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Early occurrence of lion (*Panthera spelaea*) at the Middle Pleistocene Acheulean site of Notarchirico (MIS 16, Italy)

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ABSTRACT: The long sedimentary sequence of Notarchirico has yielded evidence of one of the earliest Acheulean manifestations in Europe and of recurrent hominin occupation, spanning from the end of the interglacial MIS 17 to the glacial MIS 16 (~695–610 ka). Here, we report the new discovery of a lion, *Panthera spelaea*, from the site, based on a metatarsal from layer A. This part of the sequence dates to ~660–612 ka (MIS 16, $^{40}Ar/^{39}Ar$ age). Therefore, Notarchirico's lion represents the earliest confirmed occurrence of the species in southwestern Europe, although older findings are known from adjacent areas. Lions and several other large mammal species dispersed into Europe during the Early–Middle Pleistocene Transition, which also witnessed the spread of the Acheulean. Ecological and behavioural adaptability was probably key, for hominins and other species, to cope with the intense and recurrent environmental fluctuations that occurred during this period.

KEYWORDS: Carnivora; Early–Middle Pleistocene Transition; Europe; Hominin occupation; *Panthera fossilis*

Introduction

Between the end of the Early Pleistocene and the beginning of the Middle Pleistocene, the Earth's climate system witnessed a substantial change known as the Early–Middle Pleistocene Transition, EMPT (or Mid-Pleistocene Revolution; MPR), characterised by an increase in the amplitude of the glacial–interglacial cycles and of their periodicity, which shifted from 41 ka to ~100 ka (Lisiecki and Raymo, 2007; Clark et al., 2006; Head and Gibbard, 2015; Maslin and Brierley, 2015).

The Acheulean technological mode, denoted by the production of bifaces and the occurrence of more complex core technologies, reached Europe during the EMPT (Moncel et al., 2020; Ollé et al., 2023). The European Acheulean has been variously hypothesised to derive from local traditions or from the diffusion or new ideas or populations from outside (Moncel et al., 2023). In any case, the very late emergence of the Acheulean in Europe (around one million years later than in Africa) and its sudden spread to the northern and southern regions (Moncel et al., 2013; Ollé et al., 2013), calls for a study of the factors that might have favoured or triggered this diffusion. In this regard, large mammals are an important source of indirect information (Kahlke et al., 2011; Palombo, 2014; Iannucci, 2024).

Multiple bioevents occurred between ~900 and 700 ka, collectively characterising the Epivillafranchian–Galerian faunal turnover, a crucial event of intercontinental dispersal and faunal replacement (see Azzaroli, 1983; Iannucci and Sardella, 2023, for discussion). For example, the local extinction of the giant hyena *Pachycrocuta brevirostris* and the appearance of *Crocuta* occurred at ~800 ka (Iannucci et al., 2021). Many other large mammals appeared in the European fossil record arriving from Asia and Africa, including the straight-tusked elephant *Palaeoloxodon antiquus*, the red deer *Cervus elaphus*, and the wild boar *Sus scrofa*, among others (Kahlke et al., 2011; Martínez-Navarro and Rabinovich, 2011; Bellucci et al., 2015; Van der Made et al., 2017; Iannucci et al., 2021).

The onset of the Acheulean in Europe emphasises the ongoing changes, although its timing and modality remains enigmatic, due to the paucity of early well-dated archaeological sites. Some species, like *Palaeoloxodon antiquus* and *Cervus elaphus*, are sporadically documented in some latest Early Pleistocene localities, becoming widespread during the Middle Pleistocene (Rocca et al., 2023). Similarly, the latest Early Pleistocene site of Barranc de la Boella, in Spain, yielded some crudely made large cutting tools (Vallverdú et al., 2014; Ollé et al., 2023), while elaborate biface production appeared suddenly ~700 ka in western Europe (Moncel et al., 2020).

