles, the latter of a bigger size (Fig. 4D). Recently, based on highly divergent nucleotide sequences, the subspecies *Mi. agrestis lavernedii* (Crespon, 1844) and *Mi. agrestis rozianus* (Bocage, 1865) have been elevated to the species level (Wilson *et al.*, 2017). The M^2 of the species of this group presents an additional lingual triangle (T5), unlike the other species of the genus found at Cueva del Hueso (Fig. 4E). This additional triangle is also observed in the M^1, but the frequency and development degree of this character vary among the different species of this group (Krapp & Niethammer, 1982; Wilson *et al.*, 2017). The sample of Level 0 of Cueva del Hueso shows a low proportion of M^1 presenting a well-developed T5 (6.1%; Appendix 1, Tab. S1), which, according to Krapp and Niethammer (1982), is within the range of *Mi. lavernedii*.

Biochronology and ecology. This species preferentially inhabits humid meadows with a dense herbaceous cover with no grazing or gathering pressure. However, it can also be observed in more wooded environments (Palomo *et al.*, 2007). Nowadays, regarding the Iberian Peninsula, the species of the group occupy the Eurosiberian Biogeographic Region (Palomo *et al.*, 2007; Wilson *et al.*, 2017). Throughout the Late Pleistocene and the Holocene, its abundance and distribution have been conditioned by the alternations between glacial and interglacial periods: in the warmer moments, a rise in the abundance of this species is recorded, while in the cooler and dryer periods, its abundance is reduced in favour of *Mi. arvalis* (Álvarez-Vena *et al.*, 2021). *Microtus lavernedii* is a recently recognised species that diverged from *Microtus agrestis* in the Late Pleistocene. Therefore, it had not been previously considered in palaeontological sites. For this reason, the species is here reported for the first time in the palaeontological literature.

Subgenus *Terricola* Fatio, 1867

Microtus (Terricola) lusitanicus (Gerbe, 1879)

Figure 4F–4G

Material. The studied remains of this species include 3 right mandibles with a complete dental series (I_1–M_3); 6 left mandibles with a complete dental series; 1 right mandible fragment with a complete dental series; 1 left mandible fragment with a complete dental series; 3 right mandibles with I_1–M_2; 3 left mandible fragments with I_1–M_2; 1 right mandible with I_1–M_1 and M_3; 1 right mandible with I_1–M_1; 1 left mandible with I_1–M_2; 3 right mandible fragments with I_1–M_1; 1 right mandible fragment with I_1–

M_1; 1 left mandible fragment with I_1–M_1; 1 right mandible with M_1–M_2; 1 right mandible fragment with M_1–M_2; 1 left mandible with I_1–M_1; 2 right mandibles with M_1; 40 isolated lower molars (13 right M_1 and 27 left M_1); 1 cranial fragment with a complete right molar series (M^1–M^3) and the left M^1–M^3 alveoli; 1 right maxilla fragment with a complete molar series; 1 cranial fragment with the complete right dental series and the left I^1–M^2; and 45 isolated upper molars (26 right M^3 and 19 left M^3).

Remarks. The first lower molars of the subgenus *Terricola* (voles with subterraneous habits) present an exclusive feature of this group of species: the pitymyan rhombus (Fig. 4F) (originally these species belonged to the *Pitymys* genus (McMurtrie, 1831), which named this feature), resulting of the connection between T4 and T5. Analysing the M^3 of *Terricola*, it can be appreciated that T2 is reduced compared to the imaginary line connecting the anterior loop and T4 (Fig. 4G). This trait is shown in *Mi. (Te.) duodecimcostatus* (de Sélys-Longchamps, 1839) and *Mi. (Te.) lusitanicus* (Román, 2019), so the morphology of the anterior lobe of the first lower molar (Fig. 4F) has been used to determine which one of the two is present at the site. All the *Terricola* M_1 from Level 0 present a high degree of closure in the anterior loop, characteristic of *Mi. (Te.) lusitanicus*, since in *Mi. (Te.) duodecimcostatus* the degree of closure is much lower (Román, 2019).

Biochronology and ecology. It mainly occurs in humid and soft soils with a dense vegetal cover. Crops, forest environments, or riverbanks are also suitable habitats for this species (Palomo *et al*., 2007). Nowadays, Lusitanian pine vole is distributed around the north-western quadrant of the Iberian Peninsula, reaching Navarra or Huesca in its eastern limit and south of Lisbon in its meridional extreme (Palomo *et al*., 2007). Its oldest occurrence in the Cantabrian Region dates to MIS 5, at Level Q of the Covalejos cave (Sesé, 2021).

Family MURIDAE Illiger, 1811
Subfamily MURINAE Illiger, 1811

Genus *Rattus* Fischer, 1803

Type-species. *Rattus rattus* Linnaeus, 1758. It is distributed from all of Europe to Eastern and South-eastern Asia, the islands of Indonesia, the East coast of Australia and New Zealand, the South-eastern and Northern coast of Africa, Mexico, the United States, and most of the coast of South America. However, it is invading new territories due to its affinity to human settlements.

Rattus sp.
Figure 5A

Material. A single M^3 has been recovered from the remains of Level 0.

Remarks. The family Muridae presents rooted brachydont molars with rounded cusps and poorly sharpened crests (bunodont). Rat molars (Fig. 5A) present a significantly larger size than the genera *Mus* and *Apodemus*. Accordingly, the large size of the M3 recovered in Level 0 has been assigned to the genus *Rattus*. However, lacking other dental diagnostic elements, it has not been possible to reach an identification at the species level.

Biochronology and ecology. *Rattus rattus* is a species found in several types of habitats, given a vegetal cover is available, even though it can also live in small urban settlements, being less commensal than *R. norvegicus* (Berkenhout, 1769), which prefers urban and rural environments. However, it is also found in natural habitats (Palomo *et al*., 2007). This genus currently occupies the totality of the Iberian Peninsula, although *R. rattus* does so in a more dispersed way than *R. norvegicus* (Palomo *et al*., 2007). The first record of this genus in the Iberian Peninsula is documented at the beginning of the Roman occupation (*ca*. 2 ky BP), according to Domínguez-García *et al*. (2019).

Genus *Mus* Linnaeus, 1758

Type-species. *Mus musculus* Linnaeus, 1758. This species is widely distributed worldwide, missing in Northern Russia, Africa (except North of the Sahara), North of Canada, and South America (except the coastline). However, in America, Oceania and South Africa, it has been introduced by humans.

Mus musculus Linnaeus, 1758
Figure 5B–5D

Material. It has been found 3 isolated upper molars: 1 left M^1 and 2 right M^2.

Remarks. The mice of the genus *Mus* are characterised by the absence of t7 in the first and second upper molars (Fig. 5B–5D). According to Darviche *et al*. (2006), the morphology of t1 of the M1 (Fig. 5B), elongated in an oblique direction, and the t1 of the M2, elongated towards the labial side (Fig. 5C–5D), allowed us to assign these materials to the species *Mus musculus* (house mouse).

Biochronology and ecology. The house mouse is a commensal species of humans. Wild populations in rocky margins or herbaceous zones are located around farmlands, avoiding forests or dry areas (Palomo *et al*., 2007). This rodent, linked to human-populated areas, is found nowadays in the whole Iberian Peninsula. Domínguez-García *et al*. (2019) discussed the chronology of this species' arrival to the Iberian Peninsula. After a bibliographic review of previous findings, they conclude that this event must have occurred in the second half of the Iron Age (later than 3 ky BP).

