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# A review on Iberian and Italian occurrences of Quaternary lions

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ABSTRACT

The cave lion lineage records from Spain, Portugal, and Italy hold immense paleobiological significance, offering both recent insights and future potential for discoveries. The Iberian record is particularly noteworthy as it includes the earliest evidence of steppe lions in Western Europe, illuminating their possible migration routes. Additionally, the occurrence of cave lions in low latitude regions below 40° in both the Iberian Peninsula and Italy provides crucial information about the environmental requirements and adaptability of this lineage. Furthermore, these regions are key to understanding the replacement or substitution of cave lions by the extant lion species. Collectively, the records from the Iberian Peninsula and Italy are essential for unravelling the paleobiology of this iconic species, enhancing our understanding of their migration patterns, environmental adaptability, and evolutionary transitions.

## 1. Introduction

### 1.1. Research background on Eurasian Cave lion lineage

The Quaternary epoch witnessed the rise and downfall of a formidable array of megafauna, including that of the cave lion lineage (*Panthera fossilis* and *P. spelaea*) (see Sommer, 2020). This extinct feline lineage was one of the largest and most powerful predators of its time, despite nowadays we do not have evidence on their putative degree of sociality. The size of cave lion, its morphological adaptations, and extensive fossil record have made it a focal taxon of paleontological research for the last two centuries since the pioneering work of Goldfuss (1810). Understanding the cave lion paleobiology provides valuable insights into the ecosystems of the Pleistocene, the evolutionary history of large carnivores, and the interactions between these predators and early hominins (Rodríguez-Gómez et al., 2017).

Fossil occurrences of the cave lion were uncovered across a broad swath of Eurasia, ranging from the Iberian Peninsula in the west to the remote reaches of Siberia in the east. In fact, the Eastern range of *P. spelaea* included Beringia, Alaska and Yukon, where the North Atlantic ice sheet separated it from the American lion (*P. atrox*) (Stuart and Lister, 2011). Notable fossil sites in Germany, such as the Zoolithen and Vogelherd Cave, yielded a wealth of bones and teeth, contributing significantly to our understanding of the species' morphology and distribution patterns (von Koenigswald and Heinrich, 1999; Diedrich, 2008). In Russia and Siberia, the preservation of cave lion remains in permafrost has provided remarkably intact specimens, including entire mummified carcasses, which offer unparalleled insights into their anatomy and possibly their physiology and behavior (Boeskorov et al., 2018).

The importance of cave lions as element within the European carnivore guilds cannot be overstated. As one of the apex predators of the Pleistocene, it played a crucial role in the trophic dynamics of its environment. Studying the morphological adaptations of cave lions,

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such as their robust build and specialized dentition, allows to infer their hunting strategies and dietary preferences. Stable isotope analyses of their bones and teeth have revealed a diet predominantly composed of large herbivores, including horses, deer, reindeer, bison, and even cave bears highlighting their role as dominant predators (Bocherens et al., 2011; Bocherens, 2015; Chernova et al., 2016; Wißing et al., 2016).

The distribution and morphological variations of cave lion fossils across different regions reflect their adaptations to the climatic and environmental pressures of the Pleistocene, as well as their interspecific ecological relationships with other large carnivorans. For instance, changes in the size and robustness of cave lions have been correlated with glacial and interglacial periods, suggesting that these predators were highly adaptable to fluctuating environments (Marciszak et al., 2014, 2019; Barnett et al., 2016).

Interactions between cave lions and early humans are another area of significant interest. Archaeological evidence indicates that cave lions were both feared and revered by ancient human populations (Hussain and Floss, 2015). Depictions of cave lions in prehistoric art, such as those found in the Chauvet Cave in France, or the Armintxe cave in Biscay (González Sainz, 2019–2020), and the presence of cut-marks in different chronological contexts (e.g., Blasco et al., 2013; Cueto et al., 2016) suggest a complex relationship between different human groups and these formidable predators (Speth, 2024). These artistic representations, along with the discovery of cave lion remains in human settlements, provide a unique window into the cultural and survival strategies of early humans (Pike-Tay et al., 2008; Russo et al., 2023).

The physical characteristics of cave lions reveal much about their adaptations to the Pleistocene Eurasian environment. It is estimated that cave lions were up to 10 % larger than modern lions, with robust, and powerfully built limbs that enabled them to take down and easily subdue large prey. The presence of a thick, insulating coat is inferred from their habitation in northern latitudes and during glacial periods, indicating their ability to survive in cold climates. Cave paintings and carvings sometimes depict cave lions with faint stripes or spots, akin to the juvenile markings of modern lions, providing further insights into their appearance (Guthrie, 2005). It is noteworthy that none of the depictions, both in parietal and portable art, show any signs of a mane (Yamaguchi et al., 2004; Clottes and Azéma, 2005; Sigari et al., 2024).

In summary, the cave lion symbolizes the grandeur and complexity of the Pleistocene epoch across Eurasia. Its extensive fossil record, broad distribution, and crucial role in ancient ecosystems make it a focal point of paleontological research. Through the study of cave lions, scientists continue to unravel the intricate web of life that once dominated the prehistoric landscapes of Eurasia. As research progresses, new discoveries will undoubtedly shed further light on the life and times of this remarkable predator.

### 1.2. Research background on Iberian and Italian Cave Lions

Similarly to other European regions, during the XIX century several pioneers identified the first cave lion bones in Iberia and Italia (e.g. Vilanova and Piera, 1867) normally associated with archeological contexts.

#### 1.2.1. Spain

The oldest publications on cave lions in Spain date back to the late 19th and early 20th centuries (Vilanova and Piera, 1867; Harlé, 1908a, 1908b; Alcalde del Río et al., 1912) in sites like Santimamiñe. These early studies primarily involved the discovery and initial description of cave lion remains found in various prehistoric sites. Later, numerous Pleistocene sites yielded cave lion remains, providing a detailed picture of their presence and ecological roles. The Sierra de Atapuerca site complex, particularly the sites of Galería and Gran Dolina, has produced a wealth of fossils (García García, 2003). In addition to Atapuerca, other significant Spanish sites are those found in the northern cantabric fringe, where the most abundant and complete specimens of *P. spelaea* are found: the complete skeleton from Arrikrutz (Oñati, Gipuzkoa; Altuna, 1981) and the recently discovered skeleton from Torca del León (Álvarez-Lao et al., 2020). Several caves in Asturias provided a rich assemblage of faunal remains, including those of cave lions, which further illustrate their wide distribution and ecological impact in the region (Rodríguez-Vidal et al., 2014). Additionally, the paintings from La Pileta cave and the engravings from Armintxe cave, which include representations of lions, offer a glimpse into the relationship between early humans and these predators, suggesting a significant presence of lions in human cultural contexts (Utrilla et al., 2014; González Sainz, 2019–2020). It is also noteworthy the record of lions at the low latitude of the Carigüela Cave in Southern Iberia during MIS 6 (Riquelme-Cantal et al., 2024).

#### 1.2.2. Portugal

The first findings of cave lions in Portugal dates back to the early 20th century, with several pioneering works contributing to the initial understanding of these prehistoric animals (Zbyszewski, 1943). Portuguese Pleistocene record of lions, while less extensive compared to Spanish records, is nonetheless significant. The Almonda cave system is one of the key sites where cave lion remains have been found, contributing to the understanding of their geographical range and adaptability within the Iberian Peninsula (Antunes, 1992). These findings suggest that cave lions could inhabit diverse environments, from open steppes to mountainous caves, adapting their hunting strategies to the available prey and terrain. The discovery of lion remains at sites like Gruta da Oliveira has provided further evidence of their presence in the region and their role within the Pleistocene ecosystems (Marks et al., 2002). Then, the latest discovers to be published come also from the archeological context of Figueira Brava Cave and, despite its fragmentary nature, it has a well-defined chronological, faunistic and environmental context (Zilhão et al., 2020). Finally, Portugal displays the southernmost occurrence of cave lions in Europe (37.189°N), with several remains at the Vale Boi site dated between 25 and 20.3 ka (Cascalheira et al., 2012).

#### 1.2.3. Italy

The first findings and descriptions of cave lion remains in Italy also date back to the early 20th century, with significant contributions from pioneering researchers in paleontology and archaeology (Regalia, 1925; Pasa, 1947; Del Campana, 1954). Notably, sites such as Grotta del Cavallo and Grotta di Fumane have provided important fossils, which, alongside other faunal remains, offer insights into the ecosystem dynamics and predator-prey relationships of the time (Benazzi et al., 2011). Especially significative are the findings of *P. spelaea* in Sicily for its low latitude and paleoenvironmental context in Maccagnone and Cannita Caves (Bonfiglio et al., 2022; Di Patti and Piccione, 2004).

Research on cave lions from Spain, Portugal, and Italy continues to evolve with new discoveries and advanced analytical techniques. Genetic studies, for instance, have provided insights into the phylogenetic relationships between different populations of Pleistocene lions across Europe (Barnett et al., 2009). These studies enhance our understanding of Pleistocene ecosystems and provide broader insights into megafaunal extinctions and the impacts of climatic and anthropogenic factors on large predators. Ongoing excavations and interdisciplinary research efforts continue to uncover new data, shedding light on the complex interactions between these formidable predators and their environments.