Pleistocene lions (or lion-like felids) form a group close to the extant *Panthera leo*, but they had already diverged from it in the Early Pleistocene, being assigned to distinct species (*Panthera fossilis* and *Panthera spelaea*) or subspecies of the cave lion *Panthera spelaea* (the latter approach is followed herein), based mainly on craniodental metrics and morphology (Argant and Brugal, 2017; Prat-Vericat et al., 2022; Sabol

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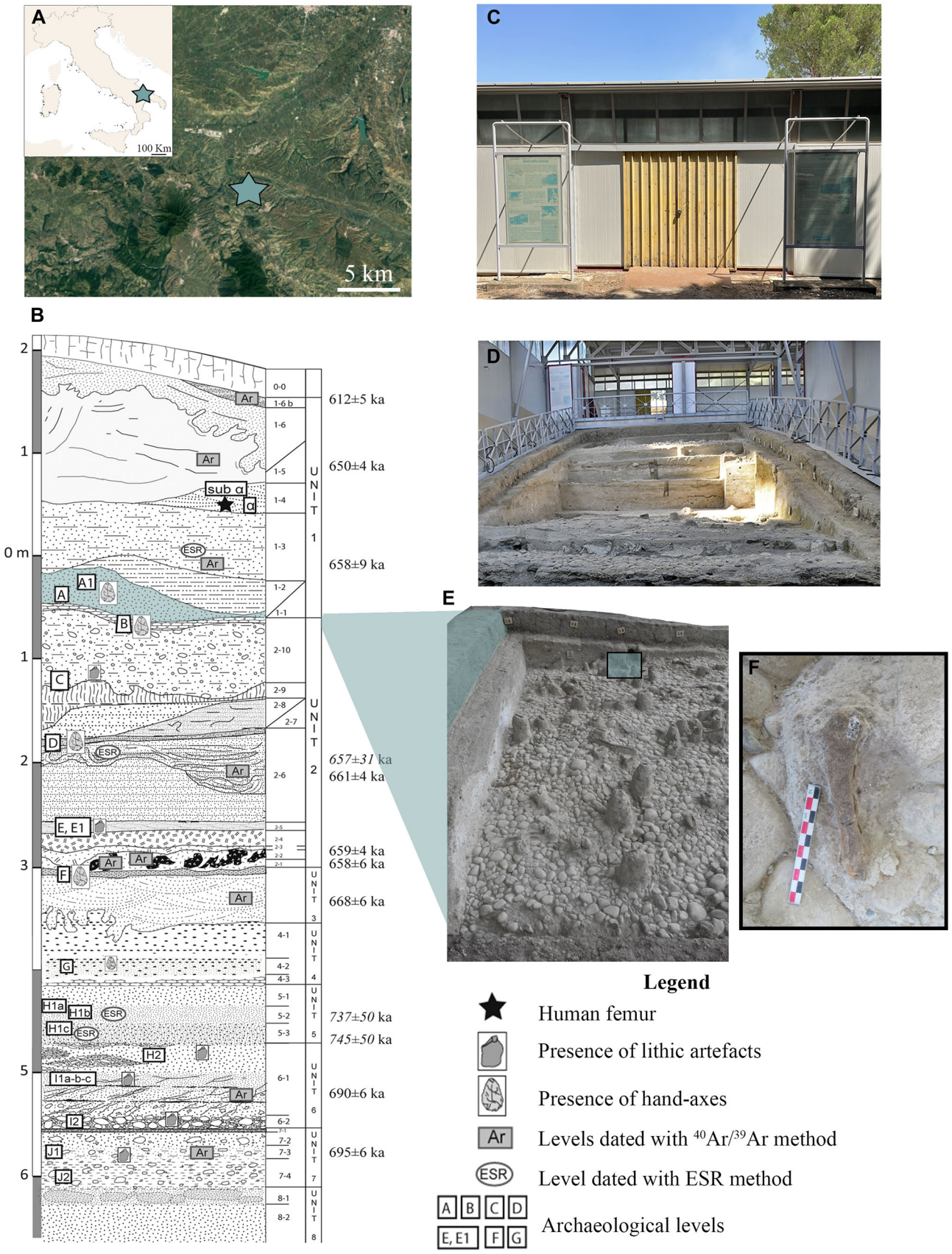


