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# A critical review of the Pliocene and Pleistocene European Felidae fossil record

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*ABSTRACT - The fossil record of European Pliocene and Pleistocene felids reveals a rich diversity of taxa and provides key insights into their evolutionary, ecological, and biogeographic dynamics. This review synthesises current knowledge on felid species across Europe, highlighting the effects of climatic oscillations and human interactions on their survival and extinction. The study integrates fossil, morphological, isotopic, and genetic data to trace evolutionary trajectories, shedding light on adaptation strategies such as dietary specialisation, morphological shifts, and resilience to environmental stressors. Additionally, unresolved questions about lineage origins, intercontinental dispersals, and evolutionary responses to fluctuating climates highlight avenues for future research. By combining palaeontological and archaeological evidence, this review underscores the ecological significance of felids in shaping Pleistocene ecosystems and provides a comprehensive framework for understanding their evolutionary history. It emphasises the need for further studies to clarify taxonomy, improve chronological resolution and explore biogeographic patterns across Europe's fossil record.*

## INTRODUCTION

Felids represent one of the most specialised and enduring lineages within the order Carnivora, tracing their origins to over 30 Ma. Throughout their evolutionary history, felids have developed specialised traits that made them apex predators in various ecosystems, including the diverse and challenging landscapes of Pleistocene Europe (Turner & Antón, 1997; Werdelin et al., 2010). The European Pliocene and Pleistocene was a period marked by dramatic climatic oscillations, with repeated glacial and interglacial phases that significantly altered habitats and species geographical distributions. This fluctuating climate created a dynamic environment in which felid species exhibited remarkable adaptability and resilience, with the fossil record revealing a diverse assemblage of genera that ranged in size and ecological specialisation.

Fossilised remains of European Pliocene and Pleistocene felids provide insight into their role within ancient ecosystems, suggesting that these predators played a vital part in shaping the trophic structures of their time. Different genera adapted to the varied environments created by glacial cycles, occupying roles as both solitary and pack hunters, and targeting a range of prey from small mammals to larger herbivores. Their morphological adaptations, evident from skeletal remains or dentition, demonstrate a highly specialised predatory strategy that responded dynamically to environmental changes. These fossils, often recovered from cave sites, river deposits, and open excavation areas, offer critical information on the geographical distribution and temporal range of each felid lineage, contributing to our understanding of their ecological niches and adaptation strategies over time (Antón, 2013; Diedrich, 2014).

The relationship between Pleistocene felids and early humans adds another layer of complexity to the study of these vanished carnivorans. Archaeological and fossil evidence indicates that early human populations, including *Homo neanderthalensis* King, 1864 and later *Homo sapiens* Linnaeus, 1758, shared landscapes with these predators. Human activities likely influenced felid populations through both direct competition for resources and incidental interactions, as early humans increasingly relied on large game and engaged in hunting practices that potentially impacted prey availability (Rodríguez-Gómez et al., 2017). Evidence of felid remains in anthropogenic contexts, such as cut marks on bones or felid artifacts in early human settlements, suggests that humans may have occasionally hunted these predators or scavenged from felid kills, while also developing strategies to avoid predation (Villa & Roebroeks, 2014). This complex interaction between felids and humans during the Pleistocene highlights a dynamic period of ecological overlap, where humans were both competitors and observers of these apex predators.

The study of Pleistocene felid fossils not only contributes to our understanding of predator-prey dynamics but also illuminates broader questions about adaptation and resilience in the face of environmental pressures. As apex predators, these felids occupied critical positions within their ecosystems, influencing species diversity and community structure. Their ability to survive, albeit intermittently, through glacial cycles reflects their remarkable adaptability; however, the eventual disappearance of many Pleistocene felids coincides with significant climatic and ecological shifts, which were further compounded by the expanding influence of human populations. By examining the fossil record of Pleistocene felids and their interactions with early humans, researchers can better understand how climate and interspecies dynamics influenced both the survival and extinction of these carnivorans (Stuart & Lister, 2011).

The present paper offers a comprehensive synthesis of European Pliocene and Pleistocene felids fossil record from a personal point of view.

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## MATERIALS AND METHODS

To conduct a comprehensive update of the European Pliocene and Pleistocene Felidae fossil record, several key tasks were undertaken. First, all available literature pertaining to the topic was gathered and reviewed. Additionally, previously published historical collections and unpublished materials from numerous institutions were examined. These institutions include: Museu de Ciències Naturals de Barcelona; Museu del Seminari Conciliar, Barcelona; Institut Català de Paleontologia, Sabadell; Museu Arqueològic Comarcal de Banyoles; Museu d'Olot, Olot; Museu de Puigcerdà, Puigcerdà; Museu de Prehistòria, Valencia; Museo Arqueológico Municipal, Cartagena; Museo Arqueológico, Granada; Museo Nacional de Ciencias Naturales, Madrid; Museo Geominero, Madrid; Museo Arqueológico y Paleontológico, Madrid; Museo Arqueológico Nacional Madrid; Institut Català de Paleoecologia Humana i Evolució Social, Tarragona; 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 Palaeontology Section); Museo di Geologia e Paleontologia dell'Università di Torino; Museo Civico di Storia Naturale di Verona; Museo Paleontologico di Montevarchi; Museo di Scienze della Terra di Sapienza, Università di Roma; Museé des Confluences, Lyon; Departement de Geologie, Université de Lyon; Natural History Museum of Perpignan; Collections of the Department of Geology, Université de Poitiers; Natural History Museum of Paris; Naturhistorisches Museum, Basel ; Natural History Museum of Berlin; Natural History Museum of London; Georgian National Museum, Tbilisi.

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 are summarised with data related to the specific site or archaeological-palaeontological layer of the find.

## RESULTS

*Eurasian scimitar-toothed cat (Fig. 1)*

European species - *Homotherium crenatidens* (Fabrini, 1890).

Synonyms - *Homotherium sainzelli* (Aymard, 1854); *Homotherium nestianus* (Fabrini, 1890); *Homotherium moravicum* (Woldrich, 1916); *Homotherium nihowanensis* (Teilhard de Chardin & Piveteau, 1930); *Homotherium ultimus* (Teilhard de Chardin, 1939); *Homotherium davitasvili* Vekua, 1972; *Homotherium darvasicum* Scharapov, 1986; *Homotherium teildardipivetaui* Sharapov, 1988; *Homotherium hengduanshanense* Zong, 1996.

European Chronological range - ca. 3.07 Ma (Kvabebi) to ca. 300 ka (MIS 9, Schoningen) and an isolated find at the North Sea at 28 ka.

Main Sites - Kvabebi (3.07 Ma; Georgia; Fig. 1a, g); Perrier-Les Etouaires (2.78 Ma; France); Roca-Neyra (ca. 2.6 Ma; France; Fig. 1b); Saint-Vallier (France, 2.5 Ma); Senèze (ca. 2.25 Ma; France; Fig.1c, h); Upper Valdarno (1.8 Ma; Italy); Pirro Nord DE11.1 (ca. 1.5 Ma; Italy); Dafnero 3 (ca. 2.3 Ma; Greece; Fig. 1d); Ceyssaguet (ca. 1.0 Ma; France; Fig. 1i); Incarcal Complex (ca. 0.86 Ma; Iberia; Fig. 1e-f, j-o).

Key References - Ballesio (1963); Ficcarelli (1979); Reumer et al. (2003); Antón et al. (2005, 2014); Barnett (2014); Serangeli et al. (2015).

History and Taxonomy - The first known fossils probably ascribable to European scimitar toothed cats were coming from the British Kent's Cavern (Late Pleistocene) and described by Richard Owen in 1846 as *Machairodus latidens* Owen, 1846. However, recent researchers on the canines described by Owen (Barnett, 2014) suggested that the teeth are not native of the Devon area but were instead transported there by Palaeolithic people. According to these assertions and not knowing the site and stratigraphical provenance (could be Miocene or Pliocene also) of the Kent's Cavern fossils the species erected by Owen is not considered here, albeit being valid according to the International Code of Zoological Nomenclature. However, other authors followed the publication of Owen and in 1854 Aymard erected the species *Machairodus sainzelli* for the French site of Sainzelles. This last species is however a nomen nudum according to the code, has type locality but not definition or description of the taxon.

The genus *Homotherium* was erected by Emilio Fabrini in 1890 as a new subgenus of *Machairodus.* In the same publication focused on the Upper Valdarno felids (ca. 1.8 Ma) Fabrini erected two new species *H. crenatidens* and *H. nestianus.* Fabrini described firstly *H. crenatidens* who here is considered the first described and valid species for the European remains. Later on, Woldrich (1916) erected the species *H. moravicum* on the basis of Czech fossils from the Stránská Skála site. Other European species of *Homotherium* were described afterwards, including *Epimachairodus boulei* Kretzoi, 1929, *E. hungaricus* Kretzoi, 1929 and *Homotherium davitasvili.*

Throughout the last decades European researchers have traditionally divided *Homotherium* in two chronospecies: *H. crenatidens* from the Early Pleistocene and *H. latidens*

Fig. 1 (color online) - *Homotherium crenatidens* remains from Europe. a) Cranium from Kvabebi (K-14) in lateral view. b) Cranium from Roca-Neyra (PET-2000) in lateral view. c) Cranium from Senèze (FSL210911) in lateral view. d) Cranium from Dafnero 3 (DFN3-152; Photo G. Koufos). e) Cranium from Incarcal I (IN-I-929) in lateral view. f) Cranium from Incarcal-I (IN-I-825) in lateral view. g) Mandible from Kvabebi (K-9) in right buccal view. h) Right hemimandible from Senèze (FSL2109111) in buccal view. i) Cast of right hemimandible from Ceyssaguet (CEY-2083) in buccal view. j) Right hemimandible from Incarcal-V (IN-V-312) in buccal view. k) Right hemimandible from Incarcal-I (IN-I-1524) in buccal view. l) Right hemimandible from Incarcal-V (IN-V-1) in buccal view. m) Right hemimandible from Incarcal-I (IN-I-1057) in buccal view. n) Right hemimandible from Incarcal-I (IN-I-826) in buccal view. o) Left hemimandible from Incarcal-I (IN-I-826; reversed) in buccal view. Scale bar = 5 cm.


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from the Middle and Late Pleistocene basically because of size and shape of upper canine (Antón et al., 2005; Barnett, 2014). However, several researchers have pointed that there are no substantial differences between European Early and Middle Pleistocene *Homotherium* (Antón et al., 2014; Jiangzuo et al., 2022a), point of view I share. Then, all the Early and Middle Pleistocene European *Homotherium* are included in the hypodigm of *H. crenatidens.*

The situation of the Late Pleistocene European *Homotherium* is complex. Traditionally several British specimens were included on this chronology, however recent findings make their stratigraphic provenance unclear or assigned to the early Middle Pleistocene (Barnett, 2014). The only clear remain from the Late Pleistocene is the North Sea mandible published by Reumer et al. (2003) which displays a pocketing on the rostral margin of the masseteric fossa. This mandibular character is used by the supporters of a different Late Pleistocene Holartic population of *Homotherium*, namely *H. serum* (Cope, 1893), also distinguished by wider frontals (Antón et al., 2014). However, the North Sea Mandible being the only isolated European specimen can be an American immigrant and this mandibular character variable within a population. Additionally, the wider frontals are only observed in the Texan Friesenhahn Cave sample which includes the only complete North American sample available (Rawn-Schatzinger, 1992).

The Pliocene European record of *Homotherium* is more problematic, basically there are two sites with well-recorded specimens: Odessa Catacombs (probably ca. 3.5-3.0 Ma; Sotnikova, 2004) and Kvabebi (3.07 Ma; Vekua, 1972; Figs. 1a, g). Several scholars have pointed to differences between Pliocene and Pleistocene Eurasian *Homotherium* including larger, high-crowned C1, wider P4, larger, bi-rooted p3/P3, p4 proportionally smaller with respect to m1 and presence of a preparastyle on P4 (Scharapov, 1988; Sotnikova, 2004; Antón et al., 2014; Jiangzuo et al., 2022a among others) which has justified separate species ascription as compared with Pleistocene European remains. My personal observations on the Kvabevi specimen show that there are practically no differences in the morphology of this specimen and the European Pleistocene specimens, only the high-crowned C1 which probably is a tendency on the *Homotherium* lineage. The Odessa specimens are more fragmentary and reconstructed; it is true that the p3 and p4 are proportionally larger, but this seems – as in the former case – to be a tendency to specialisation in the Machairodontine subfamily more than a real anatomical difference with taxonomical value.

From all the former arguments I prefer a parsimonious point of view and include all the Pliocene and Pleistocene European forms in a single species with high intraspecific variability and moderate sexual dimorphism, *Homotherium crenatidens*.

PHYLOGENY AND EVOLUTIONARY TENDENCIES - According to the traditional point of view of the last decades, *Homotherium* probably descended from the paraphyletic Miocene *Machairodus* s.l. group and more specifically from the most advanced forms, namely *Machairodus kurteni* (Sotnikova, 1991). These later forms differ from *Homotherium* in larger p3, an absent or very reduced diastema between p3 and p4, longer and more complex p4, a longer and lower corpus and a relatively large coronoid process, with only a small distance between the caudal border of the coronoid and the mandibular condyle (Antón et al., 2014 and references therein). However, Werdelin (2003) described a new genus and species of this lineage from the Miocene/Pliocene boundary of Lothagam (Kenya), *Lokotunjailurus emageritus* Werdelin, 2003 which displays a narrow P4 with a reduced protocone and a reduced single rooted p3, with a large coronoid process in an apparent mosaic of primitive and specialised features that led Werdelin (2003) to propose it as a sister taxon to *Homotherium*. Despite the presence a singular character in the morphology of the manus first digit the Kenyan skeleton is similar to *Homotherium* in many aspects which did not justify the erection of a new genus. In fact, *H. emageritus* shares with the only known complete Late Pliocene *Homotherium*, the American *H. ischyrus* (Merriam, 1905), some primitive characters as the lesser shortening of the lumbar area and the less shortening of the legs tendency seen in the Late Pleistocene *H. serum* (Rawn-Schatzinger, 1992; Hearst et al., 2011; Antón et al., 2014). However, the specimen from Idaho bears a double-rooted p3/P3 less reduced than the Kenyan specimen pointing to intraspecific variability or to more primitive characters which justify the idea of separate evolution between Old and New World Homotherinii.

Concerning European and Asian *Homotherium*, the near absence of Pliocene record hampers the possibility to trace a certain link between Miocene *Machairodus* s.l. and Eurasian forms or link it with the specimen from Lothagam, the two more parsimonious possibilities with the available record. As said in the previous section, the Pliocene and Pleistocene record shows a tendency to simplify the p3/P3 morphology and a shortening of p4 relative to m1, a tendency interpreted by many authors as an increase of specialisation towards hypercarnivory (Sotnikova, 1991; Antón et al., 2005, 2014).

DNA ANALYSIS - In the pioneering study of *Homotherium* DNA Paijmans et al. (2017) reconstructed partial mitochondrial genomes from three *Homotherium* samples and compared them with other carnivores, confirming that *Homotherium* and *Smilodon* form distinct lineages within the subfamily Machairodontinae, diverging approximately 18 Ma. The genetic data show limited diversity between American and the single "European" *Homotherium* specimens, suggesting that all Late Pleistocene *Homotherium* should be classified as a single species. This conclusion is supported by the recent common ancestor of approximately 145 ka for the sampled individuals, indicating low genetic diversity like other widespread Pleistocene carnivores. The European *Homotherium s*equence is nested within the diversity of the two American sequences, reinforcing the idea of a single species rather than distinct regional species.

Alternatively, Barnett et al. (2020) generated a nuclear genome and exome of a *Homotherium* individual from Pleistocene permafrost sediments in Canada. The analyses confirmed *Homotherium* as a highly divergent lineage from all living cat species, with an estimated divergence time of around 22.5 Ma, supporting its classification as a distinct subfamily, Machairodontinae. Comparative genomic analyses revealed signatures of positive selection in several genes related to vision, cognitive function, and energy consumption. These genetic adaptations are putatively linked to *Homotherium*'s diurnal hunting behaviour and social interactions. The presence of genes under selection for cursorial hunting suggests that *Homotherium* was adapted for running and pursuing prey in open habitats, with enhanced endurance and visual capabilities. The study also found relatively high levels of genetic diversity in the *Homotherium* individual, suggesting that the species was more abundant than previously inferred from the fossil record. This challenges the notion that *Homotherium* had low population densities and highlights its success as a widespread and adaptable predator.

