



Last population of cave lion (*Panthera (Leo) spelaea*) in the extreme south-west of Europe: Carigüela cave (Southern Iberian Peninsula)

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ARTICLE INFO

Keywords:

Cave lion

Late Middle Pleistocene

U/Th dating

Southern Iberian

ABSTRACT

The revision of the fauna of Carigüela (Píñar, Granada) has yielded the remains of a cave lion hitherto unknown at this site. The comparative morphometric study of the distal humerus fragment has led to its attribution to *Panthera spelaea* Goldfuss. From two samples of the bone and using the U/Th technique, an absolute dating of 145–148 ka (MIS 6) has been established. The geographical location of the site makes the cave lion of Carigüela, together with that of Solana del Zamborino, the two most southerly records of this species in Europe. In the case of the former, it is the most recent reference of this species for southern Iberia.

1. Introduction

The Eurasian big cat, since its initial description as *Felis spelaea* (Goldfuss, 1810), has been referred to by various taxonomic names, including *Panthera (Leo) spelaea cloueti* (Filhol and Filhol, 1871), *Panthera leo fossilis* (Reichenau, 1906), *Panthera leo spelaea* (Kurten, 1985; Argant, 1991), and others. In the second half of the last century, *Panthera (Leo) spelaea* or *Panthera spelaea* (Dietrich, 1968) has been the commonly used name by authors for all lions of the Middle and Late Pleistocene. Since the beginning of this century, the existence of three chronosubspecies of lion has been accepted: *Panthera spelaea fossilis* in the first half of the Middle Pleistocene (MIS 19–11) with a large size (Barycka, 2008; Marciszak and Stefaniak, 2010), *Panthera spelaea intermedia* in the second half of the Middle Pleistocene (MIS10–6) (Argant & Brugal, 2017), and *Panthera spelaea spelaea* in the Upper Pleistocene (MIS 5–1) with a small size (Marciszak et al., 2021). In recent decades, morphometric arguments have been supplemented by

studies of ancient DNA that demonstrate genetic isolation between the Pleistocene lion and current African forms (Burger et al., 2004; Barnett et al., 2009, 2016; Ersmark et al., 2015).

The oldest presence of the lion in Europe is recorded at the Italian site of Isernia La Pineta during the Lower Middle Pleistocene (Sala, 1990). In the Iberian Peninsula it appears for the first time in level TD10 of the Gran Dolina of the Atapuerca complex (MIS 9) and is present during the Middle Pleistocene at La Galería and the Sima de los Huesos (García, 2003). It is also the rarest feline species in archaeological contexts (Villaluenga, 2016: 190–193; Sanchís and Pascual Benito, 2017) and palaeontological contexts (Álvarez-Lao et al., 2020: 2). The greatest number of evidence of this species is in the Cantabrian Region, although it is also cited in other peninsular areas. In a review, the fossil record of the lion appears in 16 caves in the Cantabrian area and 20 in the rest of the Iberian Peninsula (Villaluenga, 2016). This estimate has become obsolete with the findings of recent years, mainly from the north of the Iberian Peninsula. An archaeological collection from the Spahni

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<https://doi.org/10.1016/j.jasrep.2024.104584>

Received 14 November 2023; Received in revised form 2 May 2024; Accepted 7 May 2024

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excavations deposited in the Archaeological and Ethnological Museum of Granada, consisting of faunal remains and carved lithic industries, has been reviewed and, among the remains of fauna from the site of Carigüela, remains attributed to a lion have been found. The aim of this paper is to offer the morphometry and chronology as well as the taxonomic attribution and paleobiogeography of this new evidence of lion from Carigüela cave, a Late Middle Pleistocene site geographically close to Solana del Zamborino (Fig. 1).

1.1. Carigüela cave

Carigüela cave is a site with a broad chronostratigraphic sequence ranging from late Middle Pleistocene to recent Holocene times (Carrión et al., 1998, 2019). The deepest levels correspond to deposits of several metres of sediments with very rich Middle Paleolithic occupations (Vega, 1988; Vega et al., 1988).

The first news about the archaeological wealth of the region of Píñar (Granada) dates back to 1916 and is due to Hugo Obermaier (1934), although this researcher only collected materials on the surface. Later,

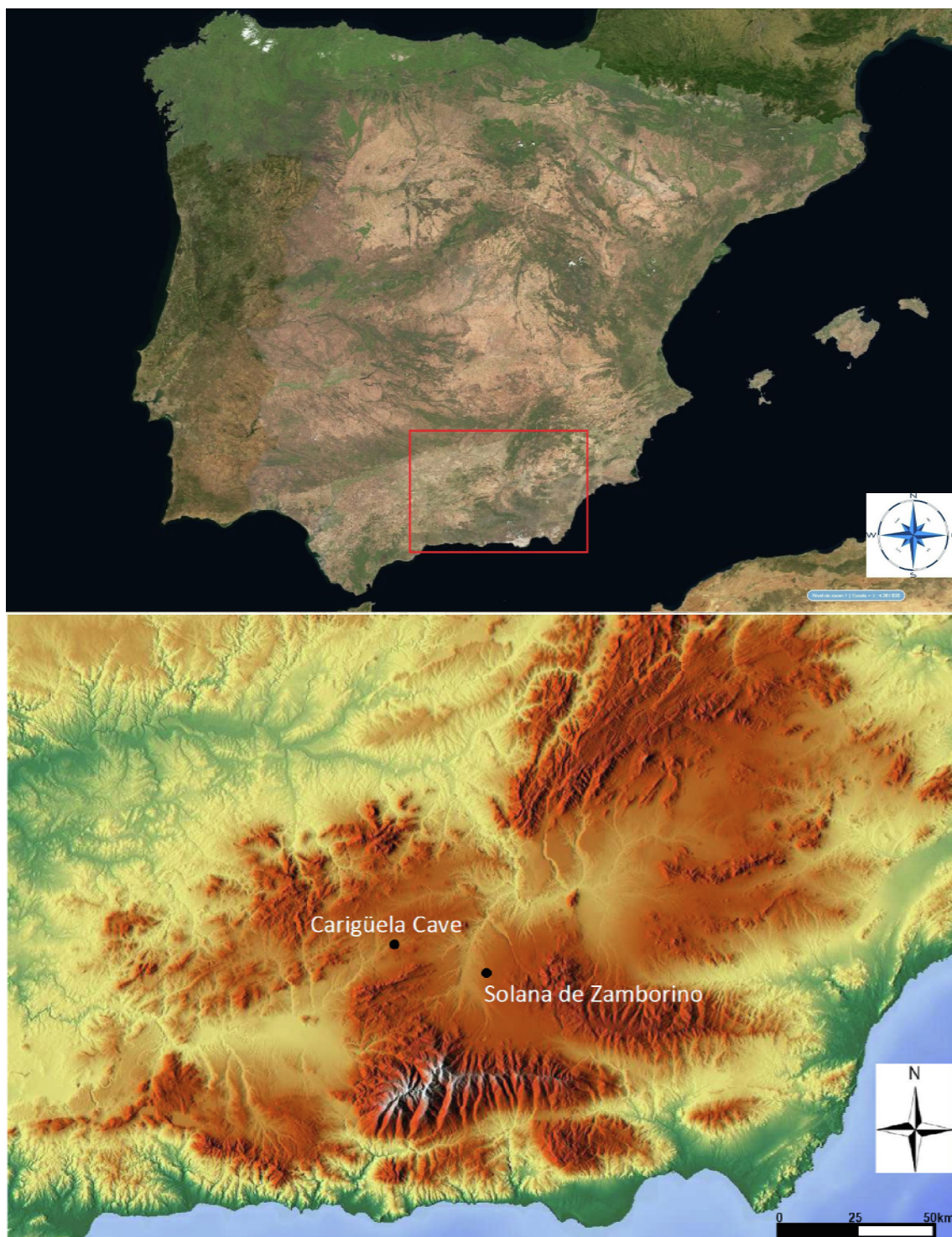


Fig. 1. Location of the Carigüela cave and Solana de Zamborino.

the Swiss archaeologist Jean Christian Spahni carried out some explorations in the Pñar area and became interested in the study of the Paleolithic in this region, excavating in Carigüela cave in 1954 and 1955 (Spahni, 1955a; Spahni, 1955b; Spahni, 1955c; Riquelme Cantal, 2002:50). The latter (Fig. 1) is located ~700 m east of the village of

Pñar, on a limestone outcrop belonging to the last foothills of Sierra Harana (Fig. 1). Its geographical coordinates UTM are 30S 461845.43 E4143896.95 and it opens up at an altitude of 1020 asl.

