



A cave lion (*Panthera spelaea*) skeleton from Torca del León (NW Iberia): Micromammals indicate a temperate and forest environment corresponding to GI-11 (MIS 3)

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ABSTRACT

The Torca del León site (Asturias, NW Spain), discovered in 2014, provided an interesting fossil assemblage including a *P. spelaea* partial skeleton and a rich micro-mammal community with palaeoenvironmental significance. The bone accumulation was formed in a karstic cave that acted as a natural trap, as indicated by the geomorphology of the cavity (connected to a 16 m deep shaft) and the lack of signs of human or carnivore activity on the bones. The large-mammal assemblage is composed of carnivores, of which the most striking is the partial skeleton of the cave lion, an exceptional find for this region, which allowed a detailed comparative study. Its skull and teeth retained features of systematic relevance, which agree with its ascription to *P. spelaea*. Sexing of the specimen points to it possibly being from a male, whose body weight was estimated at 360 kg. Other identified large mammals in the site include *P. pardus* and *Canis lupus*. The rich small mammal assemblage, comprising 14 taxa, allowed inferring that the environment during site formation corresponded to a mature forest developed under humid and temperate conditions, located at just 15 km from the glacial fronts of the Cantabrian Mountains. AMS dating yielded 43.0 ± 0.5 cal ka BP, coinciding with Greenland Interstadial GI-11, a warming event poorly known in NW Iberia, coeval with the onset of the regional glacial retreat occurred after the local glacial maximum of ~ 45 ka. This episode is also coeval with the Middle to Upper Paleolithic transition in Northwestern Iberia.

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1. Introduction

Large felid remains are scarce in the Late Pleistocene fossil assemblages from North Iberia. The main reason may be related to the fact that these animals are rare in mammal communities (Elton, 1927; Colinviaux, 1978), so it would be expected for them to be even rarer in the fossil record. Finds of cave lion (*Panthera spelaea*/*P. leo*) have been documented in eighteen sites from the Cantabrian Region (NW of Iberian Peninsula), comprising normally only isolated bone fragments or teeth (Harlé, 1908, 1909; 1912; Carballo, 1910, 1960; Alcalde del Río et al., 1911; Hernández-Pacheco, 1919; Altuna, 1967, 1972; 1981, 1986; 1990; Castaños, 1980, 1984; 1988, 2001; 2005; Dari, 1999; Altuna et al., 2002; Álvarez-Lao and García-García, 2006; Pinto Llona, 2007; Altuna and Mariezkur-

rena, 2011; Cueto et al., 2016). However, well-preserved lion skeletons are exceptional in the fossil record from this area, the most remarkable being the extraordinary findings from the cavities of Arrikrutz, in Guipúzcoa (Altuna, 1967, 1981); Lezetxiki, also in Guipúzcoa (Altuna, 1972); Azoleta, in Álava (Castaños, 2005) and La Garma, in Cantabria (Pablo Arias, pers. com, 2017).

The Torca del León cave (Llanes, Asturias) was discovered in 2014 by the Sociedad Espeleológica y Barranquista Escar. During their first explorations, speleologists discovered a few lion fossils scattered over the cave floor, suggesting that part of the fossil assemblage remained probably buried in the sediment. The cave was named Torca del León (which means "Lion's Shaft") after this discovery. Excavation of the fossil assemblage was carried out in January and February 2017, providing 214 identifiable large-mammal fossils, as well as more than 1900 remains of small mammals. This fossil assemblage documents an interesting faunal association including three large carnivore taxa: cave lion (*Panthera spelaea*), leopard (*Panthera pardus*) and wolf (*Canis lupus*). The lion remains correspond to a partially preserved skeleton,

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which provides relevant information about the morphology and biometry of the Late Pleistocene populations of this felid from North Iberia.

Fossils from Torca del León, most of them well preserved, lack any evidence of human or carnivore activity, suggesting that the origin of the bone accumulation was related to a natural trap. This is consistent with the geomorphology of the cavity, whose entrances are represented by shafts (vertical conduits), and with the location of the fossil remains, placed in the distal part of the debris cone formed at the bottom of one of the entrance shafts, 16 m depth.

The rich small-mammal assemblage provided an interesting paleoenvironmental context documenting the development of a wet forest associated with Greenland interstadial GI-11 (MIS 3), a poorly known episode in the Cantabrian Region, characterized by temperate climatic conditions. This is of special interest since most of the MIS 3 studied faunal assemblages from North Iberia include cold-adapted species, evidencing cold environmental conditions (e. g. Altuna, 1972; Castaños, 1996; Galobart et al., 1996; Altuna and Mariezkurrena, 2000, 2011; Álvarez-Lao and García, 2010; Álvarez-Lao, 2014; Álvarez-Lao et al., 2015, 2017, Álvarez-Lao and Méndez, 2016). In addition, the chronology of this site is coeval with the episode of Middle to Upper Paleolithic transition in Northwestern Iberia, so this study sheds new light on the environmental context in which this remarkable event occurred.

The main aim of this work is to characterize the site and to provide a paleontological comparative study of the large and small mammal fossil remains, with special attention to those of the cave lion (*Panthera spelaea*), which comprise one of the most complete skeletons of this species known from the Iberian Peninsula. Its paleoenvironmental, chronological, and geomorphological context is also established.

2. Setting

Torca del León (TL) (43°24'9.83"N, 4°49'51.58"W, 123 m altitude) is a karst cave (1.1 km length, 55 m depth) located in the east of As-

turias, a province in the middle part of the Cantabrian Region, northern Iberian Peninsula (Fig. 1). The surroundings of TL are dominated by marine terraces ranging from 5 to 220 m above sea level (a.s.l.), from the result of the emersion of sea wave-cut platforms during the Quaternary (Flor and Flor-Blanco, 2014). Littoral ranges (such as El Cuera, 1300 m a.s.l.) define the southern limit of the marine terraces, where TL is located (Fig. 1C). This regional configuration meant that the Cantabrian Region was used as a natural corridor for faunal and human distributions between Europe and the Iberian Peninsula since, at least, the Middle Pleistocene (e.g. Álvarez-Lao and García, 2011; Marín-Arroyo et al., 2018).

The upper marine terraces developed mainly in Ordovician quartzite while the lower terraces are cut in Carboniferous limestone (Domínguez-Cuesta et al., 2015); these lower terraces were karstified prior to 350 ka (Jiménez-Sánchez et al., 2006; Ballesteros et al., 2017). During, at least, Marine Isotope Stage (MIS) 4, the erosion of the quartzite upper terraces produced the development of alluvial fans covering the lower calcareous terraces and introducing detrital sediments inside the karst caves. After this, the alluvial fans were eroded, exposing the karst developed in the lower calcareous terraces and allowing the entrance of the macrofauna and humans inside the caves (Ballesteros et al., 2017), as evidenced by abundant findings of cold-adapted fauna (e.g. Álvarez-Lao et al., 2015) and vestiges of *Homo neanderthalensis*/*H. sapiens* during MIS 3-2, including cave paintings declared part of World Heritage Site 310 (UNESCO, 2019).

From a regional point of view, a glacial local maximum would have occurred at 48-35 ka (Serrano et al., 2016), probably at ~45 ka (Jiménez-Sánchez et al., 2013). This maximum was followed by a general glacial retreat associated with the development of cold and dry conditions in mountain areas (Moreno et al., 2010, 2012). Lower areas, such as the surroundings of TL, were characterized by open landscapes with presence of cold-adapted mammals at 45, 38, 36 and 30 ka (Álvarez-Lao, 2014; Álvarez-Lao et al., 2015) and reduced stalagmite growth during MIS 3 (Stoll et al., 2013).

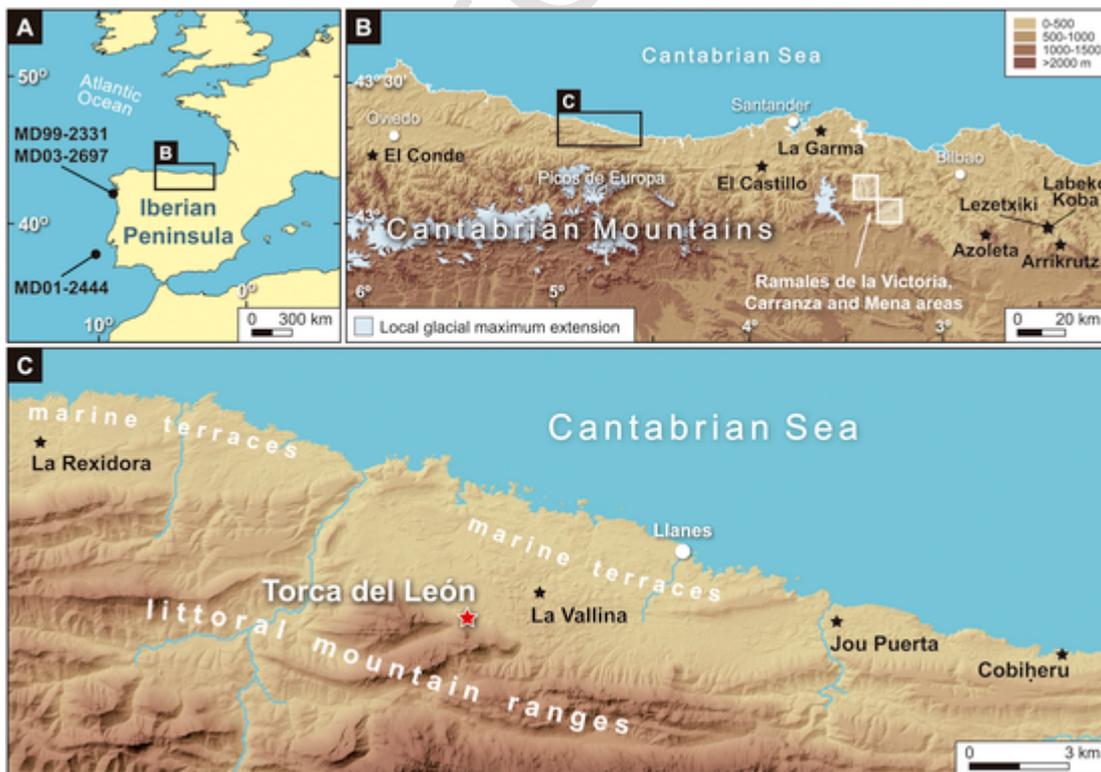


Fig. 1. Setting of the Torca del León site in the coast of the Cantabrian Region (NW Iberian Peninsula). Digital Elevation Model from the National Geographical Institute of Spain, and glacial maximum extension from Rodríguez-Rodríguez et al. (2014) and Serrano et al. (2016).

Nowadays, TL is located in an Atlantic climatic domain, characterized by temperate summers and without a dry season (type Cfb according to the Köppen-Geiger classification; Cunha et al., 2011). Precipitation is distributed along the year reaching values of ~1400 mm, while the average temperature is 13.4 °C, with annual maximum and minimum values of 19.3 and 8 °C, respectively. These conditions allowed the natural development of deciduous forest in the surroundings of the study cave; however, anthropic activities produced the reduction of the forest extension, the increase of pasture area and the introduction of allochthonous *Pinus* and *Eucalyptus*.

3. Material and methods

3.1. Geomorphology

The geomorphological study of TL was carried out to characterize the paleontological site and to establish its origin. This study includes the underground geomorphological mapping of the site using a Geographical Information System and the elaboration of a stratigraphic section of the deposit that hosts the fossil fauna assemblage. The topographic base of the geomorphological map corresponds to the cave survey elaborated in 2017 by the Sociedad Espeleológica y Barranquista Escar using the laser distance measurer DistoX.

3.2. Large mammals

The large mammal assemblage comprises 214 fossil remains, all belonging to carnivores (Table 1), 169 of them (79%) corresponding to the lion (*Panthera spelaea*) skeleton: the skull is incomplete and preserved in two main portions, including the majority of the upper teeth. The mandible is well preserved, comprising the right branch and most of the left one. Postcranial remains are abundant: vertebrae, ribs, and scapulae are very damaged, but the anterior limbs are reasonably well preserved, especially radii, ulnae and metacarpals. The posterior part of the skeleton is very fragmentary: only an incomplete tibia, a patella and three metatarsals could be measured. Leopard (*P. pardus*) pro-

vided 34 fossils (16% of the large mammal assemblage), most of them corresponding to limb bones (some of them well preserved) and two teeth. Eleven remains (5% of the large mammals) from other species are very fragmentary: 7 remains correspond to cranial fragments and teeth from wolf (*Canis lupus*), two mandibles and one cranial fragment to weasel (*Mustela nivalis*), and one mandible to polecat (*Mustela putorius*).

The fossils were recovered using the archaeological methodology and stored at the Department of Geology of the University of Oviedo (Spain). Fossil preparations consisted basically in removing the silt and clay sediment and consolidating them with Paraloid B-72, since most of the remains were very fragile because of the site's moisture. Some of them required exhaustive and careful laboratory work to remove the speleothem or to recombine them, in the cases in which they were heavily fragmented (for instance, the lion skull).

The Minimum Number of Individuals (MNI) of each species was calculated comprehensively, taking into account every skeletal element. Measurements taken on the fossils are given in millimeters following the standards of Argant (1988) and Marciszak et al. (2014) for the *P. spelaea* skeletal remains, Schütt (1969a) for *P. spelaea* and *P. pardus* upper carnassials (P⁴), Marciszak et al. (2017a) for mustelid mandibles and teeth, and Driesch (1976) for all other elements and taxa. Sexing of the lion followed Turner (1984). Morphometric and morphologic data were compared with an extensive sample from Europe and Siberia, detailed in Section 5.1.

To estimate the body weight of the lion specimen from Torca del León, we produced predictive equations based on simple and multiple variable regression. A detailed description of this method is provided in Appendix A.

3.3. Small mammals

The small-mammals assemblage comprises more than 1900 remains, 1645 of which (87%) were identified, at least, to the anatomical level. Some of the elements were found in anatomical connection (see Section 5.2. for more detailed information).