Genus *Apodemus* Kaup, 1829

Type-species. *Mus agrarius* Pallas, 1771. Its distribution area comprises Eastern Europe, the Caucasus and Russia to the Baikal Lake, China, the Korean Peninsula and Taiwan.

Apodemus sylvaticus (Linnaeus, 1758)
Figure 5E

Material. This *Apodemus* remains studied in this work consist of 3 right maxilla fragments with a complete molar series (M^1–M^3); 1 left maxilla fragment with a complete molar series; 5 right maxilla fragments with M^1–M^2; 2 right maxilla fragments with M^2–M^3; 3 left maxilla fragments with M^1–M^2; 3 left maxilla fragments with M^2–M^3; 5 left maxilla fragments with M^1; 3 right maxilla fragments with M^1; 1 right maxilla fragment with M^2; and 209 isolated upper molars (68 right M^1, 57 left M^1, 41 right M^2 and 47 left M^2).

Figure 5. Murines, glirids, and eulipotyphlans of Cueva del Hueso. **A,** Right M^3 of *Rattus* sp. in occlusal view; **B,** left M^1 of *Mus musculus* in occlusal view; **C,** right M^2 of *Mus musculus* in occlusal view; **D,** right M^2 of *Mus musculus* in occlusal view; **E,** left M^1–M^2 of *Apodemus sylvaticus* in occlusal view; **F,** left M$_2$ of *Eliomys quercinus* in occlusal view; **G,** left humerus of *Talpa occidentalis* in posterior view; **H,** left maxilla fragment of *Crocidura gueldenstaedtii* with P^3–M^3 series in labial view; left mandible of *C. gueldenstaedtii* in labial (**I**) and posterior (**I'**) views; **J,** left maxilla of *Crocidura russula* with I^1–M^3 series in labial view; left mandible of *C. russula* with I$_1$–M$_3$ series in labial (**K**) and posterior (**K'**) views; left mandible of *Neomys fodiens niethammeri* in labial (**L**) and posterior (**L'**) views; left mandible of *Neomys anomalus* in labial (**M**) and posterior (**M'**) views; left mandible of *Sorex* ex gr. *coronatus-araneus* in labial (**N**) and posterior (**N'**) views; left mandible of *Sorex minutus* with I$_1$–M$_3$ series in labial (**O**) and posterior (**O'**) views. **t,** tubercle, **mf,** mental foramen; scale bars = 2 mm.

Remarks. Following Román (2019), all the upper molars showing the tubercule t7 have been assigned to the genus *Apodemus*. Conversely, those molars which do not display this t7 have been ascribed to the genus *Mus*. In the *Apodemus* genus, there is considerable overlap in the size and morphology of both species currently inhabiting the Iberian Peninsula (*Ap. sylvaticus* and *Ap. flavicollis* (Melchior, 1834)). The discriminant criteria between the two species of the genus are the development of the t9 in the M^2 (Pasquier, 1974; Nores, 1988; Knitlová & Horácek, 2017) and the relation between length and width index for this molar (Pasquier, 1974). The presence of t9 in all the M^2 of this sample (49.5% pronounced; 43.4% reduced; 7.1% not recognisable by dental wear or fracture), as well as the relation between length and width of these molars (1.025), has allowed us to assign the *Apodemus* remains of Level 0 the *Ap. sylvaticus* species (Fig. 6).

Biochronology and ecology. It is found in most of the described habitats in the Peninsula. However, it often inhabits zones with shrubby or arboreal cover, which provides them with better protection against predators such as birds of prey (Palomo *et al*., 2007). Nonetheless, in the case of forested areas, it prefers the forest margins, and its density decreases towards the inner zones, a habitat more suited for *Ap. flavicollis* (Wilson *et al*., 2017). The oldest occurrence of the genus in the Cantabrian Region dates to MIS 7 (García-Ibaibarriaga *et al*., 2018). However, the oldest remains from the region ascribed to *Apodemus sylvaticus* come from Level Q (MIS 5) of Covalejos (Sesé, 2021). In the Upper Layer of Torca del León (MIS 3), Álvarez-Lao *et al*. (2020) reported the cooccurrence of *Ap. sylvaticus* and *Ap. flavicollis*.

Family GLIRIDAE Muirhead, 1819
Subfamily LEITHIINAE Lydekker, 1895

Genus *Eliomys* Wagner, 1840

Type species. *Eliomys melanurus* Wagner, 1840. It is currently found in Algeria, Egypt, Iraq, Israel, Jordan, Lebanon, Libya, Morocco, Saudi Arabia, Syria, Tunisia and Turkey.

Eliomys quercinus Linnaeus (1766)
Figure 5F

Material. This species is represented in the site by 9 isolated teeth: 1 left P_4; 1 left M_1; 1 left M^2; 2 left M^1/M^2 (either of those molars, since they are similar and they are not found in their anatomical position); 1 right M_1/M_2; 1 right M^1/M^2, 1 left M^1/M^2 and 1 right M^3.

Remarks. Glirids present brachydont rooted molars (with rounded cusps and poorly sharpened crests). The occlusal surface of the *Eliomys* molars is markedly concave, with transverse ridges that form cusps at its labial end (Román, 2019).

Biochronology and ecology. The garden dormouse is a generalist species, as it can live in numerous terrestrial and arboreal habitats. They are frequently found in rocky areas, although they also inhabit scrub zones and varied types of forests (Palomo *et al*., 2007). This species can be found nowadays in the Iberian Peninsula (Palomo *et al*., 2007). Its oldest record at the Cantabrian Region dates from MIS 7, at Level K of Lezetxiki II (García-Ibaibarriaga *et al*., 2018).

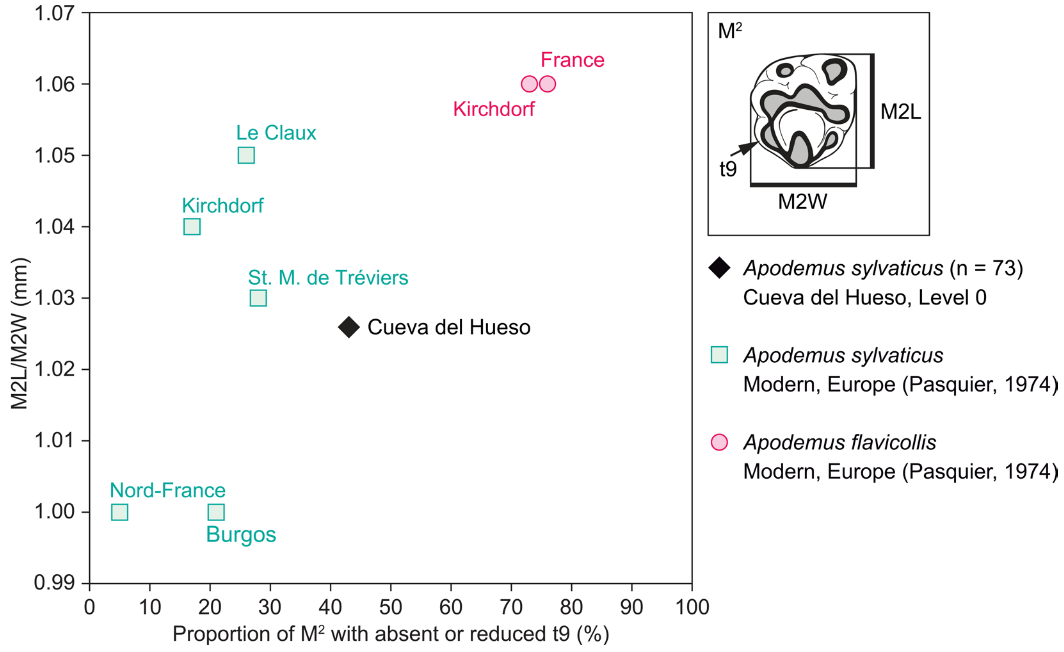

Figure 6. Characterisation of the *Apodemus* sample of Cueva del Hueso based on the upper second molars (M^2). Bivariate graph comparing the M^2 length/width ratio with the percentage of M^2 in which the t9 is reduced or absent. Current samples used for comparison were obtained from Pasquier (1974).