Carigüela was originally referred to by this name in the earliest publications (e.g., Fusté, 1956, 1957; García Sánchez, 1957; Pellicer

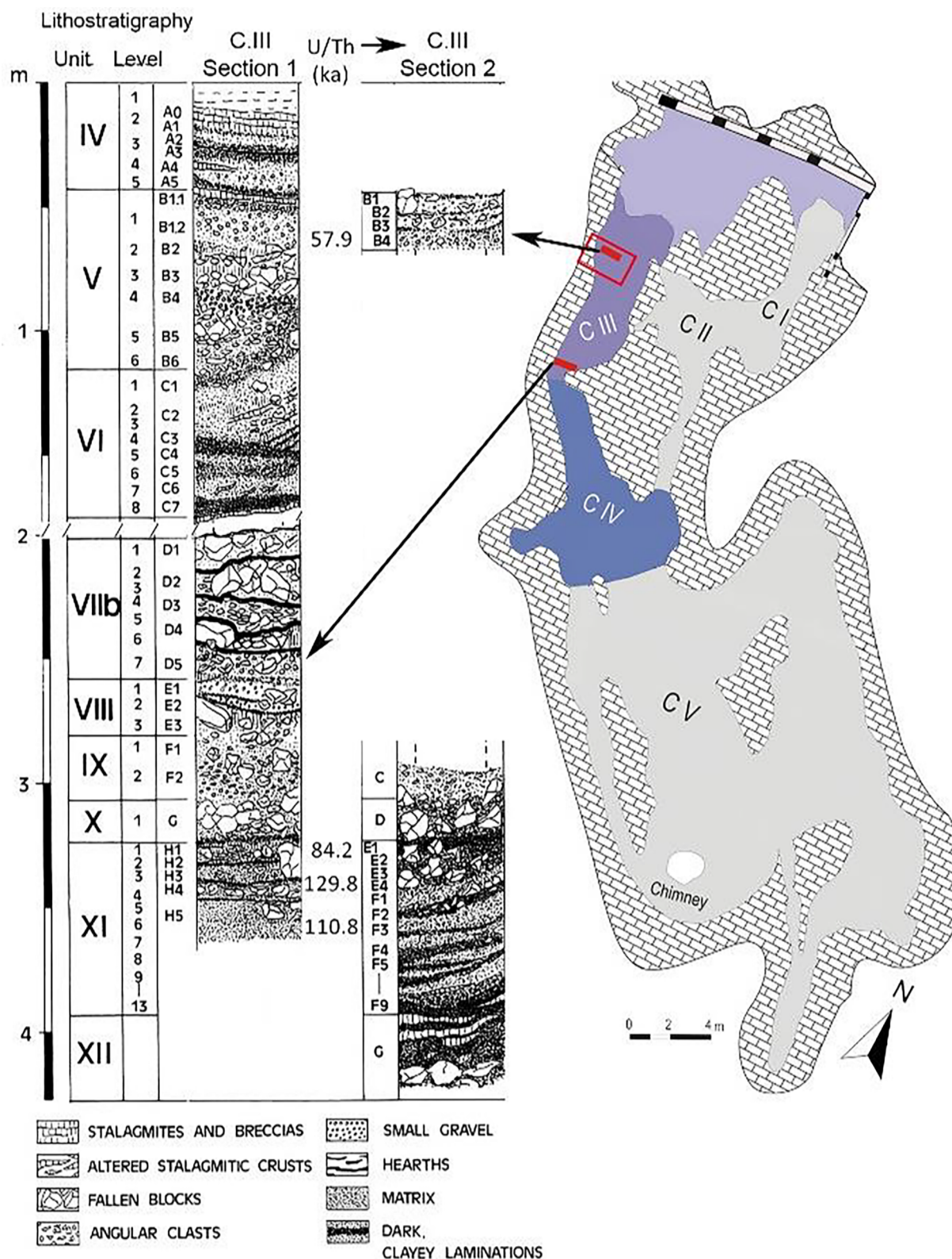


Fig. 2. Topographic plan of Carigüela and chronostratigraphic summary of the Spahni excavation (based on Carrión et al., 2019).

Catalán, 1964; Almagro et al., 1970; Göksu et al., 1974; Ruiz Bustos & García Sánchez, 1977a, 1977b). This designation remained in use until it was renamed, in the mid-1980s, by G. Vega as Cueva de la Carigüela (Vega Toscano et al., 1988 and some subsequent authors). In this historiographical context, we believe that the original name that the cave received for three decades, and which was used by numerous researchers, should prevail. Moreover, it is the name we typically use in our publications when referring to the site.

In relation to his work at Carigüela, Spahni (1955c: 4) comments: ["Under this layer, several Mousterian levels (Middle Paleolithic, 80,000 to 200,000 years ago) have appeared, the latter showing a mixture of small tools and others of Acheulean tradition (i.e. bearing the influence of an even older civilization). The richness of these Mousterian levels in tools (arrowheads, burins, scrapers, etc.) and in fauna (lion, panther, horse, deer, bear, rhinoceros bones, etc.) is very great....."] (Fig. 2).

Spahni did not leave an excavation diary, nor did he publish the results of his campaigns, but the material obtained was deposited in the Archaeological and Ethnological Museum of Granada. This institution sent a selection of pieces (161) to the National Archaeological Museum (Madrid) (Almagro et al., 1970; Vega Toscano, 1988). Of the material deposited in the first institution, the human remains, the lithic industry and part of the faunal material have subsequently been studied (Fusté, 1956; García Sánchez, 1957; M.A. de Lumley & García Sánchez, 1971; M.A. de Lumley, 1973; H. de Lumley, 1969; Bouchud, 1969, Vega Toscano, 1988). To date, the information available on the fauna of Carigüela is limited to the aforementioned publication by Bouchud and the faunal list published in Gerardo Vega's doctoral thesis (Vega Toscano, 1988). However, in neither of them does the presence of the cave lion appear.

Subsequently, in September 1959, Professor M. Pellicer (1964) conducted an initial excavation campaign, followed by a second one the following year. The main objective of these campaigns was the stratigraphic study of the post-Paleolithic levels of corridor or chamber D and chamber G (Carigüela III and IV, Fig. 2). During both interventions, it was evident that the equivalent of layer 1 of Spahni's stratigraphy (Neolithic) developed in the innermost area of the cave, due to the strong dip of the Paleolithic levels towards the cave's interior (Vega Toscano, 1988). The publication of Professor Pellicer's work at Carigüela (Pellicer Catalán, 1964) became one of the fundamental references on the Neolithic in the south of Iberia.

In 1968, Washington State University professors H.T. Irwin and R. Fryxell proposed a research project in the cave to carry out a systematic re-excavation of its Paleolithic levels. An international team led by Drs. Irwin and Almagro was formed as a result. Three excavation campaigns were conducted during the years 1969, 1970, and 1971, the results of which have not yet been published (Almagro et al., 1970).

In the mid-1980s, Gerardo Vega Toscano resumed the research at Carigüela, conducting a series of interventions focused on the outermost area of the cave. He also reviewed the sections opened by previous excavations, examined some of the materials from these interventions, and recovered archival material from the excavations of Irwin and Fryxell. The main objective was to establish a paleoclimatic and cultural sequence serving as a reference for the southern Iberian Peninsula, from the Middle Pleistocene to the Holocene (Vega Toscano, 1987, 1988, 1990; Vega Toscano et al., 1988) (Fig. 2).

2. Material and methods

An archaeological collection from the Spahni excavations deposited in Archaeological and Ethnological Museum of Granada consisting of faunal remains and carved lithic industries, has been reviewed. In a study aimed at identifying the species of mammals present in the bone collection carried out by one of the authors (JAR) concerning the fauna from Spahni's excavations (1954–1955) at La Carigüela cave, the remains of a dozen mammal species have been identified: *Equus* sp., *Bos/Bison*, *Cervus elaphus*, *Capra pyrenaica*, *Panthera pardus*, *Lynx pardinus*, *Crocota*

spelaea, *Ursus arctos*, *Canis lupus*, *Vulpes vulpes*, *Meles meles*, and *Oryctolagus cuniculus*. In this fauna sample, preserved in two boxes with bone material selected by the same excavator, a distal fragment of the humerus (number 6567) of *Panthera spelaea* was found.

