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Note on the taxonomy of the Pleistocene sabre-tooth felid *Homotherium* (Mammalia, Carnivora, Machairodontinae)

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Abstract

The specific nomenclature of the Pleistocene sabre-toothed felid *Homotherium* in the northern hemisphere has been a matter of contention for over a century up till the present day. Its correct taxonomy and systematics have, however, implications for our understanding of evolutionary patterns and biogeography of the genus. Here, we briefly review the literature and conclude that there existed only one intra-specifically variable species, to be called *Homotherium latidens* (Owen, 1846). It has priority over the name *H. crenatidens* (Fabrini, 1890). *H. latidens* had a wide distribution in time and space, i.e. the Early, Middle and Late Pleistocene and the northern hemisphere (Eurasia and North America). The large intra-specific morphological variation over time does not exceed that of a single population of large felines showing sexual dimorphism, supporting the long-term survival of a single species of feline top predator.

Keywords

Felidae – Homotherini – sabre-tooth cat – junior synonyms

Introduction

The discovery of a well-preserved mandible of the Late Pleistocene sabre-toothed felid *Homotherium latidens* (Owen, 1846) in the North Sea (Reumer et al., 2003) initially sparked discussions whether or not the species existed as part of the *Mammuthus-Coelodonta* faunal complex of the Weichselian glaciation (or Last Glacial Period; c. 115–11.7 ka), named after two abundant and iconic species, the woolly mammoth and woolly rhinoceros (Kahlke, 1999). Subsequent finds in Central Europe (e.g. by Varga et al., 2010) have confirmed its presence as part of this Late Pleistocene ecosystem. It is now generally accepted that sabre-toothed felids lived in Europe as late as 28 thousand years ago.

It is an as yet unresolved question whether the species went extinct in Europe after the occurrence around 300 ka recorded from Schönningen in Germany (MIS9; Serangeli et al., 2015), to be subsequently replaced by a later re-immigration from North America, or that *H. latidens* remained in Europe but below the detection threshold, being a relatively rare top-predator. The absence, as far as presently known, of *Homotherium* during later intervals (MIS8 through MIS3) as well as the proven conspecificity of *H. latidens* and North American *H. serum* (Paijmans et al., 2017) may support the former hypothesis of extinction and re-immigration. New research on the exact age and status of Late Pleistocene *Homotherium*, e.g. the Kessingland specimen (Backhouse, 1886) and the Hungarian material (Varga et al., 2010) is presently being planned (Dick

Mol, pers. comm.) and may provide new information.

However, the taxonomy of the Pleistocene Eurasian species of the machairodontine genus *Homotherium* Fabrini, 1890 has been subject to much confusion (e.g., Koufos et al., 2020). Already in 1992, Turner (1992., p. 117 and Table 5) considered all European *Homotherium* between 3.0 Myr and 0.5 Myr to be *H. latidens*. Also Galobart et al. (2003) united all late Pliocene-late Pleistocene material of Europe in the single species *H. latidens*. Antón et al. (2014) also included the Asian material, concluding that all Pleistocene Eurasian *Homotherium* fossils are more accurately grouped into a single though somewhat morphologically variable species, *H. latidens*. Phylogenetic analyses based on craniodental characters by Werdelin & Flink (2018) supported the monophyly of *Homotherium* within Machairodontinae. This might have seemed a consensual conclusion, followed by most researchers, but recently Madurell-Malapeira (2025) suggested that the species be named *H. crenatidens*. He thereby cited several synonyms, but omitted *Homotherium latidens* (Owen, 1826), increasing the confusion. He choose to neglect the type material of *H. latidens* from Kent's Cavern, "not knowing the site and stratigraphical provenance (...) albeit being valid according to the International Code of Zoological Nomenclature" (Madurell-Malapeira, 2025: 134). Here, we briefly investigate and discuss the taxonomic history of the Pleistocene Eurasian *Homotherium* in order to clarify the situation.