LOCOMOTOR BEHAVIOUR - The physical characteristics of *Homotherium* suggest it was built for endurance and speed rather than ambush. *Homotherium* had long limbs, a relatively short tail, and a body structure that indicates it was a cursorial predator, adapted for running (Antón, 2013). This anatomical evidence suggests that *Homotherium* relied on a combination of speed and stamina to chase down prey over open terrain, a significant departure from the ambush tactics employed by its contemporaries. The elongated limbs and the structure of the elbow and wrist joints imply a gait that was efficient for long-distance running.

Studies of *Homotherium*'s skeletal morphology have highlighted its robust forelimbs and strong claws, which would have been advantageous in grappling and subduing prey (Rawn-Schatzinger, 1992). The axial skeleton of *Homotherium*, particularly the vertebrae, indicated a flexible but powerful neck and back, supporting the large head and providing leverage for capturing and holding prey. The cervical vertebrae were massive, contrasting with the lightweight appearance of the appendicular skeleton, suggesting strong neck muscles to support the large skull. The thoracic vertebrae were robust with well-developed processes for muscle attachment, supporting a powerful forelimb musculature. *Homotherium*'s hindlimbs were shorter and less robust compared to the forelimbs, indicating probably a cursorial adaptation for running down prey in open habitats. The pelvis, femur, tibia, and fibula were all structured to provide a combination of speed and stability. The hindlimbs bore strong muscles for propulsion, while the feet had non-retractile claws, providing traction and stability during high-speed pursuits (Rawn-Schatzinger, 1992).

DIETARY BEHAVIOUR - DeSantis et al. (2021) explores the dietary ecology of the scimitar-toothed cat *Homotherium serum*, with a focus on specimens from Friesenhahn Cave in Texas. The analyses reveal that *Homotherium* consumed both soft and tough foods, with high anisotropy values indicating the consumption of tough flesh, such as that of juvenile mammoths, and lower complexity values suggesting a diet that avoided bone processing. Stable carbon isotope data further support the dietary preferences inferred from DMTA. *Homotherium serum*'s isotope values indicate a clear preference for C4 grazers, which thrive in open, grassland environments. This preference for open-habitat prey is consistent with the morphological adaptations of *Homotherium*, which suggest it was a cursorial predator, capable of running moderate distances to chase down prey.

*Eurasian Cave lion lineage*

EUROPEAN SPECIES - *Panthera fossilis* (von Reichenau, 1906) and *Panthera spelaea* (Goldfuss, 1810).

EUROPEAN CHRONOLOGICAL RANGE - 1.0 Ma (MIS 30; Vallparadís Section) to ca. 20 ka.

MAIN SITES - Vallparadís Section (ca. 1.0-0.86 Ma; Iberia); Château Breccia (0.6 Ma; France); Zoolithen Cave (MIS 3; Germany); Torca del León (MIS 3; Iberia); Srbsko Chlum-Komín Cave and other sites in the Bohemian Karst (Late Pleistocene; Czech Republic).

KEY REFERENCES - Sotnikova & Nikolskiy (2006); Argant & Argant (2007); Diedrich (2008); Sabol (2011); Stuart & Lister (2011); Marciszak et al. (2014); Álvarez-Lao et al. (2020); Puzachenko et al. (2024).

HISTORY AND TAXONOMY - The European cave lion lineage has been central to palaeontological investigations into the European Pleistocene for over two centuries. Early interest in these Pleistocene felids began in 1810 with Georg August Goldfuss's description of large feline remains from European cave sites, which he initially assigned to *Felis spelaea* (Goldfuss, 1810). This marked the first scientific attempt to categorise what would later become known as the cave lion. Throughout the 19th and early 20th centuries, the systematic study of these fossils advanced, as prominent palaeontologists, including Wilhelm von Reichenau, contributed to understanding cave lion morphology and taxonomy (Von Reichenau, 1906). Von Reichenau notably described *Panthera fossilis* from Mosbach, Germany, in 1906, establishing it as an older, more robust predecessor to *Felis spelaea* (Von Reichenau, 1906).

In the 1920s, Max Hilzheimer furthered the distinction between cave lions and modern lions by proposing the inclusion of *Felis spelaea* in the genus *Panthera* (Hilzheimer, 1924). This taxonomic distinction set the foundation for understanding European cave lions as a lineage separate from *Panthera leo* Linnaeus, 1758, with *P. fossilis* and *P. spelaea* occupying different ecological niches and representing different adaptive stages within the Pleistocene. Over time, Hilzheimer's and Reichenau's proposals were largely validated through detailed morphological studies, which demonstrated the unique adaptations of cave lions to the challenging climatic conditions of the Pleistocene.

Since the late 20th Century, research on European cave lions has accelerated, thanks to the increased use of advanced morphological analysis, radiometric dating, and an expanded fossil record. Recent studies have refined our understanding of *P. fossilis*, a species that flourished in the relatively temperate latest Early Pleistocene, and *P. spelaea*, which emerged during the Late Pleistocene and adapted to colder environments. Fossil analyses indicate that *P. fossilis* was one of the largest known felids, possessing a robust build and unique cranial features suited to preying on the large herbivores that dominated Europe's open habitats at the time (Turner & Antón, 1997). By contrast, *P. spelaea* fossils reveal further morphological specialisation, such as thicker limbs and adaptations suited to more arid, open landscapes and colder climates typical of the Late Pleistocene. These adaptations likely positioned *P. spelaea* as a highly efficient predator of megafauna in periglacial environments, as evidenced by their remains found throughout Europe and into Eurasia (Diedrich, 2014; Marciszak et al., 2014).

In recent decades, high-resolution stratigraphic and morphometric analyses have deepened our understanding of the chronological and ecological distinctions between *Panthera fossilis* and *Panthera spelaea*. Researchers have pinpointed *P. fossilis* as a more basal member of the cave lion lineage, present in the fossil record from approximately 1 Ma. This species gradually gave rise to *P. spelaea* and persisted until the late stages of the Pleistocene (Baryshnikov, 2011). Fossils of *P. spelaea* are found across a vast range, from Western Europe through Siberia, with skeletal and dental morphology indicating adaptations to high-latitude climates and a diet primarily consisting of large ungulates, which included bison, horses, and reindeer (Bocherens et al., 2011). These studies highlight the degree of ecological specialisation that allowed *P. spelaea* to occupy cold and resource-scarce environments during the Pleistocene glaciations.

This recent research has also shed light on the factors contributing to the eventual extinction of *Panthera spelaea* near the end of the Pleistocene. Fossil evidence from Late Pleistocene deposits indicates that, despite their ecological dominance, cave lions faced growing pressures from environmental shifts and possibly competition with expanding human populations. Large-scale climatic changes during the Last Glacial Maximum likely reduced the availability of suitable prey, particularly the large herbivores that *P. spelaea* depended on. Combined with increased human hunting pressures, these factors likely accelerated the decline of cave lion populations across Europe and Eurasia, culminating in their extinction approximately 13 ka (Stuart & Lister, 2011).

Fossil Record - See a detailed review in Puzachenko et al. (2024) and Madurell-Malapeira et al. (2025).

Evolutionary Tendencies - The evolutionary history of the European cave lion lineage reveals a marked tendency toward decreasing body size, spanning the progression from *Panthera fossilis* in the late Early Pleistocene to *Panthera spelaea* in the Late Pleistocene. This trend has been interpreted as an adaptive response to shifting climatic and ecological pressures. *Panthera fossilis*, identified in deposits from the late Early to the early Middle Pleistocene, is thought to represent the ancestral form of the European cave lion lineage (Von Reichenau, 1906). Fossils of *P. fossilis* display a robust morphology and massive body size, traits that likely allowed these large predators to hunt the megafaunal prey prevalent in Europe's relatively temperate Pleistocene environments.

The transition from *Panthera fossilis* to *Panthera spelaea* occurred as Europe experienced increased climatic fluctuations. Early *P. spelaea* specimens exhibit both primitive and advanced morphological characteristics, suggesting a lineage in transition. These changes included modifications in dental morphology, which became more specialised, reflecting a diet increasingly composed of smaller or more variable prey as megafaunal populations shifted with the changing environment (Baryshnikov, 2011; Marciszak et al., 2014).

By the onset of the Late Pleistocene (MIS 5), *P. spelaea* exhibited more pronounced reduction in body size. Fossils from this period show a steady decrease in size and robustness compared to *P. fossilis*, likely in response to a less stable prey base and colder, more open landscapes (Argant & Argant, 2007). By MIS 3-2, the cave lion population had undergone a dramatic reduction in genetic variability, likely a consequence of repeated climatic pressures and declining prey availability, which intensified selection for smaller, more efficient body sizes and reduced resource demands (Baryshnikov & Tsoukala, 2010). This phase produced the smallest known specimens of *P. spelaea*, some of which reached dimensions comparable to modern lions, though they retained adaptations suited to Pleistocene environments.

The size decrease within the Cave Lion lineage, from the large *P. fossilis* to the comparatively smaller *P. spelaea*, is influenced by a complex interplay of factors, including sexual dimorphism, local environmental adaptations, and possible migration events that may have introduced genetic diversity from other populations. Despite the morphological shifts across this lineage, the size variability within each species remains significant, making size alone an unreliable biochronological indicator. Instead, the evolutionary patterns observed in *P. fossilis* and *P. spelaea* highlight their dynamic adaptability to Europe's challenging Pleistocene climate and provide a broader context for understanding megafaunal responses to environmental pressures (Diedrich, 2014; Marciszak et al., 2014).

DNA Analysis - Recent advancements in ancient DNA analysis have significantly refined our understanding of the evolutionary history and taxonomic classification within the European cave lion lineage. While morphological studies initially suggested a close relationship between cave lions and extant lions, genetic research has provided strong evidence supporting a more complex phylogenetic relationship.

In an influential study by Barnett et al. (2016), researchers analysed complete mitochondrial genomes from cave lions and modern lions, establishing that the divergence between these lineages' dates back to the Early Pleistocene, approximately 1.89 Ma (with a 95% credibility interval of 1.23 to 2.93 Ma) (Barnett et al., 2016). This significant temporal split suggests that *Panthera spelaea* should be recognised as a distinct species within the *Panthera* genus, rather than as a subspecies of *Panthera leo*. The phylogenetic findings place cave lions on a separate evolutionary path from modern lions, confirming their status as a unique lineage adapted to the Pleistocene's harsh and variable climates.

Building on these findings, Stanton et al. (2020) expanded the dataset to include 31 mitochondrial genomes sampled across the geographic range of *P. spelaea* in the Holarctic region. This study provided robust evidence for the existence of two reciprocally monophyletic clades within cave lions: a Eurasian clade, which was distributed across Europe and western Asia, and a Beringian clade, isolated to the Beringian region of northeastern Siberia and North America. Phylogenetic analyses suggest that these clades diverged around 578 ka (95% credibility interval of 124 ka to 1.08 Ma), indicating that distinct genetic lineages of cave lions were established well before the end of the Middle Pleistocene. This divergence likely reflects adaptations to the distinct environmental conditions and prey availability in Beringia and Eurasia, supporting previous morphological and ecological assessments that proposed the Beringian subspecies *Panthera spelaea* *vereshchagini* Baryshnikov & Boeskorov, 2001 (Stanton et al., 2020).

Additionally, Stanton et al. (2020) observed that the Beringian and Eurasian lineages displayed differing temporal distributions, with certain haplogroups in the Beringian clade appearing to disappear from the fossil record around 41 ka. Meanwhile, the Eurasian clade persisted until the end of the Pleistocene, approximately 13 ka. These findings highlight a pattern of restricted gene flow between populations across Eurasia and Beringia, a factor that may have contributed to the cave lion's eventual extinction by reducing genetic diversity within isolated populations (Stanton et al., 2020).

These molecular findings, alongside morphological analyses, establish a clearer taxonomic boundary between *P. fossilis*, *P. spelaea*, and their extant relatives. With mitochondrial divergence dating to the Early Pleistocene and significant regional differentiation within *P. spelaea*, the genetic data support the distinct evolutionary path and speciation of cave lions, highlighting the complex biogeography and adaptive responses of these apex predators to the Pleistocene's challenging climatic shifts.

*Eurasian pantherine lineage (Fig. 2)*

European species - *Panthera toscana* (Schaub, 1949) and *Panthera gombazoegensis* (Kretzoi, 1938).

Synonyms - *Panthera schreuderi* (Von Koenigswald, 1960); *Jansofelis vaufreyi* Bonifay, 1971; *Panthera onca georgica* Hemmer et al., 2010.

Chronological range - 2.0 Ma (Olivola) to 0.35 Ma (Belle Roche).

Main sites - Olivola (ca. 2.0 Ma; Italy; Fig. 2d), Gerakarou (ca. 2.0 Ma; Greece); Upper Valdarno (ca. 1.8 Ma; Italy; Fig. 2e-g); Untermassfeld (ca. 1.1 Ma; Germany); Vallparadís Section EVT7 (ca. 0.86 Ma; Spain; Fig. 2a); Trinchera Dolina (ca. 0.85 Ma; Spain; Fig. 2j-k); L'Escale (0.6 Ma; France); Château Breccia (ca. 0.6-0.5 Ma; France; Fig. 2c, l); Belle Roche (0.35 Ma; Belgium; Fig. 2b, h-i).

Key references - Fabrini (1892); Del Campana (1915); Ficcarelli & Torre (1968); Hemmer (2001); Argant & Argant (2011); Marciszak (2014); Chatar et al. (2022); Marciszak & Lipecki (2022).

Fossil Record - see a review in Marciszak & Lipecki (2022).