## 2. Materials and methods

To conduct a comprehensive update of the Iberian and Italian fossil records of the cave lion lineage, several key tasks were undertaken. First, all available literature pertaining to cave lion finds in the Iberian and Italian Peninsulas was gathered and reviewed. The key references for each case are detailed in Tables 1 and 2. Additionally, previously published historical collections and unpublished materials from numerous Iberian and Italian institutions were examined. These institutions

**Table 1**
Cave lion verified occurrences from the Iberian Peninsula.

| N° | Country | Region | Site | Town | layer | Period | Age | MIS | Species | References |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 | Sp. | Barcelona | Vallparadís Estació Lower Unit | Terrassa | EVT9-EVT12 | Early Pl. | 1 Ma | MIS31 | *P. fossilis* | Madurell-Malapeira et al., (2024) |
| 1 | Sp. | Barcelona | Vallparadís Estació Middle Unit | Terrassa | EVT6-EVT8 | Early Pl. | 0.86 Ma | MIS21 | *P. fossilis* | Madurell-Malapeira et al., (2024) |
| 2 | Sp. | Murcia | Cueva Victoria | Cartagena | - | Early Pl. | ca. 0.9 Ma | MIS25? | *P. fossilis* | Madurell-Malapeira et al., (2024) |
| 3 | Sp. | Burgos | Galería (Sierra de Atapuerca) | Ibeas de Juarros | GIII | Middle Pl. | 466 ± 39; 256 ± 23 ka | MIS12–8 | *P. fossilis* | García and Arsuaga, (2001); Rodríguez et al., (2011) |
| 3 | Sp. | Burgos | Galería (Sierra de Atapuerca) | Ibeas de Juarros | GIIa/b | Middle Pl. | 503 ± 95; 422 ± 55 ka | MIS13–12 | *P. fossilis* | García and Arsuaga, (2001); Rodríguez et al., (2011) |
| 4 | Sp. | Burgos | Gran Dolina (Sierra de Atapuerca) | Ibeas de Juarros | TD10–1 | Middle Pl. | 337 ± _x005F_x005F_x0002_29; 379 ± 57 ka | MIS10–9 | *P. fossilis* | Rodríguez et al., (2011) |
| 4 | Sp. | Burgos | Gran Dolina (Sierra de Atapuerca) | Ibeas de Juarros | TD10–2 | Middle Pl. | 244 ± 26; 337 ± 51; 418 ± 63 ka | MIS11–10 | *P. fossilis* | Rodríguez et al., (2011) |
| 4 | Sp. | Burgos | Gran Dolina (Sierra de Atapuerca) | Ibeas de Juarros | TD10–3 | Middle Pl. | 430 ± 59 ka | MIS12–11 | *P. fossilis* | Rodríguez et al., (2011) |
| 4 | Sp. | Burgos | Gran Dolina (Sierra de Atapuerca) | Ibeas de Juarros | TD10–4 | Middle Pl. | < 480 ka | MIS12–11 | *P. fossilis* | Mosquera et al., (2024). |
| 5 | Sp. | Burgos | Sima de los Huesos (Sierra de Atapuerca) | Ibeas de Juarros | 7 | Middle Pl. | 447.9 ± 15.5 ka - 412.3 ± 2. ka | MIS12–11 | *P. fossilis* | García and Arsuaga, (2011) |
| 5 | Sp. | Burgos | Sima de los Huesos (Sierra de Atapuerca) | Ibeas de Juarros | 6 | Middle Pl. | 413 ka | MIS11 | *P. fossilis* | García and Arsuaga, (2011) |
| 6 | Sp. | Madrid | Arenero de Manuel Soto | Getafe/Ribas-Vaciamadrid | - | Middle Pl. | 350 ka | MIS10 | *P. fossilis* | van der Made et al., (2023) |
| 7 | Sp. | Granada | Solana del Zamborino | Fonelas | - | Middle Pl. | 300–480 ka | MIS9 | *P. fossilis* | Díez Fernández-Lomana, (1993); Riquelme-Cantal et al., (2024) |
| 8 | Sp. | Soria | Ambrona | Ambrona | - | Middle Pl. | 332–152 ka | MIS9–6 | *P. fossilis* | Sesé and Soto, (2005); Falguères et al., (2006) |
| 9 | Sp. | Gipuzkoa | Lezetxiki | Arrasate | VIII | Middle Pl. | > 240; > 164 ± 9 ka | MIS7 or older | *P. spelaea* | Altuna, (1972); Falguères et al., (2006) De-la-Rúa et al., (2016) |
| 9 | Sp. | Gipuzkoa | Lezetxiki | Arrasate | VII | Middle Pl. | > 240 ka | MIS7 or older | *P. spelaea* | Altuna, (1972); Falguères et al., (2006); Villaluenga et al., 2012 |
| 9 | Sp. | Gipuzkoa | Lezetxiki | Arrasate | VI | Middle Pl. | c. 240 ka | MIS7 | *P. spelaea* | Altuna, (1972); Falguères et al., (2006) Villaluenga et al., 2012 |
| 10 | Sp. | Asturias | La Parte | Siero | C | Middle Pl. | > 150 ka (141 ± 8; 188 ± 11 ka) | MIS6 | *P. fossilis* | Álvarez-Lao & García-García, (2006) |
| 11 | Sp. | Valencia | Molí de Mató | Agres | - | Middle Pl. | - | - | *P. fossilis* | Sarrión Montaña, (1990); Sanchis, (2015) |
| 12 | Sp. | Valencia | Cova del Corb | Ondara | - | Middle Pl. | - | - | *P. fossilis* | Sarrión Montaña, (1990); Sanchis, (2015) |
| 13 | Sp. | Barcelona | Avenc de la Pepi | Gavà | - | Middle Pl. | - | - | *P. fossilis* | J. M.-M. Unpublished |

(*continued on next page*)

**Table 1** (*continued*)

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|---|---|---|---|---|---|---|---|---|---|---|
| 14 | Sp. | Nafarroa | Koskobilo | Olazti | No stratigraphical context | Indet. chr. | Middle-Late Pl. | MIS7–2 | *P. spelaea* | Gómez-Olivencia et al., (2020) |
| 15 | Sp. | Valencia | Bolomor | Tavernes de Valldigna | IV | Late Pl. | - | MIS−5 | *P. spelaea* | Blasco et al., (2013) |
| 16 | Sp. | Granada | Carigüela | Piñar | - | Late Pl. | ca. 145ka | MIS6 | *P. spelaea* | Riquelme-Cantal et al., (2024) |
| 17 | Sp. | Madrid | Cueva Des-Cubierta | Pinilla del Valle | 5 | Late Pl. | 135 ka and 185 ka | MIS6 | *P. spelaea* | Baquedano et al., (2023) |
| 18 | Sp. | Lugo | Valdavara 3 | Becerreá | - | Late Pl. | 113–103 ka | MIS5d | *P. spelaea* | Vaquero et al., (2018) |
| 19 | Po. | Lisboa | Figueira Brava | Serra da Arrábida | 2 | Late Pl. | 106–86ka | MIS5 | *P. spelaea* | Antunes and Cardoso, (2000) |
| 20 | Sp. | Gipuzkoa | Imanolen Arrobia | Deba | - | Late Pl. | 100ka | MIS5 | *P. spelaea* | Castaños et al., (2017) |
| 21 | Sp. | Gipuzkoa | Artazu VII | Arrasate | - | Late Pl. | c. 93 ka | MIS5c | *P. spelaea* | Suárez-Bilbao et al., (2016); Castaños et al., (2019) |
| 22 | Po. | Leira | Oliveira | Almonda | (7−13)(20)(26) | Late Pl. | 95–70 ka | MIS5–4 (MIS5a) (MIS5b) | *P. spelaea* | Antunes and Cardoso, (2000) |
| 23 | Sp. | Madrid | Cueva del Camino | Pinilla del Valle | 5 | Late Pl. | ca. 90 k a | MIS5 | *P. spelaea* | Arsuaga et al., (2012) |
| 24 | Sp. | Segovia | Pinarillo−1 | El Pinarillo | - | Late Pl. | 90 ka | MIS5b | *P. spelaea* | Arribas Herrera et al., (2008) |
| 9 | Sp. | Gipuzkoa | Lezetxiki II | Arrasate | F | Late Pl. | Between 74 (level D) and 70–86.8 ka (level J) | MIS5a | *P. spelaea* | Villaluenga et al., 2012; Arriolabengoa et al., (2018) |
| 25 | Sp. | Madrid | PRERESA | Getafe | - | Late Pl. | ca. 84 ka | MIS5 | *P. spelaea* | van der Made and Mazo, (2015) |
| 26 | Sp. | Madrid | Abrigo de Navalmaillo | Pinilla del Valle | F-D | Late Pl. | ca. 77ka | MIS5a−4 | *P. spelaea* | Moclán et al., (2021) |
| 27 | Sp. | Cantabria | Castillo | Puente Viesgo | 22 | Late Pl. | Mousterian Beta (70.1 ± 9.4 ka) | MIS5–4 | *P. spelaea* | Rink et al., (1997); Castaños et al., (2018) |
| 28 | Po. | Vinhais | Lorga de Dine | Dine | - | Late Pl. | - | MIS5? | *P. spelaea* | Antunes and Cardoso, (2000) |
| 17 | Sp. | Madrid | Cueva Des-Cubierta | Pinilla del Valle | 3 | Late Pl. | - | MIS4 | *P. spelaea* | Baquedano et al., (2023) |
| 29 | Sp. | Huesca | Cueva de los Moros 1 (Gabasa) | Peralta de Calasanz | e | Late Pl. | > 51900; 46500 + 4400–2200 | - | *P. spelaea* | Utrilla et al., (2010) |
| 17 | Sp. | Madrid | Cueva Des-Cubierta | Pinilla del Valle | 2 | Late Pl. | 51 ka | MIS3 | *P. spelaea* | Baquedano et al., (2023) |
| 30 | Sp. | Barcelona | Cova del Toll | Moià | 4 | Late Pl. | > 49 ka | MIS3 | *P. spelaea* | Ramírez et al., 2019 |
| 31 | Sp. | Barcelona | Abric Romaní | Capellades | I | Late Pl. | c. 49–46 ka | MIS−3 | *P. spelaea* | Cáceres et al., (1993) |
| 32 | Po. | Alentejo | Escoural | Santiago do Escoural | 3 | Late Pl. | 48 ka | MIS3 | *P. spelaea* | Cardoso, (1992) |
| 27 | Sp. | Cantabria | Castillo | Puente Viesgo | 20 | Late Pl. | Mousterian alpha (>47.3 ka uncal BP; >45.7; 45.7 ± 1.7; >43.8; 42.1 ± 1.5; 42.9 ± 1.4) | MIS3 | *P. spelaea* | De Quirós Guidotti et al., 2006; Castaños, 2018 |
| 33 | Sp. | Burgos | Prado Vargas | Cornejo | 4 | Late Pl. | 46.6 ka (AAR) | MIS3 | *P. spelaea* | Alonso-García et al., (2020) |
| 34 | Sp. | Asturias | Jou'l'Llobu | La Robellada | - | Late Pl. | 46,4 ± 2,1 ka uncal BP | MIS3 | *P. spelaea* | Pinto Llona, (2007); Stuart and Lister, (2011) |
| 35 | Sp. | Asturias | Torca del León | Porrua | Upper layer | Late Pl. | 43,0 ± 0,5 ka cal BP | MIS3 | *P. spelaea* | Álvarez-Lao et al., (2020) |
| 26 | Sp. | Valencia | San Luis | Buñol | - | Indet. chr. | Würm/Mousterian | - | *P. spelaea* | Fernández-Peris & Martínez-Valle, (1989) |
| 37 | Sp. | Segovia | Cueva de la Zarzamora | Perogordo | - | Late Pl. | > 44.4 ka | MIS3 | *P. spelaea* | Sala et al., (2020) |
| 27 | Sp. | Cantabria | Castillo | Puente Viesgo | 14 | Late Pl. | Aurignacian | MIS3 | *P. spelaea* | Castaños, 2018 |
| 27 | Sp. | Cantabria | Castillo | Puente Viesgo | 12 | Late Pl. | Aurignacian | MIS3 | *P. spelaea* | Castaños, 2018 |
| 38 | Sp. | Girona | Reclau Viver | Serinyà | - | Late Pl. | 40–30 ka | MIS3 | *P. spelaea* | Maroto et al., (2017) |
| 39 | Sp. | Barcelona | Riera dels Canyars | Castelldefels | - | Late Pl. | c. 39.6 ka cal BP | MIS−3 | *P. spelaea* | Daura et al., (2013) |
| 40 | Sp. | Tarragona | Cova Foradada | Calafell | IIIc | Late Pl. | 39–34ka | MIS−3 | *P. spelaea* | Rodríguez-Hidalgo et al., (2019) |
| 41 | Sp. | Girona | Cellera d'Amont 1 | Serinyà | - | Late Pl. | - | - | *P. spelaea* | Maroto et al., (2017) |

