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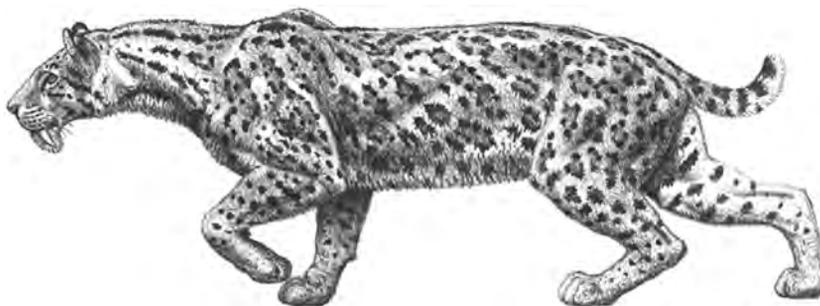
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Phylogeny and evolution of cats (Felidae)

Lars Werdelin, Nobuyuki Yamaguchi, Warren E. Johnson, and
Stephen J. O'Brien



Artist's reconstruction of the sabre-toothed cat *Megantereon cultridens* stalking its prey. (Illustration courtesy of Mauricio Antón.)

Introduction

Cats, wild as well as domestic, fossil as well as living, are familiar to people around the world. The family Felidae has a worldwide distribution and has been associated with humans in various ways throughout history (Quammen 2004). Their functional morphology, ecology, and behaviour have been the subject of intense scrutiny by scientists for over 200 years. The fossil record of cats is extensive and some of its members are among the most recognizable of extinct animals. Despite all this, the phylogeny and evolution of the family Felidae, and even the content of the family, have remained poorly understood. In this review, we will first present the current state of knowledge with regard to the interrelationships of living Felidae and the timing of the radiation of modern cats. We will also present the fossil record of Felidae in broad outline, focusing first on describing the different groups of species and their characteristics, and then discussing the general patterns of cat evolution that we can deduce from current data. Provided with this overview, we will attempt to identify those areas most in need of further research in order to achieve the aim of a fuller understanding of

felid evolution, especially that of the living felids and their ecological and functional relationship to the extinct sabre-toothed felids.

In this discussion, we will synthesize the available data, distinguishing as far as possible monophyletic groups of taxa, suggesting the most likely interrelationships of the fossil lineages, but also pointing out that there are many problem areas that need to be resolved. This section should be viewed as a challenge to investigators to use old data or discover new data to corroborate or refute the scenarios proposed herein. We end the paper with a small section demonstrating some evolutionary patterns among extant Felidae, suggesting that there is much to be gained from the deeper analysis of the current phylogenetic information.

Felid morphology is described and discussed elsewhere (Kitchener *et al.*, Chapter 3, this volume) and will not be reiterated here except as needed. Teeth of the upper jaw are referred to in upper-case letters (I, C, P, and M) and teeth of the lower jaw in lower-case letters (i, c, p, and m), followed by the appropriate number in the sequence. Character mapping on cladograms was carried out with Mesquite, version 1.12 (Maddison and Maddison 2004). Stratigraphic

ages of taxa as given in the text and figures were obtained from either primary literature or (for North America) the Paleobiology Database (www.paleodb.org) and (for Eurasia) the NOW database (www.helsinki.fi/science/now/database.html).

Phylogeny

Many attempts have been made to investigate the interrelationships of Felidae. These have followed two broad approaches. Some, like Matthew (1910), Kretzoi (1929a, b) and Beaumont (1978) have incorporated both fossil and extant felids in their analyses, while others, such as Pocock (1917a), Herrington (1986), and Salles (1992) have focused exclusively on the living members of the family. A new era in felid phylogenetics was ushered in with the introduction of molecular evidence (Collier and O'Brien 1985; O'Brien *et al.* 1985a; Johnson *et al.* 1996), while the first study to use a total evidence approach was that of Mattern and McLennan (2000).

