

Phylogeny of the sabertoothed felids (Carnivora: Felidae: Machairodontinae)

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Abstract

In recent years, advances in our understanding of feline relationships have cast light on their evolutionary history. In contrast, there have been no phylogenetic analyses on machairodont felids, making it difficult to develop an evolutionary hypothesis based on the recent surge of studies on their craniomandibular morphology and functional anatomy. In this paper, I provide the first phylogenetic hypothesis of machairodont relationships based on 50 craniomandibular and dental characters from a wide range of sabercats spanning more 11 Myr. Exact searches produced 19 most-parsimonious trees, and a strict consensus was well resolved. The Machairodontinae comprise a number of basal taxa (*Promeganteron*, *Machairodus*, *Nimravides*, *Dinofelis*, *Metailurus*) and a well-supported clade of primarily Plio-Pleistocene taxa (*Meganteron*, *Smilodon*, *Amphimachairodus*, *Homotherium*, *Xenosmilus*) for which the name *Eumachairodontia taxon novum* is proposed. Previous phenetic grouping of machairodont taxa into three distinct groups, the Smilodontini, Homotherini and Metailurini, was not supported by cladistic parsimony analysis, and forcing monophyly of these groups was significantly incompatible with character distribution. Machairodonts as a clade are not characterized by sabertooth, i.e. hypertrophied, blade-like upper canines, but by small lower canines, as well as small M¹; and large P³ parastyle. True sabertooth arose later and are a synapomorphy of the *Eumachairodontia*.

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The carnivoran family Felidae is traditionally considered to consist of a number of basal taxa from the Oligocene–Early Miocene, such as *Proailurus lemanensis* and *Pseudaelurus*, and a few less well known forms such as *Stenogale* (Turner and Antón, 1997; Hunt, 1998; Rothwell, 2001), branching out into two major clades: the Felinae, or conical-toothed cats, to which all extant species belong; and the extinct Machairodontinae, in which most known species were sabertoothed to a greater or lesser extent (Turner and Antón, 1997; Werdelin et al., 2010). The sabertoothed felids were a widespread and morphologically diverse group of medium-sized to large predators throughout the Miocene–Late Pleistocene across North and South America, Eurasia and Africa (Emerson and Radinsky, 1980; Radinsky and Emerson, 1982; Turner and

Antón, 1997; Martin, 1998; Werdelin et al., 2010). Throughout much of their evolutionary history sabercats appear to have been more numerous than conical-toothed felids, and thus undoubtedly constituted an important part of large predator diversity. Although a wide variety of machairodont taxa have been described, most often based on craniodental material, the majority of taxa are fragmentary and may have suffered post mortem damage, making taxonomic inferences difficult. Additionally, the distinct morphological heterogeneity within several traditionally recognized genera, such as *Machairodus* (Beaumont, 1978; Sotnikova, 1992; Geraads et al., 2004), gives reason to suspect that they may not be monophyletic, as no synapomorphies other than a superficial resemblance of the upper canines are usually presented.

Morphologically, the crania and mandibles of the Plio-Pleistocene sabercats, such as *Homotherium* or *Smilodon*, differ markedly from those of extant felids

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in a large number of respects (e.g. Emerson and Radinsky, 1980; Turner and Antón, 1997; Christiansen, 2006). Analyses of craniomandibular, dental and cervical morphology indicates that they constituted a different type of predator ecomorph not present in extant ecosystems, which was constrained to large-prey predation using a shearing bite and where cranial depression played a crucial part in prey capture, unlike any extant carnivore (Akersten, 1985; Duckler, 1997; Salesa et al., 2005; Therrien, 2005; McHenry et al., 2007; Christiansen, 2008b,e, 2011; Slater and Van Valkenburgh, 2008). Other studies have focused on the early evolution of sabercats through new discoveries of early taxa which were previously poorly known (e.g. Antón et al., 2004a; Salesa et al., 2005, 2006; Christiansen, 2006, 2008a).

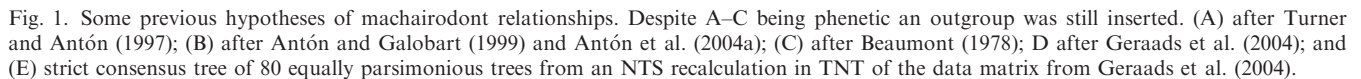
In recent years, cladistic analyses have provided major advances in our understanding of the phylogenetic relationships and evolutionary history of extant felids (e.g. Collier and O'Brien, 1985; Salles, 1992; Johnson and O'Brien, 1997; Mattern and McLennan, 2000; Johnson et al., 2006). In contrast, hypotheses of the evolutionary history of the sabertoothed felids have been tentative, and presently their evolutionary interrelationships are not well understood, as a cladistic hypothesis has not previously been attempted. Previous hypotheses of machairodont relationships have with few exceptions been phenetic (Fig. 1), and are most commonly based on overall similarity or the presence of certain features among several taxa, purportedly key characters such as the shape of the upper canine, C^1 , or the morphology of the mandible. The lack of a cladistic hypothesis for sabercat phylogeny is a serious problem for understanding their evolutionary radiation. This only becomes exacerbated with the recent surge of increasingly sophisticated morphological analyses of craniomandibular shape and inferred functional morphology and muscle mechanics. Without a phylogenetic framework to underscore the wealth of novel information, the evolutionary history and the selective hypotheses governing craniomandibular evolution of this group of unusual predators remains tentative.

A pioneering study by Berta and Galiano (1983) represented one of the first attempts to produce a phylogenetic hypothesis of sabercat relationships according to cladistic principles. Pre-dating available cladistic computer programs, it was fitted by hand and the authors only analysed *Megantereon* and its relationship to *Smilodon*. Geraads et al. (2004) made a phylogenetic analysis, but did not state which algorithms or which program were used for analysis; as outgroups they used two hypothetical taxa with inferred ancestral states but it was not explained how these were derived. Their analysis focused on specimens assigned to the *Machairodus* group, although it

included other genera as well, such as *Homotherium* and presumably *Megantereon* (Fig. 1D). Recalculation of their data matrix (New Technology Search in the program TNT; retaining 500 trees; 857 178 073 rearrangements; all multistate characters additive) failed to capture the reported topology, and resulted in a tree of 85 steps not 87, as reported. Also the recalculated analysis did not find only a single shortest tree, as reported, but 80, of which a strict (Nelsen) consensus is shown in Fig. 1E; this tree is substantially different from the reported one. Branch supports were extremely poor, as indicated by bootstrapping, jack-knifing and symmetric resampling analyses, and nearly 50% of the characters in the data matrix (381 of 770) were unknown. Recently, Rincón et al. (2011) depicted a phylogeny, the derivation of which also was unexplained but which did not appear to have been based on parsimony analysis.

Traditionally, three groups of sabercats are phenetically inferred (e.g. Beaumont, 1964; Martin, 1980, 1998; Kurtén and Werdelin, 1990; Turner and Antón, 1997; Sardella, 1998; Antón and Galobart, 1999; Werdelin et al., 2010; Rincón et al., 2011): the Homotherini, or scimitar-toothed cats, comprising *Machairodus*, the two most well-known species of which are *M. aphanistus* and *M. giganteus*, and *Homotherium*; and the Smilodontini, or dirk-toothed cats (*Paramachairodus* [see below], *Megantereon* and *Smilodon*). The third group, Metailurini, is then thought to comprise a number of other taxa, which cannot be incorporated into either of the first two groups, of which the two most well-known genera are *Metailurus* and *Dinofelis* (see Fig. 1). The recent discovery of *Xenosmilus* (Martin et al., 2000) expanded the Homotherini, adding a new taxon with postcranial characters reminiscent of those of smilodontines. Berta and Galiano (1983) assigned Beaumont's (1964) term Machairodontini to the Homotherini, and also included *Nimravides* within it (see also Fig. 1B). In contrast, Berta and Galiano (1983) assigned *Paramachairodus* ("*Pontosmilus*") to the Metailurini. Werdelin et al. (2010) questioned whether *Nimravides* should be included in the Machairodontinae at all.

The fossil record of sabercats is very uneven, and some taxa are enormously abundant, such as the Pleistocene *Smilodon fatalis*, primarily known from many hundreds of specimens from the Late Pleistocene Californian La Brea tar seeps (Miller, 1968; Duckler, 1997; McCall et al., 2003; Carbone et al., 2009). Its close relative *S. populator* from the plains of the South American Pleistocene is known from far fewer specimens, but often these are quite complete, and are sometimes represented as partial or nearly complete skeletons (Zapfe, 1956; Kurtén and Werdelin, 1990; Turner and Antón, 1997). In contrast, other species are known from only a single or very few specimens, such as several species of *Dinofelis* (Werdelin and



Basal sabercats have been known to science for well over a century, but only recently have Late Miocene deposits in Spain resulted in the discovery of near complete and often well-preserved crania, mandibles and abundant postcranial material of *Paramachairodus ogygia* (Salesa et al., 2005, 2006; but see below) and *Machairodus aphanistus* (Antón et al., 2004a), enhancing our knowledge of these species (e.g. Antón et al., 2004b; Salesa et al., 2005; Christiansen, 2007, 2008a,e, 2011). This patchy fossil record poses severe limitations for character analysis, and postcranial material is

known from too few taxa and is often too incomplete to be of value in a systematic evaluation of the entire Machairodontinae. In this paper, I provide the first cladistic hypothesis of the relationships of machairodont felids based on craniomandibular and dental morphology, and discuss the functional and evolutionary implications of the resulting phylogeny.