History and Taxonomy - Fabrini (1892) and Tuccimei (1896) were the first authors to study remains now attributed to *Panthera toscana*, initially classifying them as *Felis arvernensis* Croizet & Jobert, 1828. Fabrini first examined specimens from the Upper Valdarno and Olivola sites, noting their resemblance to tigers in cranial morphology and to leopards in dental features. Later, Tuccimei (1896) described additional specimens from Villa Spinola (Perugia, Italy). Del Campana (1915) revisited the Valdarno and Olivola specimens, proposing a closer relationship with leopards than with other large pantherines, which led him to reclassify them as *Leopardus arvernensis* (Croizet & Jobert, 1828). Some years later,

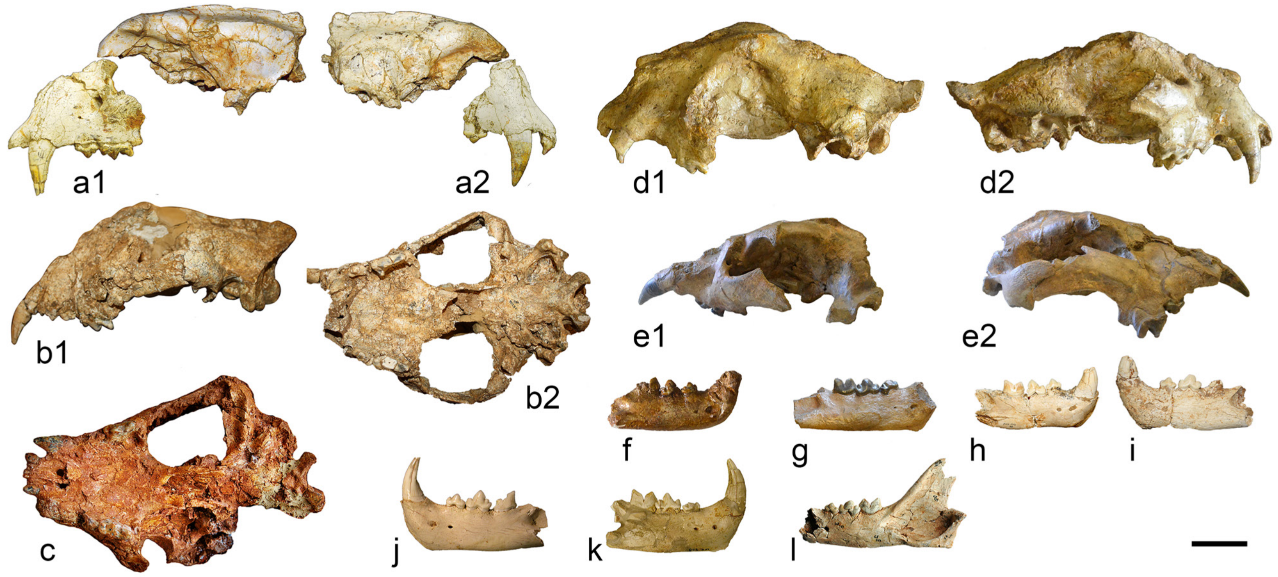

Fig. 2 (color online) - *Panthera toscana-gombaszoegensis* remains from the Early and Middle Pleistocene of Europe. a) Cranium of *Panthera gombaszoegensis* from layer EVT7 of the Vallparadís Section (EVT21072) in left lateral (a1) and right lateral (a2) views. b) Cranium of *Panthera gombaszoegensis* from La Belle Roche (ULg-BR-II-81-146; Photos N. Chatar) in left lateral (b1)and ventral (b2) views. c) Cranium of *Panthera gombaszoegensis* from the A. & J. Argant excavations at Château Breccia (CHA.1-F.8-73; Photo A. Argant) in ventral view. d) Cranium of *Panthera toscana* from Olivola (IGF4378) in left lateral (d1) and right lateral (d2) views. e) Cranium of *Panthera toscana* from Upper Valdarno (IGF10038) in left lateral (e1) and right lateral (e2) views. f) Right hemimandible of *Panthera toscana* from Upper Valdarno (IGF4375) in buccal view. g) Right hemimandible of *Panthera toscana* from Upper Valdarno (IGF851) in buccal view. h) Right hemimandible of *Panthera gombaszoegensis* from La Belle Roche (ULg-PA-BR-III-M13-455; Photo N. Chatar) in buccal view. i) Left hemimandible of *Panthera gombaszoegensis* from La Belle Roche (ULg-PA-20210823-01; Photo N. Chatar) in buccal view. j) Left hemimandible of *Panthera gombaszoegensis* from Trinchera Dolina (IPS951a) in buccal view. k) Right hemimandible of *Panthera gombaszoegensis* from Trinchera Dolina (IPS951b) in buccal view. l) Left hemimandible of *Panthera gombaszoegensis* from the A. & J. Argant excavations at Château Breccia (CHA.1-G.8-359; Photo A. Argant) in buccal view. Scale bar = 5 cm.

the Hungarian palaeontologist Milos Kretzoi described a new species, *Leo gombaszoegensis* Kretzoi, 1938, based on isolated teeth from the Gombasek quarry in Slovakia (Kretzoi, 1938). In 1949, Schaub re-examined both the French and Italian specimens, identifying significant differences between the holotype of *Felis arvernensis* and the Italian specimens. Consequently, he designated the Italian specimen from Santa Maria near Il Tasso in Upper Valdarno (IGF851) as the type specimen for a new species, *Felis toscana* Schaub, 1949.

In 1968, Giovanni Ficcarelli and Danilo Torre published a foundational study on Villafranchian pantherines from Tuscany, re-evaluating the material from Upper Valdarno and Olivola and comparing it with extant large felids (Ficcarelli & Torre, 1968). Their findings suggested strong similarities between *P. toscana* and both *P. tigris* Linnaeus, 1758 and *P. onca* Linnaeus, 1758. In 1971, French Marie-Françoise Bonifay studied Quaternary carnivorans from southeastern France, describing four individuals of a medium-sized pantherine from L'Escale, which she attributed to *Jansofelis vaufreyi*. Shortly thereafter Helmut Hemmer (1974) explored the phylogeny of Early to Middle Pleistocene pantherines, concluding that *J. vaufreyi* is a junior subjective synonym of *Panthera gombaszoegensis* and further classifying the lineage into two chronosubspecies, *P. g. toscana* and *P. g. gombaszoegensis*.

In palaeontological literature, *P. gombaszoegensis* has commonly been considered closely related to the extant jaguar or even as a subspecies of it (Hemmer, 1981; Hemmer et al., 2001; O'Regan, 2002; O'Regan & Turner, 2004). However, many of these earlier studies were based exclusively on teeth and mandibular remains. Hemmer, one of the principal proponents of this theory, later proposed *Panthera onca georgica* as a subspecies based on remains from Dmanisi, in Georgia (Hemmer et al., 2010). Additionally, most researchers consider *P. gombaszoegensis* a single species that existed from approximately 2.0 Ma to the late Middle Pleistocene (O'Regan, 2002).

In a recent study, Chatar et al. (2022) analysed cranial and mandibular remains from La Belle Roche (Belgium), concluding that the mandibular morphology of *P. gombaszoegensis* is more similar to that of extant jaguars, whereas cranial morphology aligns more closely with modern tigers.

In my view, the morphology of specimens traditionally assigned to *P. gombaszoegensis* are more closely related to the ancestral Asian pantherine lineage, currently represented by *P. tigris* and *P. uncia* Schreber, 1775, rather than resembling tigers specifically. Furthermore, the basicranial and dental morphology of specimens from Upper Valdarno, Gerakarou, and Olivola exhibits distinct differences compared to later specimens from Vallparadís Estació EVT7, Château, and La Belle Roche. Based on this evidence, I suggest a tentative division into two chronological groups, represented by distinct species, *P. toscana* and *P. gombaszoegensis*, pending further detailed study.

Finally, the origin of *P. toscana-P. gombaszoegensis* is far from being resolved. Most authors hypothesise an African origin for this lineage (Hemmer et al., 2010; Argant & Argant, 2011) linking their first appearance in Europe at ca. 1.8 Ma with the record of a large pantherine form in the Late Pliocene of Laetoli Upper Beds (ca. 3.7 Ma) ascribed by Barry (1987) to *Panthera leo* aff. *gombaszoegensis*. Other authors, on the other hand, included the first pantherine material of Laetoli in *Panthera leo* (Turner, 1990). Eventually, in a more parsimonious hypothesis, Werdelin & Peigné (2010) pointed out that African pantherine specimens older than 2 Ma are not diagnostic at species level. From 2 Ma onward, all the African material can be ascribed to *P. leo* and *P. pardus* Linnaeus, 1758 (Werdelin & Peigne, 2010). I agree with the latter authors supporting the idea that there is not a direct link among the African specimens and European *Panthera gombaszoegensis* s.l.

Palaeoecology and habitat preferences - The postcranial morphology of *P. toscana-gombaszoegensis* is largely unknown. Scanty post-cranial remains were recovered from few sites such as the better collection the French Châteu Breccia (Argant & Argant, 2011), where a partial skeleton was unearthed. This specimen allowed the former authors to describe *P. gombaszoegensis* as a stout large felid with a body mass estimation of 130 kg. In the literature, this lineage is often referred to as a jaguar-like despite that their post-cranial morphology is noticeably slenderer and with proximodistally longer long bones than the living jaguar.

The ecology and habitat preferences of this lineage are poorly known. Most authors suppose an ecology like the extant jaguar, but in fact no stable isotope, microwear or functional anatomy studies have been performed so far. Authors like Hemmer (2001) and O'Regan (2002) supposed that they were likely adapted to both forested and open environments, like modern jaguars and other large cats.

### *European* Dinofelis *(Fig. 3)*

European species - *Dinofelis diastemata* (Astre, 1929).

Synonyms - *Therailurus diastemata* (Astre, 1929).

Chronological range - 3.8-3.6 Ma (Serrat d'en Vaquer) to ca. 2.0-1.8 Ma (Senèze and Etulia).

Main sites - Perpignan and Tuilerie Chefdebien (ca. 3.8-3.6 Ma; France; Fig. 3a-j); Odessa Catacombs (3.5 Ma; Ukraine) Balaruc II (ca. 3 Ma; France); Zemo Melaani (ca. 3 Ma; Georgia); Senèze (2.25 Ma; France); Novaja Etulia 2 (1.8 Ma, Moldova).

Key references - Astre (1929); Piveteau (1948, 1961); Beaumont (1983); Ballesio (1985); Gabunia & Vekua (1998); Averianov & Baryshnikov (1999); Werdelin & Lewis (2001).

Fossil Record - See a review in Werdelin & Lewis (2001).

History and Taxonomy - The genus *Dinofelis* comprises medium to large-sized felids from the Pliocene and Pleistocene, found across Eurasia, Africa, and North America. These felids are characterised by slightly compressed but not elongated upper canines, which lack serrations but retain mesial and distal crests.

Otto Zdansky first established the genus *Dinofelis* in 1924, based on a complete cranium and mandible from the Pliocene of Lok. B in China (Zdansk, 1924). A few years later, Astre (1929) erected the species *Felis diastemata*, describing it from a right hemimandible discovered in a quarry near Perpignan, France. Notably, this mandible,

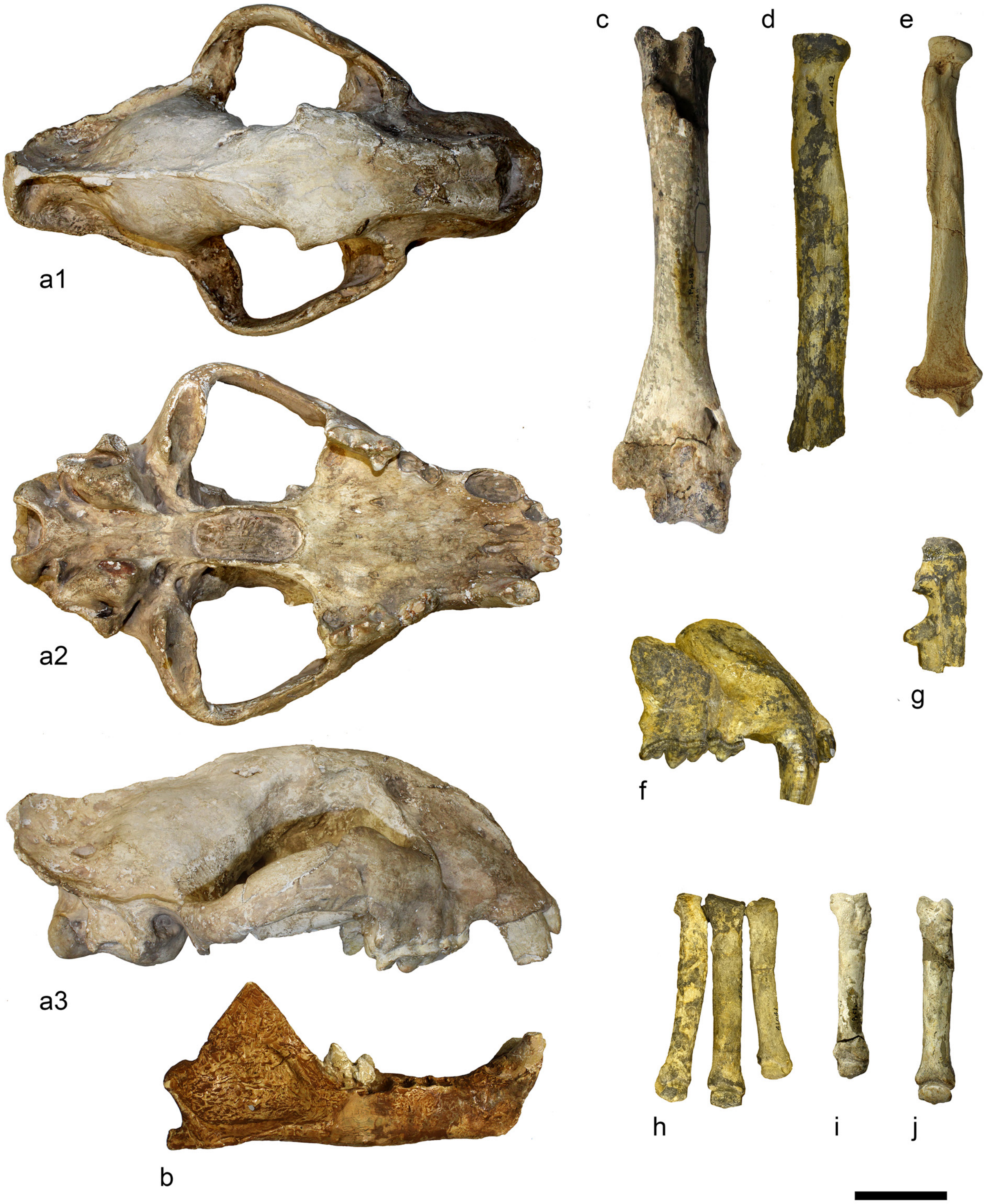

Fig. 3 (color online) - *Dinofelis* remains from Europe. a) Cranium from Tuilerie Chefdebien (cast Pp66) in dorsal (a1), ventral (a2) and right lateral (a3) views. b) Mandible from Perpignan (undetermined site; PP429) in buccal view. c) Partial left humerus (Coll. Donnezan, Pp287) in anterior view. d) Left radius proximal portion from Perpignan undetermined site (Pp 28). e) Left radius of *Megantereon*? from Serrat d'en Vaquer (Pp 297). f) Cranium fragment from Perpignan undetermined site (Pp 28) in buccal view. g) Left ulna proximal fragment from Perpignan undetermined site (FSL41026). h) Left metatarsals II-IV in (FSL41042) from Perpignan undetermined site in anterior view. i) Metacarpal II from Perpignan undetermined site (PP68a) in anterior view. j) Metacarpal III from Perpignan undetermined site (PP68b) in anterior view. Scale bar = 5 cm.

along with most other *Dinofelis* specimens recovered from Perpignan and its surroundings, originate from the Chefdebien Quarry, rather than the more famous Serrat d'en Vaquer site, also located in Perpignan.

In 1941, a complete *Dinofelis* cranium was recovered by workers from the Chefdebien Quarry (Perpignan) who gave it to the General Perruche of the French Army. Piveteau described this specimen in 1948, assigning it to the genus *Therailurus*. Both this cranium and Astre's specimen were found without detailed stratigraphic context. Although the Rousillon Basin is generally dated to the Early Pliocene, and the nearby Serrat d'en Vaquer site has been dated to approximately 4 Ma, an exact chronology for these *Dinofelis* remains cannot be confirmed beyond an Early Pliocene age.

Hemmer (1965) examined various *Dinofelis* specimens and noted that the European species differ from *D. abeli* Zdansky, 1924 by their smaller incisors, lower coronoid process, and less reduced P4 protocone. In 1983, Gérard de Beaumont described a *Dinofelis* hemimandible found by an amateur in the karstic fissure of Balaruc II, located in Frontignan near Montpellier. According to Michaux (1983), the site dates to approximately 3 Ma. The hemimandible is relatively small, with a smaller lower canine and a buccolingually narrow p4, leading Beaumont (1983) to classify it as *Dinofelis* sp.

In 1985, Ronald Ballesio described some post-cranial *Dinofelis* specimens from Perpignan, previously identified by Depéret (1890) as *Homotherium* (Fig. 3c, g-j). Although I have not reviewed Ballesio's publication, these specimens likely correspond to the post-cranial remains illustrated in Fig. 3, housed in various scientific institutions in Lyon. I concur with Ballesio (1985) that most of the Perpignan specimens are probably *Dinofelis,* pending a more detailed study. However, the radius in Fig. 3e most probably belongs to *Megantereon* due to its stoutness, small dimensions and comparatively low development of the radial head. Nevertheless, the former comparisons were based on African *Dinofelis* specimens given the absence of known Eurasian post-cranial material.

In 1998, Gabunia & Vekua described a complete *Dinofelis* cranium from Zemo Melaani (dated to around 3.5-2.0 Ma), characterised by compressed canines and assigned to *Dinofelis* sp.

