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The Plio-Pleistocene scimitar-toothed felid genus *Homotherium* Fabrini, 1890 (Machairodontinae, Homotherini): diversity, palaeogeography and taxonomic implications

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ABSTRACT

The systematics of the Plio-Pleistocene scimitar toothed felid *Homotherium* have remained problematic after more than a century of fossil findings in Eurasia, Africa and the Americas. Ranging in age between around 4 million and 10,000 years, fossils of this genus display considerable variation, but the distribution of that variation has largely failed to fit a consistent pattern that would allow a clear distinction between species, especially in the Eurasiatic record. The study of undescribed mandibular and cranial fossils of *Homotherium* from Pleistocene sites in Spain and Alaska provides new insights into the morphological variability within this widespread genus. The results of our study and comparison of the new material with the published fossils of *Homotherium* confirm the difficulty in dividing the sample into clear-cut species. The new mandible from Incarcal (Spain) shows in a more dramatic way than before how the sample from that Spanish site encompasses the range of variability observed in the Villafranchian and Pleistocene Eurasiatic record, while older, possibly Ruscinian fossils of *Homotherium* from East Europe display less reduced lower premolars and probably correspond to a different species. The Alaskan fossils, on the other hand, add to the variability in mandibular and cranial morphology of the late Pleistocene North American record. 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. A comparable pattern is found in the American record, where the same mandibular feature is observed in late Pleistocene fossils, although in that continent the "primitive" features of some older *Homotherium* fossils of Blancan (Pliocene) age are consistent enough to justify their classification in a separate species, *Homotherium ischyrus*. Only the finding of more complete cranial fossils of middle and late Pleistocene age will reveal if there are additional morphological features (besides the pocketing of the masseteric fossa) that could one day allow the separation of younger populations from those of Late Pliocene and Early Pleistocene age.

1. Introduction

Homotherium is a genus of lion-sized, highly successful Plio-Pleistocene sabre-toothed felids, and it was the last member of the long-lived machairodontine tribe Homotherini. Traditionally it has been known from many localities in Africa, Eurasia and North America, but in recent years there have been unquestionable records from South America, making *Homotherium* the most widespread machairodontine genus known to date (Turner and Antón, 1997; Antón et al., 2005; Rincón et al., 2011). In spite of its wide distribution and a relatively rich fossil record, with several complete skulls and almost complete skeletons, the specific and sometimes even the generic status of many *Homotherium* fossils have remained problematic (Sardella and Iurino, 2012).

In morphological terms, *Homotherium* differs from earlier homotherins such as *Amphimachairodus* in the following traits: proportionally larger upper and lower incisors, which are arranged in a more pronounced arch; reduced diastema between I3 and C;

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more laterally compressed C; absence of P2 and p2; P3 and p3 greatly reduced; proportionally larger P4 and m1; very reduced or absent ectostyle on P4; relatively larger orbit; reduced infraorbital foramen; reduced masseteric fossa in the skull; reduced jugular process; reduced distance between c and p4; overall much shorter mandible relative to the length of the m1; more convex rostral surface of the mandibular symphysis; relatively smaller coronoid process in the mandible.

The first fossils of *Homotherium* known to modern science were a collection of teeth found in the British cave of Kents Cavern, and described in 1846 by Owen under the name *Machairodus latidens*. In 1890 Fabrini set to study the Villafranchian (a European stage spanning from around 3.5 Ma to about 1.0–1.1 Ma) machairodonts of Tuscany (Italy) and coined the generic name *Homotherium* for the two larger species he recognised there, which he named *Homotherium crenatidens* and *Homotherium nestianum*. But Fabrini's name was hardly used until Arambourg (1947) applied it to specimens discovered in Ethiopia, and then Viret (1954) used it for fossils from the French site of Saint Vallier, further proposing to synonymize much of the Villafranchian material from Europe under *H. crenatidens*. During the 20th century, the taxonomic history of *Homotherium* has been very complex, with new species being named on the basis of subtle, often invalid differences in dental morphology and size.