Materials and methods

Craniodental characters were analysed in a wide variety of sabercats spanning most of the known temporal occurrence, a period in excess of 11 Myr from the Late Miocene through to the latest Pleistocene. The database encompasses most of the morphological diversity of the Machairodontinae, comprising 18 ingroup taxa (*Machairodus* [*Amphimachairodus*] *giganteus*; *Dinofelis barlowi*, *D. cristata* (= *D. “abeli”*; see Werdelin and Lewis, 2001) and *D. petteri*; *Homotherium crenatidens*, *H. latidens* and *H. serum*; *Machairodus aphanistus*; *Megantereon cultridens*, *M. nihowanensis* and *M. whitei*; *Metailurus major*, *M. parvulus*; *Nimravides pedionomus* (supplemented by literature data of *N. thinobates*); *Paramachairodus ogygia* (see below); *Smilodon fatalis*, *S. populator*; and *Xenosmilus hodsonae*; see Appendix 1). Data were examined from a wide array of museums worldwide (Appendix 1) and supplemented with cast specimens from the author's own personal collection, as well as literature data. The incorporated specimens of the important basal taxon “*Paramachairodus*” *ogygia* were from the fossiliferously rich, Late Miocene carnivore trap at Batallones-1, Spain (Salesa et al., 2005; Christiansen, 2008a). However, a recent revision of the genus concluded that the Spanish finds differ from the other species of *Paramachairodus*, *P. orientalis* and *P. maximiliani*, causing the authors to propose reassignment of the Batallones-1 material to *Promegantereon* (Salesa et al., 2010). This name is adopted here.

As successive outgroups I used the Early Miocene felid *Pseudaelurus*; an extant ailuroid, the fossa (*Cryptoprocta ferox*); a Late Eocene–Early Oligocene saber-toothed nimravid, *Dinictis felina*; and a representative of the Caniformia, the extant grey wolf (*Canis lupus*). *Cryptoprocta ferox* is a medium-sized, felid-like predator belonging to a lineage that is believed to be between 18 and 24 million years old (Yoder et al., 2003). Its skull, in particular, appears superficially felid-like, despite supernumerary dentition relative to most felids, causing some earlier scholars to place it within the Felidae (Beaumont, 1964; Thenius, 1967; Hemmer, 1978); Beaumont (1964) even suggested that *Cryptoprocta* might be an extant descendant of *Proailurus*. Current hypotheses favour a viverrid (euplerid) status of *C. ferox* (Gaubert et al., 2005; see also Veron and Catzeflis, 1993).

A total of 50 morphological (“discrete”) and morphometric characters from the cranium, mandible, and upper and lower dentition were scored on the analysed terminal taxa (Appendices 2 and 3). The character list is also available from MorphoBank (Project 681) (O’Leary and Kaufman, 2012). Definition of character states, in particular morphometric characters, remains a much debated subject in phylogeny. Morphometric characters are sometimes rejected as useful owing to the notion that they display continuous variation, making character delimitation rather arbitrary (Pimentel and Riggins, 1987; Cranston and Humphries, 1988; Cox and Urbatsch, 1990), although methods such as division of ranges and application of standard error differences have been formulated (Goloboff et al., 2006). Other systematists are of the opinion that no formal difference exists between what is called discrete and morphometric characters, and purported discrete characters in many cases simply constitute a less explicit way of delimitating what are obviously morphometric variables (Thiele, 1993; Fink and Zelditch, 1995; Zelditch et al., 1995, 2000; Poe and Wiens, 2000). The latter is the case when formulating characters that incorporate any sort of size variable, which often occurs in so-called discrete characters. Even typical discrete characters, such as presence/absence, can be morphometric and/or more simplified than traditional morphometric characters, in that presence reveals little, if anything, about size and shape (Poe and Wiens, 2000).

However, formulation of simple presence/absence characters is rarely feasible for phylogenetically narrow groups, as concluded by Macleod (2002). Even classic presence/absence characters, such as the presence or absence of particular bones, is sometimes subject to intraspecific variation (Hilton and Bemis, 1999), and thus incorporate a proportion component. Thiele (1993) noted that morphometric characters are often prone to less arbitrary coding than purported discrete characters, as the former are testable by statistical methods. As such, morphological characters incorporating a size component were expressed as morphometric characters in the current study to formulate an explicit distinction between character states. Standard gap coding using non-overlapping variables was employed (Mickevitch and Johnson, 1976; Archie, 1985). However, intraspecific variation must be expected to be present in ratio-variables, but as noted, many sabercats are represented by only a few or even a single individual. Obviously, the scarcity of many sabercat species imposes restrictions on method and approach (see Goloboff et al., 2006).

Cladistic parsimony analyses were carried out in the program TNT (Tree Analysis using New Technology; Goloboff et al., 2003a, 2008), and the size of

the dataset allowed exact searches to be made under the implicit enumeration algorithm. No character weighting schemes were employed and all multistate characters were analytically treated as non-additive. From an evolutionary perspective it may be argued that several characters are probably additive in evolutionary terms. For instance, the transition from a large, multicuspid protocone to no protocone at all, as in character 7 (P^4 protocone; see Appendix 2), may be inferred to have progressed through a gradual reduction in protocone size and morphological simplification. Nonetheless, non-additive data were used to minimize evolutionary inferences and also to minimize interference of evaluation of branch stability, as noted below.

The advantages and disadvantages of using one or the other of the various methods of branch support and stability have been a subject of debate (e.g. DeBry, 2001; Siddall, 2002; Giribet, 2003), and, accordingly, several approaches were used in the current study. Branch support and stability are logically different (Goloboff et al., 2003b; Brower, 2006, 2010) as support for a given branch is a measure of the net amount of evidence favouring the appearance of that branch in the most-parsimonious topology, whereas stability is the persistence of a given branch when characters and/or taxa are being added, removed, or re-weighted, as in bootstrap or jack-knife analysis. Branch stability was evaluated through three methods of resampling: bootstrapping, jack-knifing and symmetric resampling. Bootstrapping and jack-knifing are standard approaches for measuring branch stability, but bootstrapping results may be affected by uninformative characters and characters not informative for the monophyly of a given group. Bootstrapping and jack-knifing may be affected by character weights and transformation cost, such as making multistate characters additive; symmetric resampling should not be affected by such potential noise (Goloboff et al., 2003a). Branch support was evaluated with decay analysis, traditionally called Bremer support (Bremer, 1988, 1994).

As noted above, a non-cladistic grouping of certain sabercats into three discrete supposedly monophyletic units, the *Metailurini*, the *Homotherini* and the *Smilodontini*, is traditionally inferred. To test this proposal, monophyly of these groups were enforced and the resulting tree topologies were statistically compared with the most-parsimonious tree topology derived from cladistic parsimony analysis through Templeton's Test (Templeton, 1983; Larson, 1994). This is a two-sample non-parametric test for determination of whether a character matrix is statistically significantly incompatible with an alternative tree topology under the null hypothesis (H_0) that the matrix is equally likely to support both topologies.

Results

An exact search using the implicit enumeration algorithm of TNT yielded 19 equally parsimonious trees with a length of 117 steps; a strict (Nelsen) consensus tree indicated that topological ambiguity is not uniformly distributed and some clades are very well supported and resolved; ambiguity centres around the mutual interrelationships of some of the basal taxa, where *Promegantereon*, *Machairodus* and *Nimravides* form an unresolved stemgroup to *Dinofelis*, *Metailurus* and the eumachairodont sabercats (Fig. 2).

The sabercats (*Machairodontinae*) are a monophyletic group with rather low branch stability, united by the following unambiguous synapomorphies: small C_1 ; very small, knob-like M^1 ; and a large P^3 parastyle (Fig. 2). In the basal *Promegantereon*, some specimens have a rather small P^3 parastyle, but in others it is large, as in other sabercats, including other basal taxa such as *Machairodus* and *Nimravides*. The traditionally inferred (typological) definition of sabercats as felids possessing hypertrophied, knife-like upper canines is not a machairodont apomorphy, and among extant felids, clouded leopards (*Neofelis*), in particular the species *N. diardi* from the Sunda Islands, may have upper canines which are relatively as large and lateromedially flattened as the basal machairodonts, e.g. *Promegantereon* and *Machairodus* (Christiansen, 2006, 2007, 2008b). The small lower canine, however, is a true machairodont apomorphy upon which some authors have placed great emphasis (e.g. Werdelin et al., 2010), and not even *Neofelis* has this trait. The somewhat enlarged, flattened (as opposed to conical-shaped in cross-section, as in most extant felids except the clouded leopards) upper canine is present in several stem-group felids as well, such as *Proailurus* and some species of *Pseudaelurus* (Fig. 3), and the true sabertooth is an apomorphy of a less inclusive taxon, the Eumachairodontia, as noted below.

