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## The disappearance of European dirk-toothed cats

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### Abstract

Saber-toothed cats dominated the latest Pliocene to early Pleistocene ecosystems in the Old World, potentially competing with early hominins for food resources. However, the Pleistocene fossil records of the medium-sized *Megantereon* are often fragmented and scarce, leading to contentious debates regarding its evolutionary history.

Previously, it was commonly believed that *Megantereon* became locally extinct in Europe during the early Pleistocene, albeit without a precise timeline. In this study, we present findings from an unpublished *Megantereon* neurocranium discovered in

the Iberian Vallparadís Section. This discovery is correlated with the Jaramillo magnetostratigraphic subchron (ca. 1.0 Ma; MIS30). Additionally, we propose a connection between the disappearance of European *Megantereon* and the climatic shifts associated with the ‘*Early-Middle Pleistocene Transition*’, particularly the increase in aridity and expansion of open landscapes observed during the protracted glacial stage MIS30.

**Keywords:** Saber-toothed cats; Pleistocene; Europe; Climatic shifts; Extinction

## 1. Introduction

### 1.1. *Megantereon* in the Old World

*Megantereon* is a genus of mid-sized saber-toothed cats from the old world Plio-Pleistocene, primarily recognized for fragmented and/or isolated dentognathic remains (Christiansen and Adolfssen, 2007). As an ambush predator with massive forelimbs, it has similar size of a jaguar (Christiansen and Adolfssen, 2007).

The earliest records of *Megantereon* in Eurasia and Africa were unearthed from the Nachukui Formation at the South Turkwel site in Kenya (ca. 3.58–3.2 Ma; Werdelin and Lewis, 2000). However, WoldeGabriel et al. (1994) mentioned the presence of cf. *Megantereon* sp. in Aramis (ca. 4.4 Ma, Ethiopia), with no subsequent references to this material. On the other hand, the oldest Western European findings can be associated with the Early Villafranchian Perrier–Les Etouaires assemblage (ca. 2.78 Ma; Nomade et al., 2014). Regarding Asia, the initial mentions of this genus come from the Middle Villafranchian of Renzidong Cave and Longdan sites (ca. 2.5–2.2 Ma, Anhui and Gansu provinces, China; Liu, 2003; Qiu et al., 2004; Li and Sun, 2022). The presence of this felid can extend to the middle Pleistocene of Zhoukoudian-1 in northern China (ca. 0.5 Ma; Pei, 1934), although the latest European record is from Untermassfeld (ca. 1 Ma; Kahlke et al., 2011), roughly contemporaneous with the African one (ca. 1.3 Ma; Werdelin and Peigné, 2010).

The latest records of *Megantereon* in Europe were roughly contemporaneous with the ‘*Early-Middle Pleistocene Transition*’ (Head and Gibbard, 2015), a period during which changes in the Earth’s orbital parameters significantly affected the ecosystem of Northern Hemisphere. The European early Pleistocene was characterized by enhanced intraspecific competition within a diverse carnivoran guild (Rodríguez et al., 2012). During the latest early Pleistocene, some of these carnivoran taxa (*Homotherium*, *Megantereon*, *Pachycrocuta*, *Canis (Xenocyon)* or *Panthera gombaszoegensis*) gradually disappeared or became less common within European ecosystems, replaced by newcomer species. The precise chronology of these species’ local extinctions appears crucial to understanding the impact of the former climatic shifts on European ecological communities.

### 1.2. Taxonomic debate around *Megantereon* species

The phylogenetic relationship between the different *Megantereon* species is still under discussion today. Scholars like Ficarelli (1979) and Turner (1987) put all European *Megantereon* remains under the *M. cultridens* attribution. These authors argued that interspecific variation, sexual dimorphism, and biogeography are responsible for the differences between specimens. On the contrary, Sardella (1998) distinguished three species: the Asian remains included in *Megantereon falconeri*, the European specimens in *M. cultridens*, which putatively display several evolutionary convergences with the last one, the African in *M. whitei*. Later, Qiu et al. (2004) reviewed the Eurasian record of the *Megantereon* and concluded that *M. nihowanensis* is the species recorded in the middle Villafranchian of China (Longdan and Nihewan) and *M. lantianensis* is the species recorded in the late Villafranchian, whereas *M. inexpectatus* is from middle Pleistocene. More recently, Li and Sun (2022) synonymized *M. lantianensis* with *M. inexpectatus* and argued that during 1.7–1.3 Ma a dispersal event led to the appearance of *M. whitei* in Europe and *M. inexpectatus* in Asia, both originated in Africa.