The metric data used to compare the Carigüela specimen comes from different sites in Europe, and their relationship is provided in the discussion section. For sexual dimorphism, bivariate diagrams of humerus measurements from European sites are referenced (Diedrich, 2009, 2010, 2011a,b). Measurements of lion material are provided according to Marciszak (2021) with the following abbreviations: distal epiphysis breadth (dB), distal epiphysis depth (dL), and trochlear breadth (Btr). The comparative data used are from Pleistocene sites in South-West Europe (Table 2).

Two subsamples from a lion bone, identified as 23118-1 and 23118-2, were analyzed using the U-Th dating technique at CENIEH (Burgos) (Fig. 3). Around 40–50 mg of powdered samples were extracted from the bones. The U-Th separation sequence took place in the ultra-clean lab of CENIEH and followed the methodology as described in Pourmand et al. (2013). The elemental concentrations and isotope ratios in the analyzed samples were determined using two independent analytical sequences, employing a combination of standard bracketing and isotope dilution mass spectrometry (IDMS). Spikes (^{229}Th , ^{233}U , ^{236}U) and standards (CRM 112A for U and IRMM 35 for Th) were prepared through gravimetric dilution of commercial standard solutions and certified reference materials, ensuring direct traceability to NIST and IRMM. Age calculations were conducted using the NIL script published by Pourmand et al. (2013). To maintain quality control and ensure measurement accuracy, Cathedral Cave Speleothem (CCS) served as an internal standard in all sample groups. The obtained values for the standards closely align with the reported age range of 21.08–21.09 ka (McGee et al., 2012).

3. Results

We have obtained two Th-dates from the same bone as shown in Fig. 3. The analytical details of the Th-dates are given in Table 1. For sample 23118-1, the concentrations of U and Th were determined as $2.5 \mu\text{g g}^{-1}$ and 3.3 ng g^{-1} , respectively. The $^{230}\text{Th}/^{232}\text{Th}$ activity ratio for this sample is 1935 ± 39 , which indicates that the sample is clean and suitable for ^{230}Th dating. The measured $\delta^{234}\text{U}$ value of 172.2 ± 0.013 yielded a ^{230}Th (BP) uncorrected age of $145.3 \pm 6.2 \text{ ka}$ (Table 1). The second subsample, labeled as 23118-2, revealed U and Th concentrations of $2.5 \mu\text{g g}^{-1}$ and 4.3 ng g^{-1} , respectively. The $^{230}\text{Th}/^{232}\text{Th}$ activity ratio for this sample is 1524 ± 27 , suggesting that this subsample is also free of detrital materials as seen in the sample 23118-1. The calculated ^{230}Th uncorrected age (BP) for the sample 23118-2 is $148.3 \pm 5.7 \text{ ka}$, in agreement with sample 23118-1 with in the given uncertainties in 2σ levels (Table 1). In conclusion, the analysis of two subsamples from the lion bone using the Th-chronometer reveals that both subsamples represent an isotopically closed system. This conclusion is drawn from the comparison of closely aligned uncorrected and corrected ^{230}Th ages (Table 1). Based on these Th-ages, we can establish a minimum apparent age for the lion bone, ranging from 148 to 145 ka.

The fossil record of the cave lion from Carigüela consists of a distal fragment of the left humerus (Fig. 4). This bone exhibits the typical morphology of felids, featuring two condyles with a shallow radial fossa in cranial view and two epicondyles with a deep olecranal fossa in caudal view. Above the medial epicondyle, there is a well-developed ridge and a long, narrow foramen. The supracondyloid foramen does not connect the olecranal and radial fossa, distinguishing it from canids, and it is surmounted by a well-developed mesial epicondyle. The trochlea is well-preserved, oblique, and very acute.

On the cranial side of the medial epicondyle, there is a small abrasion. The fracture observed at the distal end of the shaft may be of fossil-diagenetic origin; however, no other traces of human activity are visible.

Complete fusion of the epiphysis indicates that it belongs to an adult individual. The bone is very robust with substantial thickness, as

Table 1
Th-Age determination results from the lion bone samples.

SAMPLE	²³⁸ U (ppb)	²³² Th (ppb)	²³⁰ Th/ ²³² Th [AR]	δ ²³⁴ U [measured]	δ ²³⁴ U [initial]	²³⁰ Th age uncorrected [yr BP]	²³⁰ Th age corrected [yr BP]
23118-1	2519 ± 7.91	3.3 ± 0.01	1935 ± 39.2	172.2 ± 1.01	256.6 ± 1.01	145305 ± 6270	145184 ± 6260
23118-2	2517 ± 5.57	4.3 ± 0.01	1523 ± 27.3	189.4 ± 2.01	287.9 ± 2.01	148325 ± 5728	148165 ± 5720

U decay constants: $\lambda_{238} = 1.55125 \times 10^{-10}$ (Jaffey et al., 1971) and $\lambda_{234} = 2.82206 \times 10^{-6}$ (Cheng et al., 2013).
Th decay constant: $\lambda_{230} = 9.1705 \times 10^{-6}$ (Cheng et al., 2013).
 $d^{234}\text{U} = ([^{234}\text{U}/^{238}\text{U}]_{\text{activity}} - 1) \times 1000$.
 $d^{234}\text{U}_{\text{initial}}$ was calculated based on ^{230}Th age (T), i.e., $d^{234}\text{U}_{\text{initial}} = d^{234}\text{U}_{\text{measured}} \times e^{\lambda_{234} \times T}$.
AR stands for activity ratio. BP stands for “Before Present” where the “Present” is defined as the year 1950 CE.
Uncertainties of the measurements are expressed as 2σ values.

Table 2
Measurements of the lion humerus from Carigüela cave are as follows: distal epiphysis bread (dB), distal epiphysis depth (dL), trochlear bread (Btr).

	Chronology	dB	BTr	dL	dL/dB × 100	Lab Code
Carigüela cave (Spain)	145 ± 6 ka	99	74.2	69.6	70.3	23,118

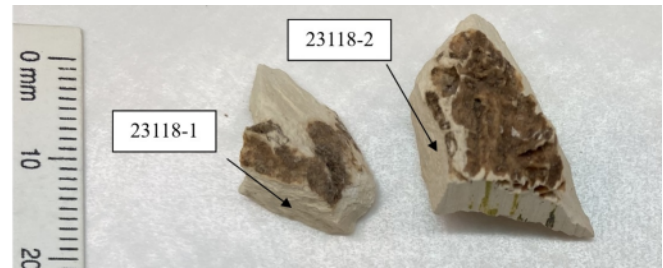


Fig. 3. Lion bone samples used for Th-chronometer. The sampling spots are shown in the figure with the sample-ID.

indicated by its measurements (Table 2).

4. Discussion

The excavation carried out by Spahni in the outermost area of Carigüela cave has been extended by several subsequent campaigns. Recent sampling of the profiles has yielded ages close to those obtained for the lion bone in CIII, unit XI, 129.88 ± 6.10 ka.

The lithic industry analyzed presents the characteristics typical of the Middle Paleolithic at Carigüela cave, including the levels of the MIS 6-MIS 5 transit (Vega Toscano et al., 1997) and is framed within the characteristics defined for the Iberian Southern Middle Paleolithic with parallels in other cave sequences with MIS 6 levels (such as Horá or Bajondillo) (Cortés-Sánchez, 2008).

The Carigüela specimen is attributed to the species *Panthera spelaea* based on its morphology and measurements. Additionally, considering its chronology, it could potentially be related to the subspecies *Panthera spelaea intermedia*. However, it is worth noting that the classification of this subspecies is primarily based on tooth morphology rather than postcranial elements (Argant & Brugal, 2017). Therefore, it would be more informative to compare the measurements (dB, dL) of the Carigüela specimen with those from European Pleistocene sites and modern lions (*Panthera leo*).