Figure 1. (A) Geographic location of Notarchirico (Venosa) in southern Italy (the star indicates the position of the site). (B) Composite section of the stratigraphic succession of Notarchirico showing dates and position of the lion specimen. (C) External view of the building within the Archaeological Park of Notarchirico. (D) View of the trench SI 2. (E) Detail of the area where the lion specimen was identified. (F) The lion specimen *in situ*. [Color figure can be viewed at wileyonlinelibrary.com]

et al., 2022; Marciszak et al., 2023). Although the lion dispersal is often considered to be an important bioevent within the Galerian faunal turnover (Palombo et al., 2008), the species is poorly documented during the early Middle Pleistocene (Prat-Vericat et al., 2022). Until now, the oldest published record from southwestern Europe was an isolated upper carnassial from Isernia La Pineta (Sala, 1990), dated at ~583–561 ka (at the end of the interglacial MIS 15; Peretto et al., 2015).

Here we report robust evidence that contribute to reliably constrain the chronology of the earliest occurrence of *Panthera spelaea* in southwestern Europe, based on material from the well-dated Layer A of Notarchirico (MIS 16).

Geological setting and chronology

The Basilicata region in southern Italy (Fig. 1a) preserves long archaeological sequences in volcano–sedimentary settings linked to the activity of the Vulture stratovolcano (Lefèvre et al., 2010). Notarchirico (Venosa Basin), systematically excavated between 1979 and 1995 (Piperno, 1999) and again since 2016, yielded a