Werdelin and Lewis (2000) erected the species *Megantereon ekidoit* from South Turkwel (ca. 3.58–3.2 Ma), the earliest African one. This species differs from the younger *M. whitei* in the absence of p3 and the morphology of the mandibular ramus. Lewis and Werdelin (2010) argued that the European remains do not belong to *M. whitei* based on analysis of specific morphological traits that differ between the European and African specimens. Therefore, they concluded that, in agreement with Pons-Moyà (1987), the more advanced European forms belong to *M. adroveri*.

Hemmer and Kahlke (2020) proposed a gene flow from East Africa into the late European populations, because the elongated upper canines and the short P3 of the Late Villafranchian *Megantereon* coincides with the *Megantereon nihowanensis* characters.

Martínez-Navarro (1992), Martínez-Navarro and Palmqvist (1995, 1996) and Palmqvist et al. (2007) included all Eurasian early-middle Villafranchian forms in *M. cultridens* and all the African ones in *M. whitei*. According to these authors, around ca. 2.0 Ma, as exemplified in the assemblage of Dmanisi (Caucasus; Bartolini-Lucenti et al., 2022), *M. whitei* dispersed from Africa to Eurasia and replaced *M. cultridens*, thus remaining the only recorded species until its disappearance.

In the present work, we describe a partial neurocranium from the latest early Pleistocene (ca. 1.0 Ma; MIS30) of the Vallparadís Section layer EVT12 which represents the last record of *Megantereon* in Western Europe, further discussing the basicranial morphology of the former lineage in the Old World.

## 2. Geological and chronological background

The Vallparadís Composite Section (VCS) includes the paleontological open-air sites of Cal Guardiola (CGR) and Vallparadís Estació (EVT) (Vallès-Penedès Basin, Northwestern Iberian Peninsula; see a synthesis in Madurell-Malapeira et al., 2010, 2017; Fig. 1).

Biochronological, magnetostratigraphic, and U-series-ESR data indicate that the

VCS ranges from before the Jaramillo paleomagnetic subchron (ca. 1.2–1.1 Ma) to the early middle Pleistocene (ca. 0.6 Ma; Madurell-Malapeira et al., 2010, 2012, 2014, 2017; Minwer-Barakat et al., 2011). Specifically, the studied specimen comes from the EVT12 layer correlated with the Jaramillo subchron and the interglacial stage MIS30 (ca. 0.99–1.07 Ma; Fig. 1). The complete faunal list of the layer EVT12 is composed of: *Macaca sylvanus* cf. *florentina*, *Lynx pardinus*, *Pachycrocuta brevirostris*, *Meles meles*, *Ursus deningeri*, *Canis (Xenocyon) lycaonoides*, *Canis mosbachensis*, *Vulpes alopecoides*, *Mammuthus meridionalis*, *Equus altidens*, *Stephanorhinus hundsheimensis*, *Hippopotamus antiquus*, *Sus strozzi*, *Caproleus* sp., *Dama vallonnetensis*, *Megaloceros savini*, *Bison schoetensacki*, *Mimomys savini*, *Allophaiomys chalinei*, *Eliomys quericinus*, *Hystrix refossa* and *Lagomorpha* indet. (Madurell-Malapeira et al., 2010, 2012, 2013, 2014, 2017; Minwer-Barakat et al., 2011; Boscaini et al., 2016; Bartolini-Lucenti et al., 2017; Cherin et al., 2020; Sorbelli et al., 2021; J.M.-M., unpublished data).

### 3. Materials and methods

The specimen studied in this work is a *Megantereon* neurocranium of layer EVT12 (IPS 125140) of EVT housed in the collections of the Institut Català de Paleontologia Miquel Crusafont, Sabadell, Spain.

To describe the material, distinctive features of this species remarked by authors like Palmqvist et al. (2007) and Li and Sun (2022) have been taken. Anatomic terminologies are taken following Barone (1976). The measurements follow Von den Driesch (1976). Furthermore, the neurocranium of *M. cultridens* of Villarroya (La Rioja, northern Iberian System; IPS 36788), the 3D model of *M. cultridens* of Upper Valdarno (Tuscany, northeastern Apennines; IGF 827) and those of *M. whitei* of Dmanisi (Georgia; D1340, D1341), and the photographed material of *M. whitei*, *M. nihowanensis*, *M. inexpectatus* of Koobi Fora (Turkana Lake, Rift Valley; AMNH 101471), Longdan (Linxia Basin; HMV 1215), Zhoukoudian-1 (Beijing; IVPP RV 39094), respectively, have been used for comparison.