All of these approaches have had their problems. In the case of fossil studies, confounding factors have included the relatively poor fossil record, the problem of finding useful characters in fragmentary material and the convergence between Nimravidae and Felidae. Though previously included in the Felidae (Matthew 1910; Piveteau 1961), the former, Nimravidae, is now known to be diphyletic. Its Paleogene (65.5–23.0 million years ago [Ma]; Gradstein *et al.* 2004) members form a basal clade within either Felformia or Carnivora as a whole (Neff 1983; Hunt 1987; Morlo *et al.* 2004), while its Neogene (23.0 Ma—recent) members are placed in a separate family, Barbourfelidae, with affinities to Felidae (see below). Morphological studies of extant felids have been hampered by the very uniform morphology of the members of the family, making it difficult to find and polarize characters for phylogenetic analysis. Molecular studies, on the other hand, have been particularly hampered by the apparently short time-span during which the clades of modern felids evolved. Thus, clades of closely related taxa have been identified but the interrelationships of these clades have been difficult to pinpoint.

Recently, two of us (Warren E. Johnson and Stephen J. O'Brien) published a phylogeny of Felidae

based on a data set of 22,789 base pairs of DNA, including autosomal, Y-linked, X-linked, and mitochondrial gene segments (Johnson *et al.* 2006b). The results of this study, while not immutable, provide a firm basis for understanding the interrelationships and evolution of the extant Felidae. The results confirm some prior results, both molecular and morphological, while providing new insights and surprises.

The study distinguishes eight clades of extant felids (Fig. 2.1). The first of these to split off from the stem lineage is the *Panthera* lineage (genera *Neofelis* and *Panthera*) at *c.* 10.8 Ma (Fig. 2.1, node A). Most previous studies of felid phylogeny have placed *Panthera* as the crown group, but a few (Turner and Antón 1997; Mattern and McLennan 2000) also have the *Panthera* lineage as basal to other cats. Within this

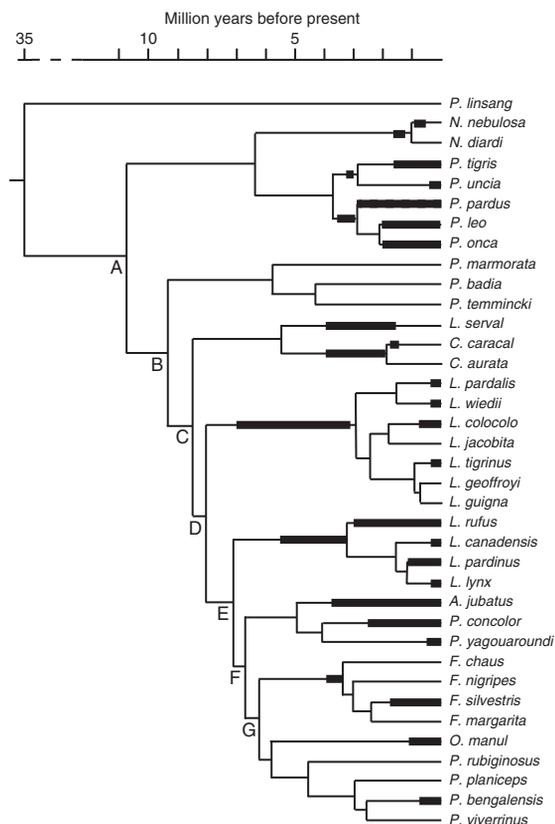


Figure 2.1 The phylogeny of the extant Felidae. Thick lines indicate the presence of a fossil record, thin lines indicate the absence of a fossil record. Node labels as in the main text. (Based on the work of Johnson *et al.* 2006b.)

lineage, the clouded leopard, *Neofelis*, with the two species *N. nebulosa* and *N. diardi* (Buckley-Beason *et al.* 2006; Kitchener *et al.* 2006) is placed basally, as would be expected from its distinctive morphology implying a long separate evolutionary lineage (Christiansen 2006), with the rest of the pantherines radiating within the last 4 million years.

The next clade to branch off, at *c.* 9.4 Ma (Fig. 2.1, node B), is the bay cat lineage (genus *Pardofelis*). This clade consists of the poorly known bay cat (*P. badia*), Asian golden cat (*P. temminckii*), and marbled cat (*P. marmorata*). The last mentioned species has been linked to the *Panthera* lineage (e.g. Herrington 1986) and this is reflected in its position here, as basal member of the clade branching off closest to the *Panthera* lineage.

The third lineage is the *Caracal* lineage, with two genera, *Caracal* and *Leptailurus*, incorporating three African species: caracal (*Caracal*), African golden cat (*C. aurata*), and serval (*S. leptailurus serval*). This lineage branches off at *c.* 8.5 Ma (Fig. 2.1, node C), with the serval basal to the other two species.