For this comparison, data from various sources are considered, including studies by Wojtusiak (1953), Diedrich (1968), Vereshchagin (1971), Clot (1980), Argant (1988, 2010), Gross (1992), Germonpré (1993), Depestele (2005), Testu (2006), Dimitrijevic et al. (2014),



Fig. 4. Carigüela cave (MAEG/6567). *Panthera spelaea* left distal humerus (a), lateral (b) and caudal (c) views.

Marciszak (2021), as well as data from *Panthera leo* (Philippe Fosse, personal communication) (Fig. 5).

A significant difference in size between the Pleistocene lion (*Panthera spelaea*) and the modern species (*Panthera leo*) is once again confirmed. The Carigüela specimen falls within the range of variation of the cave lion. Its position in the distribution is relatively high due to sexual dimorphism.

Size differences in the Pleistocene lion have been debated for decades. In the last century, these differences were attributed to the existence of two taxonomic forms (large and small) (Ballesio, 1980; Altuna, 1972). However, the prevailing hypothesis attributes differences in size in both the dentition (Turner, 1984) and the postcranial skeleton to sexual dimorphism. Postcranial bone size differences have been confirmed in modern African lions (Gross, 1992) as well as in Pleistocene sites (Baryshnikov and Boeskorov, 2001; Diedrich, 2009, 2010, 2011a,b; Diedrich and Rathgeber, 2012; Marciszak et al., 2021; Marciszak and Stefaniak, 2010).

For the sexual attribution of the Carigüela specimen, metric data from sites in Europe with information on the sexual dimorphism of the cave lion humerus have been used. The smallest values of distal width humerus attributed to males come from Zoolithen Cave (92, 94 mm), while the largest value attributed to a female is from Otterstadt-Waldwiesen (89 mm) (Diedrich, 2009, fig. 10A). This data is consistent across several sites in Europe. Therefore, it seems reasonable to assume that sex discrimination can be based on a distal depth of around 90 mm.

A female with a distal humerus width of 93 mm in Bilstein Cave (Diedrich, 2009) and another with 96 mm in Neumark-Nord (Diedrich, 2010) confirm the existence of an overlap in the metric variation of this bone, which would not affect the Carigüela specimen (99 mm). Therefore, it seems reasonable to attribute it to a male.

The low latitude of Carigüela is one of the interesting facts to highlight. References to the southern limit of the cave lion in Eurasia are scarce and imprecise (Kahlke, 1994; Stuart & Lister, 2011). For this reason, the sites of the Iberian and Italian Peninsulas located below 40° latitude have been reviewed: Cova Negra (Pérez Ripoll, 1977), San Luis (Fernández Peris & Martínez Valle, 1989) and Bolomor (Blasco, 2011) (Valencia), Cova del Corb (Sarrión, 1990) and Moli de Mato (Sarrión et al., 1987) (Alicante), Pedreira da Salemas (Antunes and Cardoso, 1987), Gruta do Escoural (Cardoso, 1993) and Gruta da Figueira Brava (Cardoso, 1993) (Portugal) Solana de Zamborino (Martin, 1988) (Granada); Grotta de la Madonna (Masetti & Mazza, 2013), Torre Talao (Marra, 2009) and Cannita (DiPatti & Piccione, 2004) (Italy) (Table 3).

Firstly, it is important to note that Solana de Zamborino and Carigüela are currently the only deposits with a latitude lower than 38° in Europe where Pleistocene cave lion remains have been documented.

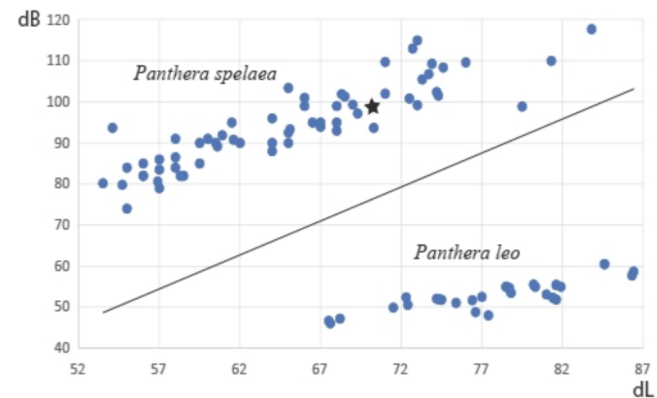


Fig. 5. Relationship between distal epiphysis breadth (dB) and distal epiphysis depth (dL) of the humerus of *Panthera spelaea* and *Panthera leo*. The specimen from Carigüela is represented by a black star on the graph.

Table 3
Geographical location and chronology of the southernmost Pleistocene cave lion sites in Europe.

Site	Latitud N	Chronology U/th C14	Reference
Solana de Zamborino	37° 23' 20"	300–480 ka	Álvarez-Posada et al., 2017
Carigüela cave	37° 26' 30"	145 ± 6 ka	This paper
Cannita	38° 04' 09"	Late Pleistocene	Di Patti & Piccione, 2004
Figueira Brava	38° 31' 28"	30390 ± 700 BP	Cardoso, 1993
Escourial	38° 38' 53"	15250 ± 95 BP	Cardoso, 1993
Moli de Mato	38° 46' 59"	Middle Pleistocene	Sarrión, 1990
Cova del Corb	38° 49' 41"	Middle Pleistocene	Sarrión et al., 1987
Pedreira da Salemas	38° 49' 41"	28890–980 BP	Antunes et al., 1989
Bolomor	39° 04'	MIS 5e	Blasco, 2011
San Luis	39° 25'	MIS 3	Fernández Peris and Martínez Valle, 1989
Cova Negra	39° 28' 11"	MIS 5–4	Pérez Ripoll, 1977
Torre Talao	39° 48' 42"	MIS 5–4	Marra, 2009
Grotta de la Madonna	39° 53' 43"	12100 ± 150 BP	Masetti & Mazza, 2013

Regarding the reference from Cueva del Agua (Torres, 1984), it is crucial to acknowledge that it is based on personal communication from a deceased researcher, and there is no detailed information available regarding the number of remains, anatomy, or measurements. Furthermore, the status of the remains is unknown as they are reported to be lost.

Similarly, the reference from Gorham's Cave raises uncertainties about the taxonomic attribution of the cave lion remains. Authors Zeuner & Sutcliffe (1964) themselves questioned the taxonomic attribution in their text and table documenting the fauna present at the site. Moreover, the absence of mention of lions in a later review of the Quaternary fauna of Gibraltar (Currant, 2000) casts doubt on the presence of cave lions in this area. Additionally, the bones attributed to the cave lion in the Virtual Museum of Gibraltar lack measurements or a scale for size estimation, and despite attempts by researchers, these remains have not been in the museum.

In contrast, Solana del Zamborino presents a more robust case for the presence of cave lions. With 15 remains (both cranial and postcranial) representing a minimum of two adult individuals, this site provides more substantial evidence. Furthermore, morphometric features of the dentition are reported to be like those of *Panthera spelaea* (Martín Penela, 1988:149). Recent magnetostratigraphic studies suggest a chronology for Solana del Zamborino ranging from 480 to 300 thousand years ago (Álvarez-Posada et al., 2017), which aligns well with Acheulean industries found at the site.

The U/Th date obtained for the Carigüela specimen, which attributes it to OIS 6, provides valuable insights into the temporal context of cave lion dispersal. This suggests that during cold phases, such as OIS 6, cave lions were able to expand their range as far south as Iberia. This interpretation is supported by evidence from several sites, including Moli de Mato, Cova del Corb, Bolomor, and Torre Talao, which indicate the presence of cave lions in southern regions during this period. However, it is important to note that the chronology of other southern sites may not align with this interpretation.

The Carigüela lion is the last example of this species for southern Iberia, framed within the end of the Middle Pleistocene. In this sense, it should be noted that important archaeofaunistic records are known for the Upper Pleistocene-Middle Paleolithic in 16 sites in the south of the

peninsula (i.e. Grajas, Zafarraya, Colomera I, Higueral de Valleja, Goram's cave, Palomas, Horá or Carigüela and Ventanas) (Riquelme Cantal et al., 2005, 2011, 2017, 2023; Riquelme Cantal and Carrión García, 2010)). The same applies for the Upper Paleolithic records both locally, Las Ventanas, 400 m from La Carigüela (Cortés-Sánchez et al., 2019), and regionally (Cortés-Sánchez et al., 2008; Riquelme Cantal and Carrión García, 2010; Riquelme Cantal et al., 2011), but in none of them *Panthera leo spelaea* has been documented, so it is possible that the dating obtained for Carigüela corresponds to a specimen from the last populations of this large carnivore in southern Iberia. Nowadays, after reviewing all the available faunal records for the Upper Pleistocene in southern Iberia, and despite significant progress in the study of faunal assemblages from the Middle and Upper Pleistocene of the southern Iberian Peninsula, the available sequence is still not sufficiently continuous and statistically significant. It should be noted that even in regions with very abundant records, the presence of cave lions is scarce (Table 4).