**Institutions abbreviations:** HMV, Hezheng Paleozoological Museum, Gansu Province, China; IGF, Natural History Museum Firenze, Italy; IPS, the Institut Català de Paleontologia Miquel Crusafont, Sabadell, Spain; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Science, Beijing, China; KNM-ER, National Museums of Kenya Koobi Fora collections, Kenya.

**Measurement abbreviations:** BA, basicranial axis; GBFM, greatest breadth of the foramen magnum; GBOC, greatest breadth of the occipital condyles; GMB, greatest mastoid breadth; GNB, greatest neurocranium breadth; HOT, occipital height.

### 4. Systematic palaeontology

Family Felidae Fisher von Waldheim, 1817

Subfamily Machairodontinae Gill, 1872

Genus *Megantereon* Croizet and Jobert, 1828

*Megantereon* sp.  
(Figs. 2–4)

**Referred specimen:** Neurocranium (IPS 125140; Fig. 2).

**Measurements:** BA: 78.4mm; GBFM: 34.6mm; GBOC: 60mm; GMB: 101.3mm; GNB: 80.7mm; HOT: 103.8 mm.

**Description:** The specimen is quite deformed and broken, ventrally at the presphenoid corpus and dorsally at the frontal level (Fig. 2B). The right mandibular fossa is fractured in the middle of the bone. The tympanic bullae are not preserved (Fig. 2A). Additionally, the specimen displays a massive and descending postglenoid and mastoid processes, lower than the basioccipital plane, characters shown in Machairodontinae.

The braincase looks rounded in the dorsal view (Fig. 2B). However, there is a remarkable lengthening of the cranium in the posterior part (previously to the rise of the nuchal crest). Furthermore, the sagittal crest is short and well-marked (Fig. 2B). The jugal process of the temporal is noticeable. As a result, the process would have encircled the lateroposterior part of the tympanic bullae. The mastoid process is developed and projected in the cranium (Fig. 2D). The mandibular fossa is broad and presents a rectangular shape. Its curvature is not as deep and close as other extant felines like *Lynx pardinus* or *Panthera pardus*, especially the last one. In ventral view, the foramen magnum has a close U-shape. The musculotubal canal is well developed. Muscle insertions of the longus capitis muscle are well marked (Fig. 2A). The mastoid process overlaps the aperture of the external ear canal. Consequently, a U-shaped is drawn between the mastoid process and the glenoid fossa. The nuchal crest is considerably noticeable. In addition, the occipital is triangular, being higher and narrower than other felids: *Felis sylvestris* presents a more rounded occipital, and *Panthera pardus* displays a width occipital, even if it is triangular-shaped. Regarding muscular insertions, the musculus rectus capitis dorsalis major insertions are highly marked. The insertions of the semispinalis muscles are also defined.

## 5. Discussion

### 5.1. Comparisons with European *Megantereon* remains

Regarding the neurocranium, the occipital condyles are well separated from each other through a narrow ventral depression (Fig. 3A). This last character is uncommon in Eurasian *Megantereon*, which normally displays the condyles united through a bone crest (Fig. 2B, D). Only the upper Valdarno *M. cultridens* skull (Italy; IGF 827) displays the two condyles separated as in the EVT12 specimen.

The fossa condylaris ventralis is more extended ventrally than other European remains such as Villarroya (Iberia; IPS 36788), Senèze (France; NMB.Se311), and Dmanisi (Georgia; D1340, D1341) (Fig. 3).

Additionally, it is worthy mentioning the rounded profile of the EVT12 neurocranium. The most primitive forms of *Megantereon* are characterized by a mesiodistally long neurocranium less rounded in overall appearance (Fig. 4). Furthermore, the studied specimen displays an enlargement of the occipital bone.

Therefore, while IPS 125140 presents an occipital height of 77.35 mm, the average between Villarroya (e.g., IPS 36788) and Dmanisi (e.g., D1340 and D1341) specimens is 64 mm.

### 5.2. Comparisons with coeval Asian *Megantereon* remains

The morphology of the fossa condylaris ventralis from the specimen of Vallparadís Section is close to the morphology shown by the specimen of *M. inexpectatus* from Zhoukoudian-1 (IVPP RV 39094), and *M. nihowanensis* from Longdan (HMV 1215), even this last specimen does not present this trait as noticeable as in IPS 125140. Regarding *M. inexpectatus*, while the lengthening of the fossa condylaris ventralis is highly marked, the condyles are united at the rostral part. However, there is a depression between each other in the caudal part, as in *M. nihowanensis*. Moreover, in IVPP RV 39094, the foramen magnum in the ventral view presents a U-shape. On the contrary, HMV 1215 display a semicircular shape, such as the EVT specimen and the other European remains sited before.