Order EULIPOTYPHLA Waddell, Okada & Hasegawa, 1999
Family TALPIDAE Fischer, 1814
Subfamily TALPINAE Fischer, 1814

Genus *Talpa* Linnaeus, 1758

Type-species. *Talpa europaea* Linnaeus, 1758. It is widely distributed in Europe and Asia, from Spain and Great Britain through most of Europe to the Siberian rivers Obi and Irtysh.

Talpa occidentalis Cabrera, 1907

Figure 5G

Material. The material belonging to this species studied in this paper consists of 10 right humeri and 5 left humeri.

Remarks. The moles (genus *Talpa*) are burrowing animals, for which its postcranial skeleton morphology is adapted to digging and its subterranean lifestyle (Reed, 1951; Yalden, 1966). This made moles develop robust and easily identifiable bones, especially humeri (Fig. 5G). In the Iberian Peninsula, two species are recorded: *Talpa occidentalis*, endemic from this territory, and *Talpa aquitania* Nicolas, Matinez-Vargas & Hugot, 2017, which occupies Cantabria and northern Burgos, the Pyrenees and the southern half of France (Nicolas *et al*., 2015, 2017). After carrying out a biometric study based on the diaphysis width of the humerus (Fig. 7A), we observed that the small values of this parameter fall in the range of variability of *T. occidentalis*, and out of the range of *T. aquitania* and *T. europaea*, both of larger size (Fig. 7B).

Biochronology and ecology. The Iberian mole requires rich-of-prey and suitable-for-burrowing soil (Palomo *et al*., 2007). This mole is evenly distributed in the northwestern third of the Iberian Peninsula, although it is not found in the Pyrenees and the Ebro Basin. Its distribution in the rest of Iberia is restricted to mountainous areas (Palomo *et al*., 2007). The oldest occurrence of this species in the Cantabrian region is in La Güelga cave (Level 9), dating to MIS 3 (Álvarez-Vena *et al*., 2021).

Family SORICIDAE Fischer, 1817
Subfamily CROCIDURINAE Milne-Edwards, 1872

Genus *Crocidura* Wagler, 1832

Type-species. *Sorex leucodon* Hermann, 1780. It currently lives from France to the Volga River and the Caucasus, Asia Minor, Israel, Lebanon, and the Lesbos Island.

Crocidura gueldenstaedtii Pallas, 1811

Figure 5H–5I’

Material. This species is represented in Level 0 of Cueva del Hueso by 4 left mandibles with a complete dental series (I_1–M_3); 1 right mandible with a complete dental series; 2 left mandibles with I_1 and P_4–M_3; 1 left mandible with I_1 and M_1–M_2; 1 right mandible with I_1 and M_1–M_2; 1 left mandible with P_4–M_2 and the ascending ramus; 1 left mandible with M_1–M_3; 1 right mandible fragment with C–M_3; 1 left mandible fragment with I_1 and P_4–M_3; 1 right mandible fragment with I_1 and P_4–

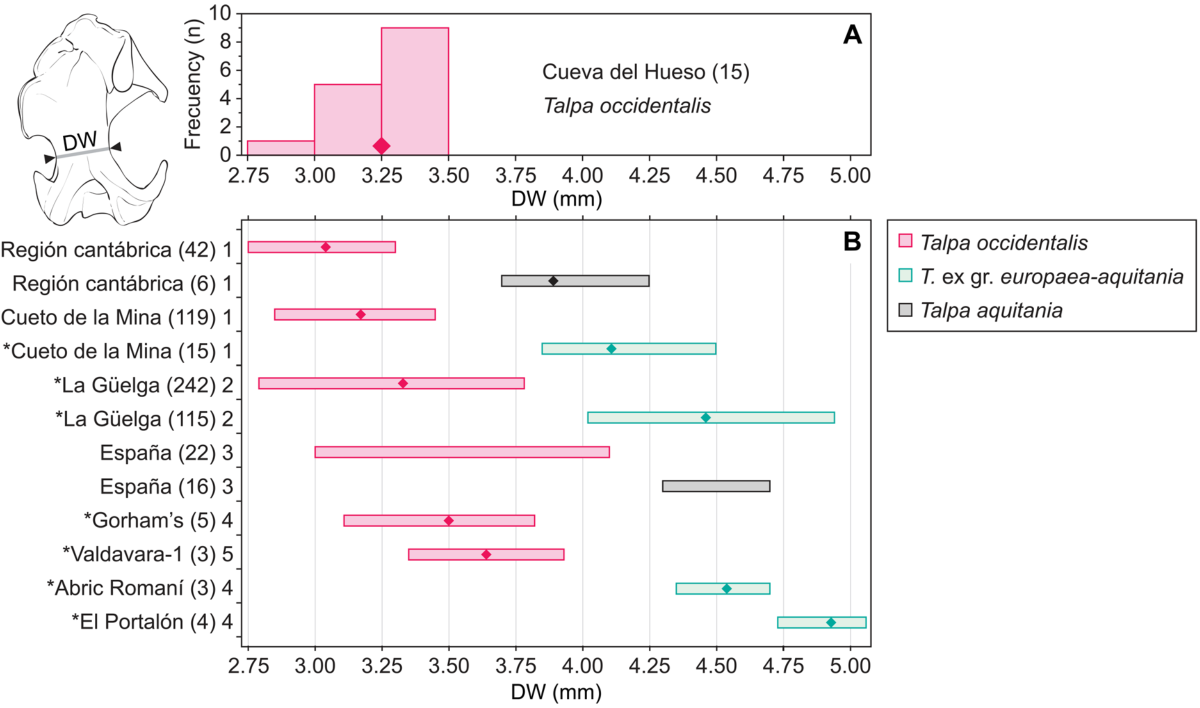

Figure 7. A, Values of the *Talpa* humeri (DW) diaphysis width from Cueva del Hueso; **B,** comparison samples from the Iberian Peninsula. Sources: 1, Castro-Bernárdez (1986); 2, Álvarez-Vena *et al.* (2021); 3, Niethammer (1990); 4, López-García (2008); 5, López-García *et al.* (2011). Numbers in brackets correspond to the number of specimens in each sample.