(*continued on next page*)

**Table 1** (*continued*)

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|---|---|---|---|---|---|---|---|---|---|---|
| 42 | Sp. | Segovia | Portalon del Tejadilla | Perogordo | CAM 1 | Late Pl. | c. 35–34.3 ka cal BP | MIS3 | *P. spelaea* | Sala et al., (2020) |
| 43 | Sp. | Gipuzkoa | Torre | Oiartzun | Sima | No chr. | Pre-gravettian | - | *P. spelaea* | Altuna and Mariezkurrena, (2010) |
| 44 | Sp. | Gipuzkoa | Amalda | Zestoa | V | Late Pl. | Gravettian | MIS3–2 | *P. spelaea* | Altuna, (1990) |
| 45 | Sp. | Gipuzkoa | Aitzbitarte III | Errenteria | Va (Entrance) | Late Pl. | Old Gravettian | MIS3 | *P. spelaea* | Altuna and Mariezkurrena, (2011) |
| 45 | Sp. | Gipuzkoa | Aitzbitarte III | Errenteria | III (Entrance) | Late Pl. | Recent Gravettian | MIS2 | *P. spelaea* | Altuna and Mariezkurrena, (2011) |
| 46 | Po. | Algarve | Vale Boi | Vale de Boi | Slope | Late Pl. | 25–20.3 ka | MIS2 | *P. spelaea* | Cascalheira et al., (2012) |
| 47 | Sp. | Gipuzkoa | Urtiaga | Deba | i | Late Pl. | Würm IIIb | MIS2? | *P. spelaea* | Altuna, (1972) |
| 27 | Sp. | Cantabria | Castillo | Puente Viesgo | 10 | Late Pl. | Solutrean | MIS2 | *P. spelaea* | Castaños, 2018 |
| 48 | Sp. | Cantabria | El Pendo | Camargo | 4-Corte Solutrense | Late Pl. | Upper Solutrean | MIS2 | *P. spelaea* | Castaños Ugarte, (2001) |
| 49 | Po. | Estremadura | Caldeirão | Tomar | F/H/I-Jb | Late Pl. | 22–18 ka | MIS3–2 | *P. spelaea* | Davis, (2002) |
| 50 | Po. | Lisboa | Pedreira e Gruta das Salemas | Ponte de Lousa (Loures) | 2_8 | Late Pl. | 33–23ka | MIS3 + 2 | *P. spelaea* | Antunes & Cardoso, 1987 |
| 51 | Sp. | Cantabria | El Juyo | Igollo | 9 | Late Pl. | Lower Magdalenian (Between 15,300 ± 700 and 14,440 ± 180 uncal BP) | MIS2 | *P. spelaea* | Klein and Cruz Uribe,(1985); González Echegaray and Freeman, (1992)/93 |
| 52 | Sp. | Gipuzkoa | Kiputz IX | Mutriku | F | Late Pl. | 18,850 ± _x005F_x005F_x0003_ 80; 19,870 ± _x005F_x005F_x0003_x005F_x005F_x0003_ 150 a uncal BP | MIS2 | *P. spelaea* | Castaños et al., (2012) |
| 53 | Sp. | Asturias | La Paloma | Soto de Regueras | 8 | Late Pl. | Lower Magdalenian | - | *P. spelaea* | Castaños, (1980) |
| 54 | Sp. | Cantabria | El Mirón | Ramales | - | Late Pl. | 19 ka | MIS2 | *P. spelaea* | Harlé, (1908a); Marín-Arroyo, (2009) |
| 47 | Sp. | Gipuzkoa | Urtiaga | Deba | f+g | Late Pl. | 17 ka BP | MIS2 | *P. spelaea* | Altuna, (1972) |
| 55 | Sp. | Nafarroa | Abauntz | Arraitz | e | Late Pl. | 13,500 ± 160 a uncal BP | MIS2 | *P. spelaea* | Altuna et al., (2002) |
| 56 | Sp. | Cantabria | La Garma (Lower Gallery) | Omoño | Zone IV | Late Pl. | 14.8 ka cal BP | MIS2 | *P. spelaea* | Cueto et al., (2016), (2020) |
| 57 | Sp. | Asturias | La Riera | Posada de Llanes | 27 (lower) | Late Pl. | 15–13 ka cal BP | MIS2 | *P. spelaea* | Altuna, (1986) |
| 58 | Sp. | Cantabria | Altamira | Santillana del Mar | - | Late Pl. | Magdalenian | MIS2 | *P. spelaea* | Castaños Ugarte and Castaños de la Fuente, (2014) |
| 59 | Sp. | Asturias | Balmorí | Llanes | - | Late Pl. | Wurm IV | MIS2–3 | *P. spelaea* | Álvarez-Lao, (2003) |
| 53 | Sp. | Asturias | La Paloma | Soto de Regueras | 6 | Late Pl. | Middle Magdalenian | - | *P. spelaea* | Castaños, (1980) |
| 53 | Sp. | Asturias | La Paloma | Soto de Regueras | 4 | Late Pl. | Upper Magdalenian | - | *P. spelaea* | Castaños, (1980) |
| 47 | Sp. | Gipuzkoa | Urtiaga | Deba | e | Late Pl. | Upper Magdalenian (Magdalenian V) | MIS2 | *P. spelaea* | Altuna, (1972) |
| 60 | Sp. | Bizkaia | Santimamiñe | Kortezubi | IV | Hol. | 9.5–7 ka cal BP | MIS1 | *P. spelaea* | Castaños, (1984) |
| 57 | Sp. | Asturias | La Riera | Posada de Llanes | 29 | Hol. | 8650 ± 300 BP, 6500 ± 200 BP | MIS1 | *P. spelaea* | Altuna, (1986) |
| 61 | Sp. | Araba | Sima de Azoleta | Orozko | - | No chr. | - | - | *P. spelaea* | Castaños, 2005 |
| 62 | Sp. | Gipuzkoa | Arrikrutz | Oñati | - | No chr. | - | - | *P. spelaea* | Altuna, (1967), (1981) |
| 62 | Sp. | Gipuzkoa | Larrayoz gallery (Arrikrutz) | Oñati | - | No chr. | - | - | *P. spelaea* | Altuna, (1981) |
| 63 | Po. | Centro | Pencova | Pencova | - | No chr. | - | - | *P. spelaea* | Cascalheira et al., (2012) |
| 64 | Sp. | Asturias | Quintanal | Llanes | - | No chr. | - | - | *P. spelaea* | Alcalde del Río et al., (1912) |