In 1999, Averianov & Baryshnikov described a partial cranium from Novaja Etulia 2 in Moldova. This specimen, similar in size to the Balaruc II mandible, is dated to the late Villafranchian (approximately 1.8-1.2 Ma). Unfortunately, only the left side of the cranium and P4 are preserved, limiting further analysis. More recently, Sotnikova revised the carnivoran assemblage from the classic Odessa Catacombs site in Ukraine (3.5 Ma; Sotnikova, 2004), assigning specimens traditionally attributed to *Megantereon* by earlier authors to *Dinofelis* cf. *abeli*. However, the material, poorly illustrated in Alexeiev (1945), does not allow for detailed assessment.

Lastly, Brugal et al. (2020) mentioned *Dinofelis* in their review of Pleistocene carnivorans from France, specifically referencing a specimen from Senèze (approximately 2.25 Ma). I had the opportunity to examine this specimen (a calcaneus housed in the collections of the Basel Naturhistorisches Museum) and concur with the authors in attributing it to *Dinofelis* sp.

PHYLOGENY - *Dinofelis* has been classified within the Machairodontinae by several authors (e.g., Beaumont, 1964) and within the Felinae by others (e.g., Hendey, 1974). Some have alternatively positioned it as an intermediate form between the two subfamilies (e.g., Piveteau, 1961). The prevailing view among scholars now places the genus within the Machairodontinae, specifically in the tribe Metailurini, alongside genera such *as Metailurus, Pontosmilus, Stenailurus*, and *Adelphailurus* (see Werdelin & Lewis, 2001; Christiansen, 2013). Beaumont (1964) further suggested an ancestor-descendant relationship between *Metailurus* and *Dinofelis.* Recently, Jiangzuo et al. (2022b) proposed a new phylogeny for the Machairodontinae subfamily, in which *Dinofelis* is positioned as a sister taxon to *Paramachaerodus* and *Megantereon*, an interpretation with which I disagree.

Focusing specifically on the phylogenetic affinities of European *Dinofelis* specimens and their relationships with African and Asian fossils, it is challenging to draw conclusions. The European material is scant and lacks clear chronological context, complicating the assessment of any definitive relationships. Nonetheless, the cranium from Chefdebien appears distinct when compared to those from Balaruc II and Zemo Melaani. Further research is needed to clarify these relationships.

PALAEOECOLOGY AND HABITAT PREFERENCES - *Dinofelis* is traditionally associated with closed environments (but see Hopley et al., 2023), where it likely functioned as an ambush predator (see Werdelin & Lewis, 2001; Antón, 2013). The European postcranial specimens are virtually limited to the scant Serrat d'en Vaquer collection, which, despite its robust morphology, are highly fragmentary.

### *Eurasian dirk-toothed cat lineage (Fig. 4)*

EUROPEAN SPECIES - *Megantereon cultridens* (Cuvier, 1823) and *Megantereon adroveri* Pons-Moyà, 1987.

SYNONYMS - *Megantereon megantereon* Croizet & Jobert, 1828; *Megantereon whitei* (Broom, 1937) partim; *Megantereon falconeri* (Pomel, 1853); *Megantereon nihowanensis* (Teilhard de Chardin & Piveteau, 1930); *Megantereon inexpectatus* (Teilhard de Chardin, 1939); *Megantereon lantianensis* Hu & Qi, 1978; *Megantereon microta* Zhu et al., 2017.

CHRONOLOGICAL RANGE - Perpignan/Serrat d'en Vaquer? (ca. 3.8-3.6 Ma; France) but more parsimoniously from 2.78 Ma (Les Etouaires) to 1 Ma (Vallparadís EVT12).

MAIN SITES - Perrier-Les Etouaires (2.78 Ma; France; Fig. 4e); Saint-Vallier (ca. 2.5 Ma; France; Fig. 4a-b, g); Senèze (ca. 2.25 Ma; France; Fig. 4d, f); Upper Valdarno (ca. 1.8 Ma; Italy; Fig. 4j-k); Dmanisi (ca. 1.8 Ma; Georgia); Fonelas-P1 (2.0 Ma; Spain; Fig. 4h-i); Taurida Cave (1.8-1.5 Ma; Crimea; Fig. 4l); Apollonia-1 (ca. 1.5 Ma; Greece; Fig. 4m); Pardines (ca. 1.2 Ma; France; Fig. 4c); Untermassfeld (ca. 1.1 Ma; Germany); Vallparadís Section EVT12 (MIS 30; Iberia).

KEY REFERENCES - Croizet & Jobert (1828); Viret (1954); Ficcarelli (1979); Vekua (1995); Sardella (1998); Christiansen & Adolfssen (2007); Palmqvist et al. (2007); Tura-Poch et al. (2025).

FOSSIL RECORD - See a review in Palmqvist et al. (2007) and Christiansen & Adolfssen (2007).

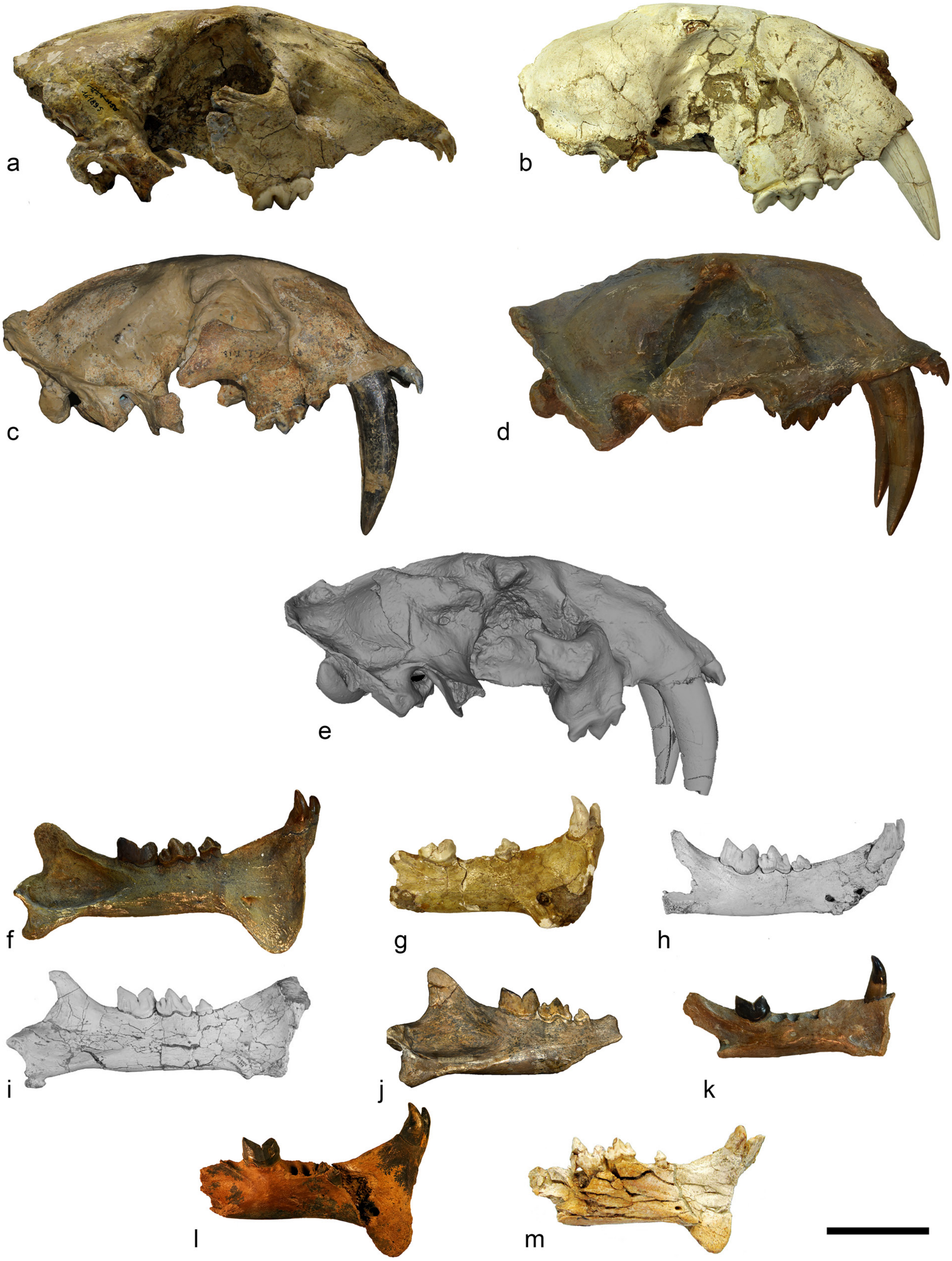

Fig. 4 (color online) - *Megantereon* remains from Europe. a) Cranium from St. Vallier (FSL20-161895) in right lateral view. b) Cranium from St. Vallier (FSL20.161892) in right lateral view. c) Cranium from Pardines (Lp18) in right lateral view. d) Cranium from Senèze (Cast SE311) in right lateral view. e) Cranium from Perrier-Les Etouaires (PET2001) in right lateral view. f) Right hemimandible from Senèze (cast SE311) in buccal view. g) Fragment of right hemimandible from Saint Vallier (FSL20-161893) in buccal view. h) Fragment of right hemimandible from Fonelas P1 (FP1-2002-5001; Photo A. Arribas) in buccal view. i) Right hemimandible from Fonelas P1 (FP1-2002-1391; Photo A. Arribas) in buccal view. j) Right hemimandibular fragment from Upper Valdarno (IGF12485) in buccal view. k) Right hemimandibular fragment from Upper Valdarno (Va-1205) in buccal view. l) Fragment of right hemimandible from Taurida Cave in buccal view (PIN 5644/95). m) Fragment of right hemimandible from Apollonia-1 (APL12; Photo G. Koufos). Scale bar = 5 cm.

History and taxonomy - The genus *Megantereon* includes several jaguar-sized machairodonts with compressed, elongated upper canines lacking crenulations. Fossils of this genus have been found across Africa, Eurasia, and North America, dating to the Pliocene and Pleistocene. The monotypic species was initially described by Georges Cuvier in 1823, based on two teeth from the Early Pleistocene of Upper Valdarno, Italy, and one *Machairodus* specimen from the Miocene of Eppelsheim, Germany, which he placed in *Ursus cultridens* Cuvier 1823 (Antón, 2013). In 1828, Jean Baptiste Croizet and Antoine Claude Jobert described a mandible from Perrier-Les Etouaires, France, naming it *Felis megantereon* Croizet & Jobert, 1828. Later, Fabrini (1890) reclassified the Tuscan machairodonts, grouping specimens with non-crenulated upper canines under *Machairodus (Meganthereon) cultridens*. This taxonomical tangle was not resolved until Ficcarelli's (1979) revision, which established *Megantereon cultridens* as the priority name according to the International Code of Zoological Nomenclature.

The phylogenetic relationships between *Megantereon* species remain debated. Scholars like Ficcarelli (1979) and Turner (1987) attribute all European specimens to *M. cultridens*, arguing that observed differences are due to interspecific variation, sexual dimorphism, and biogeography. Conversely, Sardella (1998) recognised three species: *Megantereon falconeri* from Asia, *M. cultridens* from Europe, and *M. whitei* from Africa.

Werdelin & Lewis (2000) identified *Megantereon ekidoit* Werdelin & Lewis, 2000 from South Turkwel (ca. 3.58-3.2 Ma), the earliest African species, distinguished from the younger *M. whitei* by its lack of a p3 and a distinctive ramus. Lewis & Werdelin (2010) argued that European late Early Pleistocene specimens should not be attributed to *M. whitei*, instead assigning them to *M. adroveri*. However, Martínez-Navarro (1992) and Martínez-Navarro & Palmqvist (1995, 1996) proposed that all early-middle Villafranchian Eurasian forms belong to *M. cultridens* and African forms to *M. whitei*, asserting that around 2.0 Ma, *M. whitei* dispersed from Africa to Eurasia, as evidenced at Dmanisi (Bartolini-Lucenti et al., 2022), subsequently replacing *M. cultridens*.

Notably, Eurasian *Megantereon* forms display a tendency of reduction and simplification of premolars over time, including a diastema between p3 and p4. Most African sites proposed as sources of this European advanced form (such as Kromdraai A [ca. 1.8-1.6 Ma], Sterkfontein member 5 [ca. 2-1.4 Ma] or Member 4 [ca. 3.5-2.0 Ma], Swartkrans member 1 [ca. 1.9-1.8 Ma], Elandsfontein [ca. 1.2-0.8 Ma], Schruverburg [ca. 1.8 Ma?], Koobi Fora Okote Member [1.65-1.39 Ma) and Afar [Awash Valley, unknown locality]) are, in fact, younger than the earliest putative European *M. whitei* at Dmanisi (1.8 Ma). Turner's studies (1987, 1990) add further uncertainty to the chronology, with discrepancies in assigning *M. whitei* specimen from Sterkfontein (STS-1558) between members 4 and 5. According to Werdelin & Lewis (2000), the oldest securely dated *M. whitei* specimen come from Koobi Fora (1.65-1.39 Ma).

Furthermore, slight reduction in p3 and the appearance of a diastema between p3-p4 also appear in European *M. cultridens* specimens from Fonelas P-1 (FP1-2002-1391; ca. 2.0 Ma) and Upper Valdarno and Olivola (IGF827, IGF4709, IGF4711; 2.0-1.8 Ma). Given that African specimens attributed to *M. whitei* are likely younger than 2 Ma, overall larger and stouter, it is plausible to argue either an African dispersal into Eurasia or a Eurasia-to-Africa dispersal. Until further African specimens are identified, I prefer supports an exclusively Eurasian lineage for European specimens.

Palaeoecology and habitat preferences - Based on the nearly complete skeleton from Senèze (Christiansen & Adolfssen, 2007), *Megantereon cultridens* is characterised by short, robust limbs, a short tail, and a long, muscular neck (Antón, 2013). In palaeontological literature, *Megantereon* is typically described as inhabiting wooded environments and as an ambush predator. To date, no isotopic or microwear analyses have been conducted for this genus in Eurasia. A recent study on stable isotopes in carnivorans from the Turkana Basin (Hopley et al., 2023) revealed $\delta^{13}C$ values for *M. whitei* that were similar to other machairodonts and to the extant *Panthera leo*. Additionally, another recent study by Zhu et al. (2021) on *Megantereon* remains from South China suggests that this species may not have been as well-adapted to closed environments as previously thought.

*European puma-like cat (Fig. 5)*

European species - *Viretailurus pardoides* (Owen, 1846).

Synonyms - *Panthera schaubi* (Viret, 1954); *Puma pardoides* (Owen, 1846); *P. pardoides brevipes* Hemmer & Kahlke, 2022.

Chronological range - 3.07 Ma (Kvabebi) to 0.86 Ma (Vallparadís Section EVT7).

Main sites - Kvabebi (3.07 Ma; Georgia); Saint Vallier (ca. 2.5 Ma; France; Fig. 5a-c); Graunceanu (ca. 2.0 Ma; Romania); Untermassfeld (ca. 1.1 Ma; Germany); Chaparral (ca. 1.0 Ma; Iberia); Cueva Victoria (ca. 0.9 Ma; Iberia; Fig. 5d); Vallparadís Section EVT7 (0.86 Ma; Iberia).

Key references - Owen (1846); Viret (1954); Hemmer et al. (2004); Madurell-Malapeira et al. (2010); Hemmer & Kahlke (2022); Werdelin et al. (2023).

Fossil record - See Madurell-Malapeira et al. (2010) and Hemmer & Kahlke (2022).

History and taxonomy - Eurasian puma-like cats are exceedingly rare in the fossil record, represented by only one cranium and a few postcranial bones. Consequently, their anatomy and ecology remain poorly understood, and their taxonomic classification is a subject of considerable debate (Hemmer & Kahlke, 2022).