Table 1

Composition of the faunal assemblage from Torca del León. For each small-mammal taxon is specified the most common element per specie (Element) and its distribution by habitat type: water (Wa); open humid (OH); open dry (OD); open woodland (OW); woodland (Wo).

Large mammals:										
Taxa	NISP	% NISP	MNI							
<i>Panthera spelaea</i>	169	78.97	1							
<i>Panthera pardus</i>	34	15.88	1							
<i>Canis lupus</i>	7	3.27	1							
<i>Mustela nivalis</i>	3	1.4	1							
<i>Mustela putorius</i>	1	0.46	1							
Total	214	100	5							
Small mammals:										
Taxa	NISP	% NISP	MNI	Element	% MNI	Wa	OH	OD	OW	Wo
<i>Microtus gr. Agrestis</i>	11	2.17	1	left M ₁	2.13		0.5		0.5	
<i>Clethrionomys glareolus</i>	10	1.97	2	left M ₁	4.26					1
<i>Apodemus sp.</i>	149	29.44								
<i>Apodemus flavicollis</i>	18	3.55	10	left M ²	21.28					1
<i>Apodemus sylvaticus</i>	26	5.13	10	right M ²	21.28				1	
<i>Glis glis</i>	67	13.24	7	left M ¹	14.89					1
<i>Sorex minutus</i>	58	11.46	4	right P ⁴	8.51		0.25			0.75
<i>Sorex coronatus-araneus</i>	76	15.02	6	right mandible	12.77		0.75		0.25	
<i>Neomys fodiens fodiens</i>	24	4.74	1	right mandible	2.13	0.75	0.25			
<i>Neomys f. niethammeri</i>	18	3.55	1	left mandible	2.13	0.75	0.25			
<i>Crocodyrus russula</i>	14	2.76	1	maxilla	2.13			0.75	0.25	
<i>Crocodyrus gueldenstaedtii</i>	12	2.37	1	right mandible	2.13		0.5		0.5	
<i>Talpa occidentalis</i>	4	0.79	1	right M ¹	2.13		0.75		0.25	
<i>Talpa europaea-aquitania</i>	10	1.97	1	left humerus	2.13		0.75		0.25	
<i>Rhinolophus euryale</i>	9	1.77	1	left humerus	2.13					1
Total	506	100	47		100					

More than 200 kg of sediment belonging to the upper layer (defined in Section 4), and around 50 kg from the lower layer (which resulted paleontologically sterile) were collected for collecting purposes and water-screened using superimposed sieves with 2- and 0.5-mm mesh lights. Fossil remains contained in the fine fraction (0.5–2 mm) were recovered by checking the sediment with a binocular microscope under 10x magnification.

Taxonomic identifications were carried out by means of photographs taken with a parallel-optics type stereo microscope Nikon SMZ800N equipped with a 5 Mpx digital camera. Measurements were taken on these photographs using Adobe Photoshop CC software, which allowed us to obtain the correct orientation of the images and the use of guides to adjust the measurements. For the taxonomic identification of each taxon different anatomical elements, specified in Appendix A, were used.

The number of identified specimens (NISP) was obtained by counting every taxonomically identifiable tooth and bone fragment. MNI was calculated according to the most frequent diagnostic element and considering its laterality; the selected element of each species is indicated with the MNI in Table 1. The relative abundance of each small mammal species was based on the MNI.

For a preliminary identification of the accumulating agent, molar and incisor enamel was analysed in search of alterations caused by digestion, as proposed by Andrews (1990) and Fernández-Jalvo et al. (2016).

3.4. Paleoenvironment and paleoclimate

The landscape that surrounded TL was established using the habitat weightings method (Evans et al., 1981) based on the preferences of each small-mammal taxon for one or several habitats types (López-García, 2008; Cuenca-Bescós et al., 2009; López-García et al., 2010, 2014). The environmental preferences of each species were obtained following Nores (1989), Wilson et al. (2016, 2017) and Wilson and Mittermeier (2018). The climatic conditions during the assemblage accumulation were estimated by means of the Mutual Ecogeographic Range (MER) method, which is detailed in Appendix A.

3.5. Dating

Two bone samples were selected for AMS radiocarbon dating and sent to the DirectAMS laboratory, North Creek (USA) (see Section 4). Poor preservation of collagen in one sample prevented its dating. The age obtained for the other sample was calibrated by means of INTCAL 13 database (Reimer et al., 2013) using the software OxCal v.4.3.2 (Bronk Ramsey, 2017), and considering the error as two times the standard deviation (95% probability). The calibrated date is expressed in cal ka BP.

4. Geomorphological context, origin of the paleontological site and chronology

The paleontological site is located in the entrance sector of TL (Fig. 2). This sector corresponds to ancient phreatic/epiphreatic and vadose passages, strongly modified by rock fall processes. The vadose passages include a shaft 16 m deep that constitutes the western entrance to the cave. Debris deposits dominate this entrance sector and include fallen boulders and a debris cone located at the bottom of the shaft (Fig. 2B). Cave passages preserve also minor fluvial deposits comprising quartzitic sand and pebbles.

The paleontological study site is located toward the NE of the entrance sector, within the mentioned debris cone (Fig. 2A, D). The stratigraphy of the site includes two layers (Fig. 2C) deposited over a limestone boulder fallen from the ceiling of the cave. The lower layer corresponds to a fluvial deposit with more than 0.5 m of grey silt

and sand, including dispersed quartzitic pebbles. The upper layer is a slackwater deposit with 0.2–0.4 m of fine laminated clay and silt with less than 5% of pebbles of limestone and quartzite. The upper layer contains the studied remains of small mammals and macromammals, including the cave lion, whose bones were distributed from the top to the bottom of the layer. This bone distribution points to the lion being coeval with the deposition of the upper layer, which also contains the micromammals. Thus, the age of the paleontological site is considered to be that of the lion remains.

The geomorphological study of the cave allowed us to reconstruct the formation of the cavity and its paleontological site. Groundwater flow originated the phreatic/epiphreatic passages of the cave, which were later affected by fluvial incision, resulting in the development of vadose canyons. After this, the cave was filled almost completely by fluvial terrigenous sediments (lower layer) derived from the erosion of the nearby Ordovician quartzite. According to Ballesteros et al. (2017), these sediments would come from the alluvial fans that covered the limestone marine terraces at ~65 ka. This infill was partially eroded and rock fall processes occurred along the entrance sector, probably related to the development of the entrance shaft. In this moment, the cave would connect with the topographic surface allowing macrofauna to fall into the cavity. The current position of this macromammal assemblage in the debris cone of the shaft reinforces the role of the shaft as a natural trap (Fig. 2).

The paleontological site was formed by the fall of the large mammals around 16 m into the cave. Macro and micromammal remains were deposited over a temporal pond formed by the accumulation of infiltration water. In this pond, the slackwater deposit (upper layer) was formed by clay and silt decantation, trapping all the studied fossil remains.

Regarding the small mammals, almost all the remains recovered from the upper layer (>98% of M_1 and 100% of incisors) lack any digestion evidence, suggesting that they died in the cave accidentally or naturally. Only a single tooth (*Clethrionomys glareolus* M_1) showed signs of moderate digestion suggesting that it was accumulated by a predator. Thus, since no long-distance transport of the remains by a predator is assumed, this small mammal association is considered as representative of the surroundings of the cave. This is of special relevance since all other small-mammal assemblages here compared to TL were accumulated by predators, so they represent a wider geographic area (the predator territory) and are biased by their specific feeding preferences (Andrews, 1990; Fernández-Jalvo et al., 2016).

The ^{14}C dating of the cave lion yielded an age of 43.0 ± 0.5 cal ka BP (Fig. 3) for the paleontological site. The paleoenvironmental and regional context of this episode is discussed in Section 6.

5. Systematics: results and discussion

5.1. Large mammal assemblage

The large-mammal assemblage is composed exclusively by carnivores, which are ascribed to five species: two large felids (*Panthera spelaea* and *P. pardus*), one canid (*Canis lupus*) and two mustelids (*Mustela nivalis* and *M. putorius*). Most of the remains (79%) correspond to the cave lion skeleton. Measurements of the large mammal elements are provided in Tables S1–S11 (Appendix B, Supplementary data). Comparative morphometric information of the large mammals is included in Figs. 5, 6, 8–11 and Figs S1–S9 (Appendix C, Supplementary data).

Order Carnivora, 1821
Family Felidae Fischer, 1817

5.1.1. *Panthera spelaea* Goldfuss, 1810

The lion from TL provided 169 remains (see Section 3.2), corresponding mainly to the skull, mandible and forelimbs (Fig. 4). A de-

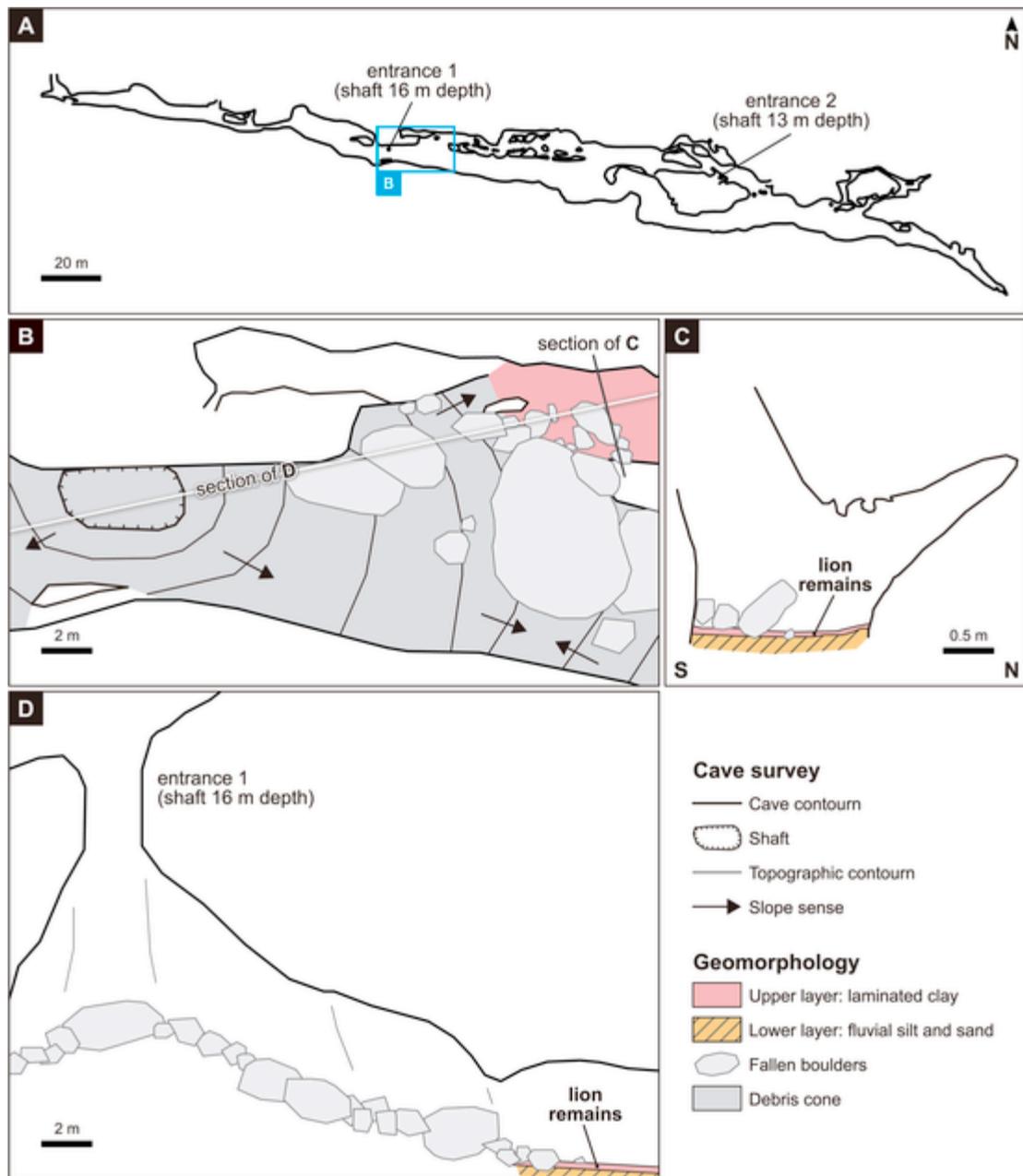


Fig. 2. Cave survey of Torca del León carried out by Sociedad Espeleológica y Barranquista Escar. B, Geomorphological map of the entrance sector that hosted the paleontological site. C, Section of B showing the cave entrance, the debris cone and the position of the paleontological site. D, Section of the paleontological site within the upper layer made of laminated clay and slit.

tailed comparative revision of the material, including measurements of the elements, as well as an estimation of the body weight of the individual, is provided in the following sections and in Tables S1–S5 (Appendix B, Supplementary data). Morphometric data were compared with an extensive sample from Europe and Siberia, detailed in the captions of Figs. 5 and 6 and Fig. S1–S6 (Appendix C).