Nimravides is found to be a basal machairodont, in line with traditional interpretation of the taxon, and not congruent with hypotheses that it is outside the *Machairodontinae* (Werdelin et al., 2010); it has all the synapomorphies of the *Machairodontinae*. *Dinofelis* is found not to be monophyletic, whereas *Metailurus* is monophyletic and it is supported by the following synapomorphies (4 [0, reversal]), rather large lower canine; and (18 [2]), absence of P^2 ; this is convergent with *Homotherium*, *Xenosmilus*, *Smilodon* and *Megantereon whitei*. The sabercat taxa *Amphimachairodus*, *Homotherium*, *Megantereon*, *Smilodon* and *Xenosmilus* are united by a whole suite of synapomorphies and their monophyly is strongly supported with high branch stability and support (Fig. 2, node 6). For this reason a new taxon is proposed, the Eumachairodontia ("true sabercats"), in reference to members of this

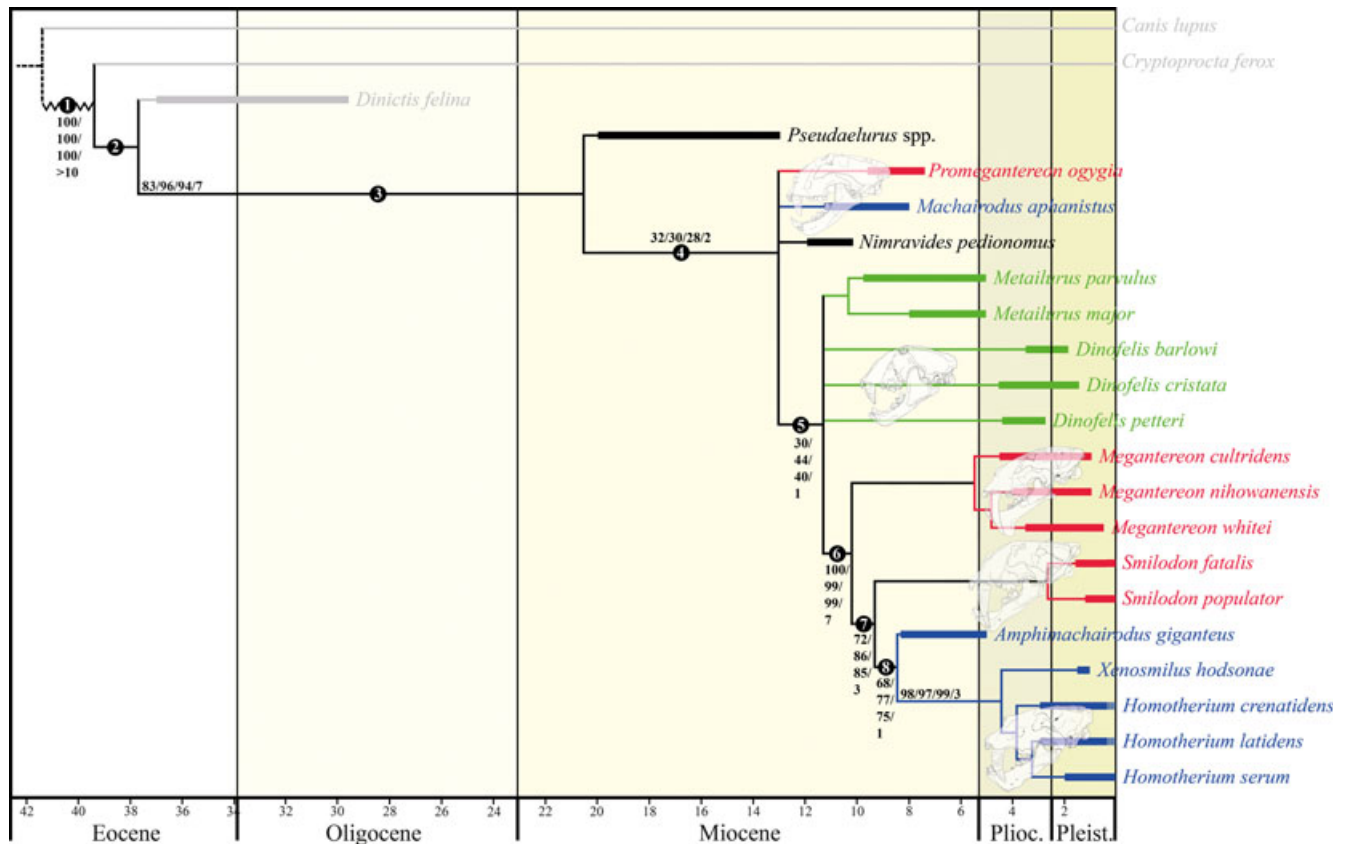


Fig. 2. A strict consensus tree of 19 equally parsimonious trees of sabercat phylogenetic relationships derived from an exact search (implicit enumeration) in the program TNT (L: 117; CI: 59; RI: 83). Traditionally inferred groups are drawn in red (Smilodontini); blue (Homotherini); and green (Metailurini). Values denote bootstrap/jack-knife/symmetric resampling (100 replications)/and Bremer Support. Thick bars denote the approximate temporal occurrence of the taxon, and thin bars denote the inferred temporal occurrence based on other fossil finds not included in the current study (see Kurtén, 1968; Turner and Antón, 1997; Andersson, 1998; Martin, 1998; Rothwell, 2001; Werdelin and Lewis, 2001; Antón et al., 2004a; Palmquist et al., 2007; Salesa et al., 2010; Werdelin et al., 2010). Nodes and synapomorphies denote: 1, Aeluroidea: 1[1]; 5[1]; 6[1]; 9[1]; 12[1]; 13[1]; 19[1]; 20[1]; 22[1]; 26[1]; 27[1]; 31[1]; 32[1]; 33[1]; 36[1]; 40[1]; 43[1]; 2, *Dinictis* + Felidae: 2[1]; 11[1]; 18[1]; 29[1]; 35[1]; 3, Felidae: 1[2]; 17[1]; 23[1]; 24[1]; 38[1]; 39[1]; 49[1]; 50[1]; 4, Machairodontinae 4[1]; 6[2]; 16[1]; 5, 8[1]; 28[1]; 44[1]; 6, Eumachairodontia (*taxon novum*): 2 [2/3]; 4[2]; 7[2]; 14[1]; 25[1]; 34[1]; 35[2]; 38[0]; 46[1]; 47[1]; 48[1]; 7, *Smilodon* + Homotherini: 3[1]; 9[2]; 11[2]; 15[1]; 42[1]; 8, Homotherini: 1[0]; 2 [2]; 3[2]; 11[0]; 37[1].

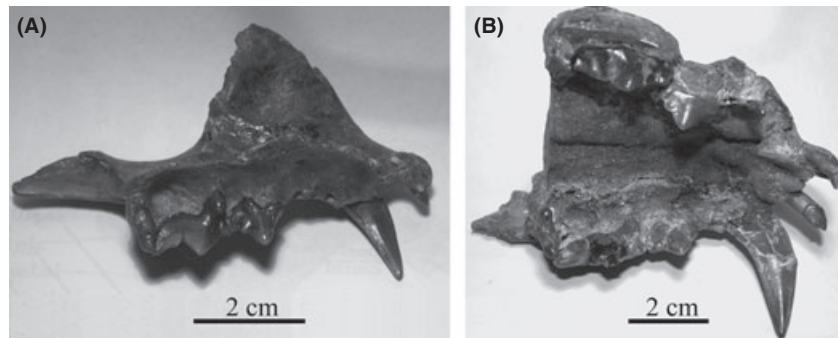


Fig. 3. Slightly to somewhat enlarged (relative to most extant felids), lateromedially flattened upper canines was a common feature of several stem-group felids, such as these premaxillae–maxillae of (A) *Proailurus lemanensis* (Late Oligocene); and (B) *Pseudaelurus quadridentatus* (Early Miocene) clearly show (ventromedial views), and this was also present in basal sabercats and in basal extant pantherines (*Neofelis*). True saber-teeth came later in sabercat evolution. Note the large, transversely situated M^1 in both species.

taxon possessing greatly hypertrophied, flattened upper canines well beyond the size of any of the felines. These, then, are the true sabertoothed felids.

Cladistic parsimony analysis failed to recover the traditionally inferred groups of Smilodontini (*Promegantereon*, *Megantereon*, *Smilodon*) and Homotherini (*Machairodus*, *Amphimachairodus*, *Homotherium*, *Xenosmilus*). Forcing monophyly of those two groups resulted in much longer trees (Smilodontini, 140 steps; Homotherini, 137 steps), both of which are significantly less parsimonious (Templeton's test: Smilodontini: $P < 0.001$; Homotherini: $P < 0.001$). The genus *Machairodus* is traditionally inferred to encompass the Miocene species *M. aphanistus* as well as the Mio-Pliocene *M. giganteus* from the Turolian (e.g. Turner and Antón, 1997; Rincón et al., 2011); however, the two do not form a monophyletic group, and the previously proposed genus name of *Amphimachairodus* (Kretzoi, 1929; Beaumont, 1975, 1978) is to be adopted for the latter species, as also concluded by Werdelin et al. (2010). The traditionally inferred taxon Metailurini (*Metailurus*, *Dinofelis*) was also not recovered and forcing monophyly of this taxon is significantly less parsimonious (127 steps; $P = 0.025$). Rather, the taxa in the "Metailurini" appear to form an unresolved stem-group to the Eumachairodontia.