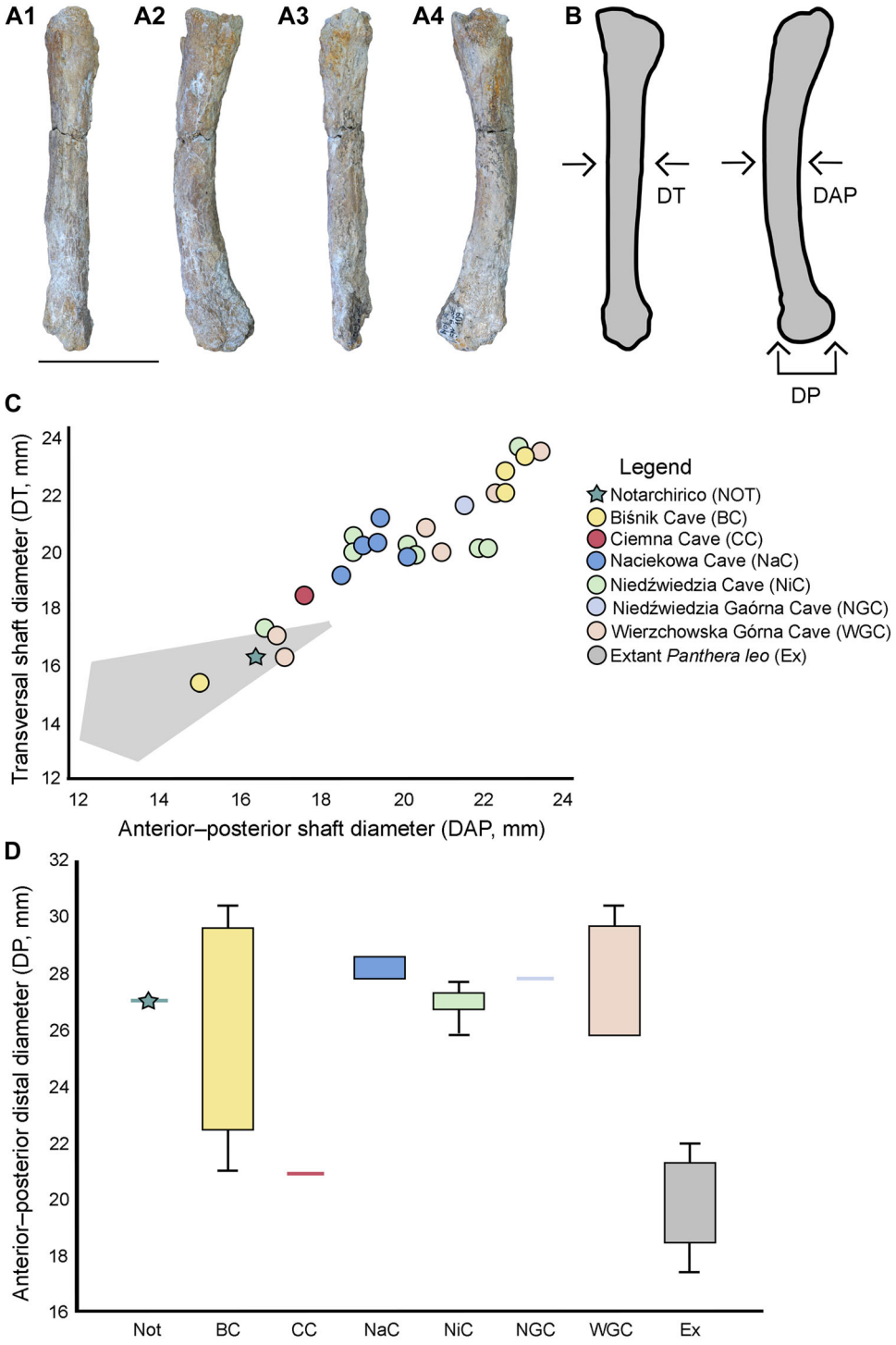
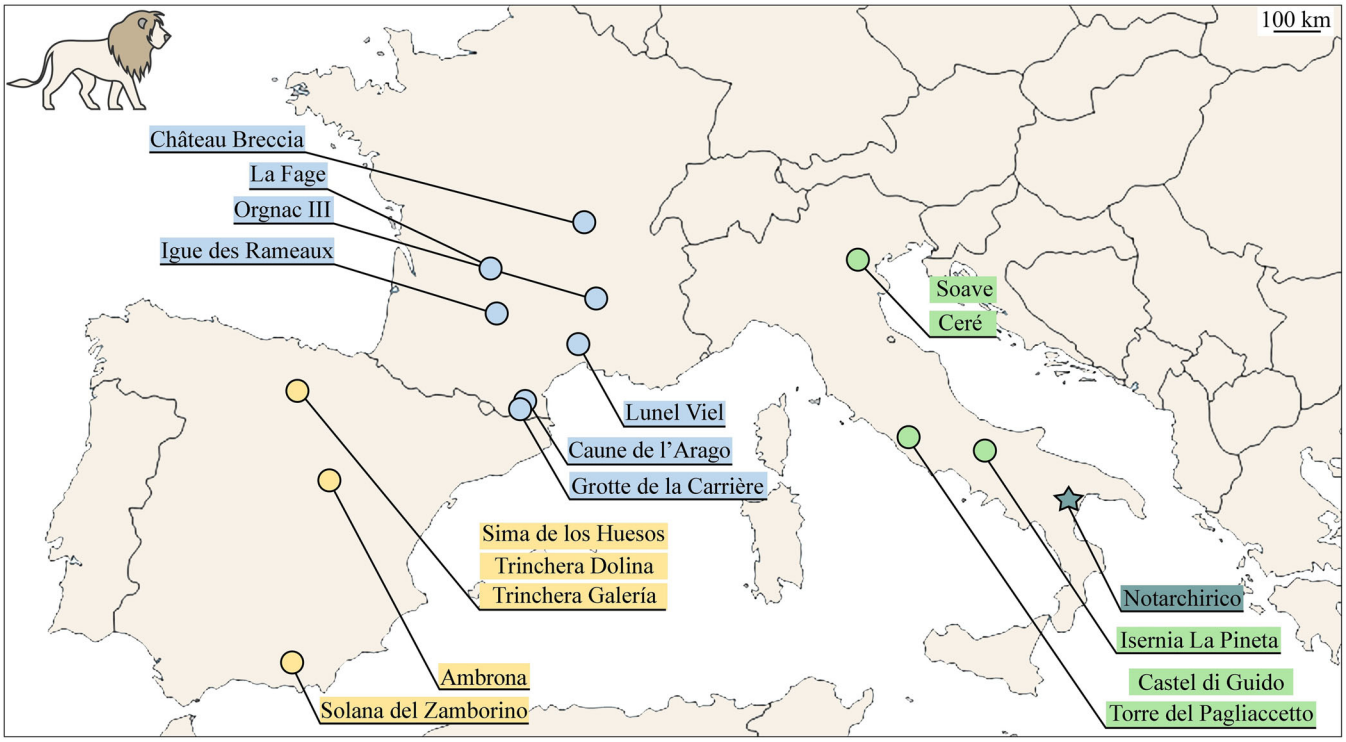