5.1.1.1. Cranium, mandible and dentition Two main regions of the skull (TL-1) are preserved: a rostral area and most of the neurocranium (Fig. 4a–c). The rostral region includes the premaxilla, the majority of the right maxilla, part of the left maxilla, and most of the upper dentition, including both dental series of I^3 , upper canine, P^4 , and the left P^3 (all of them well preserved). The neurocranium fragment comprises most of the frontal bones, the parietals (including the sagittal crest), the temporal bones (including the mastoid area) and the occipital region (comprising the occipital condyles). Cranial sutures are completely

fused and the sagittal crest is well developed. Teeth are fully erupted and show slight-medium wearing. Both dental development and cranial sutures suggest that this lion specimen was an adult. Twenty-two metric variables were taken from the skull (Table S1). Measurements have been compared to a sample of Middle and Late Pleistocene skulls from Europe and Siberia: the neurocranium length and the skull width at the canines' level are plotted in Fig. 5A. Apart from the extremely large skulls from Mokhnevskaya (Russia) and San River (Poland) (represented by the two isolated dots in the upper part of the graph), most of the specimens are spread in a continuous scattering. The neurocranium length from TL falls outside (slightly below) the average values of the total sample, whereas the facial width (at the canines' level) is slightly over the mean values of the sample. The width at the mastoid area vs. the neurocranium length of TL was also plotted (Fig. 5B), showing a noticeable wideness in this area in comparison to the other speci-

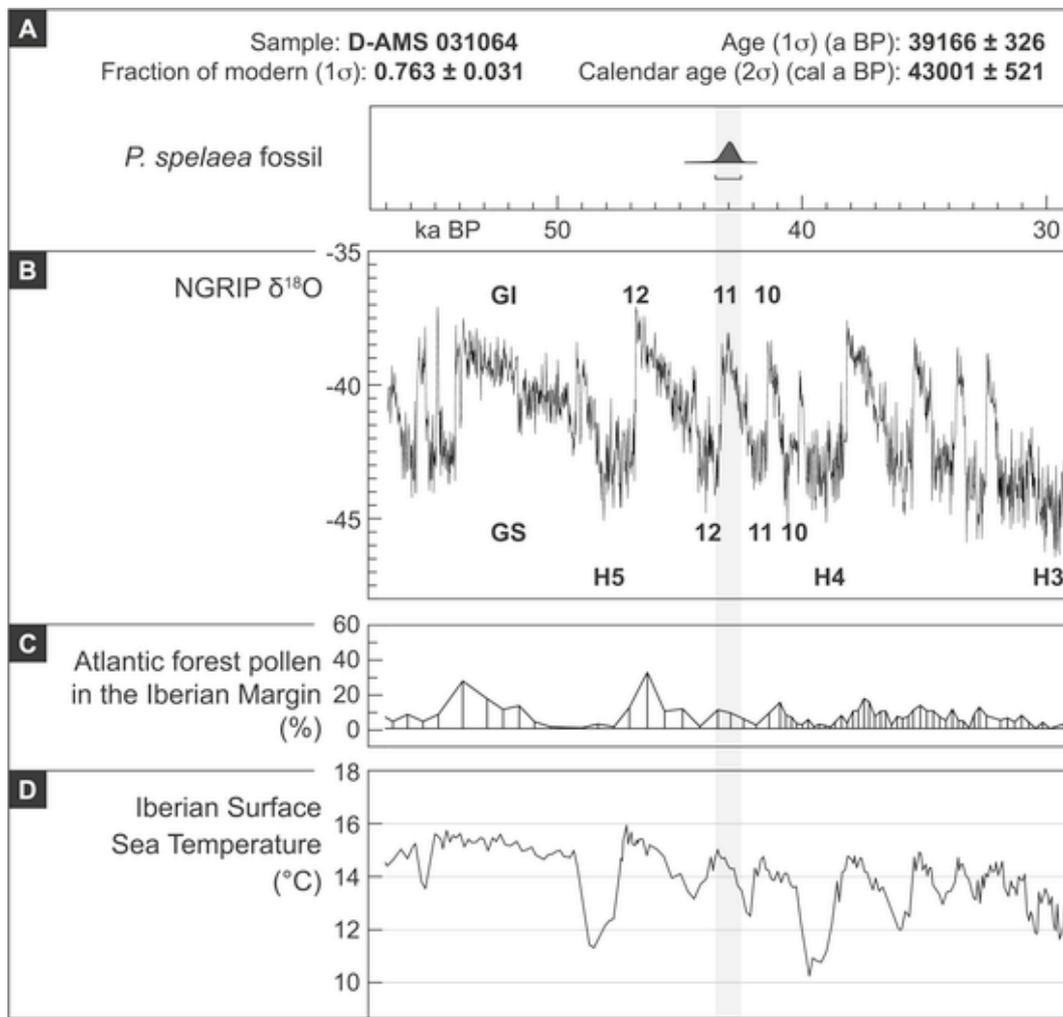


Fig. 3. (A) Radiocarbon date of the *P. spelaea* remains from Torca del León. (B) NGRIP $\delta^{18}\text{O}$ (North GRIP Members, 2004). GI: Greenland Interstadial; GS: Greenland Stadial; H: Heinrich Event. (C) Atlantic forest pollen percentage in the Iberian margin cores MD03-2697 and MD99-2331 (42°N, 9°W) (Sánchez-Goni et al., 2008). (D) 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). The position of the all cores is shown in Fig. 1A.

mens. Sotnikova and Nikolskiy (2006) analysed this trait as systematically relevant, concluding that the skull of the Middle Pleistocene species *P. fossilis* is proportionally narrower over the canines and in the mastoid region than that of *P. spelaea*. Following this criterion, the skull from TC is closer to *P. spelaea*. Measurements for the lion's upper dentition are expressed in Table S3. Following Turner (1984), Eurasian cave lions were sexually dimorphic, as recent lions are. This author found a size division in the upper canine between males and females. We compared the size of the upper canines from TC with a sample of other 83 upper canines from diverse European and Siberian sites (Fig. 6A). All specimens spread in two main size groups. The upper canines from TC are among the lower values of the larger group. If we assume that the larger group corresponds to males and the smaller to females, the individual from TC might correspond to a male. The upper carnassial (P^4 , Fig. 4f-i) is an interesting element with systematic significance. A bivariate plot graphs the relationship between the length and width of the P^4 measured on the TC specimen and on a sample of 47 Middle and Late Pleistocene specimens from Europe and Siberia (Fig. 6B). The TC specimen falls within the middle part of the dispersion but over the mean value. Morphologically, the P^4 from TC shows slightly developed preparastyles, which following Sotnikova and Nikolskiy (2006) is indicative of *P. spelaea* and different of the Middle Pleistocene *P. fossilis*, which does not present a preparastyle. An incipient cingulum anterior to the preparastyle is also present. The metastyle is slightly

longer than the paracone (Table S3): Following Sala (1990), Sotnikova and Nikolskiy (2006) and Marciszak and Stefaniak (2010), this is a typical and diagnostic feature for *P. spelaea* and is different from *P. fossilis*, which tends to reverse the values in this ratio. This trait is graphically represented in Fig. 6C, where most Late Pleistocene specimens, including the TL ones, plot above the pointed line (indicating that their metastyle is longer than their paracone), while almost all P^4 corresponding to the older part of the Middle Pleistocene (mostly ascribed to *P. fossilis*) are below the line. The shape of the P^4 buccal side (in occlusal view) is sinusoidal, also a feature typical of *P. spelaea* and different with respect to *P. fossilis*, in which it is more straight-shaped, as accepted by Schütt (1969a), Sala (1990) and Marciszak and Stefaniak (2010). The mandible (TL-2) preserves both branches (Fig. 4d and e): the right one is almost complete except for the coronoid process, which is broken, and the anterior edge, which is somewhat damaged; the left ramus lacks a significant portion of the posterior end. The left and right lower canines, P_3 , P_4 and M_1 , as well as the left I_3 , are well preserved. The right ramus provided sixteen measurements (Table S2), two of which (maximum length and height of the horizontal ramus behind M_1) have been compared with 28 other mandibles from Europe and Siberia (Fig. S2). The specimen from TL falls in the middle part of the dispersal, slightly over the average values. As shown in the graph (Fig. 6D), a comparative analysis of the lower carnassials (M_1 , Fig. 4j-m) from TL with a diverse sample ($n = 116$) from Eu-



Fig. 4. *Panthera spelaea* cranial and postcranial remains from Torca del León. Partial skull (TL-1) in right lateral (a), dorsal (b) and ventral (c) views; right mandible (TL-2) in lateral (d) and occlusal (e) views; left P³-P⁴ series in labial (f) and occlusal (g) views; right P⁴ in labial (h) and occlusal (i) views; left P₃-M₁ series in occlusal (j) and labial (k) views; right P₃-M₁ series in occlusal (l) and labial (m) views; left humerus (TL-8, TL-9) in anterior view (n); left ulna (TL-15) in medial view (o); left radius (TL-13) in medial view (p); right tibia (TL-37) in medial view (q); left metacarpals I (TL-24) (r), II (TL-25) (s), III (TL-26) (t), IV (TL-27) (u) and V (TL-28) (v) in dorsal view; metatarsals right II (TL-40) (w), left III (TL-41) (x) and right IV (TL-42) (y) in dorsal view; proximal phalanges (TL-43, TL-44, TL-45, TL-46, TL-47) (z-ad) in dorsal view; middle phalanges (TL-56, TL-59, TL-60) (ae-ag) in dorsal view; distal phalanges (TL-65, TL-66, TL-67) (ah-aj) in lateral view. Scale bars are in cm.

rope and Siberia was performed. The length of the TL specimens (Table S3) falls within the mean range, whereas width is slightly below the mean. This element has a systematic significance: following Schütt and Hemmer (1978), the M₁ of *Panthera leo fossilis* is proportionally broader than that of *P. l. spelaea*. Specimens from TL are noticeably narrower (Fig. 6D), which supports their attribution to *P. spelaea*.

5.1.1.2. Postcranial skeleton Vertebrae remains include the atlas, three cervical and five thoracic vertebrae and other 23 small fragments of vertebrae, all of them too poorly preserved to provide any reliable mea-

surements. A total of 65 rib remains, all severely fragmented, were also recovered. Scapulae fragments include both (left and right) glenoid process, however, their preservation is poor, not yielding significant measurements. All preserved limb bones (Fig. 4n-aj) show complete epiphyseal fusion, supporting the attribution of the TL individual to an adult. The left humerus (TL-9) includes two main portions (Fig. 4n), but due to fragmentation only a few measurements could be taken (Table S4). The left radius (TL-13) and ulna (TL-15) are remarkably well preserved (Fig. 4o-p, Table S4). Seven carpal bones were found: left and right scapholunate, left and right hamate, left capitate and

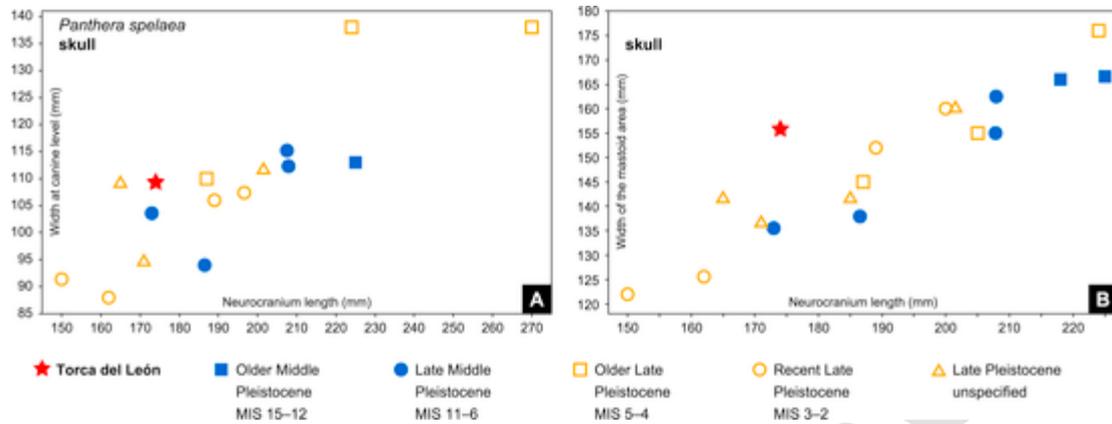


Fig. 5. Bivariate plots of *P. spelaea* skull neurocranium length/width at the canine level (A) and neurocranium length/width of the mastoid area (B) of the Torca del León specimen (TL-1) in comparison with other Pleistocene populations from Europe and Siberia. The older Middle Pleistocene specimen comes from Mauer; late Middle Pleistocene specimens come from Azé, Romain-la-Roche and Petralona PEC 90; older Late Pleistocene specimens come from L'Herm, Mokhnevskaya and San River; recent Late Pleistocene specimens come from Siegsdorf, Gailenreuth, Duvany Yar, Arrikrutz, Uzbur, and Altai. Sources: Schütt (1969a); Bonifay (1971); Kurtén and Poulíanos (1977); Clot (1980); Altuna (1981); Argant (1991, 2010); Gross (1992); Baryshnikov and Boeskorov (2001); Baryshnikov and Tsoukala (2010) and Marciszak et al. (2014). For an individual identification of each specimen/site, see Fig. S1, Appendix C.