M_3; 1 right mandible fragment with I_1, P_4–M_2 and the ascending ramus; 1 right mandible fragment with M_2–M_3; 1 cranial fragment with the right I^1 and P^4–M^3, and the left I^1 and P^4–M^3; 1 cranial fragment with the left I^1 and P^4–M^2, and the right I^1 and M^1; 1 cranial fragment with the left and the right I^1 and P^4; 1 right maxilla fragment with 1 unicuspid and the M^3; 1 right maxilla fragment with P^4–M^3; 2 left maxilla fragments with P^4–M^2; 1 right maxilla fragment with 1 unicuspid, $P^4$and M^2; 1 left maxilla fragment with I^1, 1 unicuspid, and P^4; 1 left maxilla fragment with P^4–M^1; and 2 isolated upper premolars (1 left P^4 and 1 right P^4).

Remarks. The species belonging to the genus *Crocidura* (white-toothed shrews) do not show red pigmentation in their teeth, which is characteristic of the soricines. The articular condyles of the mandible show a continuous facet, interrupted only in their labial zone (Fig. 5I', 5K') (Chaline, 1974). Recently, the *Crocidura suaveolens* group has changed its systematics: populations from Western and Central Europe are ascribed to *C. gueldenstaedtii*, while those from East Europe and Asia remain as *C. suaveolens* Pallas, 1811 (Wilson *et al.*, 2017). Güldenstädt's white-toothed shrew (*C. gueldenstaedtii*, Fig. 5H–5I') presents a broad and rounded labial outline of the parastyle of the P^4 (Fig. 5H) and a straight labial outline of the cingulum of the M_2 (Fig. 5I) (Nores, 1989).

Biochronology and ecology. It inhabits many habitats under Atlantic influence, but in Mediterranean climates, it is restricted to moister environments (Biedma *et al.*, 2018, 2020). In the Cantabrian Region, it is found in riverbank forests and the Atlantic countryside (Palomo *et al.*, 2007). In the Iberian Peninsula, it can be found all over the Cantabrian region, with some of the populations isolated in the Guadalquivir River mouth, the coast of Huelva and southern Portugal, the frontier separating Cáceres and Salamanca in the Central System, Galicia, the Cantabrian Mountain Range, the northeastern area of Catalonia and the island of Menorca (Palomo *et al.*, 2007). Its oldest occurrence in the Cantabrian Region has been reported at Torca del León dating to MIS 3 (Álvarez-Lao *et al.*, 2020).

Crocidura russula (Hermann, 1780)

Figure 5J–5K'

Material. Level 0 provided 13 right mandibles with a complete dental series (I_1–M_3); 15 left mandibles with a complete dental series; 1 left mandible with I_1–C, M_1–M_3; 4 left mandibles with I_1, P_4–M_3; 10 right mandibles with I_1, P_4–M_3; 1 left mandible with I_1, M_1–M_3; 1 right mandible with I_1, M_1–M_3; 2 right mandibles with I_1, P_4–M_2; 1 right mandible with I_1, P_4–M_1; 1 left mandible with I_1, P_4–M_1; 1 right mandible with I_1, M_1–M_2; 1 right mandible with I_1–C, M_1; 4 right mandible fragments with a complete dental series; 1 left mandible fragment with a complete dental series; 1 left mandible fragment with C–M_3; 1 right mandible fragment with I_1–M_2 and the ascending ramus; 1 left mandible fragment with I_1–M_2 with the ascending ramus; 2 right mandible fragments with I_1, P_4–M_3; 1 left mandible with I_1, P_4–M_2 and the ascending ramus; 1 right mandible fragment with I_1, P_4–M_2; 1 left mandible fragment with P_4–M_3; 5 right mandible fragments with P_4–M_3 and the ascending ramus; 1 right mandible fragment with I_1, M_1–M_3 and the ascending ramus; 1 right mandible fragment with P_4–M_2; 1 right mandible fragment with I_1, P_4–M_1 and the ascending ramus; 3 left mandible fragments with M_1–M_3; 9 right mandible fragments with M_1–M_3 (4 of them with ascending ramus); 2 left mandible fragments with M_1–M_3 and the ascending ramus; 2 left mandible fragments with I_1, M_1–M_2; 2 right mandible fragments with M_1–M_2; 3 left mandible fragments with M_1–M_2 and the ascending ramus; 2 right mandible fragment with M_2–M_3 (1 with the ascending ramus); 2 left mandible fragments with I_1, M_1 and with ascending ramus; 6 right M_2 and 4 left M_2; 1 cranial fragment with the left I^1–M^3 and the right I^1, 1 unicuspid, and P^4–M^3; 1 cranial fragment with 2 left unicuspids and the left P^4–M^2, and 3 right unicuspids and the left P^4–M^2; 1 cranial fragment with the 3 left unicuspids and the left P^4–M^3; and the complete right dental series (I^1–M^3); 1 cranial fragment with the left I^1, P^4–M^1, and the right I^1 and 2 unicuspids; 1 cranial fragment with 3 left unicuspids, and 2 right unicuspids and the right P^4–M^3; 1 cranial fragment with 3 left unicuspids and the left P^4–M^2, and 2 right unicuspids and the right P^4–M^2; 2 cranial fragments with the left and the right I^1–M^2; 1 cranial fragment with the left I^1, 1 unicuspid, P^4–M^3, and the right I^1, 1 unicuspid, and P^4–M^3; 1 cranial fragment with the left I^1–M^3, and the right I^1–P^4; 1 cranial fragment with the left I^1–M^1, and the right I^1–M^3; 1 cranial fragment with the left P^4, and 1 right unicuspid and the right P^4; 1 cranial fragment with the left I^1–P^4, and the right I^1–M^2; 1 cranial fragment with 1 left unicuspid and the left P^4, and 1 right unicuspid and the right P^4–M^3; 1 cranial fragment with the left I^1–M^2, and the right I^1 and 3 right unicuspids; 1 cranial fragment with the left I^1, and the right I^1–P^4; 1 cranial fragment with the left I^1, and the right I^1, 2 unicuspids and P^4; 1 left maxilla fragment with I^1–M^3; 1 left maxilla fragment with I^1–M^2; 3 left maxilla fragments with 3 unicuspids and P^4–M^1; 1 left maxilla fragment with I^1–P^4 and M^2; 1 right maxilla fragment with I^1–P^4 and M^2; 1 right maxilla fragment with I^1–P^4; 1 right maxilla fragment with 2 unicuspids, P^4, M^2; 1 left maxilla fragment with 3 unicuspids and P^4; 1 left maxilla fragment with 1 unicuspid and P^4–M^2; 2 right maxilla fragments with 1 unicuspid and P^4–M^2; 4 left maxilla fragments with P^4–M^2; 1 right maxilla fragment with 1 unicuspid and P^4–M^1; 7 right maxilla fragments with P^4–M^2; 1 left maxilla fragment with 1 unicuspid and P^4–M^1; 1 right maxilla fragment with I^1, 1 unicuspid and P^4; 2 right maxilla fragments with 2 unicuspids and P^4; 3 left maxilla fragments with 1 unicuspid and the P^4; 4 right maxilla fragments with P^4–M^1; 3 left maxilla fragments with P^4–M^1; 1 right maxilla fragment with 1 unicuspid and M^1; 1 right maxilla fragment with 1 unicuspid and P^4; 4 right maxilla fragments with the P^4; 4 left maxilla fragments with the P^4; 9 right P^4 and 6 left P^4.

Remarks. According to Nores (1989), the greater white-toothed shrew (*Crocidura russula*) is characterised by a reduced angular outline of the parastyle of the P^4 in labial view (Fig. 5J) and by an undulated outline of the labial cingulum of the M^2 (Fig. 5K).