Figure 2. (A) the newly identified left fourth metatarsal of a lion, *Panthera spelaea*, from Notarchirico (Venosa) in anterior (A1), external (A2), posterior (A3) and internal (A4) views. (B) The protocol for taking the measurements considered in the biometric comparison. (C) Bivariate comparison of the shaft diameters. (D) Box plot of the DP. Note that the Notarchirico specimen is damaged and the true size would have been greater than the measured values. The raw data used in the comparison are from Marciszak et al. (2021) and Prat-Vericat et al. (2022); see the supplementary dataset. [Color figure can be viewed at wileyonlinelibrary.com]

thick sequence of fluvial sediments including multiple archaeological levels dated between ~610 and 695 ka and represents one of the earliest Acheulean sites in Europe (Moncel et al., 2020, 2023; Pineda et al., 2024) (Fig. 1). A hominin femur fragment, the oldest *Homo* fossil in Italy, was also found in the upper part of the sequence (level α). The chronology of the entire sequence is constrained by $^{40}Ar/^{39}Ar$ and ESR ages obtained during the new research activities, revealing that hominins recurrently inhabited the area of Notarchirico during the period encompassing the end of the interglacial MIS 17 to the glacial MIS 16 (Moncel et al., 2020, 2023) (Fig. 1b).

Layer A (stratigraphic unit 1-1, Pereira et al., 2015), where the lion remains have been discovered, is located at the top part of the sequence. Layer A or 1-1 is stratigraphically constrained between two $^{40}Ar/^{39}Ar$-dated volcanoclastic levels; Layer 1-3, lying immediately above Layer A, and Layer 2-6, ~1.5 m below Layer A (Fig. 1b). The younger population crystals extracted from the Layers 1-3 and 2-6 yielded statistically indistinguishable ages of 658 ± 9 ka and 661 ± 4 ka, which also occur in Layers 2-1 and 2-2, ~2.5 m below Layer A, and in Layer 1-5, ~1.5 m above Layer A, suggesting that they derived from the reworking of the same pyroclastic units of the Vulture Rionero subsynthem (Pereira et al., 2015). The uppermost layer of the Notarchirico succession