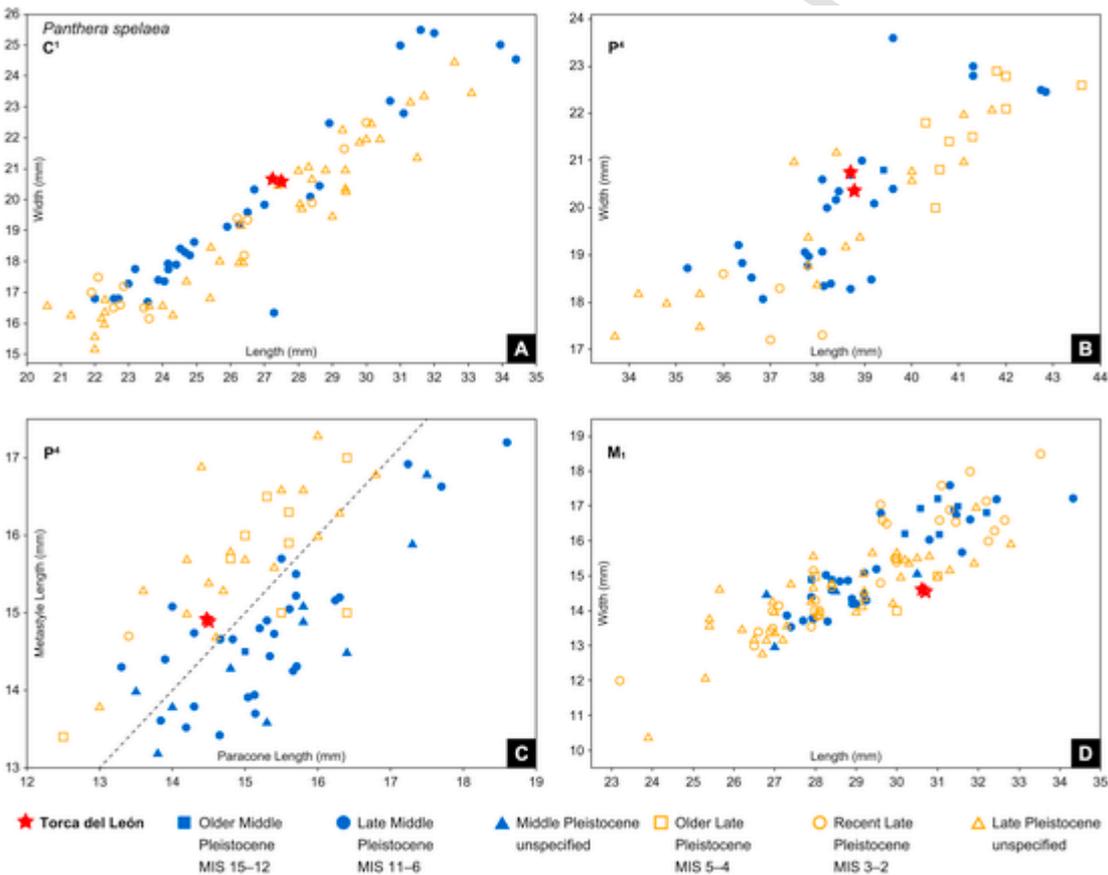


Fig. 6. Bivariate plots of *P. spelaea* teeth from Torca del León in comparison with other Pleistocene populations from Europe and Siberia: C¹ length/width (A), P⁴ length/width (B), P⁴ paracone length/metastyle length (C), and M₁ length/width (D).

left pisiform (measurements in Table S5). All 10 metacarpals were recovered in good conditions (Fig. 4r–v, Table S4). Elements of the hind limbs are very scarce and fragmentary. The femur only provided a fragment of diaphysis. A right patella and the distal epiphysis of a right fibula were also found (measurements in Tables S4 and S5). The right tibia (TL-38) was recovered with proximal and distal epiphyses damaged (Fig. 4q), so only a few measurements could be taken (Table S4). Three metatarsals were found in good conditions: right second, left third and right fourth (Fig. 4w–y, Table S4). A total of 27 phal-

anges, including 13 proximal, 9 middle and 5 incomplete distal ones (Fig. 4z–aj, Table S4), were also recovered. The dimensions of the radius, metacarpals II and V, and tibia were compared with a sample from Europe and Siberia (Figs. S4, S5 and S6). In all cases, the postcranial elements from TL are located in the middle part of their corresponding dispersions, slightly below the average values.

5.1.1.3. Body weight predictions The abundance of fossil teeth in the fossil record has inevitably resulted in an extensive use of dental dimensions (mostly carnassials -P⁴/M₁- length and canine diameter)

in studies focused on predicting body mass (Gingerich, 1977; Smith, 1984; Van Valkenburgh, 1990). However, individual teeth, despite their frequent occurrence in assemblages, show a looser relationship with body size, and therefore appear less useful for size estimations of fossil material than has been thought (Turner and Regan, 2002). The use of postcranial elements in predicting body mass has been recently found to be better for this purpose, as the forces acting on the limbs of an animal are proportional to the weight the limbs have to support (Alexander, 1991). The shape of humerus and femur are generally well-predicted by trends in average-limber felids. However, Anyonge (1993) suggests that larger-bodied felids increase in humeral robustness. In contrast, the radius of lions (and tigers) is somewhat different from that of other extant felids. The measurements on bone midshafts (depth -anteroposterior- and breadth- mediolateral-) do not follow a trend, requiring more depth than expected for their body size. This anomaly may be related to the load-bearing of ulna and radius in lions. As we do not use midshafts for the estimations, the epiphyses follow a similar pattern, resulting extremely “flat” for a given breadth. The result is that the radius does not seem to provide the best estimate. When comparing the coefficient of correlation (R) all variables are over 0.9, although the humerus shows a better correlation ($R_{\text{humerus}} = 0.98$ compared to $R_{\text{radius}} = 0.97$ and $R_{\text{tibia}} = 0.97$). Comparing the coefficient of determination (R^2), the humerus is only slightly smaller when compared to the others: $R_{\text{humerus}} = 0.97$ compared to $R_{\text{radius}} = 0.94$ and $R_{\text{tibia}} = 0.94$. While R and R^2 are often poor indicators of the robustness of a predictive equation, the Standard Error of Estimate (SEE) helps to assess how accurate they are (Van Valkenburgh, 1990; Figueirido et al., 2011). Looking at the SEE in each of the variables used for estimations, the humerus has lower values (0.10) when compared to radius and tibia (0.13 or 0.12 in all cases). This points to the humerus, in the absence of the femur, as the best candidate to estimate the weight in this particular lion specimen from Torca del León. This is in accordance with Figueirido et al. (2011)'s analyses that conclude that regression equations derived from distal limb segments (tibia, radius and ulnae) are worse predictors of body mass than those calculated from proximal ones (femur and humerus); the best mass predictor would be the one derived from femoral dimensions (more specifically the mediolateral diameter at midshaft). The *Panthera spelaea* from TL is estimated to have weighed about 360 kg (Table 2). Guzvica (1998) presented a range of cave lion weights of Middle to Late Pleistocene age. The largest body weights can reach 360 kg and are characteristic of *P. leo fossilis*, dating to the Middle Pleistocene. However, the lion weights from Guzvica (1998) are calculated from M_1 , which, as discussed above, is a less adequate predictor for body weight than postcranial elements. Moreover, no ratio estimator (RE) is applied to the analyses to reduce the underestimate in Guzvica (1998); for the RE results in this work, see Appendix A. A felid of such enormous size as the Torca del León specimen, similar to a large living brown bear,

was the best candidate for preying on the largest ungulates in the ecosystem (Cuff et al., 2015).

5.1.1.4. General discussion on the TL lion, its taxonomy and the Iberian context The lion from TL, as above specified, preserves features of systematic relevance in skull and teeth: the skull is proportionally broad with respect to its length; the upper carnassial (P^4) shows a slightly developed preparastyle, has a sinusoidal shape in the labial side (in occlusal view), and its metastyle is longer than the paracone; the lower carnassial (M_1) is noticeably narrow. In sum, all these traits are indicative of *P. spelaea* and different from the Middle Pleistocene *P. fossilis*, which is consistent with its radiocarbon dating. Sexing of the specimen points to it possibly being a male. Morphometrically, the cranial and postcranial elements of the TL lion are among the average size ranges of a comparison sample of Pleistocene populations from Europe and Siberia, often slightly under the mean values. Body weight estimation provided a value of about 360 kg. The great fossil lion that lived in Eurasia during the Late Pleistocene has been considered in the previous literature as both *Panthera leo* and *Panthera spelaea* (= *Felis spelaea* Goldfuss 1810) (Schütt, 1969a, 1969b; Hemmer, 1974, 2011; Turner, 1984; Sala, 1990; Baryshnikov and Boeskorov, 2001). In the past three decades, Eurasian cave lions have usually been treated as a subspecies of *P. leo*, *P. leo spelaea* (Kurtén, 1985; Argant, 1991), or even a chronosubspecies *P. s. spelaea* (Marciszak et al., 2014). This plethora of subspecies names associated with the *Panthera* species is also common in the North American lion specimens: *P. atrox* Leidy, 1853 (Harington, 1969), *P. leo atrox* (Harington, 1977, 1996) or *P. atrox alaskensis* (Frick, 1930). In addition to traditional classifications, molecular studies can help to clarify taxonomic problems. Phylogeographic studies of extant lion (Barnett et al., 2014, 2016; Bertola et al., 2016) indicate that lion haplotypes diversified at about 120.2–384.8 ka (divergence estimate of 244.8 ka; Bertola et al., 2016). Now most authors (including this work) consider *Panthera spelaea* a Holarctic lion species of large size that was widespread across northern Eurasia and Alaska/Yukon during the Late Pleistocene (Sotnikova and Nikolskiy, 2006; Stuart and Lister, 2011) and closely related (according to the DNA data) to an extinct subspecies of the modern African lion (Burger et al., 2004). Cave lions are present in the Iberian Pleistocene since the Middle Pleistocene and persisted in the form of *P. spelaea*, basically restricted to its northern area (Castaños, 2005), during the Late Pleistocene and up to the last Tardiglacial. The Holocene expansion of modern lion (*P. leo*) into south-east Europe reoccupied part of the former range of *P. spelaea* (Stuart and Lister, 2011), but the Late Pleistocene temporal and geographical relationships of the two species are unknown. Extinction across Eurasia of cave lion occurred in the interval ca. 14–14.5 cal ka BP while modern lions invaded south-eastern Europe during the Holocene, presumably via the Bosphorus from Turkey, perhaps as early as 8.0 cal ka BP and probably by ca. 6.5–6.0 cal ka BP (Stuart and Lister, 2011). The possible co-occurrence of *P. spelaea* and *P. leo* in the Iberian Peninsula has been considered

Table 2

Estimated body weight of the lion from TL, based in measurements of different limb bones. Abbreviations: R - coefficient of correlation; R^2 - coefficient of determination; SEE - standard error of estimate; RE - ratio estimator; EW - estimated weight.

Element	Variable used for estimation	Value (mm)	Log (value)	R	R^2	SEE	Estimated weight (kg)	RE (Felidae)	EW x RE
Humerus	Greatest Proximal Depth	106.2	2.02	0.98	0.97	0.10	315.2	1.14	360.2 kg
Tibia	Greatest Proximal Depth	96	1.98	0.972	0.94	0.13	263.3	1.8	473.4 kg
	Greatest Distal Depth	47.5	1.67	0.976	0.95	0.12	394	1.5	591 kg
Radius	Greatest Proximal Width	49.4	1.69	0.972	0.94	0.13	368	1.4	515 kg
	Greatest Proximal Depth	37.9	1.57	0.974	0.94	0.12	214.6	1.9	406 kg
	Greatest Distal Width	65	1.81	0.969	0.93	0.14	253	1.7	430 kg

by Masseti and Mazza (2013) based on the chronological attributions of the La Riera Cave (9600–7000 years old; Altuna, 1986) and Urriaga Cave (17.03 cal ka BP; García Morales, 1984–1985). The doubtful time-ranges of the Spanish lion-bearing deposits considered in Masseti and Mazza (2013) suggest to these authors two possible scenarios: either modern lions arrived in Europe earlier than assumed, or cave lions were uninterruptedly present in Western Europe surviving up until the latest Pleistocene during the Pleistocene/Holocene transition. However, although considering those hypotheses, with the absence of accurate chronologies for these lion evidences, we must analyze the most likely scenarios with supporting data. An important amount of data supports the suggested chronology for the cave lion extinction in Eurasia, at ca. 14–14.5 cal ka BP, and the subsequent expansion of modern lions into south-eastern Europe, at about 8.0–6.0 cal ka BP (Stuart and Lister, 2011). This chronology is consistent with the Iberian cave lion remains from La Garma (Cantabria), radiocarbon dated to 14.3–14.0 cal ka BP (Cueto et al., 2016). Moreover, these fossils evidence the exploitation of lion by humans during the Middle Magdalenian, which could help explain the role of hunting on the cave lion extinction in Eurasia.

5.1.2. *Panthera pardus* Linnaeus, 1758

Leopard provided 34 remains corresponding to a single individual (Fig. 7a–p). Among the dentition, only the right P⁴ (TL-168) was well preserved (the left P⁴ was also recovered but in poor conditions). Measurements of this specimen (Table S6) were compared to a sample of other 58 P⁴ (43 fossils from Europe and 15 modern specimens from Asia and Africa, Fig. 8). The size of the specimen from TL is remarkably small (length = 23.33 mm), plotting among the lower values of the fossil compilation, close to the smallest specimens from Avenc Joan Guitón (23.2–23.3 mm; Sanchís et al., 2015) and Torrejones (22.6 mm; Arribas, 1997) in Spain, Algar de Manga Larga (23.7 mm; Cardoso and Regala, 2006) in Portugal, Mauer (23.4 mm; Schütt, 1969a) and Mosbach (23.7 mm; Testu, 2006) in Germany, and Equi (22.63, 23.17 and 23.32 mm; Ghezzi and Rook, 2015) in Italy (specimens from Avenc Joan Guitón and Equi are not plotted in Fig. 8 because width data were not provided). Such small size suggests that the TL specimen could correspond to a female. Morphologically, the P⁴ from TL (Fig. 7o–p) shows a not very prominent deuterocone. The crown is high (maximum height, 11.97 mm) and the parastyle is round-



Fig. 7. Carnivore (except *Panthera spelaea*) cranial and postcranial remains from Torca del León. *Panthera pardus*: left humerus (TL-176) in anterior view (a); right ulna (TL-179) in lateral view (b); right radius (TL-177) in lateral view (c); right femur (TL-183) in posterior view (d); left tibia (TL-185) in anterior view (e); right fibula (TL-186) in posterior view (f); right metacarpal III (TL-181) in dorsal view (g); left metatarsals II (TL-191) (h) and IV (TL-192) (i) in dorsal view; proximal phalanges (TL-193, TL-194) in dorsal view (j–k); middle phalanx (TL-198) in dorsal view (l); left talus (TL-187) in anterior view (m), left calcaneus (TL-198) in anterior view (n); right P⁴ (TL-168) in lateral (o) and occlusal (p) views. *Canis lupus*: right P⁴ (TL-200) in lateral (q) and occlusal (r) views; left premaxilla fragment (TL-201) with I² (TL-204), I³ (TL-205) and C¹ (TL-203) in lateral view (s). *Mustela nivalis*: skull fragment (TL-209) in anterior view (t); right mandible (TL-207) in occlusal (u) and lateral (v) views. *Mustela putorius*: left mandible (TL-210) in occlusal (w) and lateral (x) views. Scale bars are in cm.