With the currently available data, it is evident that the presence of the lion is not documented in southern Iberia during the Upper Pleistocene.

5. Conclusion

Bone remains no. 6567 identified in the Archaeological and Ethnological Museum of Granada recovered by Spahni in the Carigüela cave is the second evidence of a cave lion at a latitude below parallel 38° N. The U/Th chronology obtained from the fossil (145 ± 6 ka) places it within the final section of MIS 6. The morphological and metric features of the analyzed bone are typical of the species *Panthera spelaea* Goldfuss.

In any case, based on the available data, the study proposes a gradual disappearance of cave lion populations, initially affecting the southernmost latitudes. Subsequently, these populations progressively vanish from the records, including those in the Portuguese area, until, by the end of the Pleistocene, the last specimens are found in the Cantabrian region. This process of gradual disappearance of cave lions is analogous to that described for other Pleistocene megafauna, such as the mammoth, whose populations experience a decline throughout the Upper Pleistocene. In the case of the Carigüela specimen, it possibly represents an initial milestone in the cave lion's disappearance process in Eurasia.

Furthermore, it is the southernmost record, along with that of Solana de Zamborino, of a cave lion in Eurasia; the latest reference of this species in southern Iberia.

Funding

This work has been carried out through the Carigüela cave archaeological project (Ref. Expt.: MH3/PU/GR/11) and has been funded by the research groups INREPA (HUM-262), PAMSUR (HUM-1089), ICAREB and the Ministry of Economy and Competitiveness (HAR2016-77789-P). Likewise, this work is a contribution to FINISTERRA project (European Research Council. CoG – 101045506). Funding for open access charge: Universidad de Córdoba / CBUA.

CRediT authorship contribution statement

José Antonio Riquelme Cantal: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Juan Manuel Garrido Anguita:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Investigation, Funding acquisition, Conceptualization. **Antonio Delgado Huertas:** Writing – original draft, Validation, Methodology, Investigation, Formal analysis. **Pedro María Castaños Ugarte:** Writing – original draft, Validation, Methodology, Investigation, Formal analysis. **Fernando Jiménez Barredo:** Writing – original draft, Validation, Resources, Methodology, Investigation, Formal analysis. **Altug Hasozbek:** Writing – original draft, Validation, Resources, Methodology, Investigation.

Table 4

Main sites of the Middle and Upper Paleolithic in southern Iberia with studied fauna and no presence of cave lion (vid. Cortés et al., 1996; Vega Toscano, 1988; Cáceres, 1997; Barroso et al., 2003; Riquelme Cantal, 2008; Riquelme Cantal et al., 2010, 2011, 2017, 2023; Bicho et al., 2013; Delgado Arcos, 2019).

Chronology	Middle Paleolithic (MIS 5–4–3)	Upper Paleolithic (MIS 3–2)
Sites	Carigüela (Granada) (panther, wolf) Colomera (Granada) Horá (Granada) (wolf) Zájara (Almería) (wolf) Grajas (Málaga) Abrigo/3 de Humo (Málaga) Zafarraya (Málaga) (panther, cuon) Higueral de Motilla (Málaga) Sima de Constantina (Sevilla) (wolf) Devi's Tower (Gibraltar) (wolf) Gorham's cave (Gibraltar) (panther, wolf) Vanguard cave (Gibraltar)	Pantano de Cubillas (Granada) Ojos (Granada) (wolf) Ambrosio (Almería) Nerja (Málaga) Victoria (Málaga) Cueva de las Ventanas (Granada) Abrigo/6 de Humo (Málaga) Tajo de Jorox (Málaga) (panther) Higueral de Motilla (Málaga) El Pirulejo (Córdoba) Higueral de Valleja (Cádiz) Gorham's cave (Gibraltar) (panther, wolf) Vale Boi (Algarbe, Portugal) (panther)

María D. Simón-Vallejo: Writing – review & editing, Writing – original draft, Visualization, Investigation. **M^a del Mar Rivas Carmona:** Writing – review & editing, Writing – original draft, Investigation. **Miguel Cortés-Sánchez:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Resources, Project administration, Investigation, Funding acquisition, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

Acknowledgements

We would like to thank the Archaeological Museum of Granada for providing us with access to the archaeological materials deposited in the Carigüela cave, especially its director, Manuel Ramos Lizana. We would like to thank the first two reviewers for their insightful comments that have allowed us to significantly improve the original manuscript. We are obliged to express our individual thanks to Dr. Philippe Fosse who, in addition to his observations, has provided us with bibliographical references and has disinterestedly made available to us measurements of the humerus of modern lions from the Muséum national d'Histoire naturelle (MNHN) in Paris. This work has been led by researchers José Antonio Riquelme Cantal, Miguel Cortés Sánchez, and Juan Manuel Garrido Anguita.

References

- Almagro, M., Fryxell, R., Irwin, H.T., Serna, M., 1970. Avance a la investigación geocronológica y ecológica de la Cueva de la Carigüela (Pñar, Granada). *Trabajos De Prehistoria* XVII 45–60.
- Altuna, J., 1972. Fauna de mamíferos de los yacimientos prehistóricos de Guipuzcoa. *Munibe* 24, 1–464.
- Álvarez-Lao, D., Álvarez-Vena, A., Ballesteros, D., García, N., Laplana, C., 2020. A cave lion (*Panthera spelaea*) skeleton from Torca del Leon (NW Iberia): micromammals indicate a temperate and forest environment corresponding to GI-11 (MIS 3). *Quat. Sci. Rev.* 229, 106–123. <https://doi.org/10.1016/j.quascirev.2019.106123>.