Results and discussion

Since the mid-nineteenth century, the number of names given to Eurasian species of the genus *Homotherium* has proliferated, but proof of consistent inter-specific differences allowing separation of taxa is lacking (Turner, 1992, 1999). An approach lumping taxa is more plausible, as it is rather unnatural to have several species of the same ultra-specialised top-predator carnivore co-existing in an ecosystem. According to Sotnikova and Titov (2009), the European fossil record includes four species of the genus *Homotherium*: *H. crenatidens* and *H. nestianus*, both with a Villafranchian age, and *H. latidens* and *H. moravicum*, both with a post-Villafranchian age. However, the intra-specific variation within *Homotherium* is large, as seen in relatively large assemblages from, for example, Untermassfeld (Germany; Hemmer, 2001) and Incarcial (Spain; Galobart et al., 2003). This large variation is probably best explained by sexual dimorphism (Serangeli et al., 2015). Koot (2008) after studying the intraspecific variation and sexual dimorphism in extant large Felidae (*Panthera leo* and *P. tigris*) came to the same conclusion when she wrote: “(...) the intraspecific variation found in lions and tigers is very similar to the variation found in the sabre-tooth cats; supporting the previous hypothesis that the genus *Homotherium* is monospecific” (see also Koot et al., 2009).

So, *H. crenatidens* and *H. latidens* are generally considered synonyms now, particularly since the revision of Antón et al. (2014) and the subsequent groundbreaking work on mitogenomics by Pajmans

et al. (2017). Antón et al. (2014) concluded: “We find no evidence to allow a species-level division within the Villafranchian-Pleistocene *Homotherium* sample from Eurasia, which for now is best classified as a single variable species, *Homotherium latidens*, but there are indications of evolution within the lineage, such as the presence of a pocketed anterior margin of the mandibular masseteric fossa, a feature found in the younger fossils of middle or late Pleistocene age but consistently absent in older specimens.” Pajmans et al. (2017) went a step further and showed the monospecificity of Eurasian *H. latidens* and North American *H. serum* on the basis of their mitochondrial DNA. Although the distribution of a carnivore species across the entirety of the northern hemisphere would be a unique situation, we consider that sufficient morphological and genomic evidence is provided to substantiate this conclusion. Thus, we cannot but conclude that *H. crenatidens* (Fabrini, 1890), *H. latidens* (Owen, 1846) and *H. serum* (Cope, 1893) are one and the same species, though somewhat morphologically variable through time and between the sexes. Of these names, *Homotherium latidens* (coined in 1846) has priority, so the two other names (published in 1890 and 1893, respectively) are junior synonyms. It is worth noting though that some authors continue to consider them separate species (e.g. Argant, 2024).

In addition, we need to spend some words on the specific epitheton *arvernensis*. Georges Cuvier, in the 1824 edition of his *Recherches sur les ossements fossiles* mentioned a large carnivore from the Valdarno in Tuscany (Italy) and provided it with the

name *cultridens*, however, without giving a formal description and without connecting it to a genus name other than to the French words 'Ours fossiles', meaning fossil bear, and thus leaving it a *nomen nudum* (Cuvier, 1824, p. 517). The first description of a true European sabre-toothed felid, found in the region Auvergne at Mont Perrier (Puy-de-Dôme, France) was provided four years later by Croizet & Jobert (1828) under the name of *Ursus cultridens arvernensis*, comparing it with Cuvier's description of the Valdarno species and naming their new species after the region, yet unfortunately retaining it in the bear genus *Ursus*. The material consisted of a typical homotherine flattened canine with a length of 165 mm and a crenulated distal or posterior border ('la dentelure du bord concave'), see Croizet & Jobert (1828: p. 191 and Planche I, fig. 6). However, the specific epitheton *arvernensis* has not been used for *Homotherium* findings ever since 1828, with only two published exceptions. Weithofer (1888) mentioned *Machairodus arvernensis*, and Kretzoi (1929) mentioned the characteristic type of canines as to belong to *H. arvernense* (see Koot, 2007; note the spelling error). A third but systematically irrelevant mention concerns *H. arvernense* in an unpublished MSc thesis (Koot, 2008). It has not been used ever since. Therefore, *H. arvernensis* (or *H. arvernense*) should be considered a *nomen oblitum*, and *H. latidens* should be considered the *nomen protectum*, as *H. latidens* has been in use ever since by more than ten authors in at least 25 works during the last 50 years (ICZN article 23.9.1.2; see also the list of synonyms and mentions presented below to prove the current usage). The epitheton *cultridens*, originally coined