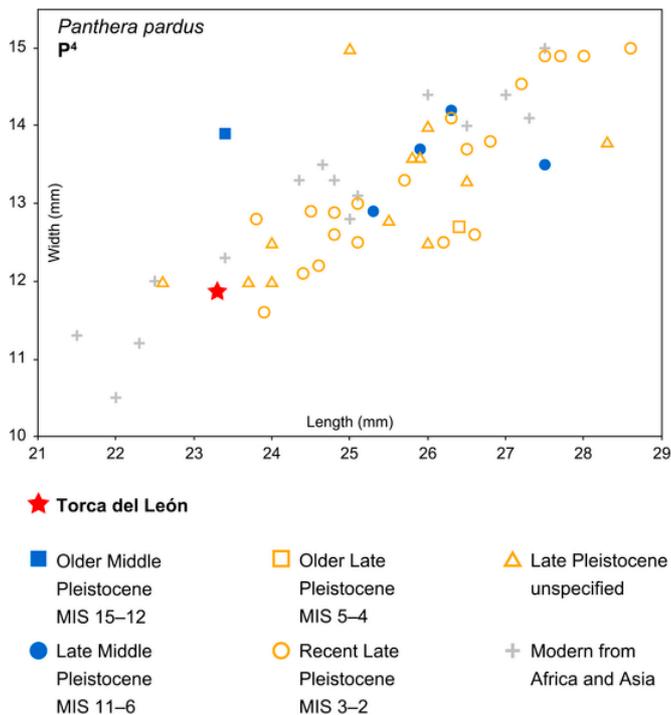


Fig. 8. Bivariate plot of *P. pardus* P⁴ length/width from the Torca del León right specimen (TL-168) in comparison with a recent sample and other Pleistocene populations from Europe. Modern specimens come from Africa and Asia; The older Middle Pleistocene specimen comes from Mauér; late Middle Pleistocene specimens come from Lunel Viel and Monte Sacro; the older Late Pleistocene specimen comes from Taubach; recent Late Pleistocene specimens come from Los Rincones, Abric Romaní, Bolinkoba, Aintzulo, Zafarraya, Figueira Brava, Escoural, Observatoire and Vraona; unspecified Late Pleistocene specimens come from Cova Negra, Torrejones, Algar da Manga Larga, Grotte des Enfants, Vence, Wildkirchli and Rübeland. Sources: Schmid (1949); Schütt (1969b, c); Bonifay (1971); Pérez Ripoll (1977); Kotsakis and Palombo (1979); Castaños (1983); Cardoso (1996); Arribas (1997); Nagel (1999); Cardoso and Regala (2006); Barroso Ruiz et al. (2006); Testu (2006); Altuna-Etxabe and Mariezkurrena-Gastearena (2013); Sanchís et al. (2015); Sauqué et al. (2016) and own data (N.G.). For an individual identification of each specimen/site, see Fig. S7, Appendix C.

shaped in lingual view, features which are considered typical of Late Pleistocene European leopards by authors such as Diedrich (2013) and Sanchís et al. (2015).

Among the postcranial elements, both radii, the right ulna, a distal fragment of the right tibia, a third metacarpal, the second and fourth metatarsals, as well as 3 tarsal/carpal elements and 7 phalanges

are reasonably well preserved (Fig. 7a–n, Tables S7 and S8). Measurements of the right radius (TL-77) and right third metacarpal (TL-181) are plotted in Fig. S8 in comparison with a sample of Pleistocene specimens from Europe. In both cases, measurements of the TL specimens are placed below the average values of the dispersal. The radius size is smaller than the specimens attributed to females published by Diedrich (2013); only the individual from Avenc de Joan Guitón is even smaller. In sum, the well-preserved P⁴ and the postcranial elements indicate that the leopard from TL is a small sized individual, most probably corresponding to a female.

The robustness index (SD/GL x 100) calculated in the metapodials yielded values of 13.47 for the right Mc III, 12.22 and 11.37 for right and left Mt II respectively, and 11.75 for the left Mt IV. These values match the ones from Late Pleistocene populations from Vraona (Greece; Nagel, 1999), Equi (Italy; Diedrich, 2013), Los Rincones (Spain; Sauqué et al., 2016), Avenc de Joan Guitón (Spain; Sanchís et al., 2015) and Lezetxiki (Spain; Altuna, 1972) and are noticeably greater than the ones from extant *P. pardus* provided by Nagel (1999).

Family Canidae Fischer, 1817

5.1.3. *Canis lupus* Linnaeus, 1758

Wolf yielded one right maxilla fragment with P⁴ and M², one premaxilla fragment and five isolated teeth (three incisors, the right upper canine and a portion of the left P⁴), all of them corresponding to a single individual (Fig. 7q–s). Slight wear at the incisors and canine as well as no visible wear in the P⁴ suggest that the specimen was about two years old at death, following the criteria of Gipson et al. (2000).

Measurements of the right P⁴ (TL-201, Table S9) have been compared to a sample of other 171 specimens from Pleistocene sites from Western Europe (Fig. 9A). A clear segregation is present between smaller Middle Pleistocene specimens and larger Late Pleistocene ones, although with a wide overlap area. Boudadi-Maligne (2010) remarks a trend of continuous increase in wolf body size through the Late Pleistocene, reaching maximum values during MIS 3 at the populations from Jaurens, Malldidier and Igue du Gral. For these larger-bodied populations, she defined the new subspecies *Canis lupus maximus*. The length of the TL specimen falls within the mean range of the Late Pleistocene populations' dispersal, while the width is visibly greater than the mean, reflecting high robustness.

The left upper canine (TL-204) was also compared to a sample of other 164 specimens from Western Europe (Fig. 9B). Again, a separation between Middle and Late Pleistocene populations, including a significant overlap area, is recognized. The canine from TL falls into the mean range of the late Pleistocene populations' dispersal.

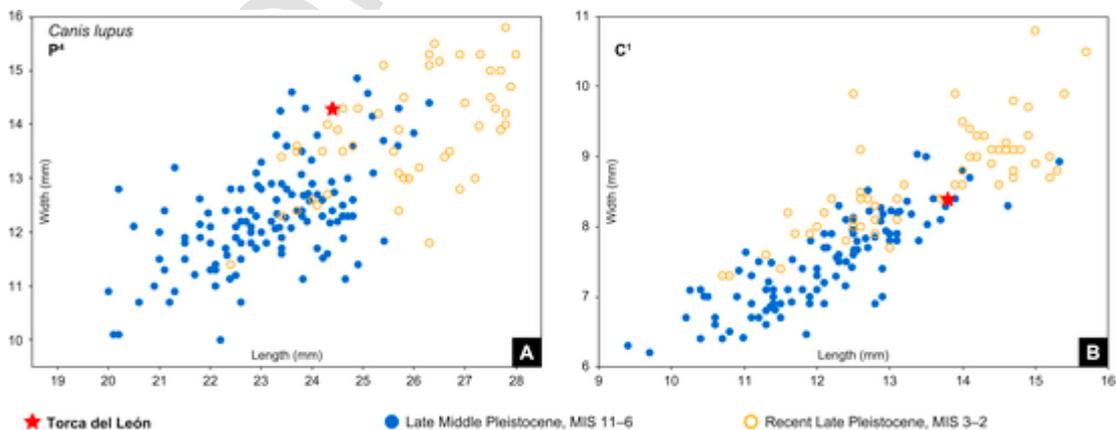


Fig. 9. Bivariate plots of length/width ratios for *C. lupus* P⁴ (A) and C¹ (B) from the Torca del León specimens (TL-200, TL-203) in comparison with other Pleistocene populations from Western Europe. Late Middle Pleistocene specimens come from Lunel Viel, Romain-la-Roche, Igue-des Rameaux, La Fage and Coudolous; recent Late Pleistocene specimens come from Aven de l'Arquet, Jaurens, Malldidier, Igue du Gral, Lezetxiki and Labeko Koba. Sources: Altuna (1972); Castaños (1986); Altuna and Mariezkurrena (2000); Argant (2010) and Boudadi-Maligne (2010). For an individual identification of each specimen/site, see Fig. S9, Appendix C.

Family Mustelidae Fischer, 1817

5.1.4. *Mustela nivalis* Linnaeus, 1766

Three cranial remains of a small mustelid, comprising a complete right mandible, a fragmented left mandible and the rostral area of a skull (Fig. 7t–v), all of them belonging to a single individual, have been recovered.

The smallest mustelids *M. erminea* and *M. nivalis* are not easy to distinguish: both species are very similar morphologically; morphometrically, while on average the stoat (*M. erminea*) is larger than the weasel (*M. nivalis*), both are extremely variable depending on geographical variation, pronounced sexual dimorphism, altitude and local environmental conditions (Marciszak, 2016; Marciszak and Socha, 2014; Marciszak et al., 2017a, b; Crégut-Bonnoure et al., 2018).

For morphometrical purposes, the small mustelid from TL (measurements in Table S10) was compared to other Pleistocene weasel and ermine populations from Western Europe (Fig. 10). The size of the M_1 from the study site (TL-207) falls into the range of *M. nivalis*, near the greatest values of the dispersal.

Morphologically, Rabeder (1976), Marciszak and Socha (2014), Marciszak (2016) and Crégut-Bonnoure et al. (2018) indicated that M_1 of *M. erminea* shows a longer trigonid and a more reduced talonid than *M. nivalis*. Thus, these authors consider the ratio M_1 talonid length to M_1 trigonid length a useful trait for separating both species: in *M. erminea* the average value of this ratio is 23–24, while in *M. nivalis* it exceeds 40 (Marciszak, 2016). The value of this ratio in the M_1 from TL is 48.6, falling clearly into the range of *M. nivalis*. In addition, Crégut-Bonnoure et al. (2018) provided a trait for the rostral area of the skull to distinguish both small mustelids: the nasal aperture in *M. erminea* is rounded, with the height comparable to

the breadth, while in *M. nivalis* this aperture is more oval, with the height exceeding the breadth. The average values for the width to height index of the nasal aperture proposed by Crégut-Bonnoure et al. (2018) is 100.4 for *M. erminea* and 90.8 for *M. nivalis*. The skull fragment from TL (TL-210, Fig. 7t) shows an oval-shaped nasal aperture (height 3.9 mm; width 3.5 mm), yielding a width/height index of 89.7, which is more comparable with the values of *M. nivalis*.

In sum, both morphometrically and morphologically, the small mustelid from TL is more comparable to the weasel, so it has been classified as *M. nivalis*. Its large size suggests that, most probably, it corresponds to a male.

5.1.5. *Mustela putorius* Linnaeus, 1758

A left mandible of a medium sized mustelid was recovered (Fig. 7w, x). This specimen (TL-211) preserves the lower canine, P_3 , P_4 and M_1 . The mandibular body, except for the presence of some erosion in the coronoid process, is well preserved. Its great robustness and the absence of P_1 are typical features of polecats (*Mustela putorius* Linnaeus, 1758/*M. eversmanii* Lesson 1827) and exclude the martens (*Martes martes* Linnaeus, 1758/*M. foina* Erxleben, 1777). While the current geographic distribution of the steppe polecat (*M. eversmanii*) ranges from Central and Eastern Europe to Western China, its Pleistocene dispersion reached also Northern and Western Europe (Krajcarz et al., 2015), including a number of sites in France (Hugueneu, 1975; Crégut-Bonnoure and Guérin, 1982; Delpech, 1989; Fosse and Fourvel, 2010; Fourvel et al., 2015; Crégut-Bonnoure et al., 2018). The potential occurrence of this species at TL, then, should not be rejected.

According to Marciszak et al. (2017a) and Crégut-Bonnoure et al. (2018), two polecat species are similar in metric and morphologi-

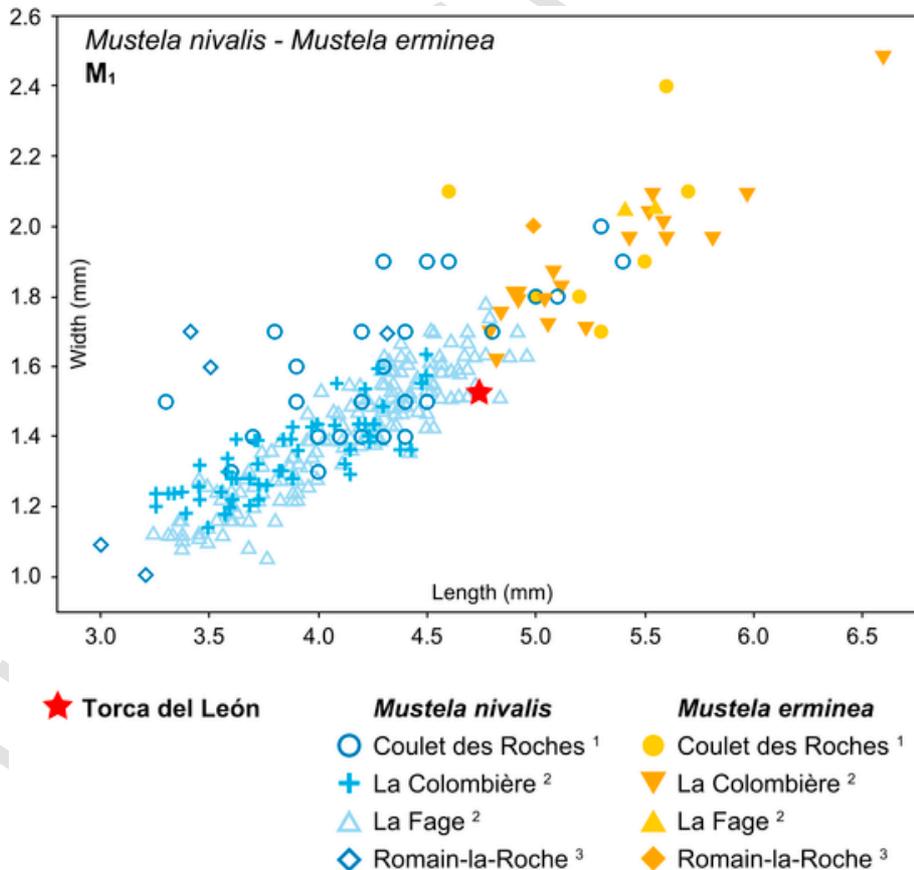


Fig. 10. Bivariate plot of *M. nivalis* M_1 length/width from Torca del León (TL-207) in comparison with other Pleistocene populations of *M. nivalis* and *M. erminea* from Western Europe. Sources: 1, Crégut-Bonnoure et al. (2018); 2, Hugueneu (1975); 3, Fosse and Fourvel (2010).

cal values. The most distinctive features are provided by the skull, mandible and teeth.