- Álvarez-Posada, C., Parés, J.M., Sala, R., Viseras, C., Pla-Pueyo, S., 2017. New magnetostratigraphic evidence for the age of Acheulean tools at the archaeological site "Solana del Zamborino" (Guadix-Baza Basin, S Spain). *Scientific Reports* 7, 13495. <https://doi.org/10.1038/s41598-017-14024-5>.
- Antunes, M.T. & Cardoso, J. 1987. O leão das cavernas, *Panthera (Leo) spelaea* (Goldfuss, 1810) em Portugal. In: *Da Pré-história à história [Em linha] : homenagem a Octávio da Veiga Ferreira*. Madrid: Editorial Delta, pp.73-81.
- Antunes, M.T., Cabral, J.M.P., Cardoso J.L., Pais, J., Soares, A.M. 1989. Paleolítico médio e superior em Portugal: datas 14C, estado actual dos conhecimentos, síntese e discussão. *Ciências da Terra (UNL)* 10, 127-138.
- Argant, A., 1988. Étude de l'exemplaire de *Panthera spelaea* (Goldfuss, 1810) (Mammalia, Carnivora, Felidae) du gisement Pléistocène moyen récent de la grotte d'Azé (Saône-et-Loire). *Rev Paléobiol* 7, 449-466.
- Argant, A., 1991. Carnivores quaternaires de Bourgogne. *Documents Des Laboratoires De Géologie De Lyon* 115, 1-309.
- Argant, A., 2010. Carnivores (Canidae, Felidae et Ursidae) de Romain-la-Roche (Doubs, France). *Rev Paléobiol* 29, 495-601.
- Argant, A., Brugal, J.P., 2017. The cave Lion *Panthera (Leo) spelaea* its evolution: *Panthera spelaea* intermedia nov. Subspecies. *Acta Zoológica Cracoviensis* 60 (2), 61-104. <https://doi.org/10.3409/azc.60.2.59>.
- Ballesio, R., 1980. Le gisement pléistocène supérieur de la grotte de Jaurens à Nespoules, Corrèze, France: les Carnivores (Mammalia, Carnivora). II. Felidae. *Nouvelles Archives Du Muséum D'histoire Naturelle De Lyon* 18, 61-102.
- Barnett, R., Lisandra, M., Zepeda Mendoza, M.L., Elias, A., Soares, R., Ho, S.Y.W., Zazula, G., Yamaguchi, N., Shapiro, B., Kirillova, I., Larson, G., Thomas, M., Gilbert, P., 2016. Mitogenomics of the extinct cave lion, *Panthera spelaea* (Goldfuss, 1810) resolve its position within the *Panthera* cats. *Open Quaternary* 2 (4), 1-11. <https://doi.org/10.5334/oq.24>.
- Barnett, R., Shapiro, B., Barnes, I., Ho, S.Y.W., Burger, J., Yamaguchi, N., Higham, T.F.G., Wheeler, H.T., Rosendahl, W., Sher, A.V., Sotnikova, M., Kuznetsova, T., Baryshnikov, G.F., Martin, L.D., Harington, C.R., Burns, J.A., Cooper, A., 2009. Phylogeography of lions (*Panthera leo* ssp.) reveals three distinct taxa and a late Pleistocene reduction in genetic diversity. *Mol. Ecol.* 18, 1668-1677. <https://doi.org/10.1111/j.1365-294X.2009.04134.x>.
- Barroso, C., Riquelme, J.A., Moigne, A.M. & Banes, L. 2003. Las faunas de grandes mamíferos de Pleistoceno Superior de la Cueva del Boquete de Zafarraya. Estudio paleontológico y paleoecológico. In: C. Barroso (coord.), *El Pleistoceno Superior de la Cueva del Boquete de zafarraya*. Arqueología Monografías, 15. Sevilla: Junta de Andalucía, pp. 169-222.
- Barycka, E., 2008. Middle and Late Pleistocene Felidae and Hyaenidae of Poland. *Fauna Pol.* 2, 1-228.
- Baryshnikov, G.F., Boeskorov, G., 2001. The Pleistocene cave lion, *Panthera spelaea* (Carnivora, Felidae) from Yakutia, Russia. *Cranium* 18, 7-24.
- Bicho, N., Manne, T., Marreiros, J., Cascalheira, J., Pereira, T., Tátá, F., Évora, M., Gonçalves, C. & Infantini, 2013. The ecodynamics of the first modern humans in Southwestern Iberia: The case of Vale Boi, Portugal. *Quaternary International* 318: 102-116. <https://doi.org/10.1016/j.quaint.2013.06.029>.
- Blasco, R., 2011. La amplitud de la dieta cárnica en el Pleistoceno medio peninsular: una aproximación a partir de la cueva del Bolomor (Tabernes de la Valldigna, Valencia) y del subnivel TD10-1 de Gran Dolina (Sierra de Atapuerca, Burgos). Tesis doctoral. Universitat Rovira i Virgili. Tarragona.
- Bouchud, J., 1969. Le faune moustérienne de Carigüela. *Anthropologie* 73, 361-364.
- Burger, J., Rosendahl, W., Loreille, O., Hemmer, H., Eriksson, Th., Götherström, A., Hiller, J., Collins, M.J., Wess, T., Alta, K.W., 2004. Molecular phylogeny of the extinct cave lion *Panthera leo spelaea*. *Mol. Phylogenet. Evol.* 30, 841-849. <https://doi.org/10.1016/j.ympev.2003.07.020>.
- Cáceres, I., 1997. Agentes tafonómicos y economía de los grupos de cazadores-recolectores de la Cueva del Higuera de Sierra Valleja (Cádiz). *Revista Atlántica-Mediterránea De Rehistoria y Arqueología Social* 1, 57-76.
- Cardoso, J.L., 1993. Contribuição para o conhecimento dos grandes mamíferos do Plistocénico superior de Portugal. Câmara Municipal de Oeiras, Oeiras.
- Carrión, J.S., Fernández, S., Jiménez-Arenas, J.M., Munuera, M., Ochando, J., Amorós, G., Ponce de León, M., Zollikofer, C., Wang, X., Alexander Jr, E.C., 2013. The sequence at Carihuela Cave and its potential for research into Neanderthal ecology and the Mousterian in southern Spain. *Quat. Sci. Rev.* 217, 194-216. <https://doi.org/10.1016/j.quascirev.2019.04.012>.
- Carrión, J., Munuera, M., Navarro, C., 1998. The palaeoenvironment of Carihuela Cave (Granada, Spain): a reconstruction on the basis of palynological investigations of cave sediments. *Rev. Palaeobot. Palynol.* 99 (3-4), 317-340. [https://doi.org/10.1016/S0034-6667\(97\)00040-7](https://doi.org/10.1016/S0034-6667(97)00040-7).
- Cheng, H., Edwards, R.L., Shen, C.C., Polyak, V.J., Asmerom, Y., Woodhead, J., Hellstrom, J., Wang, Y., Kong, X., Spötl, C., Wang, X., Alexander Jr, E.C., 2013. Improvements in 230Th dating, 230Th and 234U half-life values, and U-Th isotopic measurements by multi-collector inductively coupled plasma mass spectrometry. *Earth Planet. Sci. Lett.* 371-372, 82-91. <https://doi.org/10.1016/j.epsl.2013.04.006>.
- Clot, A., 1980. *La grotte de la Carrière (Gerde, Hautes Pyrénées). Stratigraphie et Paléontologie des Carnivores*. Thèse 3^e cycle. Travaux du Laboratoire de géologie (vol 1), Univ. Paul-Sabatier, Toulouse.
- Cortés-Sánchez, M., 2008. Variabilidad tecnológica en el Paleolítico Medio Meridional. *Treballs D'arqueologia* 14, 105-119.
- Cortés-Sánchez, M., Morales Muñiz, A., Simón-Vallejo, M.D., Bergadá Zapata, M.M., Delgado Huertas, A., López García, P., López Sáez, J.A., Lozano Francisco, M.C., Riquelme Cantal, J.A., Roselló Izquierdo, E., Sánchez Marco, A., Vera Peláez, J.L., 2008. Palaeoenvironmental and cultural dynamics of the coast of Malaga (Andalucía, Spain) during the Upper Pleistocene and Early Holocene. *Quat. Sci. Rev.* 27 (23-24), 2176-2193. <https://doi.org/10.1016/j.quascirev.2008.03.010>.