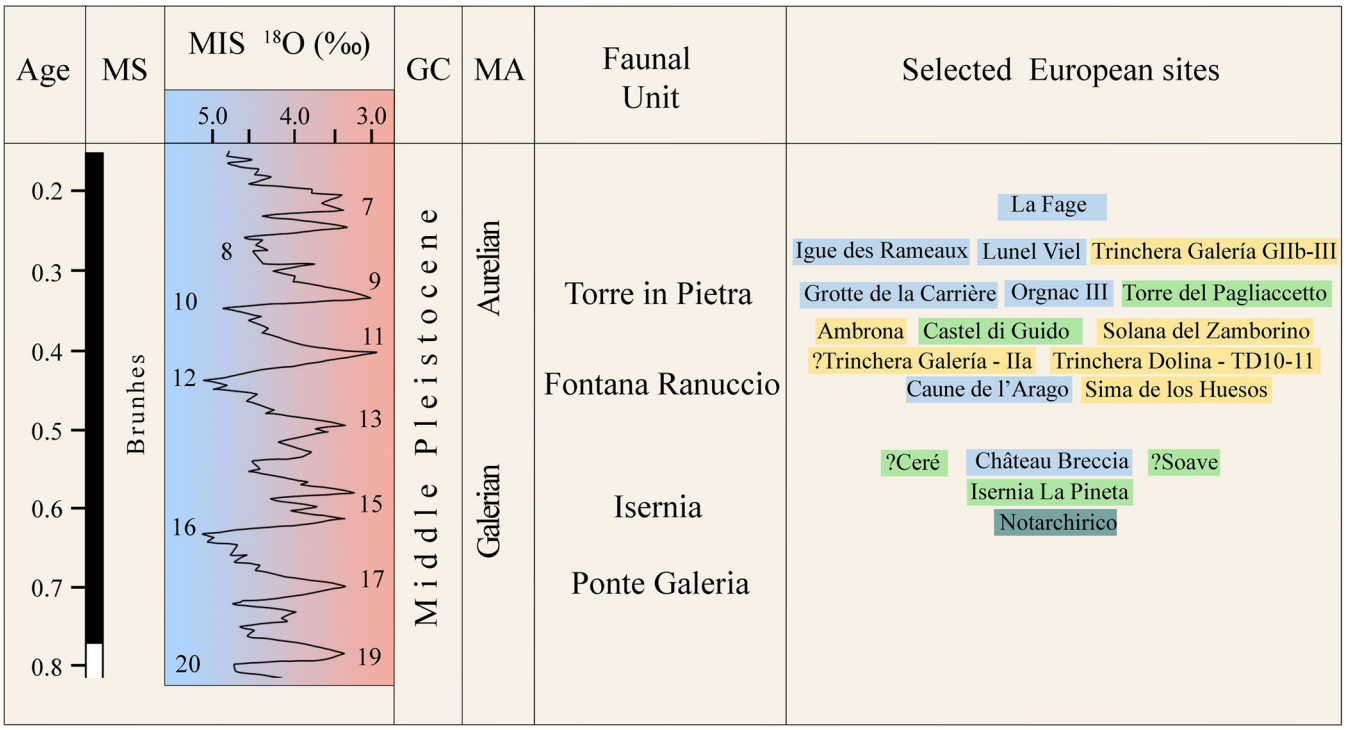


Figure 3. Geographical and chronological distribution of Middle Pleistocene lions in southwestern Europe. MS = magnetostratigraphy, GC = geochronology, MA = mammal age. For references, see Table 1. [Color figure can be viewed at wileyonlinelibrary.com]

(I-6b) is instead dated to 658 ± 9 ka (Fig. 1b). Therefore, Layer A can be confidently constrained between ~660 ka and ~612 ka, representing, respectively, terminus *post quem* and *ante quem* for its deposition. According to palynological analyses, Layer A was deposited in an open and cold environment (Piperno, 1999). It has been excavated over a large area of 120 m^2 and is a 20 cm-thick sediment of alluvial deposits with sands, silts and clays (Fig. 1d–f). This indicates low-energy fluvial sedimentation and regular inputs of volcanic material, along a lake or into channels. Layer A yielded 316 lithic tools and 544 faunal remains (Piperno, 1999). A large quantity of artefacts is in limestone (75%) composed of pebble tools or entire pebbles with percussion marks. Only two bifaces in limestone are considered to be attributed to this layer, associated with a limestone polyhedral. The light-duty tools are made of flakes, denticulates and scrapers. Few cores are described.