**Table 2**
Occurrences of cave lions on the Italian Peninsula.

| Nº in map | Country | Region | Site | Town | layer | Period | Age | MIS | Species | References |
|---|---|---|---|---|---|---|---|---|---|---|
| 65 | Italy | Molise | Isernia La Pineta | Isernia (IS) | Unit 3 | Middle Pl. | ca. 600 ka | MIS15 | *P. fossilis* | Sala, (1990) |
| 66 | Italy | Veneto | Castello (Soave) | Verona (VR) | - | Middle Pl. | ca. 500ka | MIS15–11 | *P. fossilis* | Bona and Sardella, (2012) |
| 67 | Italy | Veneto | Monte Tenda (Soave) | Verona (VR) | - | Middle Pl. | ca. 500ka | MIS15–11 | *P. fossilis* | Bona and Sardella, (2012) |
| 68 | Italy | Veneto | Sentiero (Soave) | Verona (VR) | - | Middle Pl. | ca. 500ka | MIS15–11 | *P. fossilis* | Bona and Sardella, (2012) |
| 69 | Italy | Verona | Viatelle (Soave) | Verona (VR) | - | Middle Pl. | ca. 500ka | MIS15–11 | *P. fossilis* | Bona and Sardella, (2012) |
| 70 | Italy | Veneto | Cerè Cave | Verona (VR) | - | Middle Pl. | ca. 500ka | MIS15–13 | *P. fossilis* | Ghezzo et al., (2014) |
| 71 | Italy | Latium | Castel di Guido, Via Aurelia km 20 | Roma | 4 and 5 | Middle Pl. | 412 ka | MIS11 | *P. fossilis* | Marra et al., (2022) |
| 72 | Italy | Latium | Torre in Pietra 1, Torre del Pagliaccetto | Torrimpiera (Rome) | lower level | Middle Pl. | ca. 350 ka | MIS9 | *P. fossilis* | Marra et al., (2014) |
| 73 | Italy | Lombardy | Cava Zanola | Paitone (BS) | - | Middle Pl. | ca. 350ka | MIS9? | *Panthera sp.* | Bona and Sardella, (2014) |
| 74 | Italy | Sicily | Maccagnone cave | Palermo (PA) | - | Middle Pl. | ca. 200ka | MIS7 | *P. fossilis* | Bonfiglio et al., (2022) |
| 75 | Italy | Latium | Vitina | Roma | Upper Beds | Middle Pl. | ca. 250ka | MIS7 | *P. fossilis* | Caloi and Palombo, (1997) |
| 76 | Italy | Friuli-Venezia Giulia | Grotta dell'Alce, Grotta Tilde | Sgonico (TS) | - | Middle Pl. | ca. 150ka | MIS6 | *P. fossilis* | Alice et al., (2022) |
| 77 | Italy | Camapania | Grotta del Poggio | Marina di Camerota (SA) | - | Late Pl. | ca. 100ka | MIS7, MIS5 | *P. spelaea* | J.M.-M. Unpublished Data |
| 78 | Italy | Tuscany | Maspino | Arezzo | - | Late Pl. | 130–125ka | MIS6 | *P. spelaea* | S.B.-L. Unpublished data |
| 79 | Italy | Lombardy | Cremona | Cremona (CR) | alluvial | Late Pl. | - | MIS13-MIS5 | *P. spelaea* | Persico, (2021) |
| 80 | Italy | Latium | Fosso del Cupo | Montecelio (Rome) | - | Late Pl. | 90 ka | MIS5c-MIS5a | *P. spelaea* | Petronio et al., (2019) |
| 81 | Italy | Apulia | Grotta B di Spagnoli | Rignano Garganico (FO) | Upper | Late Pl. | 60ka? | MIS5–4 | *P. spelaea* | Ricci and Toniato, (2017) |
| 82 | Italy | Abbruzzo | Grotta degli Orsi Volanti | Chieti (CH) | - | Late Pl. | ca. 100ka | MIS5–3 | *P. spelaea* | Mazza et al., (2005) |
| 83 | Italy | Salerno | Grotta della Ossa | Palinuro (SA) | - | Late Pl. | ca. 100ka | MIS5e | *P. spelaea* | Bona, (2006) |
| 84 | Italy | Latium | Valle Radice | Valleradice di Sora (FR) | - | Late Pl. | ca. 100ka | MIS5 | *P. spelaea* | Pandolfi and Tagliacozzo, (2015) |
| 85 | Italy | Apulia | Avetrana | Taranto (TA) | Layer 8 | Late Pl. | ca. 90ka | MIS5e−3 | *P. spelaea* | Mecozzi et al., (2021) |
| 86 | Italy | Lombardia | Buco dell'Orso | Laglio | - | Late Pl. | ca. 100ka | MIS5 | *P. spelaea* | Mecozzi et al., (2021) |
| 87 | Italy | Friuli-Venezia Giulia | Caverna degli Orsi/ Caverna Pocala | S. Dorligo della Valle (TS) | 120–122 | Late Pl. | ca. 125 ka | MIS5e | *P. spelaea* | Berto and Rubinato, (2013) |
| 88 | Italy | Latium | Carnello | Carnello (FR) | - | Late Pl. | ca. 70ka | MIS 4 | *P. spelaea* | Petronio et al., (2011) |
| 89 | Italy | Latium | Grotta Guattari | Circeo | - | Late Pl. | ca. 66ka | MIS4 | *P. spelaea* | Rolfo et al., (2023) |
| 90 | Italy | Apulia | Ingarano | Apricena (FO) | layer b | Late Pl. | ca. 58ka | MIS4 | *P. spelaea* | Mecozzi et al., (2021) |
| 91 | Italy | Tuscany | Montemerano-Manciano | Grosseto (GR) | - | Late Pl. | 60 ka | MIS4 | *P. spelaea* | Petronio et al., (2014) |
| 92 | Italy | Calabria | Torre Talao | Scalea (CS) | - | Late Pl. | 65 ka | MIS4 | *P. spelaea* | Marra, 2009 |
| 93 | Italy | Apulia | Grotta Romanelli | Castro (LE) | F | Late Pl. | 40 ka | MIS3 | *P. spelaea* | Sardella et al., (2014) |
| 94 | Italy | Latium | La Sassa | Sonnino (LT) | - | Late Pl. | 34 ka | MIS3 | *P. spelaea* | Gatta et al., (2022) |
| 95 | Italy | Massa-Carrara | Grotta Equi | Equi | - | Late Pl. | ca. 40ka | MIS3 | *P. spelaea* | Ghezzo and Rook, (2015) |
| 96 | Italy | Apulia | Riparo dell'Oscurusciuto | Melpignano | - | Late Pl. | 42ka | MIS3 | *P. spelaea* | Mecozzi et al., (2021) |
| 97 | Italy | Apulia | Grotta del Cavallo | Uluzzo | N-M | Late Pl. | ca. 40ka | MIS3 | *P. spelaea* | Mecozzi et al., (2021) |
| 98 | Italy | Apulia | Fondo Cattiè | Melpignano | - | Late Pl. | ca. 40ka | MIS3 | *P. spelaea* | Mecozzi et al., (2021) |
| 99 | Italy | Apulia | Grotta delle Tre Porte | Melpignano | - | Late Pl. | ca. 40ka | MIS3 | *P. spelaea* | Mecozzi et al., (2021) |
| 100 | Italy | Toscana | Buca della Iena | Roselle | - | Late Pl. | ca. 40ka | MIS3 | *P. spelaea* | Petronio et al., (2011) |
| 101 | Italy | Toscana | Grotta della Fabbrica | Grosseto | - | Late Pl. | ca. 40ka | MIS3 | *P. spelaea* | Petronio et al., (2011) |
| 96 | Italy | Apulia | Riparo dell'Oscurusciuto | Ginosa (TA) | - | Late Pl. | 42ka | MIS3 | *P. spelaea* | Mecozzi et al., (2021) |

(*continued on next page*)

**Table 2** (*continued*)

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| 102 | Italy | Emilia-Romagna | Settepolesini di Bondeno | Settepolesini di Bondeno (FE) | - | Late Pl. | 38 ka | MIS3 | *P. spelaea* | Ghezzo and Rook, (2015) |
| 103 | Italy | Friuli-Venezia Giulia | Grotta dell'Orso (di Gabrovizza) | Sgonico (TS) | - | Late Pl. | - | MIS2 | *P. spelaea* | Castello and Strazzaboschi, (2013) |
| 104 | Italy | Veneto | Grotta di Fumane | Ca' Gottolo (VR) | - | Late Pl. | ca. 30ka | MIS2 | *P. spelaea* | Peresani, (2022) |
| 105 | Italy | Latium | Palidoro | Palidoro | layers G | Late Pl. | 19ka | MIS2 | *P. spelaea* | Petronio et al., (2011) |
| 106 | Italy | Veneto | Riparo Tagliente | Grezzana (VR) | - | Late Pl. | ca. 14ka | MIS2 | *P. spelaea* | Berto et al., (2018) |
| 107 | Italy | Abruzzo | Grotta del Cervo | Carsoli (AQ) | - | Late Pl. | - | - | *P. spelaea* | Ghezzo, (2018) |
| 108 | Italy | Palermo | Grotta Cannita | Misilmeri (PA) | - | Late Pl. | - | - | *P. spelaea* | di Patti & Piccione, 2004 |
| 109 | Italy | Lucca | Grotta all'Onda | Camairoe | - | Hol. | 107ka | MIS1 | *P. spelaea* | Masseti and Mazza, (2013) |
| 110 | Italy | Calabria | Grotta della Madonna | Praia a Mare | L | Hol. | 12ka | MIS1 | *P. spelaea* | Masseti and Mazza, (2013) |
| 111 | Italy | Toscana | Riparo Fredian | Lucca | - | Hol. | ca. 13ka | MIS1 | *P. spelaea* | Petronio et al., (2011) |

include: the Museu de Ciències Naturals de Barcelona, Museu del Seminari Conciliar in Barcelona, Institut Català de Paleontologia in Sabadell, Museu Arqueològic Comarcal de Banyoles, Museu d'Olot, Museu de Puigcerdà, Museu de Prehistòria de Valencia, Museo Arqueológico Municipal de Cartagena, Museo Arqueológico de Granada, Gordailua in Irun, Arkeologia Museoa (Bilbao), Museo Nacional de Ciencias Naturales in Madrid, Museo Geominero in Madrid, Museo Arqueológico y Paleontológico de Madrid, Museo Arqueológico Nacional in Madrid, Museo de San Isidro in Madrid, Institut Català de Paleoecologia Humana i Evolució Social (IPHES), Museu Geológico de Lisboa, Museu Nacional de História Natural e da Ciência in Lisbon, Museu de Lourinhã, Museu de História Natural e da Ciência da Universidade do Porto, Museo di Storia Naturale di Milano, Museo di Paleontologia dell'Università di Napoli Federico II, Museo di Storia Naturale dell'Università di Firenze particularly the Geology and Paleontology Museum, Museo di Geologia e Paleontologia dell'Università di Torino, Museo Civico di Storia Naturale di Verona, Museo Paleontologico di Montevarchi, and Museo di Scienze della Terra di Sapienza, Università di Roma in Rome.