Regarding the neurocranium shape, the EVT one presents a rounded form, as *M. inexpectatus* from Zhoukoudian-1. However, the Longdan's cranium shows an elongation of the neurocranium. Therefore, like the European record, the ancient forms seem to present a mesiodistally elongated neurocranium (Fig. 3).

### 5.3. Comparisons with coeval African *Megantereon* remains

Only the Koobi Fora *Megantereon whitei* cranium can be compared with the studied specimen (Werdelin and Lewis, 2013). Unfortunately, the specimen from Koobi Fora is not well preserved, so a detailed comparison with our specimen is not possible. However, it appears that there is no lengthening of the fossa condylaris ventralis, but separation of the two occipital condyles (Fig. 3C). On the other hand, the general morphology of the Koobi Fora specimen in left lateral view looks more rounded like Vallparadís EVT12 neurocranium as compared with early early Pleistocene European forms (Fig. 4E).

## 6. Conclusions

The 'Early-Middle Pleistocene Transition' denotes a pivotal era characterized by significant alterations in Earth's orbital parameters, which exerted profound impacts on the ecosystems of large mammals, particularly in the Northern Hemisphere. Towards the conclusion of the early Pleistocene epoch, Europe witnessed a gradual decline in the diversity of its carnivore guild, owing to the diminishing availability of their preferred habitats. Consequently, this period marked the local extinction of iconic species such as dirk-toothed cats and giant hyenas, alongside an escalating vulnerability observed among Eurasian hunting dogs and the European Jaguar population (Madurell-Malapeira et al., 2010, 2014; Head and Gibbard, 2015; Fidalgo et al., 2023).

In this study, we scrutinized the final occurrences of dirk-toothed European cats and documented an unpublished specimen unearthed from the later EVT12 layer of the Vallparadís Section. Identified as IPS125140 and here classified as *Megantereon* sp., this specimen represents the ultimate known instance of this genus within Europe.

*Megantereon*, the pioneering large carnivoran to vanish from European ecosystems, succumbed to extinction during the Marine Isotope Stage 30 (MIS30), followed subsequently by the demise of other carnivorans during MIS21 (Madurell-Malapeira et al., 2010, 2014). The local extinction of *Megantereon* correlates with MIS30, characterized by heightened aridity and the proliferation of more open landscapes (Strani et al., 2019; Sorbelli et al., 2021).

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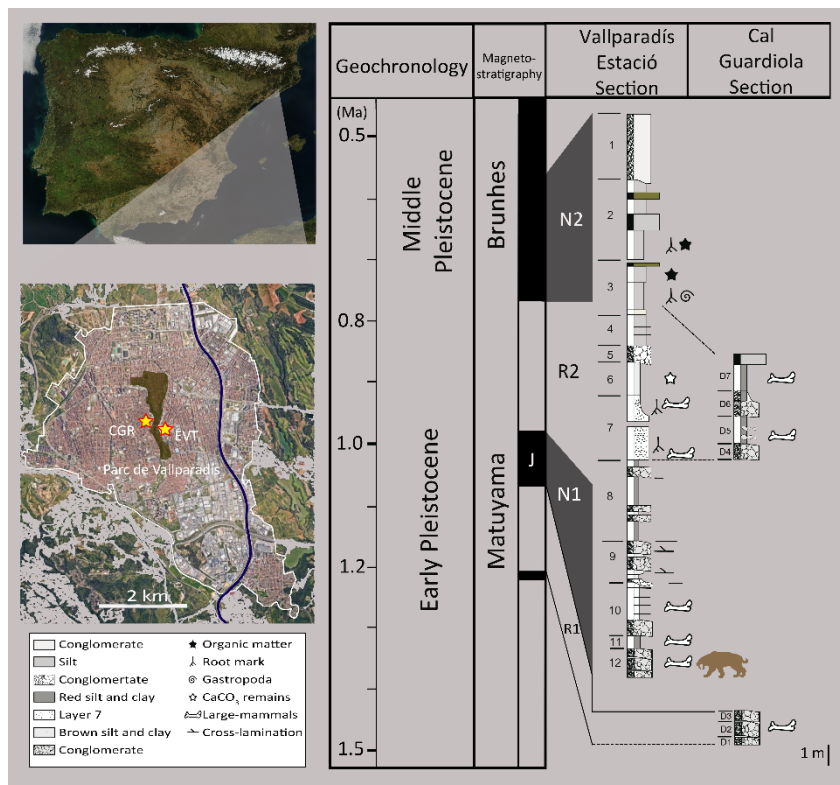
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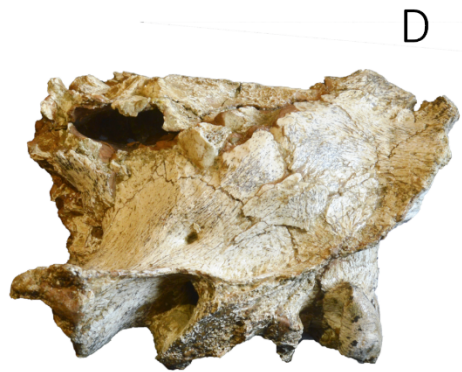
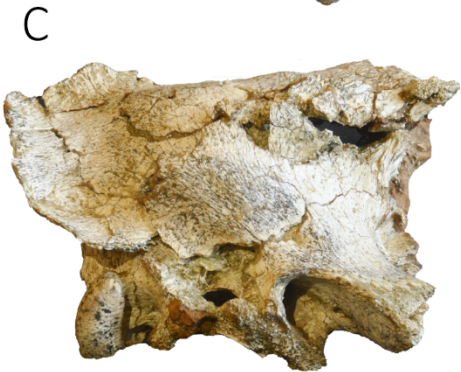
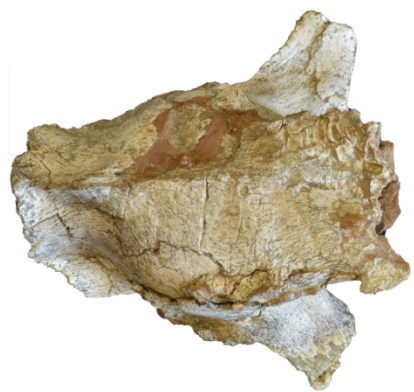
Fig. 1. Geographical location of the Vallparadís Section within the Iberian Peninsula and the city of Terrassa. Additionally, composite stratigraphic section with the layer of precedence of the studied specimen.