The faunal remains were attributed to *Elephas* (=*Palaeoloxodon*) *antiquus*, Bovinae indet., Bovinae cfr. *Bos primigenius*, *Bos primigenius*, *Sus scrofa*, Cervidae, *Cervus elaphus*, *Cervus* cfr. *elaphus*, *Dama clatoniana*, *Dama* cfr. *clactoniana*, *Dama*-like deer, *Megaceroides* (=*Praemegaceros*) sp., *Lepus* cfr. *europaeus* (Piperno, 1999).

Materials and methods

The lion specimen from Layer A of Notarchirico (NOT A 5N-9/10E 109) was identified in trench SI 2 (Piperno, 1999), during surveys on the archaeosurfaces excavated until the 1990s, which are musealised *in situ* and housed in a permanent building within the Archaeological Park of Notarchirico (Fig. 1). The fossil was removed and cleaned before the study and relocated in its original position after the morphological and biometric analyses.

The anatomical and taxonomical attribution, and the morphological characterisation of the specimen have been supported by direct comparison with modern lion material, *Panthera leo*, from the osteological collection of the PaleoFactory laboratory (Department of Earth Sciences, Sapienza University of Rome) and with fossil material of *Homotherium latidens* from Pirro Nord (see Petrucci et al., 2013). Once identified as a lion metatarsal IV, we carried out a biometric analysis based on measurements that were possible to take owing to its state of preservation, comparing it with other fossil remains from the Pleistocene of Europe and a sample of extant *Panthera leo* measured using the same protocol, as illustrated in Fig. 2.

Taphonomic analysis of the surface includes the evaluation of the portion of the preserved cortical tissue. Weathering was analysed according to Behrensmeyer's (1978) stages. Other post-depositional modifications were also examined (Lyman, 1994).

Results

NOT A 5N-9/10E 109 is a left metatarsal IV of a large felid (Fig. 2). The curved morphology of the bone aligns it to a pantherine cat (rather than, e.g. *Homotherium*) and its very large size allows us to exclude an attribution to the relatively small *Panthera gombaszoegensis* and to assign it to the lion species present in the Pleistocene of Europe, *Panthera spelaea*. The specimen preserves the shaft and part of the epiphyses. The state of preservation of the bone can be defined as poor, due to the high loss of cortical tissue affecting more than 50% of its surface. The metatarsal shows signs of weathering (stage 2, *sensu* Behrensmeyer (1978)) with cracks and signs of chemical dissolution of the surfaces. There is also dispersion of iron and manganese oxide on the surface. Proximally, the bone is severely damaged just above the base of the articular facet with metatarsal V. Distally, neither the sesamoid fossa (anteriorly) nor the sesamoid impressions (posteriorly) are clearly noticeable, although a faint notch suggests their position that separates the shaft from the head of the bone. The sagittal crest of the trochlea is eroded but visible, and it separates the better-preserved external side from the internal, which is completely missing.

The status of the bone limits the acquisition of precise measurements, though some can be taken with good reliability. The antero-posterior diameter of the preserved portion of the distal end measures ~27 mm, the minimum antero-posterior diameter of the shaft is ~16.4 mm, approximately the same value of the transversal diameter (~16.3 mm). Considering that the surface of the bone is incompletely preserved, the true size would have been greater than the obtained measurements. This is evident in the bivariate comparison of the shaft diameters, in which the Notarchirico's lion plots among the smallest fossil specimens (Fig. 2C), while the distal end, relatively better preserved, is larger and well above the range of extant lions (Fig. 2D).

Table 1. Middle Pleistocene sites with lion remains in southwestern Europe. Dubious occurrences are not included.