The Homotherini is best redefined as the taxa *Amphimachairodus*, *Homotherium* and *Xenosmilus* without *Machairodus aphanistus*, as also concluded by Werdelin et al. (2010). It is uncertain whether the alisphenoid canal, a widespread ailuroid character also present in stem-group felids, such as *Proailurus* and *Pseudaelurus*, is present in basal machairodonts as well, such as *Promegantereon* and *Nimravides*. However, it appears to be present in some specimens of *Machairodus* (Geraads et al., 2004); this constitutes another important difference from the homotherines. Expectedly, *Xenosmilus* groups with the *Homotherium* species, and the original description of this taxon as a species with the head of *Homotherium* and the body of *Smilodon* (Martin et al., 2000) appears appropriate. Combined, *Xenosmilus* and *Homotherium* form a well-supported monophyletic group supported by five unambiguous synapomorphies (7[3], very small/absent P^4 protocone; 11[0, reversal], indistinct P^4 anterior cingulum; 14[2], P^3 very small (3–4% of condylobasal skull length); 15 [2], indistinct P^3 posterior cingulum; and 42[2], extremely wide upper incisor arcade [21–23% of condylobasal skull length]), and an additional apomorphy convergently shared with *Dinofelis barlowi* and *D. cristata*, and *Megantereon nihowanensis* and *M. whitei* (22 [2], strong reduction/absence of M_1 talonid).

The implicit enumeration analyses in TNT produced (*Xenosmilus*, *Homotherium crenatidens* (*H. serum*, *H. latidens*)) because the branch illustrated in Fig. 2 from *Xenosmilus* to *Homotherium* came out as a zero-

length branch and was thus collapsed in the Nelsen consensus. However, *Homotherium* may be defined by the following characters relative to *Xenosmilus*: 10 (1, large P^4 parastyle; present in all sabercats except *Xenosmilus*); and 16 (1, distinct and lingually oriented P^3 parastyle; present in all sabercats except *Xenosmilus*), implying that *Xenosmilus* does not group within *Homotherium*. This is corroborated by *Xenosmilus*' different post-cranial morphology from *Homotherium* (Martin et al., 2000), and combined, this indicates that the Eurasian *H. crenatidens* and *H. latidens* + the American *H. serum* form a monophyletic group, with *Xenosmilus* as the sister taxon.

The Smilodontini is entirely paraphyletic and *Promegantereon* is not closely related to either *Megantereon* or *Smilodon*. *Megantereon* and *Smilodon* are also not sister taxa, as is traditionally inferred. *Megantereon* is found to constitute a monophyletic basal Eumachairodontia taxon, supported by a large mandibular flange (46[2]). The Pleistocene taxon *Smilodon* is supported by two unambiguous synapomorphies, a hugely developed mastoid process (35[3]), and a very wide palate across the centre of P^3 relative to condylobasal length (43[2]); to this may be added the virtual absence of the P_3 , as discussed below. *Smilodon* shares a very large, dirk-toothed C^1 with *Megantereon* and in part *Homotherium crenatidens* and some specimens of *Amphimachairodus giganteus*. However, other than relative size, the morphology of the C^1 is not uniform in these taxa and it should not be regarded as a synapomorphy, as has traditionally been done for *Smilodon* and *Megantereon*. It is best interpreted as convergent enhancement of an already prominent, blade-like C^1 among the eumachairodonts.

Upper canine enhancement is also seen within both genera, as the temporally later and more craniodentally specialized *M. whitei* has a larger C^1 than the more basal *M. cultridens*, as well as other specialized dental and functional characters (Palmquist et al., 2007). This is also the case in *S. fatalis* compared with the larger *S. populator*; in some *S. populator*, the C^1 is truly gigantic (e.g. in MNHN-BRD21, it is in excess of 60% of condylobasal skull length), and the C^1 of *S. populator* is also distinctly more robust in the anteroposterior plane (Kurtén and Werdelin, 1990; Turner and Antón, 1997; Christiansen, 2007). The great intraspecific variation in C^1 size and morphology among both species of *Smilodon* also argues for caution in using this as a typological character to delimit taxa.

Discussion

The division of the machairodonts into three separate evolutionary clades, as traditionally proposed, could not be recovered by parsimony analysis. This is

perhaps not surprising as it has largely been based on a few purported key characters, notably upper canine morphology, such as dirk vs. scimitar-toothed or serrated vs. smooth or weakly crenulated carinae (e.g. Kurtén, 1962, 1968; Beaumont, 1964, 1978; Martin, 1980, 1998; Berta and Galiano, 1983; Turner and Antón, 1997; Antón and Galobart, 1999; Antón et al., 2004a; Slater and Van Valkenburgh, 2008). The three groups were historically inferred to constitute separate evolutionary clades where early species convergently gave rise to increasingly morphologically specialized species: the Metailurini (*Metailurus*, *Dinofelis*); the Homotherini (*Machairodus* [*Amphimachairodus*], *Homotherium*); and the Smilodontini (*Promegantereon*–*Paramachairodus* group, *Megantereon*, *Smilodon*). This indicates convergent evolution of a great number of similar craniodental traits for the same inferred functionally adaptive purpose of efficient predation with hypertrophied upper canines, necessitating high gape angles and a concomitant reorganization of the skull and mandible (Emerson and Radinsky, 1980; Martin, 1980, 1998; Turner and Antón, 1997; Antón and Galobart, 1999; Salesa et al., 2005; Christiansen, 2006). Such scenarios are evidently unparsimonious.

In this study, the sabercat taxa *Megantereon*, *Smilodon*, *Amphimachairodus*, *Homotherium* and *Xenosmilus* were found to constitute a well-supported monophyletic taxon of felids with true “saberteeth”, i.e. hypertrophied, greatly flattened upper canines. As such, these taxa may be called true sabercats, as implied in the proposed name of Eumachairodontia. This implies that the traditionally inferred sabercat trait, the hypertrophied upper canines, is not a machairodont apomorphy (contra Berta and Galiano, 1983; Palmquist et al., 2007). Rather, the canine apomorphy characteristic of the entire Machairodontinae is a small lower canine, a trait emphasized by Werdelin et al. (2010), among others. Only later did the whole suite of characters emphasized in form–function studies (e.g. Emerson and Radinsky, 1980; Christiansen, 2006, 2008b; Slater and Van Valkenburgh, 2008) evolve. New shape studies using sophisticated digital morphometrics of the cranium and mandible of sabercats have concluded that craniomandibular shape throughout sabercat evolution was a result of mosaic evolution, where somewhat enlarged and flattened upper canines preceded the evolution of greatly modified craniomandibular shape and hypertrophied, true saberteeth (Christiansen, 2008b,c; Slater and Van Valkenburgh, 2008; Prevosti et al., 2010). These studies also support the notion that basal sabercats were not intermingled with morphologically highly specialized Plio-Pleistocene species in several separate lineages simultaneously undergoing convergent evolutionary changes.

Dinofelis was found to constitute basal machairodont taxa, but the group was not found to be monophyletic, although topological resolution and branch stability and support argue for caution in lending too much credence to this result. In their excellent monograph, Werdelin and Lewis (2001) discussed the possibility of non-monophyly for *Dinofelis*. *Dinofelis* has frequently been claimed to convergently resemble the great cats (*Panthera*), and have even been considered not to be machairodonts at all but *Panthera* relatives (e.g. Falconer and Cautley, 1836; Kretzoi, 1929; Hendey, 1974). Recently, this claim has been reiterated (Hoek Ostende et al., 2006) ignoring the results of Werdelin and Lewis (2001). The current analysis suggests that *Dinofelis* belongs in the Machairodontinae, and Werdelin and Lewis (2001) argued that hypotheses suggesting that *Dinofelis* was a relative of *Panthera* were probably based on the fact that the stratigraphically oldest and youngest *Dinofelis* species possess the most machairodont traits, whereas intermediary species appear less sabertoothed. Werdelin and Lewis (2001) and Werdelin et al. (2010) argued against a monophyletic Metailurini, but were supportive of the notion that *Metailurus* and *Dinofelis* may have shared some kind of common ancestry, noting that the mandible in early *Dinofelis* species were quite similar to that of *Metailurus major* (Werdelin and Lewis, 2001, p. 247). The hypothesis of common ancestry of *Dinofelis* and *Metailurus* is not incompatible with the result of the current analysis, but interrelationships of the basal machairodonts will need to be further analysed before this notion can be corroborated or dismissed.