Morphometrically, the size of the TL specimen is very large (measurements in Table S11). The mandible is 44.4 mm in length, reaching the size of the largest *M. putorius* mandible from Coulet des Roches (Crégut-Bonnoure et al., 2018). The length of the M_1 is also great: compared to a sample of *M. eversmanii/putorius* M_1 from Central and Western Europe (Fig. 11), the length of the TL specimen falls among the largest values. Marciszak et al. (2017b) indicated that, while *M. eversmanii* is on average larger than *M. putorius*, the extreme values in both species are almost the same, so direct measurements are not very useful for polecat identification.

Huguene (1975) noted that the mandible of *M. eversmanii* shows a bulge in the lower edge of the horizontal branch, under P_4 - M_1 , while this feature is absent in the mandible of *M. putorius*, whose lower edge is more regularly rounded. This trait is accepted by other authors such as Fosse and Fourvel (2010), Fourvel et al. (2015) and Krajcarz et al. (2015). The lower edge of the mandible from TL does not present this feature, resembling the shape of *M. putorius*.

Additionally, Crégut-Bonnoure et al. (2018) provided a list of other distinctive morphologic features in skull, mandible and teeth. Some of them are observable in the mandible from TL:

- The masseter fossa is shorter and shallower in *M. putorius* than in *M. eversmanii*: in the TL mandible, the masseter fossa is short, its anterior margin forms an open angle and does not reach the M_1 / M_2 border, agreeing with the morphology provided for *M. putorius*.
- M_1 is proportionally smaller with respect to P_4 in *M. putorius* than in *M. eversmanii*: the index of P_4 length to M_1 length in the TL mandible is 59.7, which is closer to the values indicated for *M. putorius*.
- The M_1 talonid is proportionally larger in *M. putorius* than in *M. eversmanii*: the index M_1 talonid length to M_1 total length in the TL specimen is 26.6, matching the values for *M. putorius*.
- P_4 is narrower in *M. putorius* than in *M. eversmanii*: the index of P_4 posterior width to P_4 length in the TL mandible is 57, close to the values provided for *M. putorius* by Crégut-Bonnoure et al. (2018).

Overall, while size is not generally considered as a reliable trait to identify polecat species, the morphology and proportions of the mandible from TL allow us to ascribe it to *M. putorius*. This is consis-

tent with the forested environmental conditions inferred by the micro-mammal association (see Section 6), since *M. eversmanii* prefers relatively dry habitats and avoids forests (Krajcarz et al., 2015).

5.2. Small mammal assemblage

The small mammal assemblage from TL comprises more than 1900 remains, 506 (27%) of which have been taxonomically identified (357 at species level), yielding a minimum number (MNI) of 47 individuals belonging to 14 taxa (Table 1; Fig. 12).

64% of the individuals belong to the order Rodentia, which is represented by the genera *Glis* (*G. glis*); *Apodemus* (*A. flavicollis* and *A. sylvaticus*); *Clethrionomys* (*C. glareolus*); and *Microtus* (*M. gr. Agrestis*), while 34% belong to the order Eulipotyphla, represented by the genera *Sorex* (*S. gr. coronatus-araneus* and *S. minutus*); *Neomys* (*N. fodiens fodiens* and *N. fodiens niethammeri*); *Crociodura* (*C. russula* and *C. gueldenstaedtii*); and *Talpa* (*T. occidentalis* and *T. europaea-aquitania*), and there is only one individual (2%) belonging to the order Chiroptera (*Rhinolophus euryale*).

Order Rodentia Bowdich, 1821

Family Cricetidae Fischer, 1817

5.2.1. *Microtus gr. agrestis* (Linnaeus, 1761)

Remains of this species include a complete maxilla, with both M^2 showing an additional triangle at the posterior part, and a left M_1 (Fig. 12a), whose marked asymmetry allowed us to differentiate it from the more symmetrical M_1 of *M. arvalis*.

Recently, based on highly divergent nucleotide sequences, the previous subspecies *M. a. lavernedii* and *M. a. rozianus* have been elevated to species status (Wilson et al., 2017). Although the distribution areas of their living populations are well-known, diagnostic skeletal morphologic features that allow a differentiation at species level have not yet been published. Thus, we assigned the material from TL to the *Microtus agrestis* group (*Microtus gr. Agrestis*), which includes the new taxa together with the nominal species.

5.2.2. *Clethrionomys glareolus* (Schreber, 1780)

Ten rooted-molars of *C. glareolus* (Fig. 12b-b') were recovered from TL. This arvicoline has also been cited in other MIS 3 assemblages from the Cantabrian Region: Covalejos (Sesé, 2005, 2017), Cobrante (Sesé, 2009) and El Conde (López-García et al., 2011), in all three cases related to forested and temperate environments.

Family Muridae Illiger, 1811.

5.2.3. *Apodemus flavicollis* (Melchior, 1834) and *Apodemus sylvaticus* (Linnaeus, 1758)

The occurrence at TL of four upper molar series containing the diagnostic first and second molars (Pasquier, 1974; Nores, 1988) (Fig. 12c and d) allowed us to make a confident identification of both species.

In addition, we performed a morphometrical analysis in a wider sample including all isolated M^2 (Fig. 13A) to know the relative abundances of each species. Following Pasquier (1974), a more elongated M^2 with a poorly developed or absent T9 would correspond to *Apodemus flavicollis*, while a more square-shaped M^2 with well-developed T9 would belong to *Apodemus sylvaticus*; we found 14 M^2 belonging to *A. flavicollis* and 15 to *A. sylvaticus* (see Fig. 13A).

According to Kmitlová and Horáček (2017), the absence of a T9 is a frequent feature in *A. flavicollis* from Central Europe while, conversely, a T9 is always observable in *A. sylvaticus* specimens from that region. The same happens in modern samples from the Cantabrian Region (Fig. 13B), although their size differentiation is not as clear as in Central European populations (Fig. 13B), as observed also by Niethammer (1969) and Nores (1989). Compared to a modern sam-

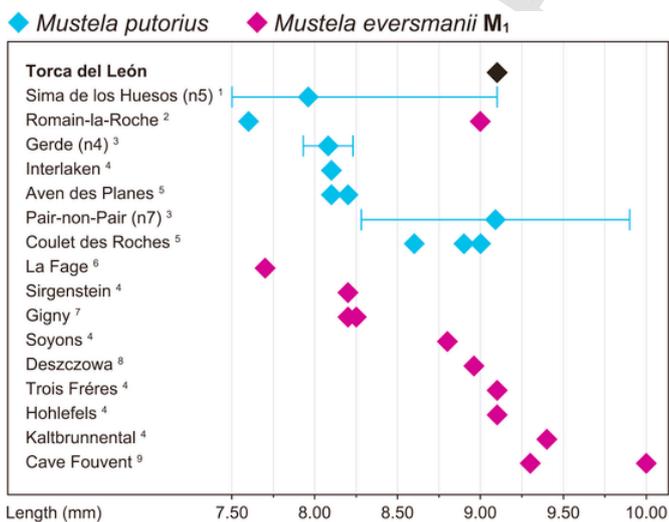


Fig. 11. Length of *M. putorius* M_1 from Torca del León (TL-210) in comparison with other Pleistocene populations of *M. putorius* and *M. eversmanii* from Europe. Sources: 1, García (2003); 2, Fosse and Fourvel (2010); 3, Clot (1980); 4, Koby (1964); 5, Crégut-Bonnoure et al. (2018); 6, Huguene (1975); 7, Delpech (1989); 8, Krajcarz et al. (2015); 9, Fourvel et al. (2015).

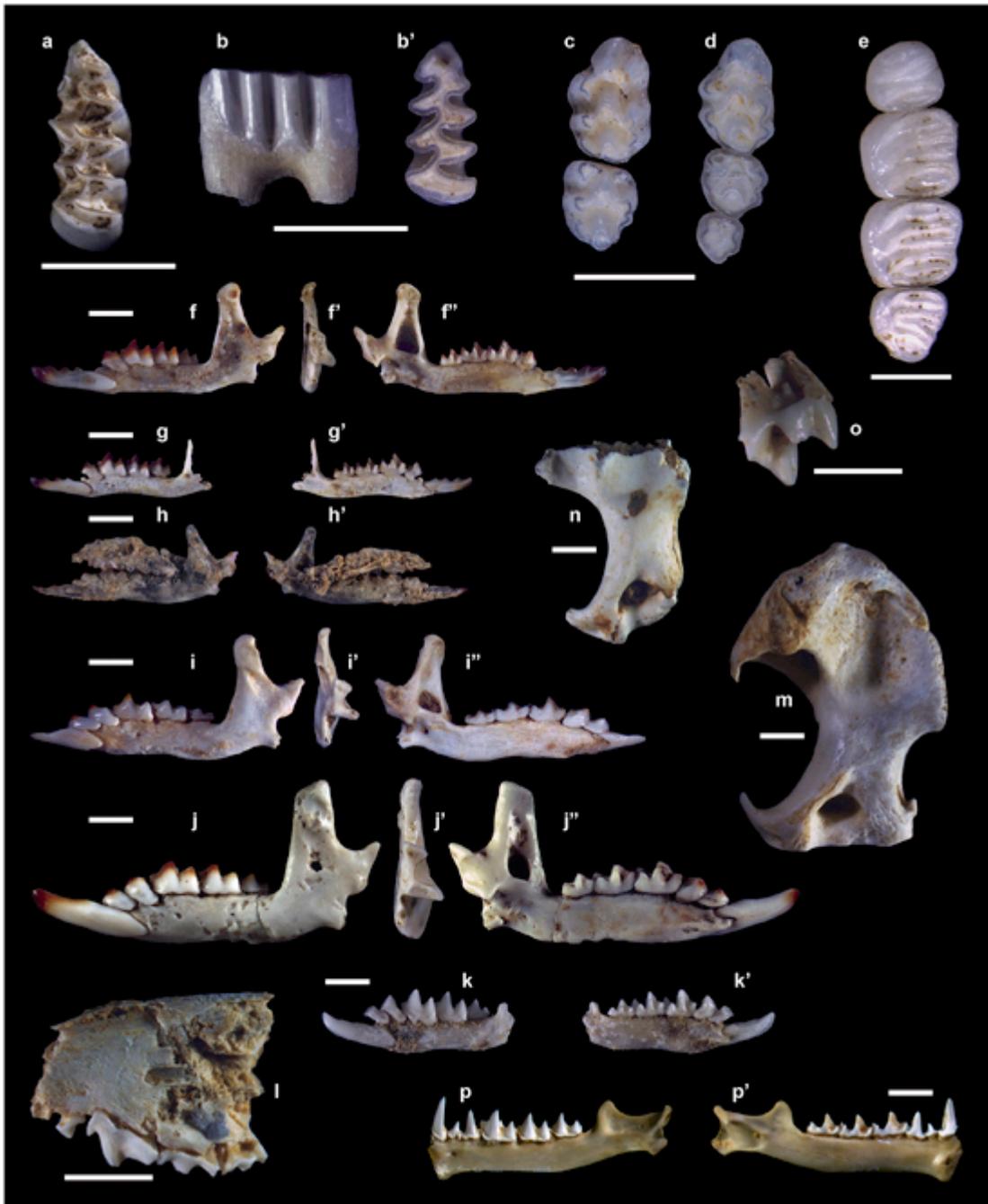


Fig. 12. Selected micromammal specimens from Torca del León. *Microtus* gr. *Agrestis*: left M_1 in occlusal view (a). *Clethrionomys glareolus*: left M_1 in labial (b) and occlusal (b') views. *Apodemus flavicollis*: left M^1 – M^2 in occlusal (c) view. *Apodemus sylvaticus*: left M^1 – M^3 series in occlusal (d) view. *Glis glis*: left P^4 – M^3 series in occlusal (e) view. *Sorex* gr. *coronatus-araneus*: left mandible in labial (f), posterior (f') and lingual (f'') views. *Sorex minutus*: left mandible in labial (g) and lingual (g') views, left mandible in anatomical connection with left maxilla in labial (h) and lingual (h') views. *Neomys fodiens fodiens*: left mandible in labial (i), posterior (i') and lingual (i'') views. *Neomys fodiens niethammeri*: left mandible in labial (j), posterior (j') and lingual (j'') views. *Crocidura gueldenstaedtii*: left mandible in labial (k) and lingual (k') views. *Crocidura russula*: left P^3 – M^2 series in labial (l) view. *Talpa europaea-aquitania*: left humerus in posterior (m) view. *Talpa occidentalis*: left humerus in posterior (n) view, right M^1 in labial (o) view. *Rhinolophus euryale*: left mandible in labial (p) and lingual (p') views. Scale bars: 2 mm.

ple from the central Cantabrian Region, fossil *Apodemus* M^2 from TL are clearly identifiable since no size-overlapping is observed between both populations. This fossil sample includes only 3 (9.4%) morphologically doubtful specimens.

Apodemus species are poorly represented in the MIS 3 record of the Cantabrian Region. The scarcity and inadequate preservation of *Apodemus* fossils normally prevent an accurate ascription to a single species, so often they are classified as *A. sylvaticus-flavicollis* or *A. sp* (e.g. Sesé, 2005, 2017; López-García et al., 2011; Sesé et al., 2018).

The relatively abundant and well preserved *Apodemus* fossils from TL allowed a differentiation of both species, which is relevant from a paleoecological perspective: *A. sylvaticus* has less strict habitat requirements, inhabiting the edges of forests and shrublands, while *A. flavicollis* needs denser forests (Wilson et al., 2017).

Since Southern European peninsulas acted as glacial refugia for *Apodemus* species through the Quaternary glaciations (Michaux et al., 2005), the co-occurrence of both species here reported is of great interest for the understanding of *Apodemus* paleobiogeography.