Site	Country	Age (MIS)	References
Notarchirico – layer A	Italy	16	This work
Isernia La Pineta	Italy	15	Sala (1990); Peretto et al. (2015)
Cerè Cave	Italy	15–13?	Ghezzo et al. (2014)
Soave (various localities)	Italy	15–11?	Bona and Sardella (2012)
Castel di Guido	Italy	11	Sala and Barbi (1996); Marra et al. (2022)
Torre del Pagliaccetto - lower level	Italy	9	Caloi and Palombo (1978); Villa et al. (2016)
Château Breccia	France	15–13	Argant and Brugal (2017)
Caune de l'Arago	France	12	Argant and Brugal (2017); Lebreton and López-García (2023)
Igue des Rameaux	France	11–7	Argant and Brugal (2017)
Orgnac III	France	10–8	Argant and Brugal (2017)
Grotte de la Carrière	France	9	Prat-Vericat et al. (2022)
Lunel-Viel	France	9 or 7	Argant and Brugal (2017)
La Fage	France	7	Argant and Brugal (2017)
Sima de los Huesos	Spain	12	García et al. (2024)
Trinchera Galería GIIa	Spain	13–9?	García (2003); Demuro et al. (2014)
Trinchera Dolina TD10-TD11	Spain	11–10	García (2003); Campaña et al. (2017)
Ambrona	Spain	11	Soto et al. (2001); Santonja et al. (2018)
Solana del Zamborino	Spain	12–9	Martín-Penela (1988); Álvarez-Posada et al. (2017)
Trinchera Galería GIIb-III	Spain	9–8	García (2003); Demuro et al. (2014)

Discussion and conclusions

Deciphering the timing of the lion dispersal into southwestern Europe is challenging. On the one hand, lion remains are known from western Siberia in sediments correlated to the Jaramillo subchron, ~1.07–0.99 Ma (Sotnikova and Forova, 2014); Kozi Grzbiet, in Poland, at ~750–700 ka (Marciszak et al., 2021); southern England, at least since MIS 17 (Lewis et al., 2010); and a large-sized phalanx of a pantherine cat has been reported from Barranc de la Boella, alongside the existence of undescribed material from Vallparadís and Cueva Victoria, all from the latest Early Pleistocene of Spain (Madurell-Malapeira et al., 2019). On the other hand, the finding from Layer A of Notarchirico described herein is the earliest in southwestern Europe with a robust chronological constraint (Fig. 3), and only dates to ~660–612 ka.

At Notarchirico, some large mammal species, like hippopotamuses and macaques, are currently documented only in the lowest portion of the sequence, which correlates with the end of the interglacial MIS 17 (Moncel et al., 2020; Mecozzi et al., 2021), while hominins regularly occupied Notarchirico, probably taking advantage of the presence of raw materials, water, plants, meat and wood (Moncel et al., 2023). Large carnivorans have long been known only from an unstratified finding of a canid humerus (Piperno, 1999), but their presence is now documented throughout the sequence, including the lion remains described herein (Layer A), recently recovered canid material (Layer I), and indirectly evidenced by tooth marks on bones (Layers G, H and I).

During the EMPT, new large mammals appeared in the European fossil record arriving from Asia (lion, deer, wild boar) and Africa (hyena, straight-tusked elephant), alongside the spread of biface production and more complex core technologies (technological Mode 2, Acheulean). In this changing world, ecological and behavioural adaptability might have played a key role, for hominins and other species (Moncel et al., 2020; Iannucci, 2024). However, our knowledge on the timing and interrelationships between the different (bio)events occurred during the EMPT is still rather imperfect, emphasising the crucial need to promptly provide data from sites with robust chronologies, like the early lion occurrence from the Layer A of Notarchirico.

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Conflict of interest—The authors declare that they have no conflicts of interest.

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Data availability statement

All data analysed during this study are included in this article or in the accompanying supporting information.

Supporting information

Additional supporting information can be found in the online version of this article.

Dataset. Raw data used in the biometric comparison.

Abbreviations. EMPT, Early–Middle Pleistocene Transition; ESR, Electron spin resonance; MIS, Marine Isotope Stage; MPR, Mid-Pleistocene Revolution.

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