Due to the extensive volume of fossil material assessed (via direct examination, bibliographic sources, or personal communication), a detailed description of each item is beyond the scope of this paper. However, the following sections will highlight some of the most significant specimens and fossil assemblages in terms of their palaeobiological, archaeological, or heritage value. These fossil assemblages

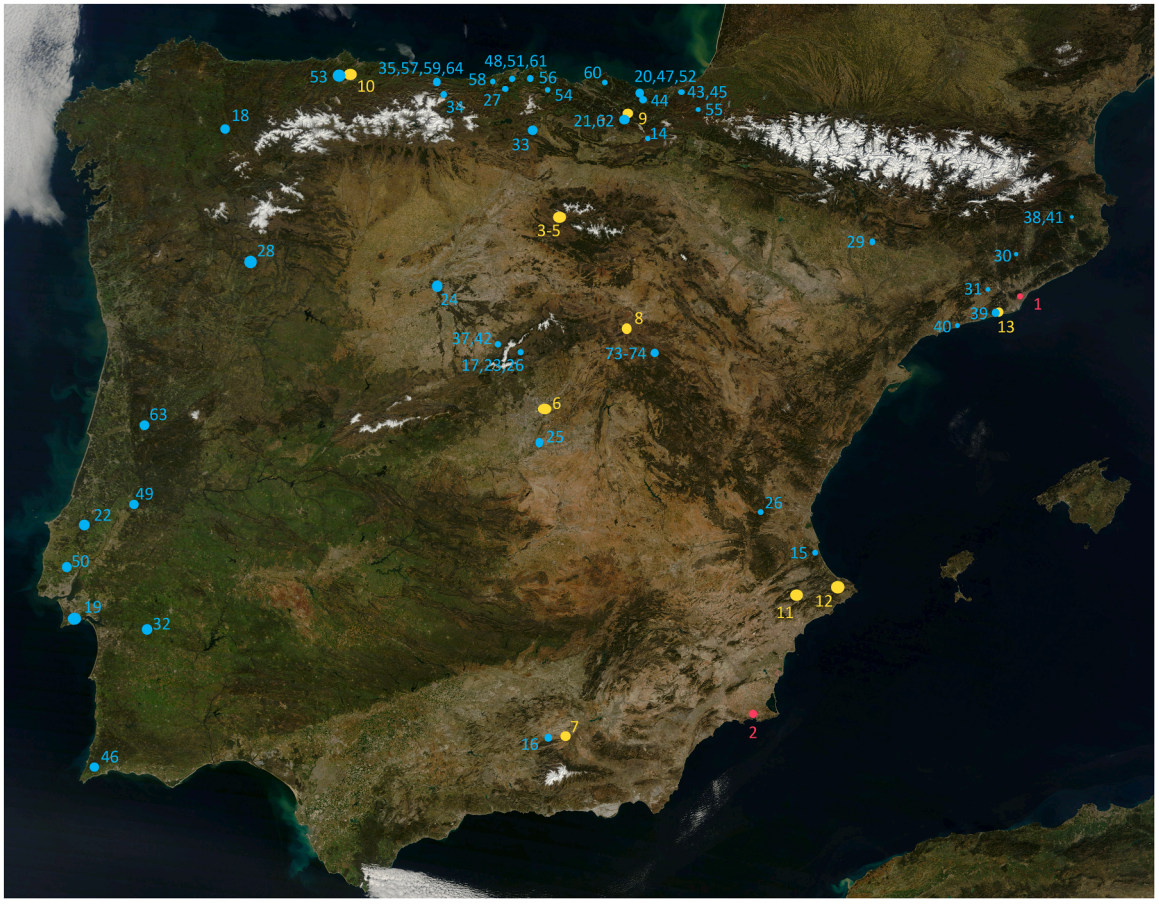


**Fig. 1.** Iberian sites with record of *Panthera fossilis* and *P. spelaea*. The sites numbers are shown in Table 1. Early Pleistocene sites in red, Middle Pleistocene sites in yellow, and Late Pleistocene and Holocene in blue.

are summarized with data related to the specific locality or archaeological-palaeontological layer of the find (refer to Tables 1 and 2). Each locality and level will be treated as a case study for analyzing the fossil record. The most up-to-date geochronology and stratigraphic framework proposed for each find has been adhered, with geochronologic ages provided in thousands or millions of years before present, abbreviated as "ka" or "Ma," respectively. The geographic location of the sites on where cave lions are recorded are depicted in Figs. 1 and 2.

## 3. Results

### 3.1. Oldest records: late Early Pleistocene

Historically, the oldest records of *Panthera fossilis* in Europe are associated with early Middle Pleistocene sites such as Mauer, Mosbach 2, Westbury-sub-Mendip, and Isernia La Pineta, dating approximately between 0.6 and 0.4 Ma (Sala, 1990; Turner and Antón, 1997; von Koenigswald and Heinrich, 1999; Stuart and Lister, 2011). However, latest discoveries in the past decade has identified even older finds in Eurasia. Notably, *Panthera fossilis* remains have been uncovered in the Western Siberian Kuznetsk Basin, dating back 1 Ma (Sotnikova and Foronova, 2014), and in Kozi Grzbiet, Poland, and Pakefield, UK, around

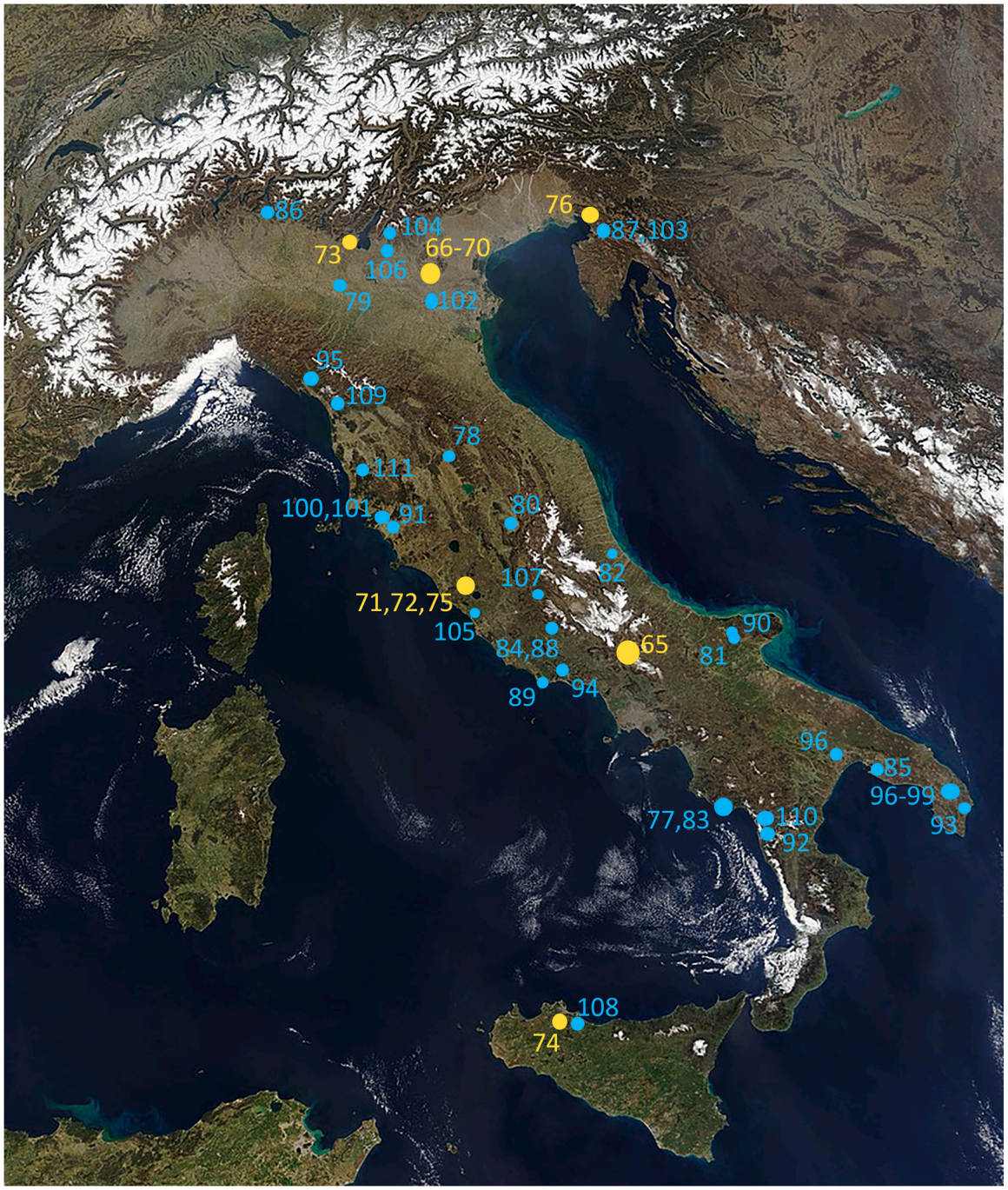


**Fig. 2.** Italian sites with record of *Panthera fossilis* and *P. spelaea*. The sites numbers are shown in Table 2. Middle Pleistocene sites in yellow, and Late Pleistocene and Holocene in blue.

750 ka (Lewis et al., 2010; Marciszak et al., 2021).

In Iberia, several finds of *Panthera fossilis* from the latest Early Pleistocene have been mentioned and illustrated in various publications, but they have not been thoroughly described until now. These early records include layers EVT10 and EVT7 of the Vallparadís Section in Terrassa, corresponding to MIS 30 and 21, respectively (Fig. 4A,E-H; Madurell-Malapeira et al., 2010, 2014, in press), and a fourth metatarsal from the historical collection of the Cueva Victoria site in Cartagena, dating to approximately 0.9 Ma (Fig. 4I; J.M.-M. unpublished data). This metatarsal is housed at the Natural History Museum of Barcelona and originates from the personal collection of J.F. de Villalta.

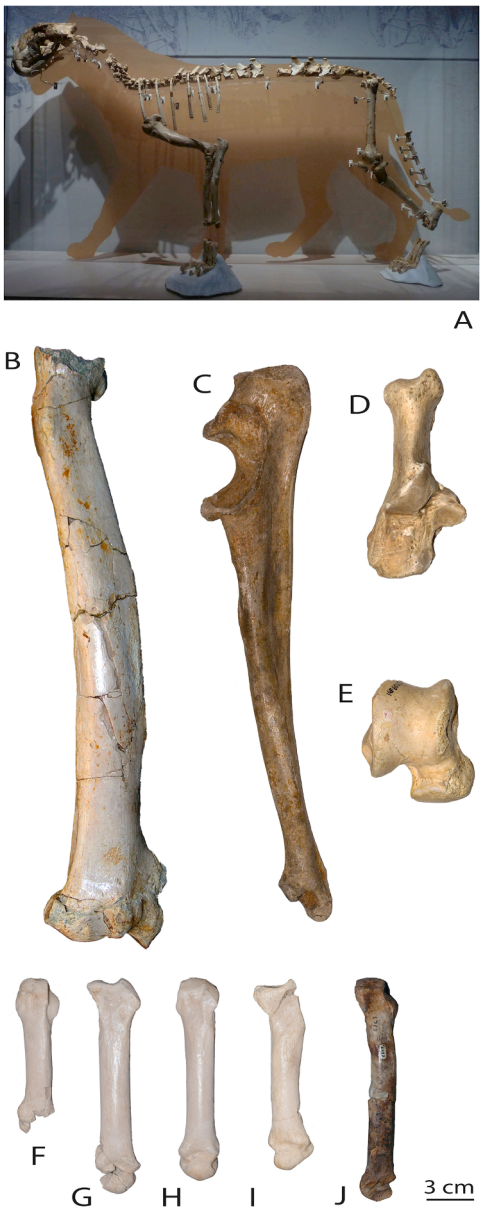


**Fig. 4.** *Panthera fossilis* and *Panthera spelaea* remains from the Italian and Iberian peninsulas. A, the Arrikrutz lion (Oñati, Gipuzkoa, Northern Iberian Peninsula). Note that only parts of the left side has been mounted as this is virtually complete specimen (see Altuna, 1981); B, right radius (EVT14269) of *P. fossilis* from the layer EVT10 of the Vallparadís Section (Spain); C, left ulna (IGF5053) of *P. spelaea* from Maspino (Italy); D, right calcaneum of *P. spelaea* from Grotta di Equi (Italy); E, Right talus of *P. spelaea* from Grotta di Equi (Italy); F, right fifth metacarpal (EVT16012) of *P. fossilis* from layer EVT10 of the Vallparadís Section (Spain); G, right fourth metacarpal (EVT16016) of *P. fossilis* from layer EVT10 of the Vallparadís Section; H, right third metacarpal (EVT14270) of *P. fossilis* from layer EVT10 of the Vallparadís Section; I, right second metacarpal (EVT14276) of *P. fossilis* from layer EVT10 of the Vallparadís Section; J, left fourth metatarsal (V6397) of *P. fossilis* from Cueva Victoria (Spain).