The first description of remains attributed to this genus was by Richard Owen (1848), who named the species *Felis pardoides* Owen, 1846 based on two lower first molars from the British Red Crags. Another species, *Panthera schaubi*, was initially described by Jean Viret (1954) from the French site of Saint-Vallier. Viret proposed that these remains displayed the dimensions and morphological characteristics of a small pantherine. However, Hemmer (1964) demonstrated that the skull from Saint-Vallier was distinctly non-pantherine and, instead, shared many features with the American puma, *Puma concolor* (Linnaeus, 1771). As a result, Hemmer reassigned the Saint-Vallier puma-like cat remains to a new genus, *Viretailurus*. Subsequently, Kurtén & Crusafont-Pairó (1976) described carnivore remains from the Iberian site of La Puebla de Valverde, some of which they identified as *Panthera* cf. *schaubi*, noting similarities with specimens from the English Red Crags. Shortly thereafter, Sotnikova (1978) reported the presence of *Felis (Puma)* sp. at Shamar and Beregovaya in Mongolia without providing detailed descriptions. In 1978, Sotnikova described *Lynx* remains from Mongolia, specifically an almost complete skull from Beregovaya (PIN2975/1), assigning it to *Lynx shansius* Teilhard de Chardin, 1938. She did not indicate whether this skull corresponded to the remains previously identified as *Felis (Puma)* sp., and she didn't revise this topic in later publications. Thanks to Alexander Lavrov, I had the opportunity to study the Beregovaya skull (PIN2975/1) in detail. Although the specimen displays some characteristics not commonly seen in *Lynx issiodorensis* (Croizet & Jobert, 1828), its small size, lack of a P2, and sharp premolars align it more closely with the genus *Lynx* than with *Viretailurus*.

In the last two decades, additional remains of this species have been identified. In 2001, Hemmer described the first mandibular fragment from Untermassfeld. Later, Hemmer et al. (2004) identified two maxillary fragments from Kvabebi, although other mandibular remains from the same site remain unpublished (J.M.-M., unpublished data). In 2010, we described several mandibular and postcranial remains from the Iberian sites of La Puebla de Valverde, Cueva Victoria, and the Vallparadís Section (Madurell-Malapeira et al., 2010). Additional Iberian remains were later noted at the Epivillafranchian site of El Chaparral (Giles-Pacheco et al., 2011). Most recently, Werdelin et al. (2023) attributed new cranial specimens from Graunceanu, Romania, to a puma-like cat. Finally, the most outstanding record of *Viretailurus* was recently described by Hemmer & Kahlke (2022) from the German site of Untermassfeld, from whence they described a partial skeleton of this taxon.

In summary, most researchers agree on placing this taxon within the subfamily Felinae rather than Pantherinae. As with *P. gombaszoegensis*, the mandibular structure shows clear puma affinities, whereas cranial affinities remain difficult to establish. While the taxonomy of this taxon lies outside the scope of this paper, and *Puma pardoides* is the more commonly accepted name, I prefer to use *Viretailurus pardoides* until its phylogenetic relationships are clarified.

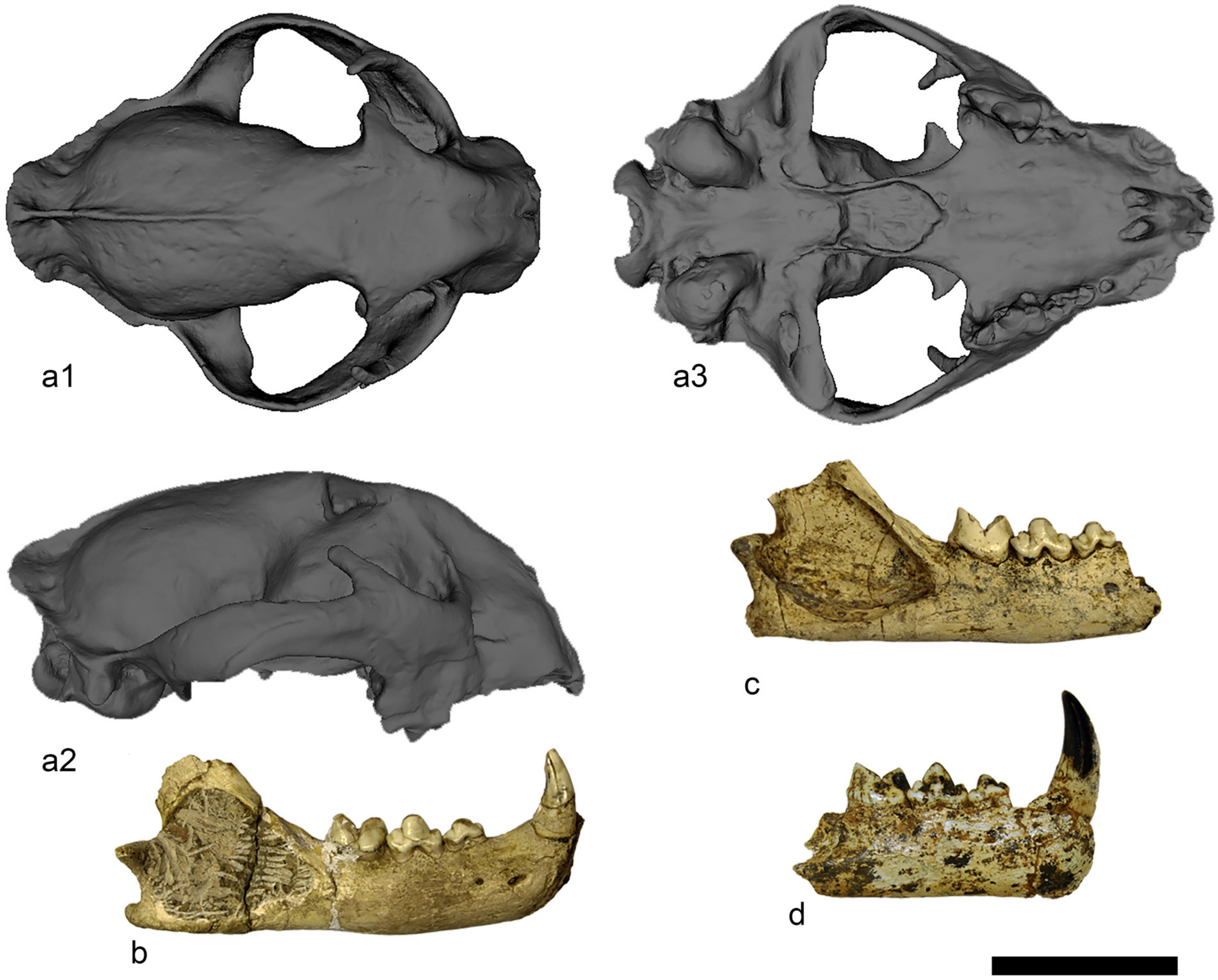

Fig. 5 (color online) - Remains of *Viretailurus pardoides* from Europe. a) Cranium from St. Vallier (QSV136) in dorsal (a1), right lateral (a2) and ventral (a3) views. b) Right hemimandible from St. Vallier (FSL20-161853) in buccal view. c) Partial right hemimandible from St. Vallier (FSL20-161855) in buccal view. d) Partial right hemimandible from Cueva Victoria (IPS46144) in buccal view. Scale bar = 5 cm.

Palaeoecology and habitat preferences - The palaeoecology, habitat preferences, and locomotor behaviour of this species remain largely unknown. However, the recently described partial skeleton from Untermassfeld offers some insights. Based on body mass estimates by Hemmer & Kahlke (2022), the German specimen weighed around 40-45 kg. The same authors also provided body mass estimates for the specimens from La Puebla de Valverde (36.1-109 kg) and Saint-Vallier (31-81.6 kg), suggesting a range of 30-50 kg for females and 60-110 kg for males (Hemmer & Kahlke, 2022).

In terms of postcranial morphology, the brachial and crural indices, though within the upper range of *Puma concolor*, also fall in the lower range for clouded and snow leopards, aligning more closely with open-habitat climbers like the latter animals. The Untermassfeld specimen notably displays shorter metapodials and a smaller hemipelvis than the cougar. Based on these features, the authors conclude that *Viretailurus* should be considered a generalist cat, without extreme specialisations, but well adapted for climbing and suited to life in wooded habitats. In my opinion, however, the habitat preferences are less clear-cut, as the postcranial morphology of the Untermassfeld specimen exhibits similarities with several climbing large cats, particularly *P. uncia*.

*European leopard (Fig. 6)*

European species - *Panthera pardus* Linneaus, 1758.

Chronological range - 1.2 Ma (Vallonnet) to 11 ka in North Iberia (several sites).

Main sites - Le Vallonnet (ca. 1.2 Ma; France); Grotte de la Carrière (MIS 9; France); Lunel-Viel (MIS 8; France); Artazu (MIS 5c; Iberia); Torrejones (MIS 4-3; Iberia); Equi (MIS 4-3; Italy; Fig. 6a-g); Avenc Joan Guitón (MIS 4-3; Iberia), Zafarraya (MIS 4-3; Iberia); Zoolithen (MIS 4-3; Germany); Imanolen Arrobia (MIS 4-3; Iberia); Baumanshöle (MIS 3; Germany); Jaurens (MIS 3; France); Vjeternica (MIS 3; Bosnia and Herzegovina); Apidima (MIS 3-2; Greece); Bolinkova (MIS 3-1; Iberia); Aintzulo (MIS 2; Iberia) Vraona (MIS 2-1; Greece).

Key references - Del Campana (1954); Schütt (1969); Bonifay (1971); Ballesio (1980); Nagel (1999); Barroso et al. (2006); Altuna & Mariezkurrena (2013); Ghezzo & Rook (2015); Sanchís et al. (2015); Castaños et al. (2016); Sala et al. (2021).

Fossil record - See a review in Marziszak et al. (2022b).

History of Research - Early European naturalists, including Georges Cuvier, Edward Lartet, and Henri Marie Ducrotay de Blainville, were instrumental in first identifying leopard remains in Pleistocene deposits and developing taxonomic approaches that distinguished *Panthera pardus* remains from other large felids. Cuvier's pioneering work in comparative anatomy laid the foundation for these distinctions, allowing him and others to differentiate leopard fossils from those of other big cats through detailed skeletal comparisons (Cuvier, 1823). Later on, Édouard Lartet's research in the Dordogne region, particularly at the Périgord cave sites, was pivotal in situating *Panthera pardus* remains within the broader context of the European Pleistocene. His findings in caves such as those at Les Eyzies, alongside the pioneering archaeological work with Henry Christy documented in *Reliquiae Aquitanicae*, provided evidence of leopards coexisting with early humans. Fossils found in stratigraphic association with human artifacts supported hypotheses of interspecies interactions and environmental sharing, illuminating the leopard's adaptability across diverse European habitats (Lartet & Christy, 1875).

In southern France's Grèzes caves, Marcellin Boule furthered the study of *Panthera pardus* remains by examining fossilised bones that displayed morphological traits specific to leopards. Boule's analysis offered a more refined view of the leopard's physical adaptations and emphasised their resilience compared to other Pleistocene predators, which were often more specialised and less adaptable to Europe's changing climates (Boule, 1906, 1910, 1019). Auguste Pomel's catalog of Tertiary and Quaternary faunal remains also referenced *Panthera pardus* fossils, reinforcing the presence of leopards in French fossil deposits and adding to the growing record of their widespread distribution across Europe (Pomel, 1853). Similarly, Paul Gervais' work *Zoologie et paléontologie françaises* (1869) provided further documentation of leopard remains across French Pleistocene sites, comparing them to those found in other parts of Europe and helping to clarify their ecological roles. These 19th Century findings not only laid the groundwork for taxonomic and ecological theories about *Panthera pardus* in Europe but also influenced future studies of species adaptation, interspecies relationships, and climate-driven migrations.

Despite two centuries of research, European leopards remain less understood than other species commonly found in Late Pleistocene karstic environments, such as cave bears, cave lions, cave hyenas, and various ungulates. One primary reason for this knowledge gap is the scarcity of leopard fossils across Europe. While *P. pardus* remains have indeed been unearthed at over 300 sites across the continent (Marciszak et al., 2022b), most of these sites contain only a few fragmentary remains of this species. Only a handful of locations, such as Equi, Zafarraya, Zoolithenhöhle, Baumannshöhle, and Vraona, preserve multiple individuals and well-preserved specimens (Del Campana, 1954; Schütt, 1969; Nagel, 1999; Barroso et al., 2006; Diedrich, 2013; Ghezzo & Rook, 2015; Sanchís et al., 2015).

Another factor contributing to this gap is that much of the research over recent decades has focused on sites associated with human activity or those that are easily accessible. Leopards, however, typically favour secluded caves in mountainous or rocky areas, which they use as dens or safe places to consume prey undisturbed. In the early 2010s, Alfred Sanchís and Víctor Sauqué pioneered the study of leopard dens in Europe, describing sites such as Los Rincones and Racó del Duc (Sauqué et al., 2016; 2018; Sauqué & Sanchís 2017). In recent years, my team has discovered additional leopard dens in the Pyrenees, all located in remote caves with difficult access, including S'Espasa, Cova 120, Tut de Fustanyà, and Grotte de la Carrière (Sauqué et al., 2018; Prat-Vericat et al., 2022). While much of the compiled data is still awaiting publication, this new focus promises to unveil a wealth of insights into the palaeobiology of this elusive species.

Palaeoecology and habitat preferences - In palaeontological and archaeological literature, the palaeobiology of European leopards is often assumed to be equivalent to that of their modern African counterparts, despite limited discussion on the subject. Similarly, few isotopic studies have focused specifically on leopards, with existing research (e.g., Bocherens et al., 2011) typically concentrating on other carnivores and providing only scattered data on leopards. Nevertheless, the palaeobiogeographic distribution of leopards in Europe appears to follow a distinct pattern, with these animals being particularly common in mountainous and rocky areas.

Some previous authors have noted anatomical features in European leopards that resemble those of snow leopards (*Panthera uncia*); for example, Sauqué et al. (2016) and others have proposed similarities, while Hemmer (2023) has even suggested the possible presence of snow leopards in Pleistocene Europe. However, despite the sparse remains of snow leopards in Europe, it is my opinion that European leopards possess several morphological traits also seen in snow leopards. One of the most notable features, cited by various authors, is the robustness of the mandible, which includes a vertically oriented symphysis and a deep masseteric fossa. Furthermore, the postcranial bones of European leopards are especially robust, with proportions differing from those of modern leopards. Specifically, the crural and brachial indices in fossil specimens are higher than in extant leopards, resembling those of pumas and snow leopards, an adaptation potentially suited to jumping and living in rocky environments.

Fig. 6 (color online) - Remains of *Panthera pardus* from Equi Cave. a) Cranium IGF10036 in dorsal (a1) and right lateral (a2) views. b) Cranium IGF185V in dorsal (b1) and right lateral (bb2) views. c) Right hemimandible IGF6102V in buccal view. d) Right partial hemimandible IGF185V in buccal view. e) Right juvenile hemimandible IGF123V in buccal view. f) Partial right hemimandible (reversed) IGF6103V in buccal view. g) Partial right maxilla IGF6120V in buccal view. Scale bar = 3 cm.

DNA Analysis - Current genetic insights into Pleistocene *Panthera pardus* are predominantly derived from mitochondrial DNA. This genetic data includes six specimens dated to approximately 45 ka from Baumannshöhle in Germany, along with one specimen from Mezmaiskaya Cave in the Caucasus, dated to around 35 ka (Paijmans et al., 2018). Comparative studies of these ancient mitochondrial sequences with both historical and modern leopard populations reveal a notable decline in mitochondrial diversity in contemporary leopards. This reduction is attributed to population bottlenecks that have led to significant genetic diversity loss since the Pleistocene.

Interestingly, the specimen from Mezmaiskaya shows closer genetic affinities with current Asian leopards than with Pleistocene populations from Europe, suggesting that distinct lineages existed. This finding implies that European leopard lineages likely did not contribute to the genetic makeup of present-day populations, suggesting that these lineages faced extinction during or following the Pleistocene.

Further complexity is introduced by recent findings from sedimentary ancient DNA (sedaDNA) extracted from Solutrean layers at El Mirón Cave. This sedaDNA analysis suggests that mitochondrial lineages in Europe during the Last Glacial Maximum (LGM) may have been more closely related to those of the Mezmaiskaya specimen than previously understood. These results point to a more complex picture of leopard population dynamics in the Pleistocene, with evidence of possible gene flow or shared ancestry between European and Caucasian populations (Gelabert et al., 2025).

### *European cheetah (Fig. 7)*

European species - *Acinonyx pardinensis* (Croizet & Jobert, 1828).