Biochronology and ecology. It is a species with Mediterranean preferences, which lives in open habitats and forest margins with vegetal cover (Palomo *et al.*, 2007). It is currently distributed all over the Iberian Peninsula, excluding areas of high altitude (Palomo *et al.*, 2007). The oldest occurrence of *C. russula* in the Cantabrian Region dates to MIS 5, from Level Q of Covalejos (Sesé, 2021).

Subfamily SORICINAE Fischer, 1814

Genus *Neomys* Kaup, 1829

Type-species**.** *Sorex daubentonii* Erxleben, 1777. Previously *Sorex fodiens* Pennant, 1771. It is currently distributed from the North of the Iberian Peninsula to the Baikal Lake, although there are some isolated populations East of this area: in the mouth of river Amur and the Russian coast of the Japan Sea.

Neomys fodiens niethammeri Bühler, 1963

Figures 5L–5L'

Material. The Eurasian water shrew is represented in this site by 1 left mandible with a complete dental series (I$_1$–M$_3$); 1 right mandible fragment with the ascending ramus and M$_1$–M$_3$ series, 1 right mandible fragment with I$_1$–P$_4$; and 1 left I$_1$.

Remarks. The molars of the order Eulipotyphla present dilambdodont morphology, different from that of the rodents, as its diet is exclusively carnivore. In Level 0 of Cueva del Hueso, the order Eulipotyphla is represented by the family Talpidae and the family Soricidae. Within the Soricidae family, this study has yielded species belonging to the subfamily Crocidurinae and the subfamily Soricinae. The soricines are different from the crocidurines by a red pigmentation in the cusps of their teeth (Fig. 5L, 5M, 5N, 5O), besides a clear separation in facets of the articular condyles of the mandibles (Fig. 5L', 5M', 5N', 5O') (Chaline, 1974). Individuals belonging to the genus *Neomys* present the occlusal margin of their lower incisors (Fig. 5L, 5M) mainly flat or with just one slope break (Chaline, 1974). The coronoid height (Fig. 8) allows for discriminating between the mandibles of the Eurasian water shrew (*N. fodiens*, the larger) and the Mediterranean water shrew (*N. anomalus*, the smaller). When this parameter is not measurable, the main diagnostic criteria is the position of the mental foramen, located below the M$_1$ talonid in the case of *N. fodiens* (Fig. 5L) and below the trigonid of the same molar in *N. anomalus* (Fig. 5M) (Barti, 2006). The mandibular length (**ML**) and the height of the coronoid process (**CH**) place the larger specimens from Cueva del Hueso within the size range of *Neomys fodiens niethammeri*, the largest species of the genus.

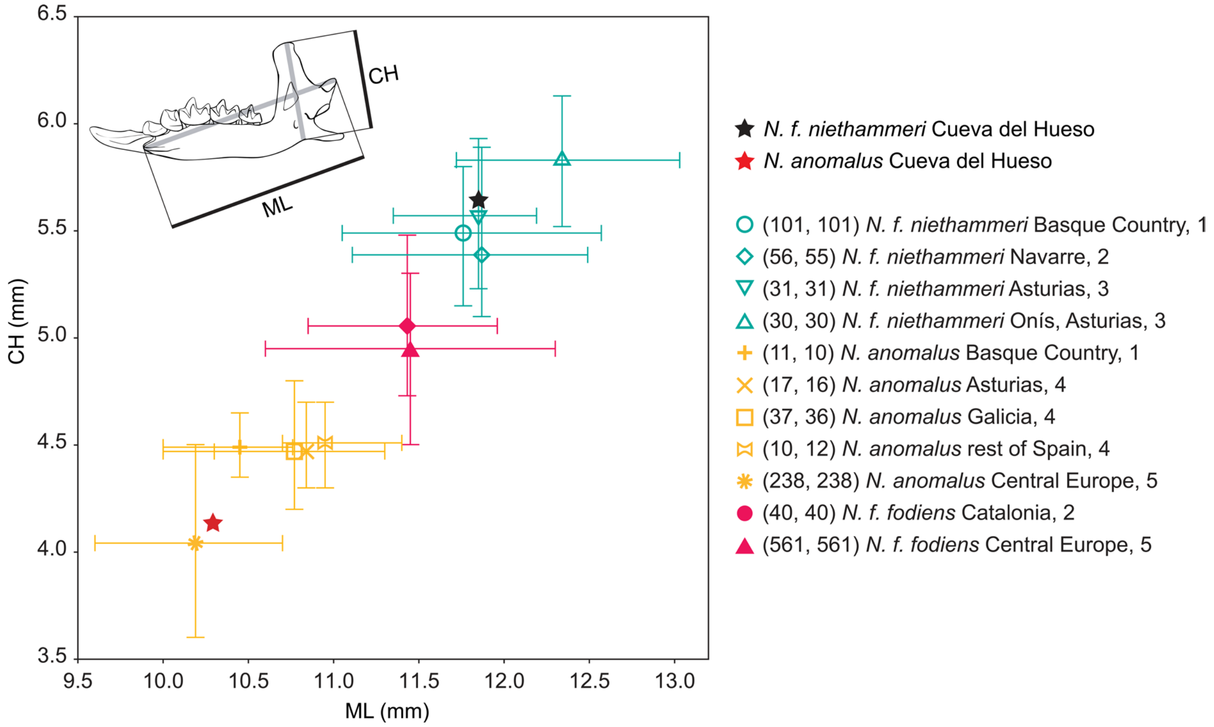

Figure 8. Characterisation of the *Neomys* specimens of Cueva del Hueso following the mandible size. Bivariate graph comparing the coronoid process's height (**CH**) with the mandibular length (**ML**). Samples used for comparison were obtained from: 1, Pemán (1983); 2, López-Fuster *et al.* (1990); 3, Álvarez-Vena *et al.* (2021); 4, Nores *et al.* (1982); 5, Ruprecht (1971).

Biochronology and ecology. The Eurasian water shrew is linked to the presence of watercourses, although sometimes it can be found in humid forests or meadows (Palomo *et al*., 2007). In the Iberian Peninsula, the species *N. fodiens* can be found throughout the northern half, from the Catalonian Pre-Pyrenees to the North of A Coruña, with its southern limit known to be in the centre of the Burgos province (Palomo *et al*., 2007). Regarding this territory, the central zone is inhabited by the subspecies *N. f. niethammeri*, which, according to some recent genetic studies (Balmori-de la Puente *et al*., 2019), could be an ecotype rather than a subspecies. The review on the remains of this genus conducted by Álvarez-Lao *et al*. (2020) located the oldest known remains of the *N. f. niethammeri* morphotype in Cueva del Castillo (MIS 3, Sánchez, 1983; Wood *et al*., 2018), an area from which it would expand until reaching its current distribution throughout the last 40,000 years, according to Álvarez-Vena *et al*. (2021).

Neomys anomalus Cabrera, 1907

Figure 5M–5M'

Material. The recovered remains correspond to just one left mandible with I_1 and M_1–M_2.

Remarks. The Mediterranean water shrew (*Neomys anomalus*, Fig. 5M–5M') is different from *N. fodiens* because of the lower height of the coronoid process (Fig. 8) and, as previously mentioned, because of the position of the mental foramen, located below the trigonid of the M1 (Fig. 5M) (Barti, 2006). The mandibular measurements have placed the individual from Cueva del Hueso in the lower limit of the range for Iberian populations, within the variability for current European populations.