All these Early Pleistocene Iberian specimens are postcranial. The remains from layer EVT10 include a nearly complete forepaw (comprising the radius, metacarpals, carpals, and phalanges). The remains from EVT7 include a femur, a tibia, and a third metatarsal, while the specimen from Cueva Victoria is a fourth metatarsal. These large, robust pantherine specimens are comparable in size and sturdiness to the remains found in Western Siberia and the early Middle Pleistocene European lions. This contrasts sharply with the small and slender remains of the latest Early Pleistocene *Homotherium crenatidens*, particularly the more than 500 remains from the Incarcal Complex, located 100 km north of the Vallparadís Section, with a similar chronology of MIS 21 (Duval et al., 2023).

### 3.2. Middle Pleistocene

The early Middle Pleistocene sites in Mediterranean Europe are not abundant, and consequently, the records of steppe lions are scarce and fragmentary. Historically, the oldest lion remains from Mediterranean Europe were dental remains from Isernia la Pineta (MIS15, Italy; Sala, 1990). However, Iannucci and colleagues (2024) recently published a putative newly discovered fourth metatarsal from Venosa Notarchirico layer A (MIS16). This newly published remain is very poorly preserved and surprisingly slender and small compared to the stouter lions of these chronologies in Europe (Sotnikova and Foronova, 2014 Marciszak et al., 2019, 2021). More surprising is the absence of biometric and morphological comparisons between this remain and an extensive record of chronologically roughly coeval sample of *Panthera gombaszoegensis* from Château (MIS15; Argant and Argant, 2011; Argant and Brugal, 2017). In fact, in the researchers' graphs, the Notarchirico remain (Iannucci et al., 2024; Fig. 2) falls outside the range of Quaternary European lions and within range of extant African lions. For the aforementioned characteristics, we deem the Notarchirico metatarsal corresponding thus to *P. gombaszoegensis* rather than to *P. fossilis* (*contra* Iannucci et al., 2024). For this reason, it will not be considered in this review.

Other Italian early Middle Pleistocene remains attributable to *Panthera fossilis* include Cerè Cave (MIS15 or 13; Ghezzo et al., 2014), Soave (MIS 15 or 13; Bona and Sardella, 2012), Castel di Guido (MIS11; Marra et al., 2022), Torre del Pagliaccetto (MIS9; Villa et al., 2016), and Cava Zanola (MIS9; Bona and Sardella, 2014).

Regarding the Iberian Peninsula, no Middle Pleistocene records are known from Portugal. In Spain, the oldest Middle Pleistocene remains probably correspond to the sites of Sima de los Huesos of the Atapuerca Complex at (MIS12, García et al., 2024), Galería IIa (MIS13 to 9; García García, 2003), and Dolina TD10 (MIS11–10; García García, 2003). Other Iberian sites include Ambrona (MIS11; Santonja et al., 2018), Solana del Zamborino (MIS12 to 9; Álvarez-Posada et al., 2017), and Arenero de Manuel Soto (MIS10; van der Made et al., 2023). Among all the above-mentioned sites, the only abundant and fairly complete remains correspond to the Gran Dolina and Galería sites, partially published by Nuria García García in her PhD (2003). However, recent excavations have provided dozens of new, yet undescribed, material.

Regarding the latest Middle Pleistocene records, Italy and Iberia have even fewer than the early Middle Pleistocene. In Italy, lions were recorded in Maccagnone Cave (MIS7; Bonfiglio et al., 2022), Grotta dell'Alce (MIS6; Alice et al., 2022), Maspino and Botro Maspino (MIS 6) and Vitina (MIS7; Caloi and Palombo, 1997). In Spain, three sites record *P. fossilis* remains from the latest Middle Pleistocene: La Parte (MIS6; Álvarez-Lao and García, 2006) and the upper layers of Galería in the Atapuerca Complex (MIS8 and 7; Rodríguez et al., 2011). Especially noteworthy is the recent publication of the lion remain from the Carigüela Cave in Piñar, with a chronology of ca. 145 ka. This humerus is located at 37° of latitude similar to the Solana del Zamborino and Vale

Boi sites, being the three southernmost records of lions in Europe (Riquelme-Cantal et al., 2024).

In summary, 30 occurrences in Italy and Iberia record Middle Pleistocene remains of *Panthera fossilis*. However, most of these finds are fragmentary and isolated, and do not represent populations or enough individuals to make paleobiological inferences.

### 3.3. Late Pleistocene

The number and quality of Late Pleistocene remains in the studied countries have significantly improved, thanks to the abundance of archaeological sites. A total of 88 sites in Spain, Portugal, and Italy recorded Late Pleistocene *P. spelaea* samples (Tables 1 and 2), with notable finds such as the complete skulls and partial skeletons from Caverna Pocala, also known as Caverna degli Orsi (MIS5e; Berto and Rubinato, 2013), and Torca del León (MIS3; Álvarez-Lao et al., 2020).

These sites are distributed across the geography of the aforementioned countries, with a high concentration in southern latitudes of the Italian Peninsula (e.g. Apulia, Sicily), and northern latitudes of the Iberian Peninsula (e.g., Gipuzkoa)(Tables 1 and 2).

Spain has the highest concentration of records, with 55 sites. Among the older Late Pleistocene records, the Cantabrian sites of Castillo and Urtiaga have the majority of remains (Altuna, 1972; Castaños et al., 2018), as well as the various sites in the Pinilla del Valle area (Arsuaga et al., 2012; Moclán et al., 2021). Concerning MIS3, the most abundant with 39 records, the Cantabrian sites and those in Bizkaia, Gipuzkoa, and Asturias are the most numerous, including Torca del León, La Riera, Castillo, Urtiaga, and Aitzbitarte III (Altuna, 1972, 1986; Altuna and Mariekurrena, 2011; Castaños et al., 2018; Álvarez-Lao et al., 2020).

In Portugal, the records are scarce, with only nine sites, but they are distributed throughout the country. These include Caldeirão, Gruta das Salemas, Vale Boi, Escoural, and Pego do Diabo, all from MIS3 (Cardoso, 1992).

In Italy, 33 sites record *P. spelaea* remains, several of them in the Melpignano Area of Apulia, such as Grotta delle Tre Porte, Avetrana, and Grotta del Cavallo (Mecozzi et al., 2021). Additionally, complete crania have been found in Grotta della Ossa at Zandobbio (Bona, 2006) and several specimens in good state of preservation at Grotta di Equi (Toscana; Del Campana, 1954; Figs. 3 and 4). Nevertheless, the excellent record of cave bears and lions from Caverna Pocala in Trieste with dozens of remains and three complete crania, stands out as the best association of cave lions in the three studied countries (Berto and Rubinato, 2013).

### 3.4. Holocene

*Panthera spelaea* is thought to have become extinct around 15–14 ka according to paleontological literature (Stuart and Lister, 2011; but see Fosse et al., 2017 which published a direct date of 10590 ± 70 BP), being replaced around 6–5 ka by extant lion populations that presumably dispersed along the Bosphorus Strait in Eastern Europe (Stuart and Lister, 2011; Masseti and Mazza, 2013). However, records from northern Spain and Italy suggest the presence of Holocene samples attributed to *P. spelaea*, which fill this supposed gap. These sites include Cueva de la Riera, Santimaiñe, Riparo Fredian, Grotta all'Onda, and Grotta della Madonna, with findings in levels with a chronology between 14.5 ka and 8 ka (Masseti and Mazza, 2013). However, direct radiocarbon dating on lion bones would be necessary in order to test proposed chronologies.

Despite most of these sites have absolute datations on the lion sedimentary or faunistic context, except for Grotta della Madonna and Santimamiñe, the remains are fragmentary and isolated, hindering the ascertain of their taxonomical attribution. Consequently, it is challenging to determine the exact date of extinction of *Panthera spelaea* in Western Europe, and whether *Panthera leo* arrived, and if so, the timing of its dispersion into Western Europe via the Bosphorous or from Ukraine and Bulgaria (Thomas, 2014). Future DNA analysis on these specimens will shed light on this intriguing topic.