The next lineage is the ocelot lineage (genus *Leopardus*), including most of the South American small cats (Seymour 1999). This lineage branches off at *c.* 8.0 Ma (Fig. 2.1, node D). The beginning of this lineage is thus independent of the formation of the land bridge between South and North America about 3 Ma (Marshall *et al.* 1982). However, the radiation of the extant species within this lineage shows dates that are compatible with a single origin of the extant radiation from a North American ancestor, as previously proposed (Werdelin 1989).

The fifth lineage comprises the genus *Lynx*, splitting off at *c.* 7.2 Ma (Fig. 2.1, node E). This lineage has also often been linked to *Panthera* (e.g. Collier and O'Brien 1985; Salles 1992), but the recent more robust study by Johnson *et al.* (2006b) indicates that the relationship is more distant than previously thought. Within the clade, *L. rufus* is basal as has generally been thought, but *L. canadensis* and *L. lynx* are not reconstructed as sister taxa, unlike in previous analyses (Werdelin 1981).

The next lineage is the *Puma* lineage, including the genera *Puma* and *Acinonyx* which split off at *c.* 6.7 Ma (Fig. 2.1, node F). This lineage has previously been recognized in both morphological (Herrington 1986; Van Valkenburgh *et al.* 1990) and molecular

(Johnson and O'Brien 1997) studies. It is worth noting that the puma and jaguarundi probably split before the Great American Biotic Interchange that followed the formation of the land bridge between South and North America (Marshall *et al.* 1982), and thus both are of North American origin.

The seventh and eighth lineages are the small cats of the Old World—the leopard cat and domestic cat lineages. They split from each other at *c.* 6.2 Ma (Fig. 2.1, node G). The former includes the genera *Otocolobus* and *Prionailurus* and the latter the genus *Felis*. The splits within the former are much deeper than within the latter, suggesting that the genus *Felis* may be oversplit. This is also the conclusion of Driscoll *et al.* (2007), who distinguish only four species in *Felis*: *F. chaus*, *F. nigripes*, *F. margarita*, and *F. silvestris*. The last mentioned species now also includes *F. ornata*, *F. bieti*, and *F. lybica*, making it one of the most widespread small cat species.

Most of the nodes in this phylogeny are robustly supported (Johnson *et al.* 2006b). A few, however, are still unstable, showing either low support or incongruence between different analyses and data sets. These as yet incompletely resolved nodes are: the relative positions of *Panthera leo*, *P. pardus*, and *P. onca*, as well as the relative positions of *P. tigris* and *P. uncia* within this clade; the position of *L. jacobita*; the position of *O. manul*; the position of *F. nigripes*; and the clade uniting *Felis* and *Prionailurus/Otocolobus* to the exclusion of *Puma/Acinonyx*.

The most notable fact about this phylogeny of extant cats lies in the short time intervals between the splits of the eight lineages. The radiation of lineages along the entire stem of the felid clade occurs within the Late Miocene (over a period of *c.* 6.3 Ma) and such a short space of time suggests the occurrence of some sort of functional or ecological release, but what that may be is at present unknown. We shall return to the fossil record of extant cats below.

The fossil record

According to available molecular data, the Felidae originated some time at or just after the end of the Eocene (Gaubert and Véron 2003). This accords well with the fossil record. The earliest forms placed in the felid lineage, *Proailurus* and possibly *Stenogale*

and *Haplogale* (Hunt 1998; Peigné 1999), occur after the 'Grande Coupure' marking the Eocene/Oligocene boundary (*c.* 33.9 Ma; Gradstein *et al.* 2004). In the Mammals Paleogene (MP) level system of Paleogene terrestrial mammal stratigraphy in Europe, this boundary is placed between MP 20 and MP 21 (Schmidt-Kittler 1990). In the fissure fillings of the Quercy region, France, where most of our knowledge of early European carnivorans originates, feliforms are not known before MP 21 (Hunt 1998). Owing to the scarcity of their remains, modern excavations have yet to establish the first occurrence of the Felidae. What we know, however, suggests that some older known finds may be from the Early Oligocene, that is, before 28.4 Ma (Gradstein *et al.* 2004). Thus, the earliest felids appeared sometime between *c.* 35 Ma (age of the sister group) and 28.5 Ma (minimum age of the earliest fossils).