Fig. 2. *Megantereon* sp. neurocranium from Vallparadís Section EVT12 (Terrassa, Northeastern Iberian Peninsula). (A) ventral view; (B) dorsal view; (C) right lateral view; (D) left lateral view; (E) caudal view.

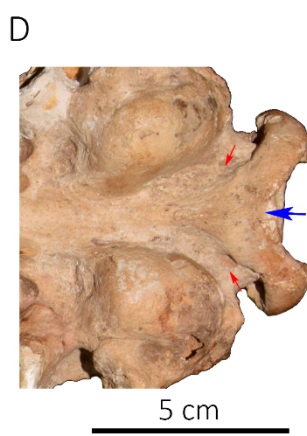
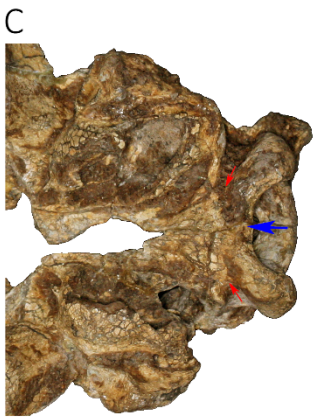
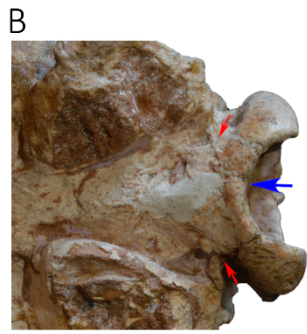
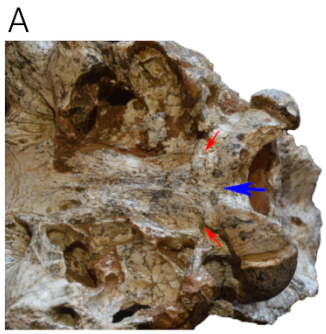
Fig. 3. Ventral view of the *Megantereon* Vallparadís Section (A), compared with the Villarroya (Spain) IPS 36788 (B), Koobi Fora (Kenya) KNM-ER 793 (C), and Zoukoudian-1 (China) IVPP RV 39094 (D). Red arrows indicate morphology of fossa condylaris ventralis and blue ones morphology of occipital condyles.

Fig. 4. *Megantereon* fossils from the Old World in lateral view. (A) Vallparadís Section layer EVT12. (B) Les Pardines (France) LP18. (C) Upper Valdarno (Italy) IGF827. (D) Dmanisi (Georgia) D1340. (E) Koobi Fora (Kenya) KNM-ER 793A. (F) Zoukoudian-1 (China) IVPP RV 39094.





5 cm





5 cm