Synonyms - *Felis (Cynailurus) etruscus* Del Campana, 1915; *Cynailurus pleistocaenicus* Zdansky, 1925; *Sivapanthera arvernensis* (Croizet & Jobert, 1828); *Acinonyx arvernensis* (Croizet & Jobert, 1828) or *Leopardus arvernensis* (Croizet & Jobert, 1828).

Chronological range - 3 Ma (Villafrancha d'Asti) to ca. 0.5 Ma (Mosbach).

Main sites - Villafrancha d'Asti (3 Ma; Italy; Fig. 7g); Perrier-Les Etouaires (2.78 Ma; France); Saint-Vallier (France; 2.5 Ma; Fig. 7a-f); Senèze (ca. 2.25 Ma; France); Villarroya (2.2 Ma; Iberia); Upper Valdarno (1.8 Ma; Italy); Untermassfeld (1.1 Ma; Germany).

Key references - Fabrini (1892); Del Campana (1915), Hemmer et al. (2011); Spassov (2011); Hemmer & Kahlke (2022); Jiangzuo et al. (2024); Gimranov et al. (2024).

Fossil record - See review in Hemmer et al. (2011) and Hemmer & Kahlke (2022).

History and taxonomy - In 1828, Jean-Baptiste Croizet and Antoine Claude Jobert became the first naturalists to describe remains that we now attribute to the European cheetah. They identified two new species, *Felis pardinensis* Croizet & Jobert, 1828 and *Felis arvernensis* Croizet & Jobert, 1828, based on fossils unearthed from the sites of Les Étouaires and Côte d'Ardé. These descriptions were published in their 1828 seminal work, *Recherches sur les ossemens fossiles du département du Puy-de-Dôme*.

Following their work, several other researchers made notable contributions to the study of European cheetah remains. In 1892, Fabrini described additional finds, followed by Tuccimei in 1896 and Del Campana in 1915, who studied the felids from the Upper Valdarno basin in Tuscany (Italy). A few years later Kretzoi (1929) and Pilgrim (1932) introduced the genera *Sivapanthera* and *Sivafelis*, respectively, for fossils that we now recognise as belonging to the European cheetah. Josep Fernández de Villalta (1954) included several cranial remains of *Sivapanthera arvernensis* in his PhD research on the Early Pleistocene large mammals of Villarroya (northeastern Iberia). That same year, Jean Viret described what is likely the most comprehensive collection of cheetah fossils from the Early Pleistocene site of Saint-Vallier. Later, Helmut Hemmer extensively studied European cheetah remains from sites including Untermassfeld, Dmanisi, and Mosbach Sands (Hemmer, 2001; Hemmer et al., 2008, 2011; Hemmer & Kahlke, 2022). In their most recent publication, Hemmer & Kahlke (2022) propose recognising several species and subspecies of European cheetah based on variations in body mass throughout the Pleistocene. However, in my view, the European record of *Acinonyx* remains too sparse and superficially analysed in terms of chronological context to support such taxonomic distinctions. To justify this separation, further statistical analyses are essential but are notably absent in the referenced study. Future research will be crucial to clarifying the phylogenetic and taxonomic status of the European cheetah.

Palaeoecology and habitat preferences - The European cheetah exhibits similar features to its living counterpart, including a small head, sharp dentition, enlarged frontal sinuses, long and slender limb bones, and a flexible vertebral column. However, its body mass is considerably greater than that of the extant cheetah. Hemmer & Kahlke (2022) estimate the body mass of the *A. pardinensis* specimens from Untermassfeld to range between 110 and 140 kg. The postcranial morphology of this larger cheetah species likely did not support high-speed pursuit hunting and agility to the same degree as the modern cheetah. Instead, it appears adapted for hunting at moderately high speeds in open terrain.

In a recent study, Camille Gröhé et al. (2018) discuss the evolutionary specialisation of the inner ear in the modern cheetah, which supports its high-speed hunting capabilities. Their findings show that the cheetah's vestibular system is exceptionally large and morphologically distinct from other felids, including the extinct European cheetah, *A. pardinensis*. This specialisation, characterised by elongated anterior and posterior semicircular canals and an enlarged utricle, enhances the cheetah's sensitivity to head movements, thereby improving postural stability and visual focus during pursuits. Notably, these features are absent in *A. pardinensis*, suggesting that these inner ear adaptations likely evolved after the Middle Pleistocene, potentially around the time of the last population bottleneck of modern cheetahs.

### *European snow leopard (Fig. 8)*

European species - *Panthera uncia* (Schreber, 1775).

Synonyms - *Panthera pardus tautavelensis* Testu et al., 2011; *Panthera uncia pyrenaica* (Hemmer, 2023).

Chronological range - 0.5 Ma (Arago, France; Fig. 8c) to MIS 3 (Algar da Manga Larga, Portugal; Fig. 8a-b).

Main sites - Arago (0.5 Ma; France; Fig. 8c) and Algar da Manga Larga (MIS 3; Portugal; Fig. 8a-b).

Key references - Nagel (1999); Hemmer (2023); Cardoso & Regala (2006); Testu et al. (2011); Sauqué & Cuenca Bescós (2013); Jiangzuo et al. (2025); Estráviz et al. (2024).

Fossil record - See a review in Jiangzuo et al. (2025).

History and taxonomy - The possible presence of snow leopard remains in Europe has been a topic of intense debate over the past decades. The first mention of potential snow leopard traits in a *Panthera pardus* sample was made by Nagel in 1999 in her description of leopard remains from Vraona, Greece. Subsequently, Hemmer (2001) attributed a mandible from glacial stage 14 in the Arago Cave, France, to this species, based on the vertical alignment of the symphysis and the morphology of the masseteric fossa. However, this identification was later refuted by Testu et al. (2011), who proposed the subspecies *P. p. tautavelensis*, designating the same mandible as its holotype. Other researchers, such as Cardoso & Regala (2006) and Sauqué et al. (2013), described traits resembling snow leopard characteristics in various Iberian samples that were ultimately attributed to *P. pardus*.

Recently, a comprehensive study of the Chinese and European record of medium-sized leopards, using multivariate analysis, geometric morphometrics, and finite element analysis, concluded that snow leopards did exist in Europe. This study included specimens from

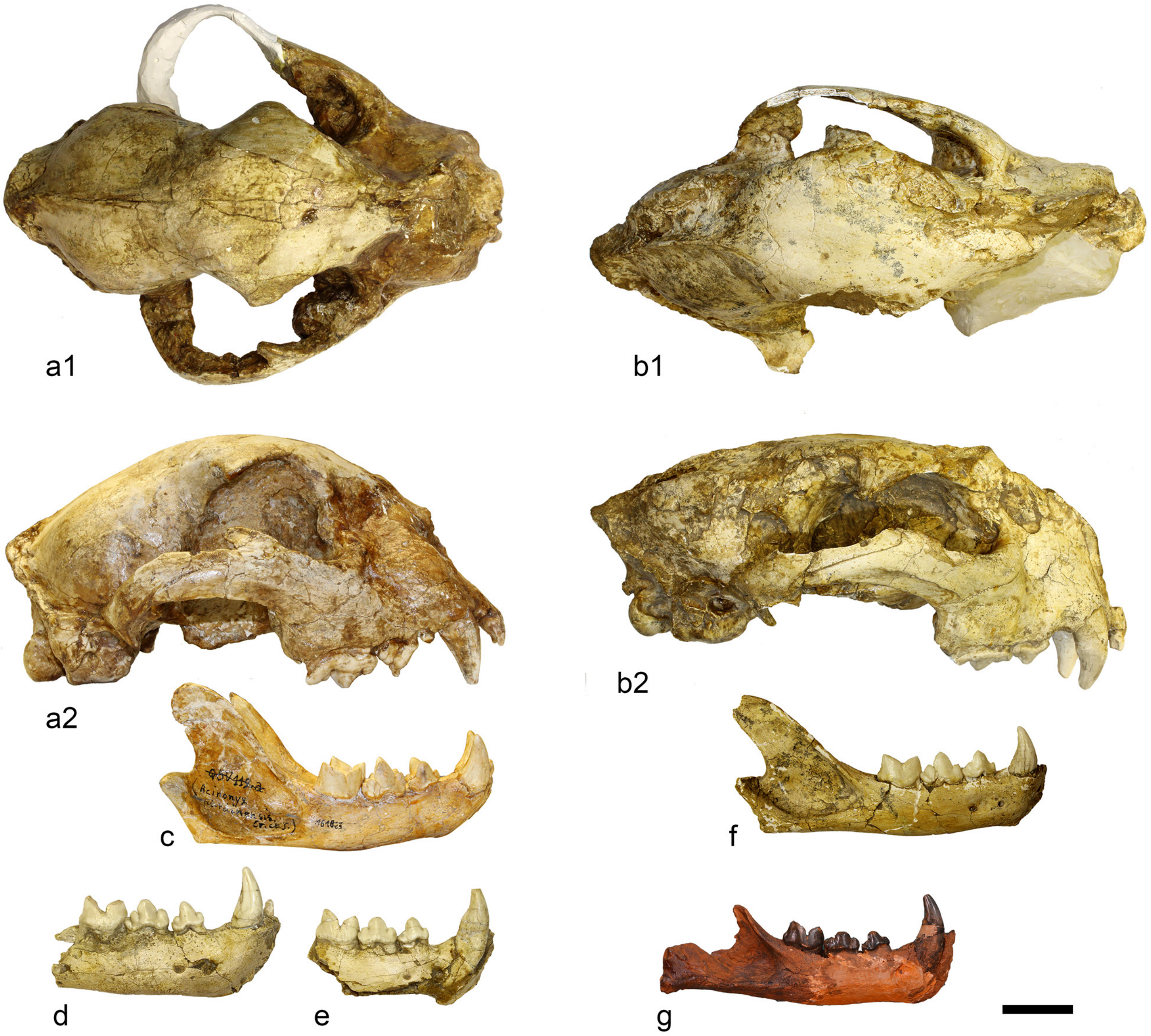

Fig. 7 (color online) - Remains of *Acinonyx pardinensis* from Europe. a) Cranium from St. Vallier (MC161827) in dorsal (a1) and right lateral (a2) views. b) Cranium from St. Vallier (MC161825) in dorsal (b1) and right lateral (b2) views. c) Mandible from St. Vallier (MC161823) in right buccal view. d) Partial right hemimandible from St. Vallier (MC161828) in buccal view. e) Partial right hemimandible from St. Vallier (MC161829) in buccal view. f) Partial right hemimandible from St. Vallier (MC161819) in buccal view. g) Partial mandible from Villafranca d'Asti (VJ132 ) in buccal view. Scale bar = 3 cm.

Fig. 8 (color online) - Remains of *Panthera uncia* from Europe. a) Cranium from Algar da Manga Larga (MG1355-001) in right lateral (a1) and dorsal (a2) views. b) Mandible from Algar da Manga Larga (MG1355-002) in right buccal view. c) Mandible from Arago Cave (E14-EFNI-1001) in right buccal view. Scale bar = 5 cm.

Algar da Manga Larga and Arago in the species *P. uncia* (Jiangzuo et al., 2025). These findings were further supported by a study of the endocranial morphology of the Algar da Manga Larga cranium, which revealed brain morphology completely comparable to *P. uncia*, along with an enlargement of the frontal sinus consistent with that species (Estráviz et al., 2024).

These recent studies may soon allow the identification of additional remains attributable to this species. However, it is true that the anatomical differences between *P. pardus* and *P. uncia* are minimal, and only complete cranial or post-cranial remains permit reliable identification. This issue is further complicated by the morphology observed in European Pleistocene leopards, which show evolutionary convergences with snow leopards. As shown in Fig. 8, external cranial morphology is clearly distinguishable by the flat cranial profile and enlarged frontal sinuses of the skull, as well as the verticalisation of the symphysis and incisors in the mandible.

Palaeoecology and habitat preferences - The postcranial morphology of European snow leopards remains unknown, as the postcranial bones from Algar da Manga Larga are too fragmentary for analysis. In Jiangzuo et al. (2025), we propose that the environmental requirements of Middle to Late Pleistocene European snow leopards were similar to those of the extant species, which inhabit mountainous rocky environments. Their primary prey was likely Caprini, originating from Asia's high altitudes.

### *Mediterranean lynx lineage (Figs 9 and 10)*

European species - *Lynx issiodorensis* (Croizet & Jobert, 1828) and *Lynx pardinus* (Temminck, 1827).

Synonyms - *Felis brevirostris* Croizet & Jobert, 1828; *Felis perrieri* Croizet (unknown year); *Lynx spelaeus* Boule, 1910.

Chronological range - 2.78 Ma (Perrier-Les Etouaires; France) to present.

Main sites - Les Etouaires (2.78 Ma; France; Fig. 9a-b and Fig. 10a-c); Saint-Vallier (2.5 Ma; France; Fig. 9d-e and Fig.10d-f); Olivola and Upper Valdarno (2-1.8 Ma; Italy; Fig. 9f-g and Fig. 10h-i); Dmanisi (1.8 Ma; Georgia); Taurida (1.6 Ma; Crimea; Fig. 9h); Avenc Marcel (1.6 Ma; Iberia; Fig. 9i); Pirro Nord (1.4 Ma; Italy); Vallparadís Section EVT12-7 (MIS 30-21; Iberia; Fig.10n; Cueva Victoria (0.9 Ma; Iberia; Fig.10m); L'Escale (0.6 Ma; France; Fig. 9j); Ingarano (MIS 3; Italy; Fig. 9k and Fig. 10o-p); Avenc del Marge del Moro (MIS 2; Iberia; Fig. 9l).

Key references - Ficcarelli & Torre (1975a, 1977); Kurtén (1978); Werdelin (1981); Kurtén & Werdelin (1984); Boscaini et al. (2015, 2016); Lavrov et al. (2021); Mecozzi et al. (2021); Tura-Poch et al. (2023).