It is well established on morphological grounds, basicranial as well as dental, that *Proailurus*, known from the Quercy fissure fills, but also from excellent material from the Early Miocene site of Saint-Gérard-le-Puy, France, (MN 2 in the Neogene mammal zonation of Europe; 22.8–20 Ma) is a felid. Despite this, the morphological path leading to the felid

condition is not well delineated. Hunt (1998) discusses changes to the auditory bulla seen in a variety of early feliforms, including *Haplogale* and *Stenogale*, and leading to the bulla of *Proailurus*. However, the placement of Asiatic linsangs (genus *Prionodon*) as the sister group to Felidae on molecular grounds by Gaubert and Véron (2003), instead of with the Viverridae, in which they have traditionally been placed, adds complexity to the story. Hunt (2001) placed *Prionodon* in a clade with 'true' viverrids, for example *Genetta*, on the basis of basicranial anatomy (but without consideration of other features). What this conflict between separate data sets consisting of non-overlapping characters means for our understanding of the fossil record of the precursors of Felidae and for the origins of the family has yet to be established.

Early felids

As noted, the earliest well-established felid is *Proailurus* (Figs. 2.2, letter A; 2.3, and 2.4). Peigné (1999) provides a discussion of the evolution of this species and its relationship to other early putative felids.

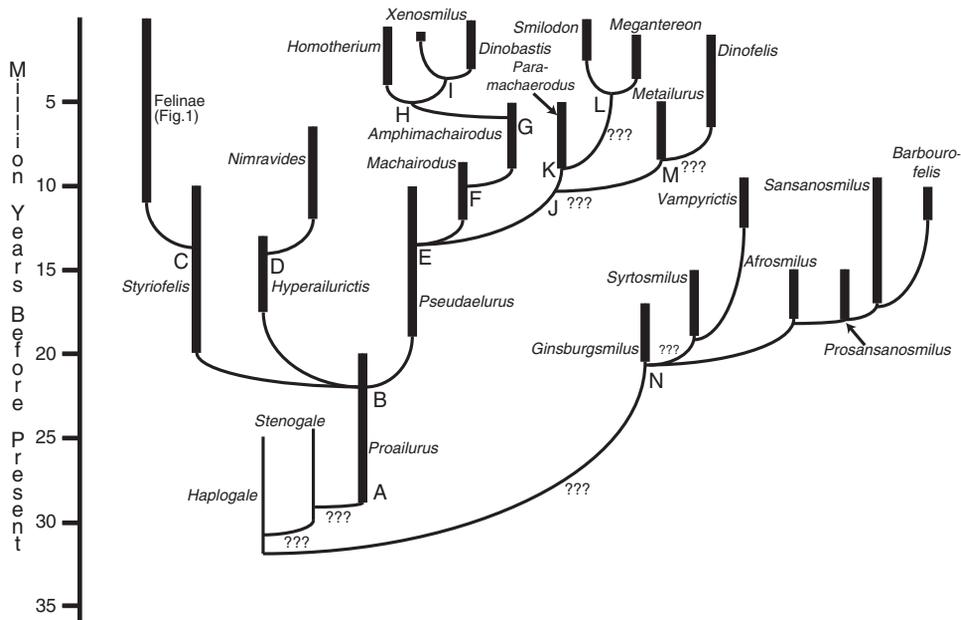


Figure 2.2 Summary of the proposed evolutionary tree of Felidae discussed herein. Thick lines indicate the presence of a fossil record, thin lines indicate the absence of a fossil record. Labels as in the main text and Table 2.1.

Table 2.1 The internal nodes of Fig. 2.2: content, place of origin, and age.

Letter	Content	Continent	Age, Ma (approximate)
A	Felidae <i>sensu stricto</i>	Europe	27
B	Pseudaelurine radiation and later felids	Eurasia	22
C	Felinae (radiation of extant felids)	Eurasia	14–13
D	<i>Nimravides</i>	North America	14
E	Machairodontinae	Europe	14–13
F	<i>Amphimachairodus</i> lineage	Eurasia	10
G	Homotheriini	Eurasia	6
H	Derived Homotheriini	Africa	5
I	North American Homotheriini	North America	4–3
J	<i>Paramachaerodus</i> lineage	Eurasia	11–10
K	<i>Paramachaerodus</i> and derivatives	Eurasia	9
L	Smilodontini	Eurasia, Africa, and North America	5–4
M	Metailurini	Eurasia	9–8
N	Barbourofelidae	Eurasia and Africa	32