The Smilodontini was also found not to be monophyletic. Although most authors have argued that this taxon should consist of the basal *Promegantereon*–*Paramachairodus* group and *Megantereon* and *Smilodon*, Werdelin et al. (2010) noted that the morphological distance between the former and the latter was great and their purported relationship was not based on any synapomorphies (contra Hodnett, 2010). The current study also failed to find evidence for a monophyletic group uniting *Promegantereon*, *Megantereon* and *Smilodon*. A potential autapomorphy of *Promegantereon* appears to be the marked development of the lateral cingulum on P⁴ adjacent to the paracone, forming a large, sometimes almost triangular shelf in some specimens (e.g. MNCNB-1377; MNCNB-5797; MNCN no number), although it is not ubiquitously present and in some specimens (e.g. MNCNB-7021) it is larger in one side than in the other. In other taxa, e.g. *Megantereon* and *Smilodon*, a lateral P⁴ cingulum is sometimes present but not to this extent. The functional significance of this remains elusive. *Promegantereon ogygia* may be distinguished from *Paramachairodus* by several dental characters, such as lack of C¹ crenulations, large P⁴ protocone and double-rooted M¹ (Salesa et al., 2010).

Traditionally, the Asiatic *Megantereon nihowanensis* is synonymized with *M. cultridens* (Palmquist et al., 2007), but there are dental differences between the two, and in the current analysis *M. nihowanensis* was found to be the sister taxon of *M. whitei*, not *M. cultridens*. *M. cultridens* appears more plesiomorphic in that it has a larger M_1 talonid (character 22), sometimes with a cusp, whereas *M. whitei* and *M. nihowanensis* have a very small or next to no talonid. *M. nihowanensis* also has a slightly smaller P^3 with smaller cusps (except for a large paracone) than *M. cultridens*, although not as small as that of *M. whitei*, and the P^4 protocone appears to be situated further posteriorly; in these respects, *M. nihowanensis* also appears more similar to *M. whitei*. *M. cultridens* also, on average, has a slightly smaller C^1 than *M. whitei*, as noted above, but, as with *Smilodon*, there is great overlap owing to size variation of the C^1 . Further studies are needed to elucidate the interrelationships of the widespread genus *Megantereon*, and from China there are numerous very well-preserved skulls which are as yet undescribed, and which could contribute with new important knowledge of the taxon.

Reduction in the size of P_3 is characteristic of some eumachairodont sabercats (*Megantereon* spp., in particular *M. whitei*; *Homotherium*, *Xenosmilus*), and a synapomorphy of *Smilodon* may be the virtual absence of this tooth; usually not even a trace of alveoli is present. In a series of 678 mandibles of *S. fatalis*, 41 (6%) had P_3 present (Merriam and Stock, 1932). In *S. populator*, the tooth is usually also absent, although some specimens possess it. As in *S. fatalis*, specimens of *S. populator* which have the tooth may have it in one mandibular ramus but the other usually shows no sign of even an alveolus (e.g. MNHN-BRD21). When present, the tooth is usually morphologically simple with only small cusps; sometimes, only a low, bulbous protoconid is present. The tooth is also absent in the holotype of the homotherine *Xenosmilus*.

Amphimachairodus and *Megantereon* are stratigraphically older and less craniodentally specialized than *Smilodon*, *Homotherium* and *Xenosmilus*. *Amphimachairodus* in some respects appears more specialized than *Megantereon*, for instance in the presence of crenulated or serrated carinae along C^1 , or the presence of a P^4 ectoparastyle. *Megantereon* also has a more elongate, plesiomorphic overall skull shape than *Amphimachairodus* rather than the taller cranial shapes present in the homotherines and *Smilodon*. However, in several other respects, *Amphimachairodus* appears more plesiomorphic than *Megantereon*, for instance in often (but not always) having a larger P^4 protocone; a distinct P^2 ; a distinct, although small P_2 ; a smaller mastoid process; and larger paroccipital and coronoid processes. *Megantereon* lacks a P_2 , and its P^2 is very small. In other respects, both appear equally

specialized, such as having a distinctly anterolaterally deflected mastoid process; very large and blade-like C^1 ; very small although not incisiform C_1 ; and ventrolaterally deflected angular process. *Megantereon whitei* is dentally and functionally more specialized than *M. cultridens* (Palmquist et al., 2007), and in this taxon even P^3 and P_3 are small.

Remarkably, even *Smilodon*, arguably the quintessential sabertoothed felid, has been proposed not to have been a machairodont at all, but rather to have been a close relative of the extant great cats (*Panthera*), as noted above for *Dinofelis*. This was based on morphological comparisons (Neff, 1982) and mitochondrial 12S RNA gene sequence analyses (Janczewski et al., 1992). Craniodental and postcranial morphology of *Smilodon* is so different from any species in the Felinae that this would imply great convergence with other sabertoothed cats. Unsurprisingly, there is a complete lack of fossil evidence for this claim, and further genomic research (Barnett et al., 2005) has also failed to corroborate the idea that *Smilodon* should group within the evolutionary radiation of the extant Felinae. *Smilodon* very evidently is no pantherine relative.

Many authors (e.g. Kurtén, 1962, 1968; Beaumont, 1964, 1978; Martin, 1980, 1998; Berta and Galiano, 1983; Turner and Antón, 1997; Antón and Galobart, 1999; Martin et al., 2000; Werdelin et al., 2010) have noted that the Smilodontini were quite different from the Homotherini on a number of points, and have argued that this means that they were members of different evolutionary lineages within the Machairodontinae, but in a cladistic context it does not constitute a valid argument against a close relationship. It is the potential synapomorphies shared by taxa rather than their mutual differences that bear witness to phylogenetic relationships (e.g. Hennig, 1966). Other than craniodental characters, the monophyly of the Eumachairodontia is also supported by the short tail known to have been present in *Megantereon*, *Smilodon* and *Homotherium* and inferred in *Amphimachairodus* and *Xenosmilus*, an unusual characteristic among sabercats and felids in general. The sister-group relationship of the Homotherini and *Smilodon* is also supported by a tall, slender scapula which differs proportionally from those of most other large felids (Merriam and Stock, 1932; Rawn-Schatzinger, 1992); the more plesiomorphic *Megantereon* does not share this morphology. Generally, the postcranial morphology of *Megantereon* is in some respects not as similar to that of *Smilodon* as has previously been surmised (Christiansen and Adolfssen, 2007). The robust postcranial build of *Xenosmilus* (Martin et al., 2000) is also compatible with a close relationship of homotherines to *Smilodon* although the basal homotherine *Amphimachairodus* appears to have been more gracile

and *Homotherium*-like, but its post-cranial morphology is not well known.

Nonetheless, the morphological distinction between homotherines and *Smilodon* could indicate a long separate evolutionary history, which is corroborated by the considerable age of the problematic *Amphimachairodus* group, but could also imply differences in predatory ecology. The latter is borne out in analyses of craniomandibular shape (Christiansen, 2008b; Slater and Van Valkenburgh, 2008; Prevosti et al., 2010), inferences of bite forces (Christiansen, 2007, 2008b), and mandibular adductor mechanics (Christiansen, 2011). Some dental differences other than canine morphology also point to differences in predatory ecology. In virtually all felids, there is an angle between the long axis of the M_1 paraconid and protoconid of around $140\text{--}150^\circ$ (my pers. obs.) implying that their shearing blades are not in horizontal alignment. However, in *Homotherium* and *Xenosmilus* the blades form a larger angle of around or more than 170° , indicating development of a more uniform shearing blade; not even *Megantereon whitei* or *Smilodon* have such upper carnassial morphology, which is convergently shared with the barbourfelids (Schultz et al., 1970). The above is corroborated by taphonomy studies indicating a predatory preference for juvenile proboscideans in *H. serum* (Rawn-Schatzinger, 1992; Marean and Ehrhardt, 1995; Turner and Antón, 1997). This appears to differ from the predatory ecology of its stem group among the *Megantereon*-like machairodonts (Palmquist et al., 2003) and also from the powerful *Smilodon* (Coltrain et al., 2004; Feranec, 2004), both of which appear to have had prey profiles more similar to those of the extant great cats (see Sunquist and Sunquist, 2002).

No character differences were recovered between the European *Homotherium crenatidens* and *H. latidens*, other than potentially character 36 (morphology of the jugal–maxilla suture), which is rather straight in *H. crenatidens* (36[1]) but could not be scored in the examined specimens of *H. latidens*. Other recovered differences, e.g. slight differences in morphology and/

or proportions of dental cusps, fell within the intraspecific variation of each taxon. However, *H. crenatidens* and *H. latidens* appear not to be morphologically identical, in that the examined specimens of *H. latidens* have smaller, more gracile upper canines, a larger diastema anterior to the C^1 and distinctly more prognathous upper incisors; in this respect they bear a closer resemblance to *Homotherium serum* than to *H. crenatidens*. In the latter characters, *Xenosmilus* also resembles *H. crenatidens* more than it does *H. serum*. Curiously, the typical scimitar-tooth condition of *H. serum* is not present in several other members of this group, and some specimens of *Amphimachairodus* and *H. crenatidens* approach the dirk-toothed condition, although they are not scored as such, as they do not have upper canines of a size and morphology like *Smilodon* and *Megantereon*. The diversity of canine morphology in closely related species argues for caution in placing as much emphasis on this one character for sorting out sabercat phylogeny as has traditionally been done.