by Cuvier (1824) is to be reserved for the smaller machairodontid *Megantereon cultridens*. Contrary to *Homotherium*, their sabers have unserrated distal and mesial margins, see Palmqvist et al. (2007).

Taking the wide temporal and spatial distribution of *Homotherium* into account, it should come as no surprise that this sabre-toothed felid displayed a large amount of variation as a result of adaptations to the different climates, habitats and assemblages of prey found throughout its geographical range, as well as by sexual dimorphism. This is in analogue to what we see in the tiger (*Panthera tigris*) today (Kitchener, 1999). In extant tigers, this has led to a consensus that there are (or were until recently) eight distinctive subspecies of *P. tigris*, which vary in body size, skull characters, coloration and coat pattern, and which are apparently insufficiently different to raise these subspecies to species level. Were *Homotherium* still living today, a similar situation might have occurred. In addition, similar to the case of *Homotherium*, *P. tigris* has a broad temporal distribution as well, ranging from the Early Pleistocene to today, with significant fluctuations in body size (e.g. Volmer et al., 2016).

In this study, we did not include taxa from outside the Nearctic and Palearctic realm, or geologically older (Pliocene) taxa, such as *H. ethiopicum* Arambourg, 1947 from Omo, Ethiopia (identified by multiple authors as belonging to the genus *Dinofelis*, e.g. Howell & Petter, 1976; Geraards et al., 2015), *H. problematicum* (Collings, 1972) (junior synonym *Homotherium hadarensis* Petter et Howell, 1988) from the Pliocene of Afar, Ethiopia or *Homotherium venezuelensis* Rincón, Prevosti et Parra, 2011

from the Plio-Pleistocene of El Breal de Orocuá, Venezuela, or *Epimachairodus romeri* Şenyürek, 1957 from the Pontian of Anatolia. For now, we consider these to be either valid taxa or in any case dissimilar from *H. latidens*. We also leave the Pliocene–Early Pleistocene North-American taxon *Machaerodus ischyryus* Merriam, 1905 outside our consideration. An exception is *Epimachairodus* / *Hemimachairodus zwierzyckii* from Java, Indonesia. Von Koenigswald (1934, 1974) described this material as a different taxon on the basis of an upper canine having crenulation on the posterior (mesial) edge only. It appears that also the anterior (distal) edge is crenulated, allowing us to rank this material, which Von Koenigswald (1940) considered related to ‘*Machairodus latidens*’ and ‘*Machairodus crenatidens*’ (see also Mohler, 1946), as a *Homotherium*. We therefore include it in our list of synonyms.

Systematic paleontology

Order Carnivora Bowdich, 1821
 Family Felidae Fischer von Waldheim, 1817
 Subfamily Machairodontidae Gill, 1872
 Genus *Homotherium* Fabrini, 1890
Homotherium latidens (Owen, 1846)
 (*nomen protectum*)

Selected synonyms and literature mentions

[ours fossiles] *cultridens* Cuvier, 1824 (partim): p. 517 (*nomen nudum*)
Ursus cultridens – Devèze de Chabriol et Bouillet, 1827: p. 75