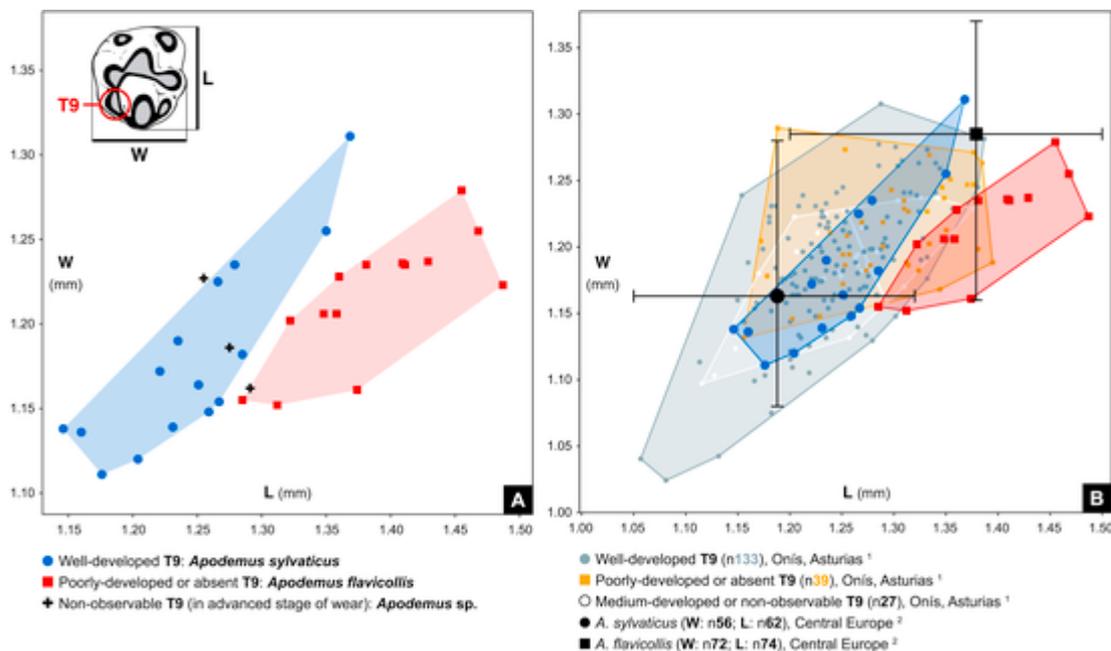


Fig. 13. (A) Characterization of the *Apodemus* specimens from Torca del León based on the measures and morphology of the M². (B) M² from Torca del León compared with modern populations from the TL area (central Cantabrian Region) and Central Europe. 1, own data A.A.-V. (this work); 2, Knitlová and Horáček (2017).

Family Gliridae Muirhead, 1819

5.2.4. *Glis glis* (Linnaeus, 1766)

The remains pertaining to *Glis glis* make up the third most abundant sample (Table 1), consisting mainly of several isolated teeth, but also a maxilla with both molar series (Fig. 12e) and a mandible with M1–M3.

This species inhabits deciduous forests in natural burrows (Palomo et al., 2007; Wilson et al., 2017). As the TL cave was inaccessible to Paleolithic humans and other potential predators, the site constituted a suitable place for *G. glis* hibernation. This could explain the great abundance (14.9%) of this species here in comparison with its absence in other contemporary Cantabrian sites with a rich small-mammals record, such as El Castillo (Sánchez, 1983; Sesé, 2017) and La Güelga (in preparation). *G. glis* has also been registered at El Sidrón (4.8%, Sesé et al., 2018) and Labeko Koba (3.4%, Pemán, 2000).

Order Eulipotyphla Waddell, Okada & Hasegawa, 1999

Family Soricidae Fischer, 1817

5.2.5. *Sorex coronatus* Millet, 1828 - *Sorex araneus* Linnaeus, 1758 and *Sorex minutus* Linnaeus, 1766

The species contained in the *Sorex araneus* group are very similar in size and morphology, especially *S. coronatus* and *S. araneus*. Both species have been cited in the Late Pleistocene record of the Cantabrian Region (e.g. López-García et al., 2011; Sesé, 2016) but, due to their high similarity, an identification at the species level is not possible in most cases, so their remains are normally ascribed to *S. gr. coronatus-araneus* (e.g. Cuenca-Bescós et al., 2009). Fossils from TL (Fig. 12f–f') do not allow a more accurate identification, so the nomenclature *S. gr. coronatus-araneus* is used here.

S. minutus (Fig. 12g–h') is smaller and rarer than *S. gr. coronatus-araneus* (e.g. Sesé, 2017; Cuenca-Bescós et al., 2009). In this site, however, *S. minutus* has been found in a slightly high relative abundance (8.5%). These species have been found in numerous MIS 3 sites of the Cantabrian Region, being more abundant in forested environments and temperate interstadials (e.g. Cuenca-Bescós et al., 2009).

5.2.6. *Neomys fodiens fodiens* (Pennant, 1771) and *Neomys fodiens niethammeri* Bühler, 1963

Two living morphotypes of the Eurasian Water Shrew are recognized nowadays in the Cantabrian Region: the subspecies *Neomys fodiens niethammeri*, which has a larger size and inhabits most of the region, and *Neomys fodiens fodiens*, of smaller size, who occupies Galicia, the western part of Asturias, and the Pyrenean Region (Nores et al., 1982; López-Fuster et al., 1990). In the TL assemblage we found remains of both subspecies (Fig. 14): a mandible of *N. f. fodiens* (Fig. 12i–i'; Coronoid Height: 5.08 mm); and a large mandible of *N. f. niethammeri* (Fig. 12j–j'; CH: 6.64 mm). The corresponding maxillae from both mandibles have been recovered as well. The co-occurrence of both subspecies in MIS 3 and older assemblages had not been previously reported.

Sánchez (1983) identified *N. fodiens* and *N. anomalus* at level 20 of El Castillo (dated to >43 cal ka BP; Wood et al., 2018) in chronologies older than TL. However, taxonomical determinations are probably erroneous: the reported measures for the specimen ascribed to *N. f.* (CH: 6.75 mm) place it far from the *N. f. f.* range, resulting even larger than the *N. f. n.* specimen from TL; likewise, measurements of the specimens ascribed to *N. a.* are out of the species' range, falling within the *N. f.* variability. Consequently, we consider that El Castillo level 20 documents another co-occurrence for *N. f. f.* and *N. f. n.*, as well as the oldest occurrence of *N. f. n.* subspecies.

From a biogeographical perspective, based on the earliest records of *N. f. n.* here discussed, the origin of this subspecies could be located in the central Cantabrian Region. The fossil and current (Nores et al., 1982; López-Fuster et al., 1990) evidence suggests that, subsequently, it has extended its distribution area, replacing *N. f. f.* At most of its former territory in the Cantabrian Region.

5.2.7. *Crociodura gueldenstaedtii* (Pallas, 1811) and *Crociodura russula* (Hermann, 1780)

Recently, the *Crociodura suaveolens* group has changed its systematics (Wilson et al., 2017): populations from Western and Central Europe are now ascribed to the species *C. gueldenstaedtii*, while those from East Europe and Asia remain as *C. suaveolens*.

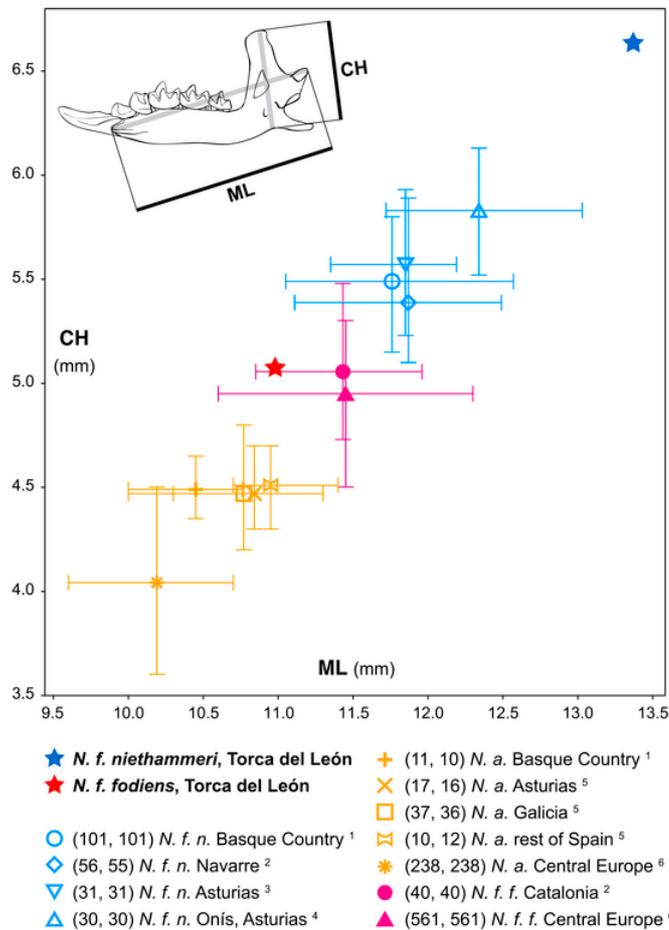


Fig. 14. *Neomys* specimens from Spain and Central Europe compared with the specimens from Torca del León. 1, Pemán (1983); 2, López-Fuster et al. (1990); 3, collection of the Department of Organisms and Systems Biology, University of Oviedo (this paper); 4, This paper (A.A.-V.); 5, Nores et al. (1982); 6, Ruprecht (1971).

Two *C. gueldenstaedtii* mandibles recovered at TL (Fig. 12k–k') show a convex shape of the M₂ cingulum, in labial view (Fig. 12k), which is visibly different than the undulated shape of the *C. russula* M₂ cingulum.

C. russula has been identified by a complete maxilla (Fig. 12l), yielding also a mandible ramus and an isolate incisor. Its P⁴ has a low-developed cingulum over the parastyle, whose upper edge has an angled profile in labial view (Fig. 12l) instead of the rounded and well-developed cingulum of *C. gueldenstaedtii*.

Fossil remains of white-toothed shrews from the Cantabrian Region are scarce in MIS 3 and become more common at the end of the Late Pleistocene, although they are not truly abundant until the Holocene (e.g. Sesé, 2005, 2017; Cuenca-Bescós et al., 2009; García-Ibaibarriaga, 2015; Álvarez-Alonso et al., 2018).

Family Talpidae Fischer, 1817

5.2.8. *Talpa occidentalis* Cabrera, 1907 and *Talpa europaea* Linnaeus, 1758 - *Talpa aquitania* Nicolas et al. (2017)

Currently, two species of the genus *Talpa* inhabit the Iberian Peninsula: *T. occidentalis*, which is present in the entire peninsula except in the Pyrenees and the Ebro basin, and the recently recognized *T. aquitania*, whose distribution extends throughout the northeast of Iberia and south of France (Nicolas et al., 2017; Wilson et al., 2017).

Two different size morphotypes of *Talpa* have been recognized in the MIS 3 record of the Cantabrian Region: the smaller, registered in El Castillo by Sánchez (1983) and in Cueto de la Mina by Castro-

Bernárdez (1986), has been ascribed to *T. caeca* (= *T. occidentalis*). Other MIS 3 sites of the Cantabrian Region where *T. occidentalis* has been identified are Cova Eirós (Rey-Rodríguez et al., 2016) and La Güelga (in preparation). The large morphotype found in many Late Pleistocene sites from the Cantabrian Region has been determined as *T. europaea* in all cases (e.g.; Cuenca-Bescós et al., 2009; López-García et al., 2011; Sesé, 2017). We cannot reject that a number of these large specimens could be ascribed to the newly defined species *T. aquitania*, so a new revision of the previously published material under this new taxonomical perspective would be needed.

One humerus of the larger morphotype recovered at TL (Fig. 12m; Fig. 15) was classified as *T. europaea-aquitania*. Ascription of this specimen to a single species was not possible due to the lack of molar series, which are the taxonomically diagnostic elements (Nicolas et al., 2015).

The smaller morphotype (*T. occidentalis*) provided one humerus (Fig. 12n; Fig. 15) and one M¹ with double mesostyle (Fig. 12o).

The co-occurrence of *T. occidentalis* and *T. europaea-aquitania* during MIS 3 has only been reported previously at sites from the central area of the Cantabrian Region, such as El Castillo (Sánchez, 1983), Cueto la Mina (Castro-Bernárdez, 1986) and La Güelga (in preparation).

Nowadays *T. occidentalis* is the only *Talpa* species at the TL area (Asturias), since the co-occurrence territory in the Cantabrian Region has moved eastwards to Cantabria and the Basque Country.

Order Chiroptera Blumenbach, 1779

Family Rhinolophidae Gray, 1825

5.2.9. *Rhinolophus euryale* Blasius, 1853

Chiroptera is represented at the TL assemblage by one complete mandible (Fig. 12p–p') and one isolated canine, identified as belonging to *Rhinolophus euryale*. This genus has been cited in the Cantabrian Region in MIS 3 records at El Sidrón cave, as *R. euryale-R. mehelyi* (Sesé et al., 2018). *R. euryale* inhabits caves of forested and temperate areas (Palomo et al., 2007).