The American *Homotherium serum* morphologically appears to be different from the Eurasian *Homotherium crenatidens*, as confirmed by simple visual inspection (Fig. 4), but appears more similar to *H. latidens*, in this case the specimens from Incarcal. However, it is presently unknown how much of these purported differences may be attributable to phylogenetic distance and how much is simply intraspecific variation. In extant felids such differences are unlikely to represent intraspecific variation. However, the huge assemblage of *Smilodon fatalis* from Rancho la Brea appear to show high levels of morphological variation relative to extant felids (Merriam and Stock, 1932; Slaughter, 1963; Meachen-Samuels and Binder, 2010) and this is also the case for *S. populator* (my pers. obs.). Most sabercat species, including *Homotherium*, are not represented by sufficiently abundant material to allow studies of intraspecific variation.

Some recent studies (Werdelin et al., 2010) have suggested that the differences primarily in craniomandibu-

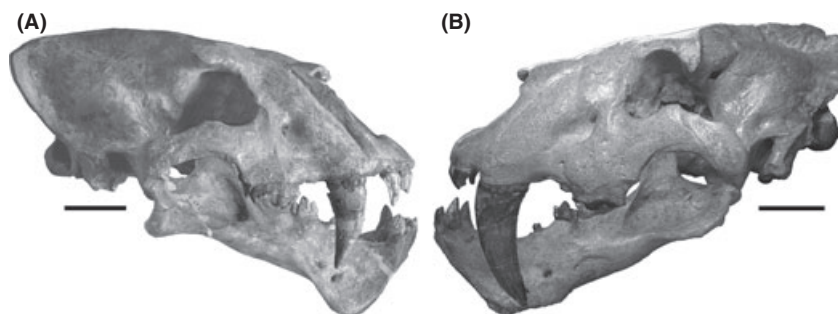


Fig. 4. Skulls of (A) *Homotherium serum* TMM3582; and (B) *Homotherium crenatidens* MNHN-per2000a/b, demonstrating the large morphological differences between the two species. Despite traditionally being labelled scimitar-toothed felids, only *H. serum* has a C^1 morphology which can appropriately be described as scimitar-toothed, whereas the C^1 of *H. crenatidens* appears closer to the traditional sabertoothed canines of *Megantereon* and *Smilodon*. Scale bars = 5 cm.

lar and dental (primarily C^1) morphology of *H. serum* from *H. crenatidens* would imply generic separation of the two, with the traditionally proposed name *Dinobastis serus* (Cope, 1893) supplanting the more recent synonymization with *Homotherium* to *Homotherium serum*. Yet, in the character matrix of the current study they are virtually identical, as a large sample of morphologically diverse sabercats tends to mask their differences, which, more importantly, are also not easily expressed in terms of discrete or morphometric characters. The interrelationships among the species of *Homotherium* and *Xenosmilus* need further clarification.

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Appendix 1

List of included specimens

Abbreviations: BF, Bolts Farm, Transvaal Museum, Pretoria; BI-OPSI, Babiarz Institute of Paleontological Studies Inc.; BM, Natural History Museum, London; CN, Zoological Museum, Copenhagen; F:AM, American Museum of Natural History (Frick Collection), New York; ICP, Institut Català de Paleontologia, Universitat Autònoma de Barcelona; IN-I, Incarcal 1, Museo Arqueológico Carmacal de Banyoles; LACMHC, Los Angeles County Museum, George C. Page Museum (Hancock Collection); MLP, Museo de La Plata;

MNCN, Museo Nacional de Ciencias Naturales (CSIC), Madrid; MNHN, Museum national d'Histoire Naturelle, Paris; NRM, Naturhistoriska riksmuseet, Stockholm; PC coll, personal collection of Per Christiansen; PMU, Paleontological Museum, Uppsala; RMNH, National Museum of Natural History, Leiden (Naturalis); SE, Naturhistorisches Museum, Basel; TMM, Texas Memorial Museum; UC, University of California.

Outgroup taxa

Canis lupus CN5335; CN5218; CN2547; CN2544; CN2349; CN5608; CN5609; CN5685; CN5688; CN5689; CN5691; CN5686; CN5786; CN6060; CN6048; CN713; CN714; CN1170; CN216; CN1239

Cryptoprocta ferox CN184; BM45.155; BM32.719.12; BM1938.11.16.1; BM1960.2.7.4; RMNH34451; RMNH34452; RMNH34454

Dinictis felina NRM (cast skull and mandible); PC coll (cast skull and mandible)

Pseudaelurus quadridentatus MNHN SA601 (type); MNHN SA602; MNHN SA603; MNHN SA963;

MNHN SA964; MNHN SA9966

Pseudaelurus skinneri F:AM61847 (Ginn Quarry specimen); F:AM61813; F:AM61816; F:AM61817

Pseudaelurus validus F:AM61835 (Echo Quarry specimen); F:AM61834; F:AM61828; F:AM61829

Ingroup taxa

Amphimachairodus giganteus BM28882 (cast); MNCN (cast skull and mandible); Ath nr. 1967/6; NRM (cast skull and mandible); NRM m3863; PC coll (2 cast skulls and mandibles, one of which is partially encased in matrix); *Homotherium serum* TMM933-3580; TMM933-3582; TMM933-1

Dinofelis barlowi BF 55-22, BF 55-23; PC coll (cast skull and mandible UC113720)

Dinofelis cristata PMU-m3657; PMU-m3658

Dinofelis petteri KMN-ER2612 (type); KMN-KP30397 (casts at the NMR)

Homotherium crenatidens MNHN-per2000a; MNHN-per2000b; PC coll (cast skull and mandible)

Homotherium latidens IN-I929; IN-I826; ICP (cast cranium and mandibles)

Machairodus aphanistus MNCNB-1523; MNCNB-2230; MNCNB-3974; MNCNB-4191; MNCNB-4272; MNCNB-4711; MNCNB-5445; MNCNBat-1'04-D5-35a; MNCNBat-1'04-E4-200; MNCNB-8-6; MNCN no numbers (4 specimens lacking numbers); *Megantereon cultridens* SE311; MNHNPer-2001a; MNHNPer-2001b

Megantereon nihowanensis NRM (2 cast skulls and mandibles); PC coll (cast skull and mandible); MNHN2003-1

Megantereon whitei KMN-ER793B (NRM cast skull and mandible); ICP20065 (cast of Dmanisi skull and mandible)

Metailurus major PMU-m3841; PMU-m3842 (type)

Metailurus parvulus PMU-m3836; PMU-m3835; PMU-m71; PMU-m72; PMU-m73; PC coll (cast skull and mandible)

Nimravides pedionomus F:AM61855; F:AM25206; F:AM25207

Promegantereon ogygia BM8959; MNCNB-134; MNCNB-751; MNCNB-847; MNCNB-1377; MNCNB-2376; MNCNB-3109; MNCNB-3434; MNCNB-3848; MNCNB-3942; MNCNB-4236; MNCNB-4322; MNCNB-4708; MNCNB-4778; MNCNB-4869; MNCNB-5198; MNCNB-5406; MNCNB-5797; MNCNB-7021; MNCNB-7022; MNCNB-7042; MNCNBat-1'04-F7-21; MNCNBat-1'05-E4-214; MNCN no number (2 specimens without numbers)

Smilodon fatalis LACMHC2001-1; LACMHC2001-2B; LACMHC2001-3; LACMHC2001-64; LACMHC2001-92; LACMHC2001-168; LACMHC2001-173; LACMHC2001-176; LACMHC2001-181; LACMHC2001-215; LACMHC2002-R15; LACMHC2002-R16; MNHN2050-21944; MNHN2051-22054; MNHN2051-28006; MNHN2737-22696; PC coll (2 cast skulls and mandibles)

Smilodon populator CN2, CN4; CN8, CN9; CN52; CN60; MLP7-47 (cast); MLP10-2; MNHN1907-10; MNHN1907-13; MNHN-BRD21; BMNH (2 cast skulls and mandibles); PC coll (cast skull and mandible)

Xenosmilus hodsonae BIOPSI101

Appendix 2

Character list

1. Upper incisor arcade: 0, strongly parabolic; 1, slightly parabolic; 2, straight [un-ordered]. Unfortunately, the state of preservation of most specimens of *Promegantereon* and *Machairodus* make this character tentative, but their incisor arcades appear to have been fairly straight. In *Nimravides* FAM:61855 the right premaxilla has empty aveoli and a relatively straight incisor arcade. According to Biknevicius et al. (1996), eumachairodont sabercats have fairly robust incisors in gently parabolic arcades, but this only applies to *Megantereon* spp. and *Smilodon* spp., whereas the traditional Homotherini (*Amphimachairodus*, *Homotherium*, *Xenosmilus*), uniquely among the sabercats, have much more robust, procumbent incisors in strongly curved arcades. In general, nimravids (e.g. *Eusmilus*, *Hoplophoneus* spp.) had large, robust incisors in strongly parabolic arcades, but basal taxa such as *Dinictis* only have a gently curved incisor arcade.