History and taxonomy - The first authors to describe fossil remains of ancient lynx were Croizet & Jobert in 1828, based on their work at the French sites in Auvergne. They identified two new species: *Felis issiodorensis* and *Felis brevirostris*. In 1869, Paul Gervais included these two forms in the genus *Lynx*. In 1890, Charles Depéret described Early Pliocene remains from Serrat d'en Vaquer (ca. 4 Ma, France; Fig. 10a), based on a single hemimandible, and assigned them to *Caracal brevirostris* (Depéret, 1890), noting similarities with the African *Caracal* as well as with the earlier specimens described by Croizet & Jobert (1828). Depéret mentioned an old label in the Paris Muséum national d'Histoire naturelle, attributed to Croizet, which originally identified the Perrier Mountain

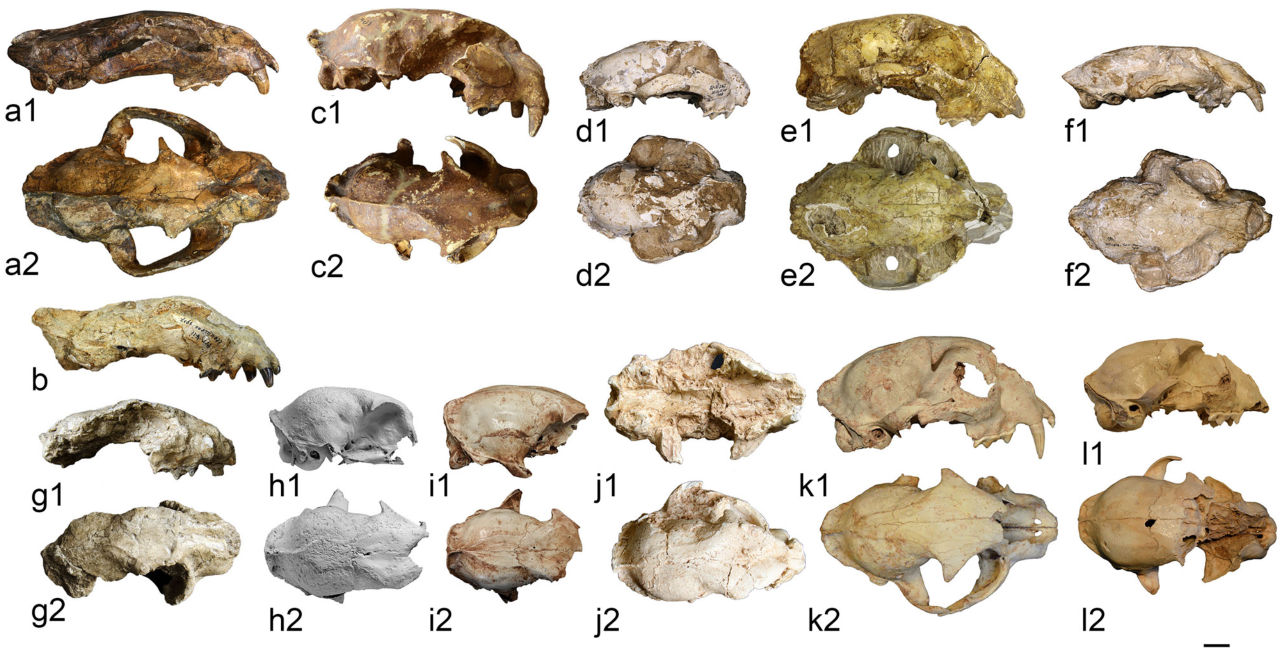

Fig. 9 (color online) - *Lynx* cranial remains from the Pleistocene of Europe. a-g) *Lynx issiodorensis.* a) Cranium from Les Etouaires (Prr200) in right lateral (a1) and dorsal (a2) views. b) Cranium from Les Etouaires (Prr411) in right lateral view. c) Cranium from Côte d'Ardé (cast IGF12277) in right lateral (c1) and dorsal (c2) views. d) Cranium from St. Vallier (St.V.767) in right lateral (d1) and dorsal (d2) views. e) Cranium from St. Vallier (MC161882) in right lateral (e1) and dorsal (e2) views. f) Cranium from Olivola (Olivola-1905) in right lateral (f1) and dorsal (f2) views. g) Cranium from Olivola (IGF4399) in right lateral (g1) and dorsal (g2) views. h) Cranium from Taurida Cave (PIN5644) in right lateral (h1) and dorsal (h2) views. i) Cranium from Avenc Marcel (IPS4170) in right lateral (i1) and dorsal (i2) views. j) Cranium from L'Escale (cast IGF678V) in ventral (j1) and dorsal (j2) views. k) Cranium from Ingarano (MGPT-PU-13415) in right lateral (k1) and dorsal (k2) views. l) Cranium from Avenc del Marge del Moro (IPS4175) in right lateral (l1) and dorsal (l2) views. Scale bar = 2 cm.

remains as *Felis perrieri*, though Croizet later favoured classification under *F. brevirostris*. Surprisingly, while Depéret accepted Gervais' inclusion of Croizet & Jobert's species in the genus *Lynx*, he later assigned the Roussillon remains to the genus *Caracal*, albeit within Croizet's species. The same year, Forsyth Major (1890) was the first to study small felid remains from Upper Valdarno and Olivola, including all specimens under *Felis issiodorensis*. This view was further supported by Fabrini in 1892.

At the beginning of the 20th Century, Marceline Boule (1919), working at the Late Pleistocene site of Grotta del Principe, noted the occurrence of *Felis lynx* Linnaeus, 1758 and introduced a new form, *Felis (Lynx) pardinus spelaea* Boule, 1919, a larger variant of the modern *L. pardinus* characteristic of the late Quaternary. Subsequent researchers studied the differences between living *L. lynx*, *L. pardinus*, and the "cave lynx" (Dubois & Stehlin, 1933). Bonifay (1971) described the oldest known cranium at L'Escale in France (0.7-0.6 Ma), assigning it to Boule's species *L. spelaeus*. Ficcarelli & Torre (1975a, 1977) compared the living lynx forms with remains from Upper Valdarno and Olivola, concluding that *L. issiodorensis* likely represented the ancestor of *L. pardinus*. These studies were followed by Kurtén's (1978) redescription of the Les Etouaires specimens and a detailed phylogenetic analysis of all known living and extinct lynxes by Lars Werdelin in 1981. Werdelin (1981) postulated that *L. issiodorensis* was the ancestor of both *L. pardinus* and *L. lynx*, proposing several subspecies of *L. issiodorensis* and a gradual evolutionary trend leading to *L. pardinus*. Later, Kurtén & Werdelin (1984) studied material from the Early Pleistocene chinese species *L. shansius*, noting its similarities to European *L. issiodorensis*.

Since these studies, most authors have included Pliocene and Early Pleistocene lynxes under *L. issiodorensis* (Garrido & Arribas, 2008; Lacombat et al., 2008; Palombo et al., 2008; Sotnikova, 2008; Brugal et al., 2020). Meanwhile, the 'cave lynx' has been reported from numerous Middle-Late Pleistocene sites in southwestern Europe, particularly southern France and northern Italy. Consistent with Werdelin's (1981) interpretation, many researchers consider this taxon a subspecies and probable ancestor of modern *L. pardinus* (e.g., *L. pardinus spelaeus*) (Kurtén & Granqvist, 1987; Palombo et al., 2008; Garrido & Arribas, 2008; Rodríguez-Hidalgo et al., 2020; Fosse et al., 2020). Others classify the "cave lynx" as a distinct species, *Lynx spelaeus* (Bonifay, 1971; Ficcarelli & Torre, 1977; Arribas, 1994; Rustioni et al., 1995; Capasso Barbato et al., 1998; Testu, 2006).

In 2010, I began an ambitious project to clarify the fossil record and phylogenetic relationships of European lynxes. In 2011, we published the first fossil DNA data of *L. pardinus*, which indicated a loss of genetic diversity in this species at least 40 ka (Rodríguez et al., 2011). In 2015, we reported the earliest evidence of *L. pardinus*, based on a partial cranium from Avenc Marcel (NE Iberia; 1.6 Ma), suggesting an Early Pleistocene origin for this species due to geographical isolation in Iberia during the Gelasian-Calabrian transition (Boscaini et al., 2015). In 2016, we analysed an extensive collection of fossil lynx from the latest Early Pleistocene sites of Vallparadís Estació and Cueva Victoria (E Iberia; ca. 1.0-0.8 Ma;

Boscaini et al., 2016). We proposed that *L. spelaeus* be regarded as a junior subjective synonym of *L. pardinus*, as the two taxa exhibit no significant skeletal morphological differences aside from fluctuating body size throughout the Pleistocene.

Rodríguez-Varela et al. (2015) analyzed mtDNA from fossils at Arene Candide (Savona, northwestern Italy), which had been previously attributed to *L. lynx* or *L.* cf. *spelaeus* based on their large size (Cassoli & Tagliacozzo, 1994). Molecular findings identified some specimens as *L. lynx* and others as *L. pardinus*. This marked the first direct evidence of *L. pardinus* in Italy, extending its ancient range beyond the Iberian Peninsula. In 2021 and 2023, we described better-preserved Late Pleistocene *L. pardinus* remains from Ingarano (Italy) and Avenc del Marge del Moro (NE Iberia), further documenting this species' wide distribution during the Late Pleistocene (Mecozzi et al., 2021; Tura-Poch et al., 2023). Our most recent publication also suggested changing the common name "Iberian lynx" to "Mediterranean lynx" to reflect this broader historical distribution.

Finally, Lavrov et al. (2021) published preliminary descriptions of key lynx fossils from the late Early Pleistocene of Taurida Cave (1.6 Ma; Crimea), identifying fragments of two crania as *L. issiodorensis*. However, the morphological characteristics of these remains align closely with the Mediterranean lynx. Recent re-evaluations of Early Pleistocene lynx fossils from Pirro Nord, Apollonia-1, and Le Vallonnet suggest these should be assigned to *L. pardinus* (Madurell-Malapeira et al., 2024a). These findings indicate a distribution of the Mediterranean lynx from the Iberian Peninsula to Crimea around 1.6 Ma, challenging the hypothesis of this species' origin in Iberia. Recent studies support a lineage of *L. issiodorensis*-*L. pardinus* (sensu Ficcarelli & Torre, 1977), while further investigation of the Late Pliocene-Early Pleistocene record in eastern Asia may clarify the origins of *L. lynx*, at least during the Early Pleistocene.

FOSSIL RECORD - See a review in Boscaini et al. (2016) and Mecozzi et al. (2021). Small to medium-sized felids typically classified as *Lynx issiodorensis* have been recorded in Europe since the Pliocene, at sites such as Serrat d'en Vaquer (Fig. 10a), Cuevas de Alzamora, Layna, La Calera or Vialette (Depéret, 1890; Montoya et al., 2001; Morales et al., 2003; Lacombat et al., 2008). However, the taxonomic classification of these early felines remains controversial due to the limited fossil record, which consists primarily of isolated teeth and some postcranial bones. Some authors, such as Depéret (1890) and Morales et al. (2001), have assigned the Pliocene record to the genus *Caracal*. The scarcity of European lynx-like forms from the Pliocene and the absence of complete crania prevents specific identification. Nevertheless, the examined material shows greater morphological and biometric affinities with the genus *Lynx* than with *Caracal*. Consequently, I prefer to classify all European Pliocene forms under *Lynx* sp.

Since the Late Pliocene, well-preserved specimens of *Lynx issiodorensis* have been recorded at several sites, including Perrier-Les Etouaires, Les Pardines, Saint Vallier, Olivola, Upper Valdarno, and Dmanisi (Ficcarelli & Torre, 1977; Kurtén, 1978; Pers. Observ.). According to some scholars, *L. issiodorensis* was the ancestor of both *Lynx lynx* and *Lynx pardinus* (Werdelin, 1981), with the earliest *L. pardinus* remains recorded in Taurida Cave at approximately 1.6 Ma (Lavrov et al., 2021). However, as mentioned in the previous section, the morphological characteristics of *Lynx issiodorensis* and its similarities with the Mediterranean lynx suggest a closer relationship, supporting an early divergence of *L. lynx* from the *L. issiodorensis*-*L. pardinus* lineage.

PALAEOECOLOGY AND HABITAT PREFERENCES - The ecological role and habitat preferences of *L. issiodorensis* and *L. pardinus* have remained largely unknown due to the scarcity of complete specimens. According to Kurtén (1978), in his study of *L. issiodorensis* from Les

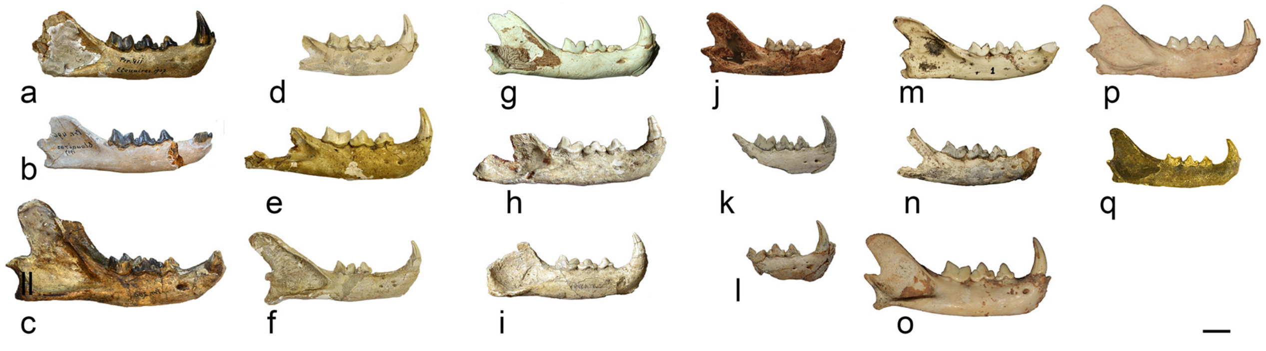

Fig. 10 (color online) - *Lynx* mandibular remains from the Pleistocene of Europe. a-j) *Lynx issiodorensis*. a) Right hemimandible from Les Etouaires (Prr411) in buccal view. b) Left hemimandible from Les Etouaires (reversed Prr492) in buccal view. c) Mandible from Les Etouaires (reversed Prr200) in right buccal view. d) Right hemimandible from St. Vallier (MC161884) in buccal view. e) Right hemimandible from St. Vallier (MC161880) in buccal view. f) Right hemimandible from St. Vallier (MC161871) in buccal view. g) Right hemimandible from La Puebla de Valverde (LPV'98-337-16) in buccal view. h) Right hemimandible from Olivola (IGF4396) in buccal view. i) Left hemimandible (reversed IGF4396) in buccal view. j) Right hemimandible from Tourkovounia-1 in buccal view. k-q) *Lynx pardinus*. k) Right partial hemimandible from Apollonia-1 (APL-14) in buccal view. l) Left hemimandible from Apollonia-1 (reversed APL-543) in buccal view. m) Right hemimandible from Cueva Victoria (IMEDEA-C9) in buccal view. n) Right hemimandible from Vallparadís Estació EVT12 (IPS60461) in buccal view. o) Right hemimandible from Ingarano (IN15NS) in buccal view. p) Right hemimandible from Ingarano (MGPT-PU-13415) in buccal view. q) Right hemimandible of *Lynx* sp. from Serrat d'en Vaquer (PP64) in buccal view. Scale bar = 2 cm.

Etouaires, this species had shorter limbs, and a stouter build appearance as compared to the modern *L. lynx*, and it likely inhabited a landscape like that of the Mediterranean lynx. Our previous studies on Early to Late Pleistocene *L. pardinus* indicated similar body proportions to the extant species, though with a variable yet generally larger body size. However, uncertainties remain regarding the habitat preferences of the Mediterranean lynx and the timeline for its dietary specialisation on lagomorphs.

*European wild cat (Fig. 11)*

European species - *Felis silvestris* Schreber, 1777.

Synonyms - *Felis ferus* De Serres, 1839; *Cattus minuta* Schmerling, 1834; *Felis lunensis* Martelli, 1906; *Felis monspesulana* Bonifay, 1971.

Chronological range - Perpignan/Serrat d'en Vaquer (ca. 3.8-3.6 Ma; France) to present.

Main sites - Perpignan/Serrat d'en Vaquer (ca. 4 Ma; France; Fig. 11c); Layna (ca. 4 Ma; Iberia); Olivola (2 Ma; Italy); Le Vallonnet (ca. 1.2 Ma; France); Montoussé 5 (late Early Pleistocene, France); Lunel-Viel (MIS 9; France); Forat de la Ruda and Avenc Sellarés (MIS 3; Iberia; Fig. 11a-b).

Key references - Depéret (1890); Forsyth-Major (1890); Martelli (1906); Kurtén (1965); Bonifay (1971); Ficcarelli & Torre (1975b, c); Clot et al. (1976).

History, taxonomy and fossil record - The fossil record of European wild cats is extremely scarce and not well understood. Several 19th Century authors, including De Serres (1839), Pomel (1853), and Bourguinat (1879), described Late Pleistocene remains. However, the first author to document remains older than the Late Pleistocene was Charles Depéret (1890) in his study of mid-Pliocene fossils from the Perpignan Basin and the Serrat d'en Vaquer site. Depéret described a corpus with p3-m1, attributing it to *Felis* aff. *maniculata* Horsfield & Vigors,

Fig. 11 (color online) - *Felis silvestris* remains from Europe. a) Cranium from Forat de la Ruda (FDR-021) in right lateral (a1) and dorsal (a2) views. b) Right hemimandible from Avenc Sellarés (SE-IPS-4262) in buccal view. c) Right hemimandible from Serrat d'en Vaquer (Pp62) in buccal (c1) and lingual (c2) views. d) Right first lower molar of "*Felis christoli*" from Sables de Montpellier (MP338) in buccal (d1) and lingual (d2) views. e) Left partial hemimandible of "*Felis christoli*" from Sables de Montpellier (MP337) in buccal view. Scale bar = 2 cm.