Biochronology and ecology. Although this water shrew usually lives linked to humid environments, it can also appear far away from water bodies. This species shows no so restricted water-related habits in the Iberian Peninsula, having a more significant affinity with Mediterranean environments than its relatives from Central Europe (Palomo *et al*., 2007). It can be found in the southern half of the Iberian Peninsula, besides the eastern half of Andalusia and in points of Huelva, Badajoz and Albacete (Palomo *et al*., 2007). Its oldest record in the Cantabrian Region dates to MIS 3, at Level 6 of La Güelga (Álvarez-Vena *et al*., 2021).

Genus *Sorex* Linnaeus, 1758

Type-species. *Sorex araneus* Linnaeus, 1758. This species is mainly European, occupying the United Kingdom, Scandinavia, and most Central and Eastern Europe, extending East to Siberia.

Sorex ex gr. *coronatus-araneus*

Figure 5N–5N'

Material. This taxon is represented in Level 0 by: 9 left mandibles with the complete dental series (I_1–M_3); 5 right mandibles with the complete dental series; 3 left mandibles with I_1–M_2, 4 right mandibles with I_1–M_2; 7 left mandibles with I_1 and P_4–M_3; 5 right mandibles with I_1 and P_4–M_3; 1 left mandible with I_1–M_1; 1 right mandible with I_1 and M_1–M_3; 2 left mandibles with I_1 and P_4–M_2; 4 right mandibles with I_1 and P_4–M_2; 1 right mandible with I_1, P_4 and M_2; 1 left mandible with I_1, P_4–M_1; 2 left mandibles with I_1 and M_1–M_2; 1 right mandible with I_1 and M_1–M_2; 2 right mandibles with I_1 and M_1; 1 left mandible fragment with I_1–M_3; 2 left mandible fragments with C–M_3 with an ascending ramus; 2 right mandible fragments with C–M_3 (1 with ascending ramus); 1 left mandible fragment with I_1–M_2; 2 left mandible fragments with P_4–M_3 (1 with ascending ramus); 1 right mandible fragment with P_4–M_3 and ascending ramus; 1 left mandible fragment with I_1, P_4–M_2; 1 left mandible fragment with I_1–M_1 and ascending ramus; 1 right mandible fragment with I_1–M_1 and ascending ramus; 1 left mandible fragment with C–M_1; 2 left mandible fragments with P_4–M_2 (1 with ascending ramus); 1 right mandible fragment with I_1, C–P_4, and ascending ramus; 1 left mandible fragment with I_1, P_4–M_1, and ascending ramus; 3 left mandible fragments with I_1–P_4, and ascending ramus; 1 left mandible fragment with C–M_1; 1 right mandible fragment with P_4–M_1; 1 left mandible fragment with M_1–M_3 and ascending ramus; 2 right mandible fragments with M_1–M_3 and ascending ramus; 2 right mandible fragments with M_1–M_2 and ascending ramus; 3 left mandible fragments with M_1–M_2 and ascending ramus; 1 left mandible fragment with M_2–M_3 and ascending ramus; 1 right mandible fragment with M_2–M_3 and ascending ramus; 3 left mandible fragments with I_1, P_4, and ascending ramus; 2 right mandible fragments with M_1 (1 with ascending ramus); 1 left mandible fragment with M_1 and ascending ramus; 1 left mandible fragment with M_2; 1 right mandible with M_2 and ascending ramus; and 21 isolated teeth (11 left incisors, 8 right incisors, 1 right P_4 and 1 right M_3).

Remarks. Among soricines, the genus *Sorex* (Fig. 5N–5O') differs from the genus *Neomys* (Fig. 5L–5M') by the serrated occlusal edge of its lower incisors; also, by the morphology of the articular condyles, which show a flat surface between facets (Fig. 5N', 5O'), while in the *Neomys* genus there is a valley (Fig. 5L', 5M'); and, also, by its lower size (Fig. 5N–5O'), among other features (Chaline, 1974). *S.* ex gr. *coronatus-araneus* (Fig. 5N–5N') is different from *S. minutus* (Eurasian pigmy shrew, Fig. 5O–5O') by the substantially smaller size of the latter (Chaline, 1974). The material of Level 0 selected to study this species consisted of mandibular remains since those were better preserved and more abundant.

Biochronology and ecology. This species prefers zones with Atlantic influence, living in a wide variety of habitats, from deciduous or conifers forests to Atlantic or alpine prairies. However, it requires the presence of humid soils and enough vegetal cover (Palomo *et al*., 2007). In the Iberian Peninsula, this shrew can only be found in the northern zone, between the East of Galicia and the West of the Catalonian Pyrenees, and to the North of the Iberian System (Palomo *et al.*, 2007). Its oldest occurrence in the Cantabrian region is in Lezetxiki II, which dates to MIS 7 (García-Ibaibarriaga *et al.*, 2018).

Sorex minutus Linnaeus, 1766

Figure 5O–5O'

Material. This species is represented in Level 0 by 3 right mandibles with I_1 and P_4–M_3; 2 left mandibles with I_1 and P_4–M_3; 1 right mandible with I_1, P_4, and M_2–M_3; 1 left mandible fragment with P_4–M_3 and the ascending ramus; 1 right mandible fragment with M_1–M_3 and the ascending ramus; 1 left mandible fragment with P_4–M_1; 1 right mandible fragment with M_2–M_3; and 2 isolated left incisors.

Remarks. The small size of this material allowed us to identify it as the *Sorex minutus* (Fig. 5O–5O'), the smallest of the Level 0 soricines.

Biochronology and ecology. The Eurasian pygmy shrew occupies various habitats, such as meadows and forests. The factor determining its presence is moisture, besides preferring a dense vegetal cover (Palomo *et al.*, 2007). The current distribution in the Iberian Peninsula comprises the northern area, from the North of Portugal to the humid Eastern region of Catalonia, with two isolated populations in the Central System and Tarragona (Palomo *et al.*, 2007). The oldest occurrence of this species in the Cantabrian Region was reported from Lezetxiki II, which dates to MIS 7 (García-Ibaibarriaga *et al.*, 2018).

DISCUSSION

Small mammal assemblage

Level-0 small-mammal remains are conformed of a total of 6,240 elements, 2,422 of those belonging to postcranial bones (cranial fragments not assigned to a specific group are included) (Appendix 1, Tab. S2). The remaining 3,818 elements belong to isolated teeth or in anatomical connection with their respective mandibles or maxillae. 2,358 of these specimens have been classified to the species level, belonging to a minimum of 286 individuals of 16 different taxa (Tab. 1). 38.81% of the studied material belongs to postcranial bones (Appendix 1, Tab. S2), which present a good preservation state. Bones with a narrow diaphysis appear fractured at times, and there have been found what appear to be small tooth marks, caused by predation from a small carnivore. Excepting these isolated cases, there are no significant taphonomic alterations produced by predators, such as excessive fracturing or corrosion caused by digestion. According to Andrews (1990) and Fernández-Jalvo *et al*. (2016), the only predators capable of generating an accumulation of such characteristics (great concentration of remains barely altered) are nocturnal birds of prey, which swallow the whole bodies and after the digestion regurgitate the bones and hair in the form of small balls (~ 2–10 cm), called regurgitation pellets.