Ursus cultridens arvernensis Croizet et Jobert, 1828: p. 195 (*nomen oblitum*)
Machairodus latidens Owen, 1846: p. 179, figs. 69, 70
Meganthereon latidens – Pomel, 1853: pp. 54, 56
Meganthereon cultridens – Pomel, 1853: pp. 54, 56
Meganthereon falconeri Pomel, 1853 (partim): p. 56
Machairodus sainzelli Aymard, 1854: p. 53
Machaerodus latidens – MacEney, 1859: pl. F
Drepanodon (*Machairodus*) *latidens* – Murchison, 1868: pl. 25, figs. 7, 8
Machaerodus latidens – Dawkins et al., 1878: pl. 25
Drepanodon latidens – Cope 1880: p. 847
Machairodus arvernensis – Weithofer, 1888: p. 31
Machairodus crenatidens – Weithofer, 1889: p. 65
Machairodus nestianus – Weithofer, 1889: p. 65
Machairodus (*Meganthereon*) *crenatidens* Fabrini, 1890: p. 161, pls. 5, 6
Machairodus (*Meganthereon*) *nestianus* Fabrini, 1890: p. 172, pl. 6
Machairodus (*Homotherium*) *nestianus* Fabrini, 1890: p. 176, fig. 7
Machairodus latidens – Fabrini, 1890: p. 165
Dinobastis serus Cope, 1893: p. 897
Machairodus latidens – Boule, 1901: p. 559, figs. 8, 9
Machairodus crenatidens – Boule, 1901: p. 561, fig. 10
Machairodus nestianus – Boule, 1901: p. 567
Machairodus crenatidens – Woldřich, 1917: p. 135
Machairodus latidens – Woldřich, 1917: p. 135, fig. 2

- Machairodus moravicus* Woldřich, 1917: p. 137, fig. 1
- Epimachairodus crenatidens* – Kretzoi, 1927: p. 131^o
- Machairodus boulei* Kretzoi, 1927 (acc. to Viret, 1954, p. 77)
- Machairodus* sp. – Zdansky, 1928: pp. 47, 48, pl. 4, fig. 5
- Meganthereon falconeri* – Matthew, 1929 (partim): p. 444
- Epimachairodus hungaricus* Kretzoi, 1929: p. 1293ff
- Epimachairodus boulei* – Kretzoi, 1929: ibid.
- Epimachairodus latidens* – Kretzoi, 1929: ibid.
- Epimachairodus crenatidens* – Kretzoi, 1929: ibid.
- Homotherium arvernense* – Kretzoi, 1929: ibid.
- Machairodus nihowanensis* Teilhard de Chardin et Piveteau 1930 (partim): pl. 22
- Machairodus* cf. *crenatidens* – Teilhard de Chardin et Piveteau, 1930: pl. 22, fig. 2
- Epimachairodus zwierzyckii* Von Koenigswald, 1934: p. 190, pl. 4
- Machairodus ultimus* Teilhard de Chardin, 1936: p. 9ff.
- Machairodus* (*Epimachairodus*?) *ultimus* – Teilhard de Chardin, 1939: p. 236, figs. 1–4
- Epimachairodus zwierzyckii* – Von Koenigswald, 1940: p. 57, Plate II, fig. 11.
- Epimachairodus ultimus* – Teilhard de Chardin et Leroy, 1945: p. 15
- Homotherium crenatidens* – Arambourg, 1947: pp. 439, 440
- Machairodus nestianus* – Arambourg, 1947: pp. 439, 554
- Homotherium crenatidens* – Viret, 1954: p. 78, pl. 13
- Homotherium nestianus* – Viret, 1954: p. 78
- Homotherium* cf. *latidens* – Hooijer, 1962: p. 25
- Homotherium zwierzyckii* – Kurtén, 1962: p. 101
- Homotherium crenatidens* – Kurtén, 1962: fig. 1
- Dinobastis?* *crenatidens* – Kurtén, 1962: fig. 1
- Homotherium latidens* – Kurtén, 1962: table 1
- Homotherium ultimum* – Kurtén, 1962: p. 101
- Homotherium crenatidens* – Ballesio, 1963: p. 17, pl. 1
- Dinobastis latidens* – Mawby, 1965: p. 585
- Homotherium serum* Churcher, 1966: p. 263ff
- Homotherium sainzelli* (*Epimachairodus crenatidens*) – Kurtén, 1968: p. 75
- Homotherium* (*Dinoblastis*) *latidens* – Kurtén, 1968: p. 76
- Homotherium serum* – Kurtén, 1968: p. 76
- Homotherium ultimum* – Kurtén, 1968: p. 76
- Megantereon problematicus* Collings, 1972: p. 87, fig. 1
- Hemimachairodus zwierzyckii* – Von Koenigswald, 1974: p. 267
- Homotherium ultimum* – Von Koenigswald, 1974: p. 270
- Homotherium* sp. indet. – Hendeby, 1974: p. 159
- Homotherium nestianum* – de Bonis, 1976: p. 163
- Homotherium crenatidens* – Ficarelli, 1979: pp. 21, 22, pl. 3
- Homotherium serum* – Rawn-Schatzinger et Collins, 1981: p. 15, fig. 1, 2
- Homotherium latidens* – Stuart, 1982: p. 43
- Homotherium sainzelli* – Stuart, 1982: p. 43
- Homotherium serum* – Rawn-Schatzinger, 1983: p. 49, fig. 1, 2