1829 (Fig. 11c). The morphology and measurements of this specimen closely resemble those of the extant wild cat *Felis silvestris*, making it likely the earliest record of this species in Europe. That same year, Forsyth-Major (1890) described remains from the Tuscan site of Olivola, noting the presence of a wild cat. Later, Martelli (1906) named a species, *Felis lunensis*, based on a corpus from Olivola, a classification later supported by Kurtén (1965). However, I agree with Ficcarelli & Torre (1975c) in including the Olivola corpus and additional postcranial remains within the hypodigm of *Felis silvestris*. Further fragmentary Early Pleistocene remains of wild cats were recorded at the French sites Montoussé 5 and Le Vallonnet (Clot et al., 1976; Moullé, 1992). Since the mid Middle Pleistocene, wild cat remains have been documented at various European sites, though they are generally fragmentary and scarce, such as the dental remains from Lunel-Viel (Bonifay, 1971). The only complete fossil cranium and skeleton, recently excavated from the catalan site of Forat de la Ruda (MIS 3), displays postcranial morphology and measurements fully consistent with those of the modern European wild cat (*Felis silvestris*) (Montesinos, 2024).

PALAEOECOLOGY AND HABITAT PREFERENCES - No detailed studies on the ecology and habitat preferences of fossil European wild cats were performed up to now, and their palaeobiology was always assumed equal to extant forms. The living species is a highly adaptable taxon occupying a wide range of habitats, including forests, grasslands, and shrublands. Its morphology, characterised by a robust build, sharp retractable claws, and keen senses, enables it to prey on small mammals, birds, and insects. The ecological niche of *Felis silvestris* includes areas with dense vegetation for cover and open spaces for hunting.

## DISCUSSION

### *Pliocene and Pleistocene European felid guilds*

PLIOCENE - The fossil record of Pliocene sites in Europe is remarkably scarce, with only a few notable exceptions, such as Les Sables Marins de Montpellier and various locations in the Roussillon Basin, both in France (Viret, 1939; Depéret, 1890). Additionally, some sites like Camp dels Ninots, Baza-1 or Layna, have provided insights into Early to Mid-Pliocene ecosystems (Jiménez-Moreno et al., 2012; Ros-Montoya et al., 2017; Grandi et al., 2023). Overall, the fossil record remains poor, and chronological precision is virtually absent. At these sites, remains of the genera *Dinofelis*, *Lynx*, and *Felis* were unearthed several decades ago. However, tracing evolutionary trends or conducting phylogenetic studies based on this sparse evidence is highly challenging. Most previous researchers have reconstructed the taphocenoses of these sites as tropical to subtropical environments, characterised by higher global temperatures during the *Early Pliocene Warmth*, along with greater humidity and rainfall compared to present-day conditions (Fedorov et al., 2013).

During this chronological period, the case of "*Felis*" *christoli* Gervais 1869 from Les Sables Marins de Montpellier (ca. 4.5 Ma) is particularly noteworthy and has not been previously discussed here. The material, consisting of a corpus with p3-p4 and an isolated m1 (Fig. 11d-e), is housed in the Basel Naturhistorisches Museum and was first described by Gervais (1869). Ficcarelli & Torre (1975b) provided a detailed description and comparison of these specimens with available Miocene, Pliocene and Pleistocene material. Notably, these specimens are lynx-sized rather than *Felis*-sized. While the material is too limited to support definitive interpretations, I concur with the earlier authors that it may represent a long-surviving member of the genus *Pseudaelurus* or a primitive *Lynx*. However, no further conclusions can be drawn from the existing evidence.

LATEST PLIOCENE/GELASIAN - Since ca. 3 Ma, has Europe experienced profound palaeoenvironmental transformations driven by global climatic shifts. During the late Pliocene, the relatively warm and humid conditions of the *Early Pliocene Warmth* gradually gave way to a cooler and more arid climate as the Northern Hemisphere began to experience extensive glaciation (Zachos et al., 2001). This period marks the beginning of the Pleistocene epoch, characterised by cyclical alternations of glacial and interglacial phases driven by orbital cycles (Hays et al., 1976). These climatic oscillations significantly impacted European ecosystems. Forested landscapes, which were widespread during warmer interglacial periods, contracted during glacial maxima, giving rise to open habitats such as steppe and tundra, especially in higher latitudes and altitudes (Ehlers & Gibbard, 2007). These changes also led to significant biogeographic shifts, as species migrated in response to advancing and retreating ice sheets. For example, some subtropical and tropical taxa that thrived during the Pliocene, such as members of the genus *Dinofelis*, become extremely rare went finally extinct around 2 Ma. Other felid taxa more adapted to open or mixed environments started to be recorded in Europe in several sites. These taxa include *Acinonyx pardinenis, Homotherium crenatidens* and *Viretailurus pardoides* and, slightly later, *Megantereon cultridens.* These four species became the most characteristic large felid forms in the European Early Pleistocene, being recorded since this period in a plethora of European localities, most of them unfortunately by fragmentary remains.

CALABRIAN - During the Calabrian, Europe experienced the continued expansion of ice sheets, particularly in northern regions, which had a significant impact on terrestrial environments. Extensive glaciation dominated Scandinavia, with ice sheets periodically advancing into northern Europe during glacial periods (Ehlers & Gibbard, 2007). In contrast, southern Europe maintained more temperate conditions, serving as a refuge for both plant and animal species during colder phases (Tzedakis et al., 2002). Vegetation patterns shifted dramatically in response to these climatic oscillations. Forests, which had been widespread during the Pliocene and early Gelasian, were increasingly replaced by open, steppe-like habitats during glacial periods, particularly in central and northern Europe. These open environments supported the spread of grazing herbivores such as *Bison* and *Equus*, which thrived in these conditions (Van Kolfschoten & Gibbard, 2000). In warmer interglacial phases, however, forests temporarily re-established themselves in many regions.

These environmental changes had a profound effect on faunal assemblages. The beginning of the Calabrian was marked by the continued dispersal and adaptation of early members of the genus *Homo*, whose survival and expansion were likely influenced by fluctuating environments that demanded behavioural flexibility and innovation (Lordkipanidze et al., 2013). As for the felid guild, established genera such as *Homotherium*, *Megantereon*, *Viretailurus*, *Acinonyx*, *Lynx*, and *Felis* continued to be recorded at numerous late Early Pleistocene sites. Additionally, the newcomer *Panthera toscana* made its first appearance around 2.0 Ma at sites such as Olivola and Gerakarou, further diversifying the carnivore community.

The Early-Middle Pleistocene transition - The EMPT, spanning roughly 1.2 to 0.6 Ma, marked a major reorganisation of Earth's climate system, driven by changes in orbital dynamics and their interaction with Earth's climate feedback mechanisms. Before the EMPT, the Earth's climate was primarily influenced by obliquity-driven 41 ka cycles, which dictated the extent of seasonal variations, especially in higher latitudes. These cycles influenced glacial growth and retreat in a relatively predictable manner. However, during the EMPT, a shift occurred, and climate patterns began to align more closely with eccentricity-driven or precession-driven 100 ka year cycles, which are associated with variations in the shape of Earth's orbit around the Sun. While eccentricity itself has a weaker direct influence on climate than obliquity or precession, its modulation of solar insolation combined with Earth's internal feedback mechanisms, such as ice sheet dynamics, greenhouse gas concentrations, and ocean circulation, resulted in more pronounced and prolonged glaciations.

This transition was likely influenced by the progressive build-up of large, persistent ice sheets in the Northern Hemisphere, which altered the Earth's albedo and energy balance. These ice sheets became increasingly stable and resistant to melting, leading to longer glacial periods interspersed with shorter, intense interglacials. The shift in orbital pacing also amplified climatic extremes, intensifying the environmental pressures on ecosystems. As glaciations grew longer and more severe, habitats were repeatedly fragmented, pushing species to adapt, migrate, or face extinction. During interglacials, the rapid melting of ice sheets and higher solar insolation allowed for the re-expansion of forested and temperate regions, but these periods were comparatively brief, challenging long-term ecosystem stability.

The EMPT represents a complex interplay between orbital forcing and Earth's internal feedbacks, fundamentally reshaping the planet's climate system. Its impacts on European ecosystems included a pronounced shift in vegetation patterns, with tundra and steppe dominating glacial periods and mixed forests recovering during interglacials. These changes also played a critical role in driving evolutionary adaptations, particularly among large mammals and early hominin populations, who had to navigate increasingly unpredictable and extreme environments. This epochal transition highlights the intricate links between orbital mechanics and terrestrial ecosystems, underscoring the role of astronomical cycles in shaping Earth's environmental history.

Specifically concerning the felid guild some of the long-lasting Early Pleistocene species like *Acinonyx*, *Homotherium*, *Panthera gombaszoegensis* start their decline being more poorly documented, whereas others like *Viretailurus* and *Megantereon* vanished from the continent around 1 Ma. Instead, the first record of newcomers like *Panthera fossilis* and *Panthera pardus* started at the beginning of the EMPT in sites like le Vallonnet and the Vallparadís Section (Moullé, 1992; Madurell-Malapeira et al., 2024a).

Middle to Late Pleistocene - The period from the Middle Pleistocene to the end of the Late Pleistocene was marked by significant climatic and ecological transformations across Europe, primarily driven by intensified glacial-interglacial cycles. These cycles, governed by orbital forcing (particularly the interplay of eccentricity, obliquity, and precession) shaped the structure of ecosystems and biodiversity. The dominant 100 ka cycles led to prolonged and intense glaciations, interspersed with shorter but warmer interglacial periods, resulting in a pattern of ecosystem contraction and expansion. A pivotal moment within this timeframe was the *Mid-Brunhes Transition* (MBT), occurring approximately 430 ka. This event marked a shift in the characteristics of interglacial climates, with interglacials following the MBT being significantly warmer and more prolonged compared to those that preceded it. The MBT has been attributed to changes in greenhouse gas dynamics, particularly higher levels of atmospheric $CO_2$ during interglacials, which amplified their warmth and impacted vegetation and hydrology. In Europe, the MBT had substantial ecological implications. Pre-MBT interglacials were generally cooler, supporting mixed but often fragmented forests, while post-MBT interglacials allowed for the expansion of temperate forests over broader areas. This warmer climate post-MBT fostered more stable and productive ecosystems during interglacials, promoting the proliferation of species adapted to temperate conditions. However, glacial periods remained harsh and dominated by tundra and steppe landscapes in the north, with the compression of ecosystems into southern refugia during these colder phases. The MBT also influenced the hydrological cycle, with evidence of increased precipitation variability and higher seasonality in many regions. These changes affected soil development, vegetation patterns, and the connectivity of ecosystems across Europe. The alternation between glacial and interglacial climates created a dynamic mosaic of habitats, driving evolutionary pressures and influencing species distributions (Hodell et al., 2003; Barth et al., 2018; Mitsui & Boers, 2022).

This period saw the Mediterranean region continue to act as a critical refugium during glaciations, preserving plant and animal diversity and enabling recolonisation during interglacials. The interaction between glaciations and interglacials throughout the Middle and Late Pleistocene shaped Europe's biogeographic patterns, with the *Mid-Brunhes Transition* serving as a key turning point in the ecological and climatic history of the region.

The once diverse felid guild became dominated in the Middle to Late Pleistocene basically by four species: *Panthera fossilis-spelaea, Panthera pardus, Lynx pardinus* and *Felis silvestris. Homotherium, Acinonyx* and *Panthera gombaszoegensis* were sparsely recorded during the Middle Pleistocene, becoming extinct before the Late Pleistocene. Finally, only two Asian newcomers were recorded: *Lynx lynx* with an imprecise chronology of arrival, but probably around MIS 5, and *Panthera uncia,* as discussed in previous sections.

### *Resilience and adaptability of Quaternary European felids*

I would like to highlight several key points concerning the resilience and adaptability of felids before concluding this work. First, it is essential to consider that most of the available records from Quaternary sites, particularly those dating to the Middle Pleistocene and later, originate from archaeological sites or locations frequented by hominin species. These records do not provide a complete representation of Quaternary ecosystems. Similarly, hyaena dens do not accurately reflect the composition of the original taphocenoses; instead, they represent only the carcasses transported to these caves or shelters by hyaenas.

An example supporting this observation is the recent data obtained from sedaDNA studies. These studies have recovered genetic material from numerous species that are otherwise unrepresented in the fossil record of the analysed geographical areas (e.g., Kjær et al., 2022; Gelabert et al., 2025). This emphasises the need to acknowledge that the fossil record offers only a partial glimpse of the true diversity and geographical distribution of species. While this may seem obvious, it is a critical point worth reiterating considering contemporary research. A further example is the recently published *Homotherium* mummy from Yakutia, a species virtually absent from the Eurasian fossil record during the Late Pleistocene (Lopatin et al., 2024).

Another important consideration in the palaeoecology of fossil felids is their preferred habitats. The habitats inferred from anatomical studies typically represent the most suitable environments for these species, but this does not imply that they were exclusively restricted to these areas. Felids could occupy other habitats, not only under unfavourable climatic or environmental conditions but also during periods of optimal environmental stability. Recent results from stable isotopic analysis of *Homotherium* specimens from Pirro Nord (Italy; Madurell-Malapeira et al., 2024b) provide a notable example. Based on anatomical evidence, *Homotherium* is considered a slender, long-legged felid adapted for running and hunting in open environments. Isotopic data from various studies also support this view. However, our analysis of 20 samples from different individuals at Pirro Nord suggests a population of *Homotherium* that hunted browsing species in closed, wooded habitats. This finding is surprising yet expected, as different populations of the same species may exhibit varying dietary habits depending on their environment or learned behaviours.

Finally, recent palaeopathological studies offer compelling examples of the resilience of certain felids. These studies have documented the survival of individuals with severe injuries that likely impaired their hunting abilities (e.g., Balisi et al., 2021; Luna et al., 2024; Salesa et al., 2024; Serdyuk et al., 2024; Fig. 12). Such injuries might have prompted changes in predatory behaviour or habitat preferences, diverging from those customarily inferred for their species. These findings underscore the remarkable adaptability of felids in responding to extreme challenges.

## CONCLUSIONS

The fossil record of European Pliocene and Pleistocene felids offers critical insights into the interplay between climatic changes, environmental pressures, and predator dynamics. These carnivorans adapted to shifting ecosystems shaped by glacial and interglacial cycles, demonstrating resilience and ecological versatility in response to fluctuating prey availability, habitat restructuring, and competition. Their evolutionary history reflects the broader impact of climate oscillations on biodiversity and ecosystem stability.

Palaeontological evidence highlights the importance of felids as indicators of environmental and climatic shifts. Their morphological and ecological adaptations reveal strategies for surviving periods of environmental stress, including dietary specialisation, changes in body size, and niche partitioning. Despite these adaptations, rapid climatic transitions, habitat fragmentation, and increasing human influence during the Late Pleistocene ultimately contributed to their decline, emphasising the fragility of apex predators in the face of compounded pressures.

The dynamic relationship between felids and their environments underscores the role of palaeoenvironments in shaping evolutionary trajectories. Shifts in vegetation, prey populations, and biogeographic barriers influenced the distribution and survival of carnivores across Europe. Climatic extremes, such as prolonged glacial maxima, placed additional stress on these species, underscoring the profound impact of climate change on terrestrial ecosystems.

Future research should aim to refine the understanding of palaeoenvironmental conditions and their influence on predator-prey dynamics. Integrating fossil data with advanced isotopic, genetic, and sedimentary analyses will enable more detailed reconstructions of past climates and their effects on ecosystem structures. Such studies are vital for contextualising the long-term impacts of environmental changes on biodiversity and for drawing parallels to the challenges faced by modern ecosystems under current climate trajectories.

This synthesis emphasises the importance of studying past ecosystems to better understand the resilience and vulnerabilities of carnivorans and the ecosystems they inhabit, both in the past and today.

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Fig. 12 (color online) - Palaeopathologies on Quaternary felids. a) Right humerus of *Homotherium crenatidens* from Senèze (FSL96133) in anterior view. b) Hemimandible of *Homotherium crenatidens* from Senèze (FSL210951) in left buccal view. c) Left radius of *Panthera pardus* from Grotte de la Carrière-S2 (GDC21-S2-Nv.2-P30-624) in lateral view. d-e) Lumbar vertebrae of *Homotherium crenatidens* from Pirro Nord (DST-DE11.1-SN) in lateral view. f) Right metacarpals of *Lynx pardinus* from Taurida Cave (PIN5644/341a) in anterior view. g) Left tibia and fibula of *Felis silvestris* from Avenc del Marge del Moro (MM-2451) in anterior view. Scale bar = 5 cm.

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