In the assemblage, the most abundant species is *Apodemus sylvaticus*, with an MNI of 78 individuals. The most outstanding species in the small mammal assemblage are *Microtus lavernedii*, *Microtus arvalis*, *Mus musculus* and *Rattus* sp. Regarding the genus *Microtus*, *Mi. lavernedii* is more abundant (6.99%) in the Level 0 of Cueva del Hueso than *Mi. arvalis* (0.70%), which can be indicative that this level was formed during a relatively temperate moment (Álvarez-Vena *et al.*, 2021).

Palaeoenvironment and palaeoclimate reconstruction

Applying the Habitat Weighing Method, we inferred a landscape dominated by forest patches alternating with open areas with herbaceous cover, the last in the way of humid meadows and dry grasslands (Fig. 9). The landscape would be like that which can be found nowadays in the rural environment of the Cantabrian Range, in the zones located behind the littoral mountain chains of Asturias; a few kilometres further inland than the current location of Cueva del Hueso.

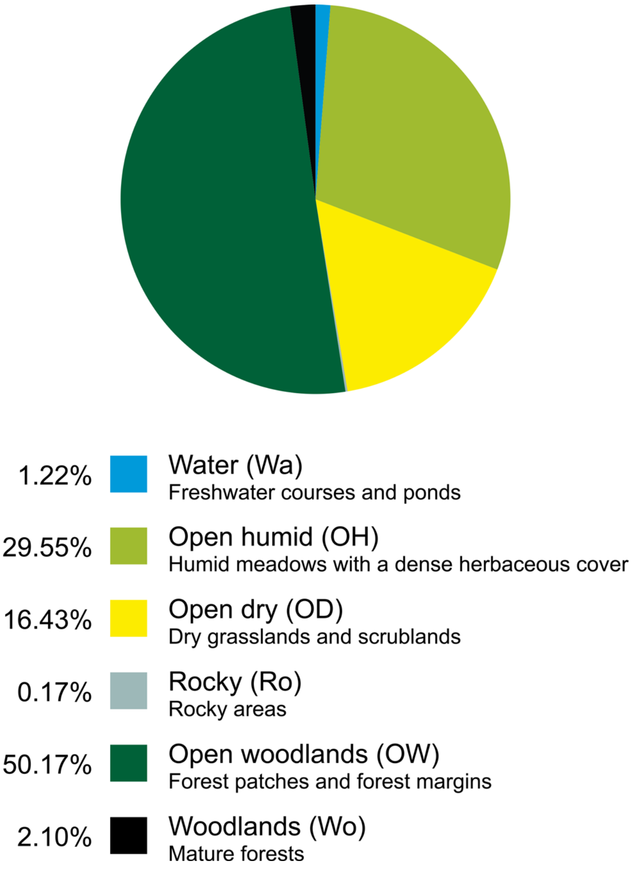

Figure 9. Type of landscape inferred by the Habitat Weighting Method for Cueva del Hueso surroundings.

Table 1. Small mammal species from Level 0 of Cueva del Hueso and their weighted habitat preferences (Álvarez-Lao *et al.*, 2020). **Wa,** water; **OH,** open humid; **OD,** open dry; **OW,** open woodlands; **Wo,** mature woodlands; **Ro,** Rocky areas.

	NISP	MNI	%MNI	Wa	OH	OD	OW	Wo	Ro
Arvicola amphibius	4	1	0.35		1				
Arvicola sapidus	4	1	0.35	1					
Microtus lavernedii	137	20	6.99		0.5		0.5		
Microtus arvalis	6	2	0.70			0.75	0.25		
Microtus lusitanicus	187	40	13.99		0.5		0.5		
Mus musculus	3	2	0.70		0.75	0.25			
Apodemus sylvaticus	292	78	27.27				1		
Sorex minutus	59	6	2.10		0.25			0.75	
Sorex coronatus	446	48	16.78		0.75		0.25		
C. russula	968	60	20.98			0.75	0.25		
C. gueldenstaedtii	164	11	3.85		0.5		0.5		
N. f. niethammeri	16	3	1.05	0.75	0.25				
Neomys anomalus	4	1	0.35	0.25	0.75				
Talpa occidentalis	58	10	3.50		0.75		0.25		
Rattus sp.	1	1	0.35						
Eliomys quercinus	9	2	0.70					0.75	0.25
Total	2358	286	100						
Weighted habitats				1.22	29.55	16.43	50.17	2.10	0.17

The superimposed current distribution of each species yielded two shared UTM grids corresponding to the municipalities of Piloña and Parres, which are in the eastern inland of Asturias (Fig. 10), between the pre-coastal range and the Cantabrian Mountains. The current climatic parameters in these two areas (Tab. 2) are extrapolated to those in the surroundings of Cueva del Hueso by the time of the accumulation of Level 0. Inferred climatic conditions are slightly colder and moister than current: Mean Annual Temperature (MAT) is 1.2 ± 0.9ºC colder, Mean Temperature of the Warmest month (MTW) is 0.5 ± 0.8ºC colder, Mean Temperature of the Coolest month (MTC) is 2.2 ± 1ºC colder, and Mean Annual Precipitation (MAP) is 225 ± 56 mm higher. The fact that these climatic parameters, nowadays registered in more inland areas of the region, existed in such a close location to the current shoreline, suggests that during the sedimentation of Level 0 it took place a climate cooling episode.

Chronology of the assemblage

The presence of the murines *Mus musculus* and *Rattus* sp. and the arvicoline *Microtus arvalis* allows us to establish a time frame for the chronology of the deposit. In Domínguez-García *et al.* (2019), the timing