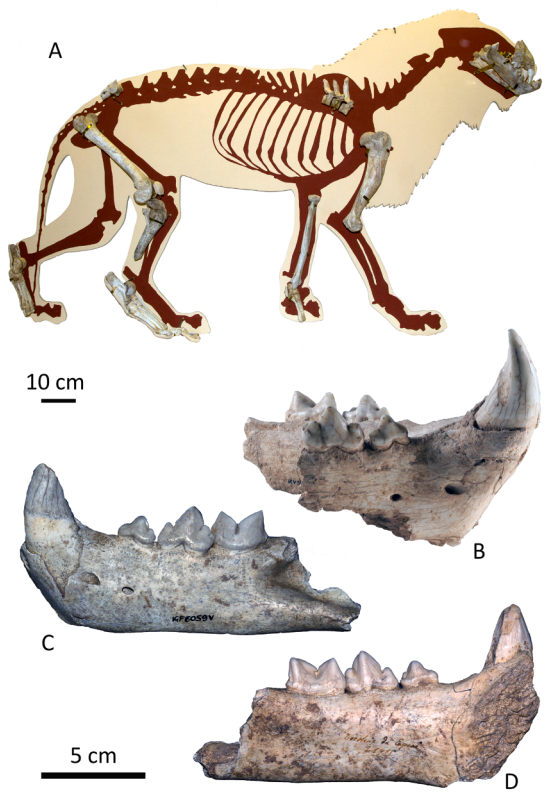


**Fig. 3.** Cranial remains of *Panthera spelaea* from the Iberian and Italian peninsulas. A, Partial skeleton from the Grotta di Equi as displayed in the Natural History Museum of Florence, Italy (IGF); B, partial mandible from Reclau Viver exhibited at the Arqueological Museum of Banyoles (Spain; MACB-329–118b); C, partial left hemimandible from Grotta di Equi (IGF 6059 v) in buccal view; D, partial left hemimandible from Grotta di Equi (IGF 6059 v) in lingual view.

## 4. Iberian and Italian Cave Lions in the Pleistocene European context: significance and future perspectives

### 4.1. The Early-Middle Pleistocene Transition and the Cave Lion Lineage

The *Early-Middle Pleistocene Transition* (EMPT), occurring around 1.2–0.6 Ma, marks a significant shift in Earth's climate system and had profound effects on European ecosystems. This period saw a transition from a 41-ka glacial-interglacial cycles to a 100-ka cycles, leading to more pronounced and prolonged glacial periods (Head and Gibbard, 2015). These climatic changes caused significant alterations in habitat distributions and the composition of flora and fauna across Europe. During the EMPT, glacial expansions led to the displacement and extinction of many species, while interglacial periods allowed for the migration and establishment of new species in Europe (Madurell-Malapeira et al., 2010). One of the notable faunal turnovers was the progressive replacement of the large saber-toothed cats, *Homotherium crenatidens*, by early *Panthera fossilis*. Also, during this period other large carnivorans such as *Megantereon adroveri, Panthera gombaszoegensis, Viretailurus pardoides, Pachycrocuta brevirostris* or *Xenocyon lycaonoides* vanished from the European ecosystems or started their decline being replaced by *Panthera pardus* and *Crocuta crocuta* (Madurell-Malapeira et al., 2024). This shift in dominant predators influenced the structure of herbivore communities, as different predation pressures would have altered their population dynamics and behaviors. The EMPT also saw the appearance and spread of early hominins with Acheulean technology in Europe, who would interact with these changing ecosystems, both as predators and agents of

ecological change (Vallverdú et al., 2014).

Concerning large felids, *Homotherium* was a specialized predator that thrived in open, grassland environments. Its morphology, including long limbs and serrated, flattened canines, was well-suited for hunting large, open-country herbivores such as mammoths and large ungulates (Turner and Antón, 1997). However, as the EMPT progressed, the glacial cycles became more severe, causing significant shifts in habitat availability and the types of European ecosystems. These changes led to the fragmentation and reduction of open grasslands, the primary habitat of *Homotherium*, thus limiting its hunting grounds and prey availability (Stuart and Lister, 2011). In contrast, *Panthera fossilis* exhibited greater ecological flexibility. This species could adapt to various environments, from open plains to more forested areas, and demonstrated a more generalized hunting strategy. *Panthera fossilis* had robust and powerful builds, allowing them to tackle a wide range of prey sizes and types. Their adaptability to different environments and broader diet made them more resilient to habitat fluctuations caused by the changing climate (Marciszak et al., 2019). Moreover, the presumed social structure of *Panthera fossilis*, which likely included living and hunting in groups, provided additional survival advantages. Social hunting strategies allowed them to efficiently pursue larger prey and provided better protection against competitors and environmental stresses (Yamaguchi et al., 2004). This social behavior is evident in modern lion populations, and it is believed to have been present in their Pleistocene ancestors (Diedrich, 2013). In the context of the EMPT it is important to highlight that the human populations present in southern Europe were probably large social predators, notable for their use of cooperative hunting (Saladié et al., 2011) contributing to interspecific competition pressure. The replacement of *Homotherium* by *Panthera fossilis* can also be attributed to competitive interactions. As habitats evolved and the ranges of these large predators overlapped, *Panthera fossilis*, with its superior adaptability and competitive advantages, would have been more successful in securing territories and resources. The decline in prey availability for the more specialized *Homotherium* further intensified its vulnerability, ultimately leading to its eventual extinction (Van Valkenburgh, 2001). Regarding the competition and interaction between these two large predators, certain contexts in the Iberian Peninsula, such as Atapuerca Gran Dolina levels TD10.3 and TD10.4, may offer further insights in the future due to the discovery of both *Homotherium* and the cave lion within the same archaeological stratum (García García, 2003; Mosquera et al., 2024; Villalobos et al. in preparation).

In this scenario, the Iberian and Italian Peninsulas play a pivotal role on the first dispersals of African and Asian species into Europe during the EMPT and the restructuration of European ecosystems. The latest Early and early Middle Pleistocene records from these peninsulas became key points for studying the ecological evolutive tendencies of the cave lion lineage (sensu Marciszak et al., 2014). In this sense, the current evidence indicates that the first European lions were very large and stout forms comparable to those from the MIS11–9 (Marciszak et al., 2019; Prat-Vericat et al., 2022) and slightly larger than the MIS15–12. Currently these collections are quite reduced but future excavations will help in shed light in the paleobiology of the earliest European lions and the putative antagonistic relationships with saber-toothed cats.

### 4.2. Low-latitudinal cave Lions

The lineage of cave lions roamed the vast expanses of Eurasia and North America during the Quaternary Ice Ages. Typically associated with the cold and arid environments of the Pleistocene epoch, cave lions inhabited a variety of habitats that were largely shaped by the climatic fluctuations of glacial and interglacial cycles. These predators were primarily found in steppe-like environments, which were characterized by open grasslands interspersed with sparse woodlands. Such habitats were prevalent during the cold glacial periods, providing an ideal setting for cave lions due to the abundance of large herbivorous prey like horses or bison (Diedrich, 2011; Barnett et al., 2009). The steppe-tundra biome, where cave lions thrived, extended across much of northern Eurasia. This biome was marked by low temperatures, limited precipitation, and a landscape dominated by grasses, sedges, and shrubs. The open terrain shaped the hunting strategies of cave lions, which likely involved stalking and ambushing their prey in a similar manner to modern lions (Yamaguchi et al., 2004). However, the distribution of cave lions was not restricted to the frigid north. Fossil evidence indicates that Pleistocene cave lions inhabited Spain, Portugal and Italy, suggesting that these regions provided suitable environments for these large predators during the Pleistocene. Specifically, several sites in these countries record cave lions below 40º latitude including Solana del Zamborino (37.388°N), La Carigüela Cave (37.399° N), Figueira Brava(38.445°N), Escoural (38.570°N), Vale Boi (37.189°N), Pedreira da Salemas (38.887°N), Bolomor (39.025°N), Cova Negra (39.015°N) or Grotta della Madonna (39.886°N) (Riquelme-Cantal et al., 2024 and references therein; Tables 1 and 2). Several ecological factors contributed to the presence of cave lions in these lower latitude regions, despite their typical association with the colder climates of the Quaternary Ice Ages. One key factor was the significant climatic variability during the Pleistocene, characterized by alternating glacial and interglacial periods. During interglacial periods, the climate warmed, leading to the expansion of temperate environments into southern regions such as Spain and Italy. These warmer intervals allowed the steppe-like habitats to extend into these areas, providing continuous suitable habitats for cave lions even in lower latitudes (Stuart and Lister, 2011). The adaptability of cave lions to various environmental conditions was another critical factor. They were not strictly cold-adapted species but rather opportunistic predators capable of exploiting different habitats as long as their prey was abundant. In Iberia and Italy, the presence of diverse and plentiful prey populations during interglacial periods would have attracted cave lions. These regions offered a mix of open grasslands, woodlands, and other environments that supported large herbivores essential for the diet of cave lions. The availability of prey species like deer, horses, and bovids in these regions during warmer periods made them attractive habitats for cave lions (Rodríguez-Vidal et al., 2011).

Additionally, southern Europe, including Spain and Italy, likely served as refugia during colder glacial periods. These areas provided relatively stable and less harsh environments where both prey and predators could survive. The milder climates and more varied landscapes of these regions would have offered cave lions the necessary resources to sustain their populations when conditions in northern Europe became too extreme. This refugial role of southern Europe is supported by the presence of other cold-adapted megafauna in these regions during the Pleistocene, indicating that these areas acted as sanctuaries during adverse climatic conditions (Álvarez-Lao and García, 2011). The topographical diversity of Spain and Italy also played a role in supporting cave lion populations. The varied landscapes, including mountains, plains, and coastal areas, created a range of microhabitats that could sustain different prey species throughout the year. This ecological diversity ensured that cave lions had access to a consistent food supply, regardless of seasonal changes. The ability of cave lions to navigate and hunt in these diverse terrains further demonstrates their ecological versatility and adaptability (Bocherens et al., 2011).

Finally, it is essential to consider additional ecological factors, such as competitive exclusion, as potential limitations on the paleogeographic distribution of cave lions. Sherani et al. (2023) recently reported the presence of cave lions in the Middle Pleistocene of North China, overlapping with the historical range of *Panthera tigris*. These authors suggested that competitive exclusion might have favored cave lions during periods when open habitats expanded in Northern China (Sherani et al., 2023). However, when considering the lower-latitude presence of cave lions in Europe, it is challenging to justify a possible dispersal of *Panthera leo* through Gibraltar or Sicily during the Late Pleistocene as a case of competitive exclusion.

### 4.3. Taphonomy of Iberian and Italian lions

The condition of lion bones found in fossil assemblages from the studied sites is highly variable, suggesting a complex interplay of natural deposition and taphonomic processes. The diversity of contexts in which these remains fossilized complicates generalizations about their taphonomic histories. However, most *Panthera fossilis/spelaea* remains in Iberia and the Italian Peninsula come from rock shelters or caves, often within karstic environments, or from open-air sites near rivers, lakes, or streams.