- Current, A.C. 2000. A review of the Quaternary mammals of Gibraltar. In: C.B. Stringer, R.N.E. Barton & J.C. Finlayson, (Eds.). *Neanderthals on the edge*. Oxford and Oakvill: Oxbow books.
- de Lumley, H., 1969. Étude de l'outillage moustérien de la Grotte de Carigüela (Pñar, Grenade). *Anthropologie* 73, 325-360.
- Lumley, M.A. de & García Sánchez, M., 1971. L'enfant néandertalien de Carigüela à Pñar (Andalousie). *Anthropologie* 75, 29-56.
- Lumley, M.A. de., 1973. Anté-néandertaliens et Néandertaliens du bassin méditerranéen occidental européen. *Études Quaternaires. Mém. n.1.2. Université de Provence*.
- Delgado Arcos, J.A. 2019. Estudio zooarqueológico y tafonómico de los restos óseos de fauna de los niveles musterienses y solutrenses de la cueva del Higuera-Guardia (Málaga-Cádiz). Inferencias en las estrategias de subsistencia y en la paleoecología. Trabajo Fin de Máster. Universidad de Granada.
- Depestele, L., 2005. De hollenleuven (*Panthera leo spelaea*) uit de Belgische grotten: osteometrie, tafonomie en paleoecologie. Gent: Universiteit Gent. Licentiaat.
- Di Patti, C., Piccione, S., 2004. La collezione vertebratologica della Grotta "Cannita" (Misilmeri-PA) conservata presso il Museo Geologico "G. G. Gemellaro" di Palermo. *Naturalis sicil.* S IV, XXVIII (2), 947-963.
- Diedrich, C., 2009. Upper Pleistocene *Panthera leo spelaea* (Goldfuss 1810) remains from the Bilstein Caves (Sauerland Karst) and contribution to the steppe lion taphonomy, palaeobiology and sexual dimorphism. *Annales De Paléontologie* 95, 117-138. <https://doi.org/10.1016/j.anpal.2009.07.001>.
- Diedrich, C., 2010. A diseased *Panthera leo spelaea* (Goldfuss 1810) lioness from a forest elephant graveyard in the Late Pleistocene (Eemian) interglacial lake at Neumark-Nord, central Germany. *Hist. Biol.* 4, 1-23. <https://doi.org/10.1080/08912963.2010.507814>.
- Diedrich, C., 2011a. A Late Pleistocene lion *Panthera leo spelaea* (Goldfuss 1810) skull and other postcranial remains from the Sloup Cave in the Moravian Karst, Czech Republic. *Acta Archaeol.* 19-28.
- Diedrich, C., 2011b. The largest European lion *Panthera leo spelaea* (Goldfuss 1810) population from the Zoolithen Cave, Germany: specialised cave bear predators of Europe. *Hist. Biol.* 23 (2-3), 271-311. <https://doi.org/10.1080/08912963.2010.546529>.
- Diedrich, C., Rathgeber, T., 2012. Late Pleistocene steppe lion *Panthera leo spelaea* (Goldfuss 1810) skeleton remains of the Upper Rhine Valley (SW Germany) and contributions to their sexual dimorphism, taphonomy and habitus. *Hist. Biol.* 24 (1), 1-28. <https://doi.org/10.1080/08912963.2010.549943>.
- Dietrich, W.O., 1968. Fossile Liiwen in europäischen und afrikanischen Pleistozän. *Paläontologische Abhandlungen* 3 (2), 323-366.
- Ermak, E., Ludovic, O., Sandoval-Castellanos, E., Barnes, I., Barnett, R., Stuart, A., Lister, A., Dalen, L., 2015. Population demography and genetic diversity in the pleistocene cave lion. *Open Quaternary* 1 (4), 1-15. <https://doi.org/10.5334/oq.aa>.
- Fernández Peris, J., Martínez Valle, R., 1989. El yacimiento del Paleolítico medio de San Luis (Buñol, Valencia). *Saguntum. Papeles Del Laboratorio De Arqueología De Valencia* 22, 11-34.
- Filhol, E., Filhol, H., 1871. Description des ossements de *Felis spelaea* découverts dans la caverne de Lherm (Ariège). Toulouse: Annales Sciences Naturelles, Masson ed.
- Fusté, M., 1956. Morfología cerebral de un ejemplar neandertalense de la Cueva de la Carigüela en Pñar (Granada). *Trabajos del Instituto Bernardino de Sahagún de Antropología y Etnología* XV (1.1), 27-39.
- Fusté Ara, M., 1957. Moldes intracraniales de dos neandertalenses españoles. Resúmenes del V Congreso Internacional de I.N.Q.U.A. p. 59. Madrid.
- García, N., 2003. Osos y otros carnívoros de la Sierra de Atapuerca. *Fundación Oso de Asturias, Oviedo*.
- García Sánchez, M., 1957. Les hommes fossiles du Paléolithique Moyen et Supérieur de la Grotte de la Carigüela, à Pñar (Grenade). In: V Congrès International INQUA. *Resumés des communications*. Madrid-Barcelona, Gráficas Marina, pp. 66-67.
- Germonpré, M., 1993. Taphonomy of Pleistocene mammal assemblages of the Flemish Valley, Belgium. *Bulletin De L'institut Royal Des Sciences Naturelles De Belgique* 63, 271-309.
- Göksi, H.Y., Fremlin, J.H., Irwin, H.T., Fryxell, R., 1974. Age determination of burned flint by a thermoluminescent method. *Science* 183 (4125), 651-654. <https://doi.org/10.1126/science.183.4125.651>.
- Goldfuss, G.A. 1810. *Die Umgebungen von Muggendorf ein Taschenbuch für Freunde der Natur- und Alterthumskunde*. Erlangen: J.J. Palm.
- Gross, C. 1992. *Das Skelett des Höhlenlöwen (Panthera leo spelaea Goldfuss 1810) aus Siegsdorf/Ldkr. Traunstein im Vergleich mit anderen Funden aus Deutschland und den Niederlanden*, Unpublished Dissertation, Tierärztliche Fakultät der Ludwig-Maximilians Universität, München.
- Jaffey, A.H., Flynn, K.F., Glendenin, L.E., Bentley, W.C., Essling, A.M., 1971. Precision measurement of half-lives and specific activities of 235U and 238U. *Phys. Rev. C* 4, 1889. <https://doi.org/10.1103/PhysRevC.4.1889>.
- Kahlke, R.-D., 1994. Die Entstehungs-, Entwicklungs- und Verbreitungsgeschichte des oberpleistozänen *Mammuthus-Coelodonta*-Faunenkomplexes in Eurasien (Großsäuger). *Abh. Senckb. Naturforsch. Ges.* 546, 1-164.
- Kurten, B., 1985. The Pleistocene lion of Beringia. *Ann. Zool. Fenn.* 22, 117-121.
- Marciszak, A., Lipecki, G., Pawłowska, K., Jakubowski, G., Ratajczak-Skrzatek, U., Zarzecka-Szubska, K., Nadachowski, A., 2021. The Pleistocene lion *Panthera spelaea* (Goldfuss, 1810) from Poland-A review. *Quat. Int.* 605-606 (2), 213-240. <https://doi.org/10.1016/j.quaint.2020.12.018>.
- Marciszak, A., Stefaniak, K., 2010. Two forms of cave Lion: middle Pleistocene *Panthera spelaea* fossilis Reichenau, 1906 and upper Pleistocene *Panthera spelaea spelaea* Goldfuss, 1810 from de Bisnik cave Poland. *Neues Jahrbuch Geol. Palaontol. Abhand.* 258, 339-351. <https://doi.org/10.1127/0077-7749/2010/0117>.