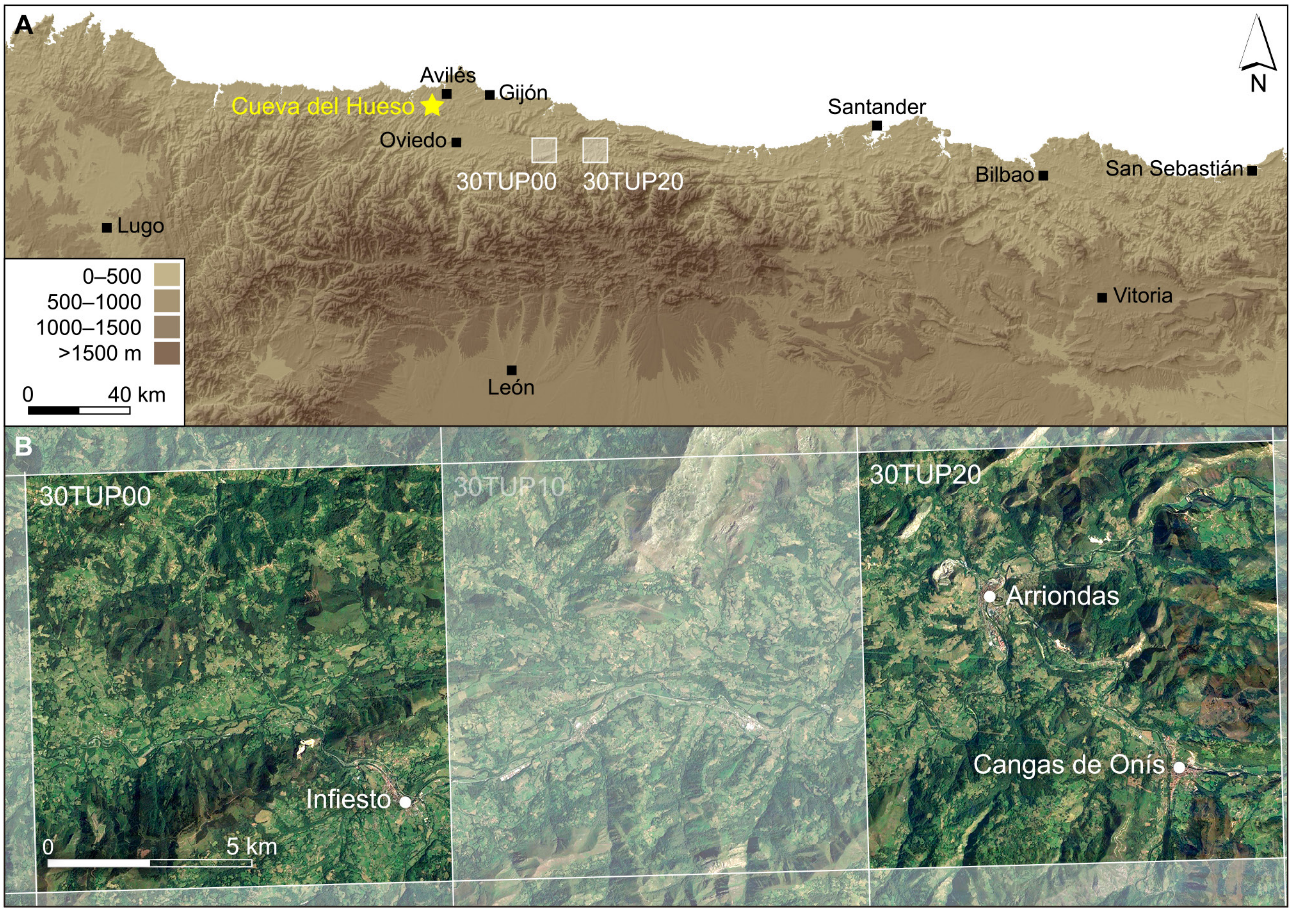

Figure 10. Location of both UTM grids (10 km × 10 km), where micromammal species identified in Level 0 of Cueva del Hueso cohabit nowadays.

Table 2. Current climatic values at Cueva del Hueso area (Castrillón, Asturias) compared with the obtained from the Mutual Ecogeographic Range.

			Mutual Ecogeographic Range			
	Current values		Mean	Minimum	Maximum	STD
Mean Annual Precipitation (mm)	1070		1295	1198	1420	56
Mean Temperature of the Warmest month (°C)	18.5		18	15.5	19.3	0.8
Mean Annual Temperature (°C)	13		11.8	9	13.4	0.9
Mean Temperature of the Coldest month (°C)	8.6		6.4	3.8	8.4	1

for the arrival of *Rattus* and *Mus* to the Iberian Peninsula is discussed. Taking into consideration the reliable records, and ignoring those which remain doubtful, *Mus musculus* entered in the second half of the Iron Age, and *Rattus* did so at the beginning of the Roman period. Therefore, this last taxon provides a maximum age for Level 0 of the cave, around 2000 yr BP.

Nowadays, *Mi. arvalis* is found at the southern slope of the Cantabrian Mountain Range, mainly in the Mediterranean biogeographic region. Conversely, Cueva del Hueso belongs to the Euro-Siberian region. Therefore, the presence of *Mi. arvalis* in a site so close to the coastline, where it is not currently found, indicates that Level 0 was formed during an episode with slightly cooler climatic conditions than those existing nowadays in the surroundings of the cave. However, the relative abundance of *Mi. lavernedii* is significatively higher than that of *Mi. arvalis*, as frequently recorded in temperate periods under Atlantic climatic conditions (Álvarez-Vena *et al*., 2021). Therefore, it would not have been an extremely cold episode. This hypothesis is supported by the climatic parameters obtained through the Mutual Ecogeographic Range, which indicates cooler and moister conditions.

In the climatic scale globally established for the Holocene (Mayewski *et al*., 2004), several cooling events are distinguished, which are recorded in stalagmites from the Northwest of the Iberian Peninsula (Martín-Chivelet *et al*., 2011) and in pollen cores (Desprat *et al*., 2003). Considering the palaeobiogeographic data previously mentioned, there are two reliable periods for the accumulation of Level 0: a cooling episode during the Dark Ages Cold Period (450 AD–950 AD) and the Little Ice Age (1400 AD–1850 AD). Regarding the lack of additional criteria that would allow us to choose between both periods, we conclude that Level 0 could have been formed during either of them or even during both if it were a condensed level comprising that time frame. In any case, the most suitable chronology for this deposit ranges between 450 AD and 1850 AD.

This small mammal assemblage in this site represents an exceptional finding, as the presence of the murids *Mus musculus* and *Rattus* sp. is not frequent in other sites of this region. Moreover, in the Cantabrian Region, most of the Holocene sites belong to the Middle Holocene, so the fact that Level 0 of Cueva del Hueso has such a recent Holocene chronology makes it an exceptional record.

CONCLUSIONS

Level 0 of Cueva del Hueso provided a rich and diverse micromammal association, with a NISP of 2,358 and an MNI of 286, corresponding to 16 taxa. The most relevant species of the assemblage are *Mus musculus* and *Rattus* sp. as their occurrences are scarce in the Cantabrian fossil record. These murine species also provided the boundaries for the chronology of the site. *Microtus arvalis* is another significant species, which provided relevant chronological and palaeoenvironmental data.

In order to characterize the palaeoenvironmental and palaeoclimatic conditions under which Level 0 was deposited, the Habitat Weighting Method and the Mutual Ecogeographic Range Method have been used. The Habitat Weighting Method indicates that the landscape would have been formed by forest patches alternating with more open areas, both humid meadows and dry grasslands. There were also small areas of mature forests and freshwater courses.

The Mutual Ecogeographic Range yielded paleoclimatic data regarding temperature and precipitation for the site. The climatic values for these parameters were obtained from the current conditions of the municipalities of Piloña and Parres, as they represent the only areas where the micromammal assemblage of Level 0 coexists nowadays. The temperature obtained was slightly lower than the current, and the precipitation was slightly higher, indicating cooler climatic conditions.

The presence of *Rattus* sp. and *Mus musculus* indicates that Level 0 must be younger than 2000 yrBP, and the presence of *Microtus arvalis* indicates that it cannot be a modern accumulation, as this species is not found in the surroundings of the site nowadays. Combining this time frame with the palaeoenvironmental and palaeoclimatic information obtained from the Habitat Weighting Method and the Mutual Ecogeographic Range, we propose that Level 0 tentatively accumulated in a period ranging from 450 AD to 1850 AD. This makes Cueva del Hueso a remarkable site in the Cantabrian Region, where it is not common to find sites with such a recent Holocene chronology.

Supplementary information. Supplementary information for this paper consists of an Appendix (Appendix I), where Table S1 and Table S2 are included. The Apendix is available at the Spanish Journal of Palaeontology web-site (https://sepaleontologia.es/spanish-journal-palaeontology/) linked to the corresponding contribution. The information provided by the author has not being copy edited or substantially formatted.

Authors contributions. DA-L codirected the fieldwork and provided the study material, AC-G processed the samples, AC-G and AA-V studied and discussed the micromammal classification and prepared the figures. AC-G and AA-V coordinated the work and prepared the final draft, which all the authors have revised.

Competing interest. We hereby declare no competing interest.

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