Based on this, we can identify four primary typologies of lion bone accumulations. These are determined by factors such as (1) the number of remains, (2) the number and age of individuals, (3) skeletal completeness, (4) surface modifications, and (5) the taphonomic context, including agents involved in the assemblage formation. These, along with environmental and sedimentary contexts, help us understand the origins of the remains, whether from natural death, predation, scavenging, human activity, or a combination of these factors.

In most Iberian and Italian sites, lion remains are scarce, usually consisting of small, isolated elements like teeth or tooth fragments (e.g. Altuna, 1972; Gómez-Olivencia et al., 2020), and carpal or tarsal bones, and phalanges (e.g. Bona and Sardella, 2012; Antunes and Cardoso, 2000). Occasionally, complete mandibles (e.g. Persico, 2021) or skulls (e.g. Bona, 2006) are found. Typically, fewer than five remains are present, often only a single bone/tooth, representing one individual, with no significant taphonomic signals to determine their origin. This pattern is seen in key sites like Ambrona, Castillo, Carigüela, and Caldeirão in Iberia, or Isernia La Pileta in Italy (Davis, 2002; Rink et al., 1997; Riquelme-Cantal et al., 2024; Sala, 1990; Sesé and Soto, 2005). These small assemblages limit detailed taphonomic analysis. Nevertheless, the origin of these isolated remains aligns with what is known as the "background noise" of the palimpsest. Though scattered, these fossils still offer critical insights into ancient ecosystems.

A second typology includes sites where there are more than a few remains but fewer than a few dozen bones or teeth, often representing more than one individual. These remains are frequently spatially concentrated and consist of specific anatomical parts, such as a hand or foot (e.g. Antunes and Cardoso, 2000; Bona and Sardella, 2012). When multiple individuals are present, juvenile remains, particularly deciduous teeth, are often found (e.g. Masseti and Mazza, 2013; Ghezzo et al., 2014). This typology of accumulation is commonly associated with palimpsests involving various taphonomic agents, particularly hyenas (e.g. Antunes and Cardoso, 2000; Arsuaga et al., 2012; Davis, 2002). Although it has been speculated that lions used caves as dens (Diedrich, 2009), carnivore tooth marks on the bones suggest most are linked to *Crocuta spelaea* scavenging activity (Diedrich, 2009; 2011).

A third typology includes rare cases where lion remains are associated with human activity. These remains are typically scarce, often isolated, representing a single adult individual, and showing anthropogenic modifications, though multiple elements can be found (Cueto et al., 2016, 2020). In Iberia and the Italian Peninsula, cut marks and, fractures link lion remains to hunting and consumption by humans (Blasco et al., 2010; 2013), use of skins (Cueto et al., 2016; Valensi and Psathi, 2004), and perforations kink to the use of teeth as “ornaments” during the Upper Paleolithic (Harlé, 1912 in Álvarez-Fernández, 2001).

The final typology involves partial skeletons, sometimes nearly complete, as seen in Arrikrutz and Torca del León (Altuna, 1981; Álvarez-Lao et al., 2020). These remains often appear in anatomical connection and are likely from lions wandering through karst systems. Some authors suggest lions prowled caves to hunt or scavenge hibernating bears, though this accumulation could also result from natural traps or refuge-seeking behavior (Diedrich, 2011).

While we propose four general typologies, exceptions exist, and many sites lack sufficient data on context, the number of remains, or taphonomy. Although lion-human interactions date back to the Middle Pleistocene, they remain rare. The role of lions as bone accumulators in caves, either as dens or refuges, is still unproven and requires more evidence. Moreover, while some sites suggest complex interactions between lions and hominins, the fragmentary nature of the data limits definitive conclusions, underscoring the need for more detailed taphonomic studies.

### 4.4. Holocene lions: Cave or Extant lions?

The putative Holocene records of lions in Spain and Italy provide valuable insights into the distribution and ecological dynamics of these large predators during a period marked by significant climatic and environmental changes. These records suggest that lions persisted in these southern European regions throughout the early Holocene, demonstrating their adaptability to a range of habitats and environmental conditions (Masseti and Mazza, 2013).

In Spain, Holocene lions remains have been found in several sites, particularly in the Cantabrian region. The Cueva La Riera and Santimamiñe sites has yielded lion remains from layers dated to Asturian, however no direct radiocarbon dating was performed directly on cave lion bones (See Table 1; Altuna, 1986; Sommer and Benecke, 2006). These findings suggest that lions were present in northern Spain during a period of climatic transition, from the colder, more arid conditions of the Late Pleistocene to the warmer, more temperate climate of the early Holocene. In Italy, significant discoveries have been made at several sites, most of them also without direct datation on felid specimens, including Grotta della Madonna, Riparo Fredian, and Grotta all’Onda. The Grotta della Madonna site, located on the Tyrrhenian coast of Calabria, has yielded lion remains radiocarbon-dated to approximately 12–9 ka (Fiore et al., 2004). This chronology places the lions in the Late Pleistocene to early Holocene transition. Similarly, the remains from Riparo Fredian, situated in the Serchio Valley in central Italy, have been dated to around 10.8 ka, and further lion fossils from Grotta all’Onda in the same region have been dated to approximately 10.7 ka. However, in the last two cases, the chronology correspond to the geological layers and no direct datation on cave lions are available (Berton et al., 2003; Cilli et al., 1998). These findings suggest that lions persisted in Italy during the early Holocene, occupying a variety of habitats.

Ecologically, these records suggest that lions in Spain and Italy were highly adaptable, capable of surviving in diverse environments, from open woodlands to semi-open habitats. The preference for such environments is consistent with the known ecology of modern lions, which thrive in areas that offer abundant prey and clear visibility for hunting (Schaller, 2009). The adaptability of lions to different habitats would have been crucial for their survival during the significant climatic fluctuations of the late Pleistocene and early Holocene. As the glaciers retreated and the climate warmed, open steppe-like habitats gave way to more temperate environments, which still supported large herbivores essential for lion predation (García and Arsuaga, 2003; Masseti and Mazza, 2013). The location of these lion-bearing sites, often at relatively high altitudes and near coastal regions, suggests that these areas may have served as refugia during periods of climatic stress or human encroachment. For example, the Grotta della Madonna site is approximately 52 m above sea level, and the Grotta all’Onda cave is located at 708 m on the slopes of Mount Matanna. These altitudes indicates that lions occupied both montane and coastal environments, which offered diverse prey opportunities and shelter from human activities (Berton et al., 2003).

The putative presence of lions in these regions during the early Holocene raises questions about their taxonomic identity. There is ongoing debate regarding whether these remains belong to the extinct cave lion (*Panthera spelaea*) or to early populations of the extant lion species (*Panthera leo*). Morphological characteristics and radiocarbon dating suggest a complex scenario where either cave lions survived longer than previously thought, reducing considerably their body size and robusticity through the Late Pleistocene (Marciszak et al., 2014), or modern

lions arrived earlier and further west than traditionally assumed. The fossil evidence from Spain and Italy could represent a population of cave lions that persisted into the Holocene or an early incursion of modern lions from Africa or Asia (Stuart and Lister, 2011). Further complicating this picture is the genetic evidence, which indicates that cave lions (*Panthera spelaea*) and modern lions (*Panthera leo*) are distinct species with no evidence of interbreeding (Burger et al., 2004; Barnett et al., 2009; De Manuel et al., 2020). This genetic distinction supports the hypothesis that the lion remained from the Late Pleistocene and early Holocene in Western Europe could indeed belong to the cave lion lineage, suggesting a longer survival period for this species than previously believed (Burger et al., 2004).

Understanding the migration routes of these lions during the Holocene involves examining the geographical and environmental corridors that would have facilitated their movement. During the Late Pleistocene, the retreat of the ice sheets opened new habitats and migration routes across Europe. The Mediterranean basin, with its diverse topography and climate, likely provided crucial migration corridors for lions moving from Africa and Asia into Europe. One possible migration route for modern lions (*Panthera leo*) into Europe during the early Holocene could have been through the Near East, crossing through Anatolia (modern-day Turkey) and into the Balkans. This route would have provided access to the southern parts of Europe, including Italy and Spain, via land bridges and narrow straits that existed during periods of lower sea levels (Spassov and Iliev, 1994). The Bosphorus land bridge and the coastal routes along the northern Mediterranean would have been particularly significant in facilitating the dispersal of lions into southern Europe (Stuart and Lister, 2011).

The persistence of cave lions in Europe until the late Pleistocene and their potential survival into the early Holocene would have required the existence of suitable refugia. Southern Europe, with its milder climate and varied topography, could have provided these refugia, allowing cave lions to survive longer than in other parts of their range. The availability of prey and the relative stability of the environment in these regions would have supported small, isolated populations of cave lions (Stuart and Lister, 2011).

However, in order to be accurate, all the former hypotheses need to be tested with radiocarbon dating directly on lion specimens and the DNA analysis of the remains. Much of the cited remains were collected in old excavations with non-precise stratigraphic control or can be older fossil remains that were collected and transported by *Homo sapiens*.

## 5. Conclusions

The cave lion lineage records from Spain, Portugal, and Italy, holds significant paleobiological importance due to the critical insights which provided recently and will provide in the near future. Firstly, the Iberian record includes the earliest evidence of steppe lions in Western Europe, shedding light on their potential migration routes. Secondly, the presence of cave lions in low latitude regions below 40º in both the Iberian Peninsula and Italy offers valuable information regarding the environmental requirements and adaptability of this species and also of its lineage. Lastly, these regions provide putative cases of the replacement or substitution of cave lions by the extant lion species. In summary, the records from the Iberian Peninsula and Italy are crucial for understanding the paleobiology of this iconic species, offering a deeper understanding of their migration, environmental adaptability, and evolutionary transitions.

## CRediT authorship contribution statement

**Joan Madurell-Malapeira:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Ibon Barrasa-Morondo:** Resources, Formal analysis, Data curation. **Saverio Bartolini-Lucenti:** Writing – review & editing, Writing – original draft, Resources, Investigation, Data curation. **Maria Prat-Vericat:** Writing – review & editing. **Ainara Badiola:** Writing – review & editing, Data curation. **Antonio Rodíguez-Hidalgo:** Writing – review & editing, Investigation, Formal analysis, Data curation. **Asier Gómez-Olivencia:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Lorenzo Rook:** Writing – review & editing, Supervision, Project administration, Investigation, Funding acquisition.

## Declaration of Competing Interest

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

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## Data availability

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

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