2. C¹ morphology: 0, conical-oval (rounded) in cross-section, absence or weakly developed posterior carina, crown not elongated (13–20% of condylobasal skull length (CBL)); 1, flattened in cross-section, occasionally posterior carina and moderately elongate (20–25% of CBL); 2, scimitar-toothed, greatly flattened with distinct posterior carina and moderately to somewhat elongate (25–30% of CBL); 3, dirk-toothed, greatly flattened with distinct posterior carina and greatly to enormously elongate (>35% of CBL) [un-ordered]. *Dinofelis cristata* has a C¹ which is only mildly flattened and it is not much larger than in extant tigers and proportionally shorter than in some clouded leopards, in particular *Neofelis diardi* (Christiansen, 2008a,b). The upper canine is broken in *D. petteri* but was not very flattened, and only *D. barlowi* has a moderately developed saberlike C¹. *Homotherium serum* is a typical scimitar-toothed form, whereas *H. crenatidens* (and many *Amphimachairodus*) approaches the dirk-toothed condition.

3. Carinae of C¹. 0, absence of carinal crenulations/serrations; 1, carinal crenulations; 2, carinal serrations [un-ordered]. The term crenulations is used for a weakly developed shearing carina, usually with small denticles, whereas the term serration is used about the condition observed in homotherines, which have large, distinct, chisel-like serrations along the posterior (and sometimes anterior) carinae, creating a saw-like carinal appearance.

4. C₁ morphology: 0, caniniform and large; 1, small; 2, very small and incisiform [un-ordered]. Lower canines in eumachairodonts, such as *Homotherium* or *Smilodon*, are often called incisiform, a term relating to extreme reduction in canine size and their apparent functional inclusion into the incisor battery (Biknevicius et al., 1996). Peigné (2003) also found that size of the upper and lower canines were not tightly coupled in nimravids (*sensu stricto*) and thus carried independent phylogenetic information.

5. M²: 0, presence of M²; 1, absence of M².

6. M¹: 0, presence of large, multi-cuspid M¹ situated in normal, anteroposterior direction; 1, presence of reduced, multi-cuspid M¹ sit-

uated transversely; 2, presence of very small, knob-like M^1 ; 3, absence of M^1 [un-ordered]. Only *Canis lupus* has a large, anteroposteriorly rectangular M^1 with large outer (paracone, metacone) and inner (protocone, protocone, hypocone, metacone) cusps. The M^1 in *Pseudaelurus*, while clearly reduced over the canid condition, is as large as the M^1 in *Dinictis*, and also has clearly discernible cusps (parastyle, paracone, metacone and protocone), but is situated transversely in the maxilla; it is double-rooted. *Homotherium crenatidens* and *H. latidens* were scored as 2, as some specimens have while others lack the M^1 .

7. P^4 protocone: 0, presence of very large, elongate and usually cusped protocone; 1, protocone small but still distinct; 2, protocone very small and usually un-cuspid; 3, protocone minute or absent [un-ordered].

8. P^4 protocone angulation: 0, strongly anteriorly directed; 1, linguallly directed. This was evaluated by drawing a straight line across the paracone–metastyle and the centre of the protocone, and evaluating the angle. In *Homotherium* and *Xenosmilus*, there is only a tiny knob which is at right angles to the long axis of the tooth.

9. P^4 protocone placement: 0, rostral to paracone; 1, at the paracone–parastyle junction; 2, medial to paracone [un-ordered]. Despite *Dinictis* having a very large, elongate and strongly anteriorly directed P^4 protocone, it originates medial to the paracone. In *Amphimachairodus*, some specimens have around a quarter of the protocone medially to the posterior part of the parastyle, but most specimens have most or all of the protocone medial to the paracone.

10. P^4 parastyle anteroposterior length: 0, parastyle absent or indistinct; 1, parastyle large. In nimravids (*sensu stricto*), there is no true parastyle, which is a derivation of the anterior cingulum. The “parastyle” of some nimravids is probably a derivation of the anterior paracone and thus an evolutionary neomorph, and has been termed the preparastyle or pseudoparastyle (Flynn and Galiano, 1982; Bryant, 1991). In *Xenosmilus*, the entire P^4 is extremely sectorial and the parastyle is indistinct, probably an autapomorphy rather than a plesiomorphy, as a large P^4 parastyle is characteristic of most ailuroids. However, the absence of the parastyle nonetheless implies a “0” scoring for *Xenosmilus*.

11. P^4 anterior cingulum: 0, indistinct; 1, distinct and often forming a ridge; 2, forming a distinct ectoparastyle [un-ordered]. Only in *Amphimachairodus* and *Smilodon* are there a distinct, pointed cusp (ectoparastyle) and little if any other trace of the anterior cingulum. In *Pseudaelurus* spp., the anterior cingulum in *P. skinneri* (Ginn Quarry) is more indistinct than in *P. validus* or *P. quadridentatus*. Given the remote relationship of Felidae and Nimravidae, it may be ruled out that the preparastyle of the latter is homologous to the cingular ectoparastyle of some felids, as also indicated by their having a large, true parastyle.

12. P^4 anterolateral edge: 0, rounded and medially directed after paracone cusp; 1, straight or sinusoid after paracone cusp; 2, distinctly medially directed, forming a wide, trough-like cingulum [un-ordered].

13. Relative size of P^4 : 0, P^4 short relative to CBL (9–10% of CBL); 1, P^4 large (12–16% of CBL).

14. Relative size of P^3 : 0, P^3 large relative to CBL (7–10% of CBL); 1, P^3 small (6–7% of CBL); 2, P^3 very small (3–4% of CBL) [un-ordered]. In some eumachairodonts, e.g. *Megantereon* and *Smilodon*, the P^3 is usually smaller than in basal taxa; yet, there is overlap on the ratios. *Canis lupus* and *Machairodus* were coded ambiguously (0/1) as some specimens have short whereas others have large P^3 . Crown sizes of P^4 and P^3 relative to CBL are not tightly coupled. In most eumachairodonts, the P^3 is markedly smaller relative to the P^4 than among extant felids and basal sabercats, but among the homotherines, P^3/P^4 ratios are much lower than among *Megantereon* and *Smilodon*. Curiously, the P^3 is greatly reduced in the otherwise rather morphologically unspecialised *Dinofelis*.

15. P^3 posterior cingulum: 0, posterior cingulum forming a ridge; 1, posterior cingulum forming a posterior accessory cusp; 2, poster-

ior cingulum indistinct [un-ordered]. *Pseudaelurus* is scored as having a cusp, as the posterior cingulum in *P. quadridentatus* is distinctly cusp-like, whereas it is more ridge-like in *P. validus*, but still markedly elevated compared with the inner part of the cingulum, rising to a peak along the lateral margin of the tooth.

16. P^3 parastyle: 0, indistinct or absent; 1, distinct parastyle cusp linguallly situated. Some specimens of *Promegantereon* have only a vestigial parastyle, but in most, it is large and distinct, sometimes rivalling the metacone in size. In *Machairodus*, *Nimravides*, *Amphimachairodus* and *Smilodon fatalis*, it can exceed metacone size.

17. Mediobasolateral width of P^3 across the metacone relative to width across the paracone: 0, narrow (70–90%); 1, wide (95–120%).

18. P^2 : 0, large with multiple cusps; 1, present but very small, usually only with a paracone cusp; 2, absent [un-ordered]. In *Metailurus*, the P^2 is absent, lending to their superficial cheetah morphology. Among *Acinonyx jubatus*, the P^2 is frequently absent, but is also often present but very small; sometimes it is present in one maxilla but not the other. It is also absent in some specimens of *Promegantereon* and *Machairodus*, whereas others have the P^2 . Its presence in *Dinofelis petteri* is inferred, as the type skull (KMN-ER2612; see Werdelin and Lewis, 2001) lacks them, but it is incomplete and weathered, and other specimens of *Dinofelis* have them, although they are not ubiquitously present.

19. P^1 : 0, present; 1, present but very small; 2, absent [un-ordered]. Some specimens of *Cryptoprocta* have this tooth, but it is not ubiquitously present. In *Pseudaelurus*, it is only clearly visible in the Ginn Quarry specimen of *P. skinneri* (F:AM61847). As in nimravids (Peigné, 2003), the presence/absence of P^1 and P_1 in sabercats appears to carry separate phylogenetic information.

20. M_3 : 0, present; 1, absent.

21. M_2 : 0, present; 1, absent. Among felids, the M_2 is present only in stem-group felids such as *Proailurus* (Rothwell, 2001). Curiously, it has reappeared in the Nordic *Lynx lynx*, where it is present in 10% of specimens (Werdelin, 1987; Russell et al., 1995). Occasionally, a small M_2 may be found in extant felids as an atavism (Hilzheimer, 1905; Christiansen, 2008c, figure 1).

22. M_1 : 0, large talonid basin with distinct hypoconid, entoconid and metaconid; 1, distinct talonid with or without a metaconid cusp; 2, little if any talonid [un-ordered]. In most *Promegantereon* and *Machairodus*, the talonid is large but un-cuspid, but some specimens have a small, but distinct metaconid (e.g. MNCNB-134; MNCNB-4708; MNCNB-2230; MNCNB-3974; MNCNB-S-8-6). *Dinofelis petteri* has a short but distinct, un-cuspid M_1 talonid whereas *D. cristata* and *D. barlowi* have only a tiny shelf or none (Werdelin and Lewis, 2001). In some specimens of *Megantereon cultridens*, there is only a tiny shelf or none, but a few specimens, e.g. SE311, have a short but distinct talonid. Some *Smilodon fatalis* and *S. populator* have a tall, distinct metaconid, but in others there is no talonid at all.