- Homotherium darvasicum* Sharapov, 1986: p. 69, pl. 22
- Homotherium latidens* – Antunes, 1986: p. 50
- Dinobastis serus* – Martin et al., 1988: p. 157
- Homotherium crenatidens* – Sotnikova 1989: p. 54, pls. 10, 11
- Homotherium davitasvilli* – Sotnikova 1989: p. 88
- Homotherium serum* – Rawn-Schatzinger, 1992: p. 1ff
- Homotherium serum* – Dundas, 1992: p. 10, figs. 2, 3
- Homotherium crenatidens* – Pons Moyà et Moyà Solà, 1992: p. 90
- Homotherium latidens* – Turner, 1992: p. 117
- Homotherium latidens* – Turner, 1995: p. 351
- Homotherium latidens* – Turner et Antón, 1997: p. 48
- Homotherium serum* – Turner et Antón, 1997: p. 51
- Homotherium latidens* – Antón et Galobart, 1999: figs. 3, 5–7
- Homotherium cf. crenatidens* – Bajgusheva, 2000: p. 35, fig. 5
- Homotherium crenatidens* – Koufos, 2001: p. 218
- Homotherium cf. crenatidens* – Koufos, 2001: p. 218
- Homotherium crenatidens* – Hemmer, 2001: p. 750
- Homotherium crenatidens* – Agustí et Antón, 2002: p. 226
- Homotherium latidens* – Agustí et Antón, 2002: p. 227
- Homotherium crenatidens* – Sotnikova et al., 2002: p. 386, pl. 2
- Homotherium latidens* – Reumer et al., 2003: p. 260, fig. 1
- Homotherium latidens* – Galobart et al., 2003: p. 99, pls. 1–14
- Homotherium latidens* – Antón et al., 2004: p. 960, fig. 2
- Homotherium cf. davitasvilli* – Sotnikova, 2004: pp. 199–202
- Homotherium latidens* – Antón et al., 2005: p. 1287, figs. 2–6
- Homotherium latidens* – Mol et al., 2007: p. 32 ff.
- Homotherium latidens* – Mol, 2008: p. 61
- Homotherium crenatidens* – Van Logchem et Mol, 2008: p. 3 ff
- Homotherium crenatidens* – Christiansen, 2008: fig. 2
- Homotherium serum* – Christiansen, 2008: fig. 2
- Homotherium latidens* – Arribas et Garrido, 2008: p. 267, figs. 8, 9
- Homotherium crenatidens* – Titov, 2008: p. 42, pl. 3
- Homotherium latidens* – Antón et al., 2009: p. 543, fig. 2
- Homotherium latidens* – Sotnikova et Titov, 2009: p. 48, fig. 3
- Homotherium crenatidens* – Sotnikova et Titov, 2009: p. 51
- Homotherium davitašvilli* – Sotnikova et Titov, 2009: p. 51
- Homotherium crenatidens* – Probst, 2009: p. 83
- Homotherium serum* – Probst, 2009: p. 83
- Homotherium latidens* – Probst, 2009: p. 93
- Homotherium latidens* – Varga et al., 2010: p. 271, fig. 5
- Homotherium moravicum* – Sardella et Iurino, 2012: p. 18, fig. 1
- Homotherium crenatidens* – Meachen-Samuels, 2012: table 4
- Homotherium crenatidens* – Meloro et Slater, 2012: p. 678
- Homotherium serum* – Meloro et Slater, 2012: p. 679, fig. 2

