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, 40Ar/39Ar 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.

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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
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 $658 \pm 9$ ka and $661 \pm 4$ 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](https://onlinelibrary.wiley.com/doi/10.1002/jqs.3639)
Materials and methods

The lion specimen from Layer A of Notarchirico (NOT A SN-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 Behrensmeier’s (1978) stages. Other post-depositional modifications were also examined (Lyman, 1994).

<table>
<thead>
<tr>
<th>Site</th>
<th>Country</th>
<th>Age (MIS)</th>
<th>References</th>
</tr>
</thead>
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<tr>
<td>Notarchirico – layer A</td>
<td>Italy</td>
<td>16</td>
<td>This work</td>
</tr>
<tr>
<td>Isernia La Pineta</td>
<td>Italy</td>
<td>15</td>
<td>Sala (1990); Peretto et al. (2015)</td>
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<td>Cervase</td>
<td>Italy</td>
<td>15–13?</td>
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<td>Italy</td>
<td>15–11?</td>
<td>Bona and Sardella (2012)</td>
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<td>11</td>
<td>Sala and Barbi (1996); Marra et al. (2022)</td>
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<tr>
<td>Torre del Pagliacceto - lower level</td>
<td>Italy</td>
<td>9</td>
<td>Caloi and Palombo (1978); Villa et al. (2016)</td>
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<td>France</td>
<td>15–13</td>
<td>Argant and Brugal (2017)</td>
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<td>France</td>
<td>12</td>
<td>Argant and Brugal (2017)</td>
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<td>France</td>
<td>11–7</td>
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<tr>
<td>Orgnac III</td>
<td>France</td>
<td>10–8</td>
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<td>9</td>
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<td>France</td>
<td>9 or 7</td>
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<tr>
<td>La Fage</td>
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<td>7</td>
<td></td>
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<td>Spain</td>
<td>12</td>
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<td>García (2003); Demuro et al. (2014)</td>
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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 Foro-va, 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 Vallparadis 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 lower portion of the sequence, which correlates with the end of the interglacial MIS 17 (Moncel et al., 2020; Meccozzi 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 bifac technology 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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References


Iannucci, A. (2024) Taphonomy and reviewed the manuscript. A. Pineda worked on taphonomy. All authors exchanged ideas and reviewed the manuscript.

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.


Lebreton, L. & López-García, J.M. (2023) Stage or sub-stage: the contribution of small mammals to the characterization of Middle Pleistocene local climate variation. Quaternary, 6(4), 54.


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