23. Anterior edge of M_1 protoconid: 0, forming a curved (sickle-shaped) edge from the carnassial notch; 1, forming a short vertical edge at the carnassial notch, followed by a long, posteriorly directed, straight crest. Owing to extreme M_1 wear, this character cannot be scored in *Xenosmilus* and *Homotherium*, although the derived state is inferred. The derived state can be observed in juvenile *Homotherium* (e.g. Friesenhahn Cave specimens of *H. serum*).

24. Relative height of the M_1 major cusps: 0, height of paraconid low compared with height of protoconid (70–90%); 1, height of paraconid tall compared with height of protoconid (95–130%).

25. Carnassial (M_1) rotation. 0: absent; 1: present. The lower carnassials are rotated laterally in some sabercats, probably in order to preserve carnassial shearing with hypertrophied upper canines, implying less ability for other than simple orthogonal mandibular action. But this trait is not tightly coupled to the size of the canines, as basal taxa with fairly large canines (e.g. *Machairodus*) do not have

it, whereas eumachairodonts with proportionally similarly sized upper canines (e.g. *Homotherium*, *Xenosmilus*) do. In some species with very large upper canines, e.g. *Megantereon* and *Amphimachairodus*, it is often less well developed than in, for example, *Xenosmilus* with proportionally shorter upper canines. Morphologically specialized nimravids also have carnassial rotation (Bryant and Russell, 1995), and in *Dinictis*, the long axis of the lower carnassial is not in line with the long axis of the horizontal dentary ramus. However, the M_1 has become pivoted about its central axis, bringing the protoconid laterally and the paraconid medially compared with extant felids. This process appears different from the lateral twisting of the entire tooth seen in many sabercats, and *Dinictis* is scored as having the primitive condition.

26. Relative size of P_4 : 0, small relative to mandible length (7.5–9%); 1, large relative to mandible length (10–14%). This metric is mirrored in the P_4/M_1 crown length ratio, where *Canis lupus* centres around 0.55, whereas all other included taxa are much higher, 0.8–>1.0, with the exception of *Homotherium* and *Xenosmilus*, which have lower P_4/M_1 ratios of 0.6–0.7 owing to their very large carnassials.

27. P_4 paraconid: 0, paraconid distinctly asymmetrical, with gently posteriorly sloping anterior face, but posterior face with posteroventral slope from apex, followed by downward-sloping ventral part of cusp (i.e. cusp not bilaterally symmetrical about its central axis); 1, paraconid bilaterally symmetrical around its central axis; most with a distinct angle between the ventral and apical part.

28. P_2 : 0, present; 1, absent. Among extant felids, the P_2 is absent, but it is occasionally present as an atavism in certain populations of lions (Mazák, 1975; Christiansen, 2008d). In *Machairodus*, the P_2 (and alveolus) is usually absent, but a tiny P_2 is present in a few specimens (e.g. MNCN B-2230), or the alveoli (MNCN BS-8-6). *Amphimachairodus* sometimes has a tall, thin P_2 , but in other specimens not even alveoli are present.

29. P_1 : 0, present; 1, absent. In *Cryptoprocta*, a small, round P_1 is sometimes present, but is much smaller than in *Canis lupus*. Among felids, the P_1 is only present in *Proailurus*.

30. Mandibular glenoid: 0, facing anteriorly; 1, facing ventrally. In some specimens of *Promegantereon*, the glenoid faces somewhat anteriorly, although primarily ventrally, but this is probably an artefact of post-mortem distortion. In the type skull of *Dinofelis petteri* (KMN-ER2612), however, the glenoid appears to be facing as much anteriorly as in *Nimravides* and outgroup taxa *Cryptoprocta* and *Canis lupus*.

31. Preglenoid process: 0, small or absent; 1, large and distinct. The process is very small in *Dinofelis petteri*, but has been broken off, and, accordingly, is inferred to have been larger, as in other species of *Dinofelis*.

32. Infraorbital fenestra: 0, situated distinctly anterior to orbit; 1, situated close to orbit.

33. Anterior rim of orbit: 0, situated above or behind P^4 meta-style; 1, situated above P^4 paracone or parastyle–paracone junction; 2, situated in front of the P^4 [un-ordered]. In *Smilodon* the orbital rim is not as far anterior as in homotherines or basal forms such as *Dinofelis cristata* or *Machairodus*, but is usually situated above the parastyle.

34. Snout area elevation compared with braincase: 0, snout area low; 1, snout area distinctly elevated. This variable is most easily gauged by drawing a straight line from the apex of the nasals at the top of the external narial aperture to the junction of the sagittal and occipital crests. In most of the included taxa, the snout area is not elevated and this implies that a large part of the skull will be situated dorsally to this line. In eumachairodonts, the portion of the skull above this line is much less and the line frequently intersects the frontal postorbital process, and sometimes the line almost follows dorsal skull profile.

35. Size of mastoid process: 0, small, sometimes knob-like; 1, large and elongate; 2, much larger relative to the condition in extant pantherines and anteriorly sloping; 3, enormously large, obscuring the auditory bulla in lateral view [un-ordered]. The size of the mastoid is not linearly related to upper canine size, and is enormously developed in *Smilodon* compared with *Megantereon*, which have almost equally large upper canines. The pantherines usually have equally large mastoid processes to *Dinictis*, despite having much shorter, conical canines. Peigné (2003) was also able to extract separate phylogenetic information from the canines and mastoid process in nimravids (*sensu stricto*).

36. Jugal–maxilla suture: 0, strongly sinusoid; 1, weakly sinusoid or almost straight. In *Canis lupus*, there is a distinct, median posterior flange from the maxilla, which is absent in felids. Unfortunately this suture is not discernible in some sabercat specimens, although it is inferred to have been straight.

37. P^3/P^4 junction relative to infraorbital fenestra: 0, posterior to infraorbital fenestra; 1, anterior to infraorbital fenestra. This character appears to be unrelated to the length of the snout (long in canids, much shorter in felids) and the size of the sabertooth. It is also not related to the position of the fenestra relative to the orbit (character 32, above). Only some specimens of *Amphimachairodus* have an anterior P^3/P^4 junction, whereas it is at level with the infraorbital fenestra in others.

38. Nasal does (0) or does not (1) extend past the maxilla–frontal suture. A posterior extension does not imply a few mm at either side of the frontal–maxillary suture, but a distinct posterior extension, as in extant tigers.

39. Size of the jugal postorbital process: 0, small, rounded, often almost absent; 1, tall, triangular and tapering. There is variation among some sabercats. For instance, in some *Promegantereon* it is reduced, whereas others (e.g. MNCNBat-1'04-F7-21; MNCNBat-1'05-E4-214 and MNCNB-7022 [partly damaged]) have a distinct, tall, triangular process, which is also the case in some *Machairodus* (e.g. MNCNB-4272; and MNCNB-4191, B-1523 and B5445 [partly damaged]). In some eumachairodonts, e.g. *Smilodon fatalis* LAC-MHC2001-92; *S. populator* (e.g. CN4, CN52, MNHNBRD-21), or *Homotherium latidens* IPS36771 the process is a distinct but low and round knob, and is not long and triangular.

40. Length of facial region of skull relative to CBL: 0, elongate facial region (52–57% of CBL); 1, abbreviated facial region (40–47% of CBL). Among felids, there appears to be little relationship between facial size and reduction of the postcanine dentition and elongation of the upper canines. *Smilodon* has a facial length/CBL ratio comparable to basal sabercats and outgroup taxa (e.g. *Cryptoprocta*), and the facial region of *Dinictis* (45%) is much shorter than that of *Canis lupus*. Rather, it would appear to be a synapomorphy of the felid-like aeluroids, although it is definitely not a character shared by all viverrids.

41. Angle of the occipital condyles: 0, low (45–60°); 1, high (70–100°). Curiously, the values in *Smilodon fatalis* (75–92°) are generally lower than in *S. populator* (85–100°).

42. Relative width across the incisor arcade: 0, narrow (12–15% of CBL), 1, wide (16–19% of CBL); 2, extremely wide (21–23% of CBL) [un-ordered]. Eumachairodonts generally have rather large incisors, but only *Homotherium* and *Xenosmilus* have incisor arcade widths approaching a quarter of CBL. Despite *Canis lupus* having fairly well-developed, procumbent incisors and a parabolic incisor arcade, the arcade is narrow. In sabercats, there appears to be slight correlation of this character and the morphology of the upper incisor arcade (character 1, above), but the relationship is a very loose one, as only some homotherines (*Homotherium*, *Xenosmilus*) have both characters in the derived state whereas *Amphimachairodus* does not. *Smilodon* has fairly although not markedly wide arcades, whereas *Megantereon* has narrower arcades, but both share the same degree of arcade curvedness. Among other included felids the

50. Posterior part of horizontal dentary ramus height relative to ramus length: 0, slender (15–17%); 1, robust (18–23%). This varies even in sabercats with seemingly slender mandibular rami, such as *Machairodus*, *Amphimachairodus* and *Dinofelis cristata*, and ranges from the extreme upper range of the outgroup taxa to considerably above (e.g. *Machairodus* is 17.4–19.8%).

Character matrix

[illegible]