Current views tend to recognise a single variable species, *Homotherium latidens*, in the Plio-Pleistocene of Eurasia (Antón et al., 2005, 2009). Turner (1999) argued that the differences that led Ficcarelli (1979) to retain *H. crenatidens* and *H. latidens* as different species, namely the smaller size and slightly different upper canines of the latter, were simply invalid. This view is also largely supported by the fact that much of the variability observed in the skulls and dentitions of fossils from different ages and sites is also found within the sample of one single locality, the Spanish early Pleistocene fossil site of Incarcal (Galobart et al., 2003). Older fossils from the Pliocene of Eastern Europe, including those from the Odessa Catacombs, display relatively unreduced lower premolars (Sotnikova et al., 2002), and they probably represent a distinct, comparatively primitive species of *Homotherium*. Sotnikova (2004) has classified the Odessa material as *Homotherium* cf. *davitasvilii*, thus assuming a close relationship with a species created by Vekua (1972) for a fragmentary sample of fossils found at the Georgian site of Kvabebi, a relationship that is discussed further below. Further east, in Tajikistan, a sample of *Homotherium* skulls, mandibles and postcranial were described by Sotnikova (1988) and ascribed to *H. crenatidens* on the basis of similarities with the material from the classic Villafranchian site of Senèze (France). These fossils represent a link between Asian, European and African populations of *Homotherium*. The abundant *Homotherium* fossils from China have mostly been attributed to the European Villafranchian species (Qiu et al., 2004), but Teilhard de Chardin (1936) created the species *Homotherium ultimus* for fossils with advanced features from the Middle Pleistocene site of Zhoukoudian. North American members of the genus are usually classified within several species, two of which appear to be more strongly supported: *Homotherium ischyrus*, from several Pliocene and early Pleistocene localities, and *Homotheriumserum*, from late Pleistocene sites (Churcher, 1966; Martin et al., 2011). A new species, *Homotherium venezuelensis*, has been proposed for the material described from the Pleistocene of Venezuela (Rincón et al., 2011). The fossil record of *Homotherium* in Africa consists of generally fragmentary material, which has been ascribed to separate species such as *Homotherium problematicus* Collings, 1972 and *Homotherium hadarensis* Petter and Howell, 1988. Turner (1990) questioned the validity of those species that in his view were indistinguishable from European material classified as *H. crenatidens* (a species that he would later consider as synonym of *H. latidens*) (Turner, 1999). More recently, all the African *Homotherium* fossils are usually cited as *Homotherium* sp. in view of the difficulties in making a species level determination (Werdelin and Lewis, 2005; Werdelin and Sardella, 2006).

The above review of *Homotherium* species reflects a conservative estimate of the diversity within the genus, and some specialists have remained convinced that there must have been more species, given its enormous geographical and temporal range, especially in the Old World. Unfortunately the incompleteness of the fossil record makes it difficult to define in a satisfactory way the morphology of each population. For instance, while there are several complete skulls from the Villafranchian and early Pleistocene of Europe (including the specimens from Perrier, Senèze and Incarcal), the material from the middle and late Pleistocene is restricted to teeth, mandibles and isolated postcranial fossils. This situation makes it impossible to compare relevant anatomical features among all samples, and as a result it is inevitable that disagreement remains about the classification. The "splitter view" of *Homotherium* classification recognises at least 3 species in the Old World, with *H. crenatidens* and *H. nestianum* being older and supposedly larger, while *H. latidens* is seen as a smaller species typical of the middle and late Pleistocene (Qiu et al., 2004). In North America the "splitter view" recognises up to 5 species: *Homotherium idahoensis*, *Homotherium johnstoni*, *H. ischyrus*, *Homotherium crusafonti*, and *H. serum* (Martin et al., 2011).

In this paper we set out to make a comparison of the craniodental morphology of *Homotherium* from the Old and New World, with special consideration to some previously undescribed, well preserved fossils from Spain and the USA. Combining our own direct observations with the published descriptions of *Homotherium* fossils from other localities, we attempt to provide an updated review of morphological variation and its implications for the taxonomy and paleogeography of this most successful of machairodontines.

2. Material and methods

2.1. Material

The new fossils of *Homotherium* described in this paper come from several localities near Fairbanks in Alaska (USA) and the locality of Incarcal (Gerona, Spain), Those from Alaska are housed at the collections of the American Museum of Natural History (New York, USA) and labelled with F:AM (Frick Collection, American Mammals). Those from Incarcal are stored at the collections of the Museu Comarcal de Banyoles (Girona, Spain), and labelled with the acronym IN (Incarcal) followed by a roman number indicating the referred karst cavity.

The Incarcal site is located in the lacustrine basin of Banyoles–Besalu (north-eastern Spain) and it is a complex of isochronic fossiliferous karst infilling developed on a Pliocene lacustrine limestone formation. Several localities have been described at Incarcal, from Incarcal I to Incarcal VI, but no differences in faunal composition have been detected between them. Three of these fillings (Incarcal I, II, and V) have yielded the majority of the faunal remains, while the others have a much lower fossiliferous richness (Antón and Galobart, 1999). The site complex has been dated as Late Villafranchian in the basis of the macro and microvertebrate fauna (Agustí and Galobart, 2003).

The Alaskan material described here was obtained during salvage operations carried over the years 1934 to late 1950s, paid for by Childs Frick of the American Museum of Natural History (New York, USA) during active gold-placer mining in the Cripple Creek area by the Fairbanks Exploration Company. The specimens