- Marra, A.C., 2009. Pleistocene mammal faunas of Calabria (Southern Italy): biochronology and palaeobiogeography. *Bollettino Della Società Paleontologica Italiana* 42 (2), 113–122.
- Martín Penela, A., 1988. Los grandes mamíferos del yacimiento Achelense de la Solana del Zamborino (Fonelas, Granada, España). *Antropología y Paleoeología Humana* 5, 29–235.
- Masseti, M., Mazza, P., 2013. Western European Quaternary lions: new working hypotheses. *Biol. J. Linn. Soc.* 109, 66–77. <https://doi.org/10.1111/bij.12032>.
- McGee, D., Quade, J., Edwards, R.L., Broecker, W.S., Cheng, H., Reiners, P.W., Evenson, N., 2012. Lacustrine cave carbonates: Novel archives of paleohydrologic change in the Bonneville Basin (Utah, USA). *Earth Planet. Sci. Lett.* 351–352, 182–194. <https://doi.org/10.1016/j.epsl.2012.07.019>.
- Obermaier, H., 1934. Estudios prehistóricos de la provincia de Granada. *Anuario Del Cuerpo Facultativo De Archiveros, Bibliotecarios y Arqueólogos* 1, 255–273.
- Pellicer Catalán, M., 1964. Actividades de la delegación de zona de la provincia de Granada durante los años 1957–1962. *Noticiario Arqueológico Hispánico VI* 304–355.
- Pérez Ripoll, M., 1977. Los mamíferos del yacimiento musteriense de Cova negra (Játiva, Valencia). *Serie de Trabajos Varios del SIP*, 53. Valencia: Diputación de Valencia.
- Pourmand, A., Tissot, F., Arienzo, M., Sharifi, A., 2013. Introducing a comprehensive data reduction and uncertainty propagation algorithm for U-Th geochronometry with extraction chromatography and isotope dilution MC-ICP-MS. *Geostand. Geoanal. Res.* 38 (2), 129–148. <https://doi.org/10.1111/j.1751-908X.2013.00266.x>.
- Reichenau, W. v., 1906. Beiträge zur näheren Kenntnis der Carnivoren aus den Sanden von Mauer und Mosbach. *Abhandlungen Grossherzoglichen Hessischen Geologischen Landesanstalt zu Darmstadt* 4(2), 189–313.
- Riquelme Cantal, J.A., 2002. Cueva de las Ventanas. *Historia y Arqueología*. Ayuntamiento de Píñar, Granada.
- Riquelme Cantal, J.A., 2008. Estudio de los restos óseos de mamíferos de El Pirulejo, Los Niveles Paleolíticos. *Antiquitas* 20, 199–212.
- Riquelme Cantal, J.A., Caro Gómez, J.A., Álvarez García, G., Beltrán Ruiz, A., Delgado Arcos, J.A., Soler López, A., Cañete Gómez, M., 2017. Presencia de grandes carnívoros cuaternarios en el interior de la cueva de La Sima (Constantina, Sevilla). In: *XI Jornadas de Patrimonio Histórico y Cultural de la Provincia de Sevilla*. Sevilla: Diputación de Sevilla, pp. 43–52.
- Riquelme Cantal, J.A., Carrión García, J.S., 2010. La Cueva de las Ventanas, Píñar (Granada): reconstrucción arqueológica de un cubil de hiena tardiglacial en el sur de la Península Ibérica. *Zona Arqueológica* 13, 344–352.
- Riquelme Cantal, J.A., Finlayson, C., Giles Pacheco, F., Rodríguez Vidal, J., Finlayson, G., Santiago, A. & Fa, D., 2011. La fauna de mamíferos solutrense de Gorham's Cave, Gibraltar. In: J.J. Fernández Caro, R. Baena Escudero (coords.), *Arqueología, Paleontología y Geomorfología del Cuaternario en España: X aniversario del seminario Francisco Sousa (La Rinconada, Sevilla)*. Sevilla: Ecomática, Industria Gráfica, pp. 61–178.
- Riquelme Cantal, J.A., Simón-Vallejo, M.D., Garrido Anguita, J.M., Cortés-Sánchez, M., 2023. La montaña neandertal. *Arqueozoología del Paleolítico Medio en el sur de Iberia*. In: J. Ruiz-Fernández, R. Luelmo-Lautenschlaeger, S. Pérez-Díaz, C. García-Hernández, J.A. López-Sáez, F. Alba-Sánchez, D. Gallinar, M. Ruiz-Alonso, A. García & B. González-Díaz (Eds.). *Socio-ecología, arqueología y geohistoria de los paisajes de montaña ibéricos: una mirada multidisciplinar*. Oviedo: CeCodet (Universidad de Oviedo) – Ed. Trabe, pp. 163–173.
- Riquelme Cantal, J.A., Simón Vallejo, M.D., Cortés Sánchez, M., 2005. La fauna de mamíferos del solutrense en la cueva de Nerja. *Munibe. Suplemento* 57–1, 255–263.
- Ruiz Bustos, A., García Sánchez, M., 1977a. Climatología del Musteriense en el Sureste de la Península Ibérica mediante el estudio de los micromamíferos de la Cueva de la Carigüela (Granada). *III Biental De La Real Sociedad Española De Historia Natural*, T. 75, 553.
- Ruiz Bustos, A., García Sánchez, M., 1977b. Las condiciones ecológicas del Musteriense en el Sureste de la Península Ibérica. *La fauna de micromamíferos de la Cueva de la Carigüela (Píñar, Granada)*. *Cuadernos De Prehistoria De La Universidad De Granada* 2, 7–17.
- Sala, B., 1990. *Panthera leo fossilis* (v. Reich., 1906) (Felidae) de Isernia La Pineta (Pléistocène moyen inférieur d'Italie). *Geobios* 23(2), 189–194. 10.1016/S0016-6995(06)80051-3.
- Sanchis, A., Pascual Benito, J.L. (Eds.), 2017. Interaccions entre felins i humans: III Jornades d'Arqueozoologia del Museu de Prehistòria de València : homenatge a Innocenci Sarrión Montañana. *Museu de Prehistòria de València - Diputació de València*, Valencia. <https://mupreva.org/pub/1009/va>.
- Sarrión, I., 1990. El yacimiento del Pleistoceno medio de la Cova del Corb (Ondara-Alicante). *Archivo De Prehistoria Levantina XX* 43–75.
- Sarrión, I., Dupré, M., Fumanal, M.P. & Garay, P., 1987. El yacimiento paleontológico de Moli de Mato (Agres, Alicante). In: *Actas de la VII Reunión sobre el Cuaternario (Santander)*. Madrid: Asociación Española para el Estudio del Cuaternario, pp. 59–62.
- Spahni, J.C., 1955a. Grotte de la Campana à Píñar (Grenade, Espagne). *Bull. Soc. Preh. Fran.* LII, pp. 248–249.
- Spahni, J.Ch. 1955b. Vestiges néanderthaliens de Píñar. *Bull. Soc. Preh. Fran.*, LII, 540. Paris.
- Spahni, J.C., 1955c. Exposición de los hallazgos arqueológicos de la Cueva de Píñar. *Granada, Diputación Provincial de Granada*.
- Stuart, A.J., Lister, A.M., 2011. Extinction chronology of the cave lion *Panthera spelaea*. *Quat. Sci. Rev.* 30, 2329–2340. <https://doi.org/10.1016/j.quascirev.2010.04.023>.
- Testu, A., 2006. Étude paléontologique et biostratigraphique des Felidae et Hyenidae pléistocènes de l'Europe méditerranéenne (sites de la Caune de l'Arago, Orgnac 3, le Portel-Ouest, Bize-Tournal, l'Hortus, la Crouzade en France, la Cova de l'Arbreda en Espagne, Karaïn E en Turquie). *These de l'Université de Perpignan*.
- Torres, T., 1984. Úrsidos del Pleistoceno-Holoceno de la Península Ibérica. Tesis Doctoral. Escuela de Ingenieros de Minas. Universidad Politécnica de Madrid.
- Turner, A., 1984. Dental sex dimorphism in European lions (*Panthera leo* L.) of the Upper pleistocene: palaeoecological and palaeoethological implications. *Ann. Zool. Fenn.* 21, 1–8.
- Vega Toscano, L.G., Hoyo, M., Ruiz, A. & Laville, H., 1988. La séquence de la Grotte de la Carihuela (Píñar, Grenade): Chronostratigraphie et Paléoeologie du Pléistocene Supérieur au Sud de la Péninsule Ibérique. In: M. Otte (ed.). *L'Homme de Néandertal Actes du colloque international de Liège* (1986). In: H. Laville (ed.): *L'environnement 2. ERAUL*. Liège: Études et recherches Archéologiques de l'Université de Liège, pp. 169–180.
- Vega Toscano, G., 1987. El proyecto de la cueva de La Carihuela (Píñar, Granada). *Investigaciones durante 1985*. *Anuario Arqueológico de Andalucía* 1985, II, 129–132.
- Vega Toscano, G., 1988. El Paleolítico Medio del Sureste Español y Andalucía Oriental. Tesis Doctoral. Universidad Complutense de Madrid.
- Vega Toscano, G., 1990. La fin du Paléolithique au Sud de l'Espagne. Ses implications dans le contexte de la péninsule ibérique. In: C. Farizy (ed.). *Paléolithique moyen récent et Paléolithique supérieur ancien en Europe, rupture et transitions. Actes du Colloque International de Nemours (Nemours 1988)*. Mémoires du Musée de Préhistoire d'Ile-de-France 3, 169–176.
- Vega Toscano, L. G. V., Villar, A., Rojas, T., Cosano, P., Escarpa, O., 1997. Las industrias de la interfase Pleistoceno Medio-Superior en la cueva de la Carihuela (Píñar, Granada). In: *II Congreso de Arqueología Peninsular*: Zamora, del 24 al 27 de septiembre de 1996. Zamora: Fundación Rei Afonso Henriques, pp. 105–118.
- Vereshchagin, N.K., 1971. The cave lion and its history in the Holarctic and on the territory of the U.S.S.R. *Trudy of Zoological Institute* 49, 123–199.
- Villaluenga, A., 2016. Presencia de felinos (Felis, Lynx y Panthera) en el registro arqueológico de la Península Ibérica durante el Pleistoceno Superior. *Archaeofauna* (25), 185–204. 10.15366/archaeofauna.2016.25.007.
- Wojtusiak, K., 1953. Remains of *Felis spelaea* Gold. from the cave "Wierzchowska Górna" in Poland. *Acta Geol. Pol.* 3 (4), 573–592.
- Zeuner, F.E., Sutcliffe, A., 1964. Preliminary report on the mammalia of Gorham's Cave, Gibraltar. In: J. d'A. Waechter. *The excavation of Gorham's Cave, Gibraltar, 1951–1954*. *Bull. Inst. Archaeol.* 14, 213–218.