6. Paleoenvironment and paleoclimate inferred from the faunal association

While none of the large mammal species recovered at TL is environmentally indicative, the micromammal community provided relevant palaeoenvironmental and paleoclimatic information. From the rela-

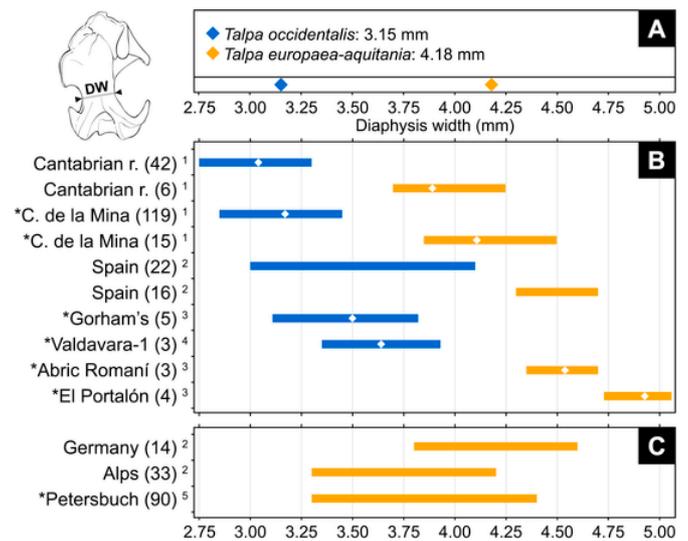


Fig. 15. Diaphysis width of the *Talpa* humerus from: (A) Torca del León, (B) Iberian current localities and archaeological sites, (C) European current and fossil specimens of *Talpa europaea*. Sources: 1, Castro-Bernárdez (1986); 2, Niethammer (1990); 3, López-García (2008); 4, López-García et al. (2011); 5, Koenigswald (1970). (*) Fossil specimens.

tive abundance of each micromammal species (Table 1), the habitat weightings method allows to infer that the landscape that surrounded the TL site during its formation (Fig. 16) was mainly a mature forest (Woodland: 48.9%), since there are 4 species exclusive of this type of habitat: *A. flavicollis*, *G. glis*, *C. glareolus* and *R. euryale*.

Open woodlands (28.2%), comprising forest margins and forest patches, are mainly represented by *A. sylvaticus* (21.8%), but there are other species whose requirements also include open landscapes (Table 1).

Humid meadows are barely represented in the assemblage (Open Humid: 18.1%): eight of the identified taxa (*M. gr. Agrestis*, *T. occidentalis*, *T. europaea-aquitania*, *S. gr. Araneus-coronatus*, *C. gueldenstaedtii*, *S. minutus*, *N. f. fodiens* and *N. f. niethammeri*) include this habitat among their environmental preferences, but none of them is exclusively indicative of it.

Water sources (3.2%), consisting of streams, lakes or ponds, are denoted by *N. f. fodiens* and *N. f. niethammeri*, and dry meadows (1.6%) are inferred from the presence of *C. russula*.

We assume that this faunal record is representative of the cave surroundings because the paleontological site corresponds to a natural trap (see Section 4). Consequently, the combination of the mentioned habitats indicates that the study cave through which these faunas fell was located in a well-developed forest and close to grasslands.

According to the relief configuration of the surroundings of TL (Fig. 1C), the mature forest formed at the bottom of littoral ranges and grasslands probably occupied nearby coastal marine terraces. The littoral ranges would act as a barrier to rainfall favoring the local development of the forest at 6–13 km from the ancient coastline, considering the current position of the study cave, the present bathymetry of the Cantabrian Coast and global sea-level oscillations (Rabineau et al., 2006). Furthermore, the fossil assemblage including the lion is coeval with the beginning of the regional glacial retreat after a local maximum, established at 45 ± 3 ka in the north of Picos de Europa (Fig. 1B) (Jiménez-Sánchez et al., 2013). During this local maximum, glaciers covered Picos de Europa above 600–900 m altitude (e.g. Rodríguez-Rodríguez et al., 2014; Serrano et al., 2016). Thus, the mature forest that surrounded TL was located at ~15 km north of the glaciers fronts.

According to the MER method results (Table 3), the paleoclimate at the cave's location when the study fauna was accumulated was humid (MAP: 1217 ± 181 mm) and temperate (MAT: 12.2 ± 0.9 °C), with warm summers (MTW: 18.9 ± 0.7 °C) and mild winters (MTC: 6.3 ± 1.0 °C). These conditions are slightly drier and colder than the Cfb type climate current ones in the surroundings of TL, according to Cunha et al. (2011). The small-mammal species association registered at TL persists nowadays in a restricted area at the central-east Cantabrian Region (Fig. 1B). This area (UTM squares 30TVN68 and 30TVN77) comprises Ramales de la Victoria and Carranza in the Cantabria-Basque Country border, and Mena Valley in Burgos (north-

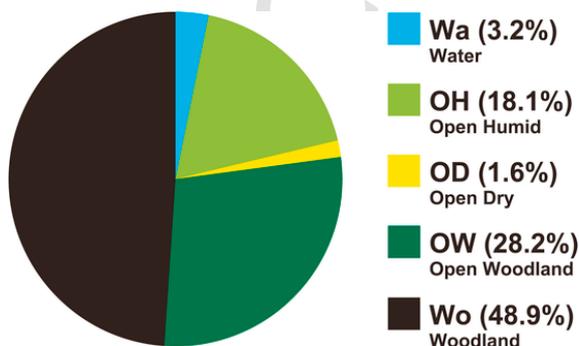


Fig. 16. Type of landscape inferred through the habitat weightings method for the surroundings of Torca del León at 43 ka.

Table 3

Temperature and precipitation values estimated for the Torca del León upper layer. Mean annual temperature (°C) (MAT); mean temperature of the warmest month (°C) (MTW); mean temperature of the coldest month (°C) (MTC); mean annual precipitation (mm) (MAP). Mutual Ecogeographic Range estimations; local current values; and difference (Δ) between the estimations for the upper layer of Torca del León and the current data.

	Mutual Ecogeographic Range			Current values		
	mean	min-max	STD	mean	STD	Δ
MAT (°C)	12.2	9.4–14.2	0.9	13.4	1.0	-1.2
MTW (°C)	18.9	16.5–20.3	0.7	19.3	1.0	-0.4
MTC (°C)	6.3	3.6–8.9	1.0	8.0	1.0	-1.7
MAP (mm)	1217	924–1640	181	1367	66	-150

ern slope and watershed of the Cantabrian Mountains). This last locality shows more continental conditions, with lower precipitations and colder winters, than the means obtained with the MER method (see min-max values at Table 3).

The radiocarbon date (43 ± 0.5 cal ka BP) indicates that the faunal association of TL occurred during GI-11, a warming event recorded also in marine-cores from the Iberian Margin (Martrat et al., 2007; Sánchez-Goñi et al., 2008). These records show an increment in Atlantic forest pollen and sea surface temperatures during this interstadial, coevally with the development of a local mature forest that surrounded the study cave. Following Fletcher et al. (2010), the landscape at the latitude of TL during GI-11 would be dominated by grassland and dry shrubland with an increase in temperate forest elements (open woodlands). This is consistent with the results obtained in this work through the habitat weighting (Fig. 16) and the MER methods (Table 3).

Other fossil assemblages corresponding to GI-11 from the Cantabrian Region are very scarce: Levels 17–16 of El Castillo (Cantabria) were dated to 44.9–41.3 cal ka BP (Wood et al., 2018); and Levels 20a and 104 of Cueva del Conde (Asturias) yielded 43.9–41.4 cal ka BP dates (López-García et al., 2011). In both cases, the relatively high abundance of temperate forest-indicative and humid-indicative species, as well as the absence of cold adapted taxa, is consistent with this temperate interstadial.

This warm episode recorded in TL is framed between two cold phases recognized at other sites in the Cantabrian Region (Fig. 1B–C): 13 km NW from the study site, a woolly rhinoceros (*Coelodonta antiquitatis*) molar from Rexidora Cave (Asturias) yielded a date of 44.4 ± 1.1 cal ka BP revealing the occurrence of local cold and open conditions during GS-12 (Álvarez-Lao et al., 2015); in the eastern Cantabrian Region, Level-IX of Labeko Koba (Guipúzcoa) includes cold-adapted taxa such as *Rangifer tarandus*, *C. antiquitatis* and *Mammuthus primigenius* (Altuna and Mariezkurrena, 2000) dated to 42.9–41.4 cal ka BP (Higham et al., 2014; Marín-Arroyo et al., 2018), coevally with cold stadial GS-11.

The chronology of the paleontological site (43.0 ± 0.5 cal ka BP, Fig. 3) is of special interest from an anthropological perspective since it is coeval with the transition between the end of the Mousterian technocomplex (~45 ka BP) and the first Aurignacian evidence (< 43.3 ka BP) in the Cantabrian Region (Marín-Arroyo et al., 2018).

7. Conclusions

The bone accumulation from Torca del León was formed in a karst cave that worked as a natural trap: lion and other carnivores fell accidentally through a vertical conduit 16 m deep. The lack of human or carnivore activity on the bones is consistent with this hypothesis. The remains of these animals were deposited in a small water pond with clay and silt deposition, which also involved micromammal remains.

The large-mammal assemblage is only composed of carnivores: two large felids (*Panthera spelaea* and *P. pardus*), one canid (*Canis lupus*) and two mustelids (*Mustela nivalis* and *M. putorius*).

The good preservation of the cave lion (*P. spelaea*) remains from Torca del León allowed a comparative study of the individual. Skull and teeth preserved features of systematic relevance allowing an ascription to the species *P. spelaea*, which is consistent with its radiocarbon dating. Morphometrically, the TL lion elements are among the average size ranges of a comparison sample of Pleistocene populations from Europe and Siberia, normally slightly below the mean values. Sexing of the specimen points to it possibly being a male. In order to estimate its body weight, the humerus was considered the most suitable element. Equations provided a value of about 360 kg.

The leopard (*P. pardus*) assemblage, while much scarcer, also allowed a comparative study: the upper carnassial (P⁴) and postcranial elements of the TL individual are noticeably small, compared to a sample of Pleistocene leopards from Europe, suggesting that it most probably corresponds to a female. The morphology of the P⁴ shows the typical features of Late Pleistocene specimens. In addition, the high robustness of the metapodials is comparable with Late Pleistocene European populations and significantly greater than in living leopards.

Wolf (*C. lupus*) provided few cranial and dental remains from a single individual which, compared to an extensive sample of Pleistocene specimens from Western Europe, fall into the mean range of the Late Pleistocene populations' dispersion. In addition, P⁴ shows a marked robustness.

The morphometrical and morphological studies of the small mustelid cranial remains, allowed an ascription to *M. nivalis*, most probably a male.

The morphology and proportions of the polecat mandible and lower teeth are consistent with those of *M. putorius* and different from those of *M. eversmanni*.

The small mammal assemblage provided 506 identifiable specimens (NISP) corresponding to a minimum (MNI) of 47 individuals, ascribed to 14 taxa (*G. glis*, *A. flavicollis*, *A. sylvaticus*, *C. glareolus*, *M. gr. Agrestis*, *S. gr. coronatus-araneus*, *S. minutus*, *N. fodiens fodiens*, *N. fodiens niethammeri*, *C. russula*, *C. gueldenstaedtii*, *T. occidentalis*, *T. europaea-aquitania*, and *Rhinolophus euryale*).

The abundant and well preserved *Apodemus* material allowed a detailed morphological and morphometrical study revealing the presence of the two species of this genus known in the northern Iberian Late Pleistocene record: *A. sylvaticus* and *A. flavicollis*. This is of special interest since the co-occurrence of both species was never verified in MIS 3 records from the Cantabrian Region.

The oldest records of the subspecies *Neomys fodiens niethammeri*, represented by the extremely large specimens of TL and El Castillo, are here reported and discussed, respectively. This taxonomic determination is of great importance for the study of this subspeciation event affecting *Neomys fodiens* species.

Two species of the genus *Talpa* have been here identified: *T. occidentalis* and *T. europaea-aquitania*. The co-occurrence of both mole species has been reported previously only from the central Cantabrian Region.

The small-mammals association allowed us to infer that the environment surrounding the TL site during its formation corresponded to a mature forest developed under humid and temperate conditions, with warm summers and mild winters. These conditions are slightly drier and colder than the current ones in the surroundings of TL. This forest was located at the bottom of a littoral range, close to grasslands developed above marine terraces. At this time, the ancient coastline was 6–13 km to the North and glacier fronts of the Cantabrian Mountains were ~15 km to the South. The assemblage was AMS-radiocarbon dated to 43 ± 0.5 cal ka BP, coincident with GI-11, a warm episode poorly recorded in NW Iberia. This is consistent with the inferred pale-

oenvironment and paleoclimate conditions and coeval with the onset of the regional glacial retreat occurred after the local glacial maximum of ~45 ka. In addition, the paleoenvironmental information of this episode is of special interest from a palaeoanthropological perspective, since it is coeval with the Middle to Upper Paleolithic transition in Northwestern Iberia.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.quascirev.2019.106123>.

Older Middle Pleistocene specimens come from Arago, Atapuerca, Petralona, Isernia la Pineta and Westbury; late Middle Pleistocene specimens come from Azé, Romain-la-Roche, Igüe-des Rameaux, Ullakhan Sullar, Bíšník, Za Hájovnou and Petralona PEC 90; unspecified Middle Pleistocene specimens come from Beresovka and various unspecified European sites, older Late Pleistocene specimens come from Baume Longe, Cajarc, L'Herm, Mokhnevskaya, Bíšník and Santenay; recent Late Pleistocene specimens come from Bolshoy, Castillo, Bois du Cantet, Siegsdorf, Jaurens, Wierzchowska, Gilenreuth, Duvany Yar and Portel-Ouest; unspecified Late Pleistocene specimens come from Oner Lake, Constantinovski Yar, Kira Sullar, Ytyk-Kuel, Mokhokho, Kondakovka, Avdevo, Azoleta, Arrikruz, Vence, Saint Romain, Genay, Prety-Lacrost, Herdengel, Bärenfalle, Postonja, Rübeland, Curtil, Broion, Pocala, Cannita, Gerde, Bear Cave, Repolusthöhle and Britain (various sites). Sources: Schütt (1969b); Bonifay (1971); Kurtén and Poulianos (1977); Altuna (1981); Clot (1984); Turner (1984, 1999); Sala (1990); Argant (1991, 2010); Baryshnikov and Boeskorov (2001); García (2003); Castaños (2005); Sotnikova and Nikolskiy (2006); Pacher (2009); Baryshnikov and Tsoukala (2010); Marciszak and Stefanik (2010); Sabol (2014) and Argant and Brugal (2017). For an individual identification of each specimen/site, see Fig. S3, Appendix C.

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