- Homotherium serum* – Widga et al., 2012: p. 549, fig. 4
- Homotherium latidens* – McFarlane et Lundberg, 2013: p. 1630
- Homotherium latidens* – Antón et al., 2014: p. 261, fig. 2
- Homotherium serum* – Antón et al., 2014: p. 265, fig. 3
- Homotherium latidens* – Barnett, 2014: pp. 20, 21, figs. 3, 4
- Homotherium crenatidens* – Barnett, 2014: p. 27
- Homotherium latidens* – Serangeli et al., 2015: p. 176, figs. 3–6
- Homotherium latidens* – Paijmans et al., 2017: p. 3334, table 1
- Homotherium crenatidens* – Diedrich et McFarlane, 2017: p. 79, figs. 2, 3
- Homotherium latidens* – Diedrich et McFarlane, 2017: pp. 78, 79, fig. 2
- Homotherium serum* – Ewald et al., 2018: p. 9, figs. 4–11
- Homotherium latidens* – Reumer et al., 2019: p. 23, fig. 1
- Homotherium latidens* – Janssens et al., 2019: p. 279, figs. 3, 4
- Homotherium* sp. – Tong et al., 2019: p. 623, fig. 3
- Homotherium latidens* – Barnett et al., 2020: p. 518
- Homotherium latidens* – Koufos et al., 2020: p. 142
- Homotherium crenatidens* – Li et al., 2021: p. 2
- Homotherium ultimum* – Li et al., 2021: p. 3, fig. 3
- Homotherium serum* – DeSantis et al., 2021: p. 2674
- Homotherium latidens* – Koufos et Tamvakis, 2022: p. 1408
- Homotherium crenatidens teilhardipive-teau* – Jiangzuo et al., 2022: p. 2758, fig. 3
- Homotherium latidens* – Antón et al., 2022: p. 2, fig. 1
- Homotherium latidens* – Verheijen et al., 2022: p. 3, fig. 37
- Homotherium latidens* – Mol et Langeveld, 2022: p. 39, figs. 8–13
- Homotherium crenatidens* – Mol et Langeveld, 2022: p. 40, fig. 5
- Homotherium latidens* – Lopatin et al., 2024: p. 6, figs. 1–7
- Homotherium latidens latidens* – Marciszak et al., 2024: p. 12
- Homotherium* sp. – Moretti et al., 2024: p. 7, table 1
- Homotherium latidens* – Chernova et al., 2025: p. 117ff
- Homotherium latidens* – Jiangzuo et al., 2025: p. 29, fig. 4
- Homotherium latidens* – Rodrigues-Oliveira et al., 2025: p. 102ff
- Homotherium crenatidens* – Madurell-Malapeira, 2025: p. 134, fig. 1
- Homotherium latidens* – Lopatin et al., 2025: p. 1, fig. 1

Conclusion

During the Pleistocene only one species of the machairodontine felid genus *Homotherium* lived in the northern hemisphere: *Homotherium latidens* (Owen, 1846). It shows large intraspecific variation, partly due to sexual dimorphism among other reasons. Other given names, especially the widely used *H. crenatidens* (Fabrini, 1890) and *H. serum* (Cope, 1893) are junior synonyms. In addition, we conclude that *Homotherium latidens* is a *nomen protectum*, while the only rarely used *H. arvernensis* or *H. arvernense* (Cuvier, 1824) should be considered a *nomen oblitum*.

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