Proailurus (with three species, *P. lemanensis*, *P. bourbonnensis*, and *P. major*) is a medium-sized cat about the size of a bobcat, *L. rufus*. Dentally, it differs from living cats in the (variable) presence of p1, p2, m2, and P1, as well as the presence of a small metaconid and talonid on m1. Overall, the dentition is thus very similar to that of living felids, but includes some elements that have been fully reduced in the modern clade. Further, the auditory bulla of *Proailurus* has a ventral process of the petrosal promontorium (Hunt 1989, 1998). This process is lost in living felids. When it was lost in felid evolution has yet to be established, but it serves to distinguish at least the modern clade from the basally situated *Proailurus*. The geologically youngest *Proailurus* is from Laugnac, France, biostratigraphically placed in MN 2b (>20 Ma). In *Proailurus* we have (as far as it is known) an essentially modern felid except for a few minor details of the dentition, auditory bulla, and postcranium, which has shorter limbs than modern felids. Coupled with the molecular date for the divergence of *Prionodon* and Felidae, this suggests that there must have been a stem lineage of perhaps 5 Ma in the Early Oligocene leading up to the full felid morphology. *Haplogale* and *Stenogale* are likely

to be members of that lineage (Hunt 1998; Peigné 1999), but the details of the process have not been worked out.

Proailurus is not known with certainty outside Europe. Hunt (1998) reports the presence of *Proailurus* sp. from the Hsanda Gol Formation, Mongolia. However, Peigné (1999) concludes, in our opinion correctly, that this specimen is better assigned to the Barbourofelidae. On the other hand, Hunt (1998) also describes the skull of a *Proailurus*-grade felid from the Ginn Quarry, Nebraska (Late Hemingfordian, c. 17–16.5 Ma). According to Hunt the basicranial structure of the Ginn Quarry felid is more plesiomorphic than that of European *Proailurus*. This suggests that phylogenetic diversification in Felidae had begun already in the Early Miocene and that North American ‘*Pseudaelurus*’ (see below) may have evolved from a *Proailurus*-grade ancestor rather than from a migration of early *Pseudaelurus* into North America. If so, felids may have migrated into North America as early as the beginning of the Hemingfordian (c. 19 Ma), along with a number of other carnivoran taxa (Qiu 2003).

The next felids to evolve belong to the *Pseudaelurus* complex (Fig. 2.2, letter B; Fig. 2.5). This is a group of



Figure 2.3 The skull of *Proailurus lemanensis*, MNHN SG 3509 (holotype) from Saint-Gérard-le-Puy, France, in ventral view. The anterior and posterior halves do not meet. (Photo courtesy of Stéphane Peigné.)

species with representatives in Europe, Arabia, Asia, and North America. The interrelationships of the species included in *Pseudaelurus* and the relationship of this genus (or genera) to the radiations of the subfamilies Felinae (conical-toothed cats) and Machairodontinae (sabretooths) are a major challenge to felid palaeontology. *Pseudaelurus* is clearly a grade rather than a monophyletic clade, and this complex includes the ancestors of all subsequent felids. A number of generic names are available for parts of this complex, including *Styriofelis*, *Hyperailurictis*, *Miopanthera*, *Schizailurus*, and *Pseudaelurus* itself. We will consider the validity and applicability of these in the discussion below. A fuller knowledge of the interrelationships within this group would go a long way towards an understanding of the evolutionary patterns of the Felidae.

Pseudaelurus is first recorded from Wintershof-West in Germany (MN 3, 20–18 Ma; Dehm 1950). Hence, it does not overlap stratigraphically with *Proailurus* in Europe. Several reviews of *Pseudaelurus* in Europe have been published in the past decades (Heizmann 1973; Ginsburg 1983; Rothwell 2003) and we refer to them for a fuller discussion of evolutionary details.

Four species of *Pseudaelurus* are known from Europe. In the order of increasing size they are: *P. turnauensis* (= *P. transitorius*), *P. lorteti*, *P. romieviensis*, and *P. quadridentatus* (type species of the genus). They range in size from a modern wildcat to a lynx or small puma. Differences between them, apart from



Figure 2.4 Artist's reconstruction of *Proailurus lemanensis*, the first cat. (Illustration courtesy of Mauricio Antón.)



Figure 2.5 Artist's reconstruction of *Styriofelis lorteti*, a member of the stem lineage leading to the extant Felidae, together with the flying squirrel *Petaurista* sp. (Illustration courtesy of Mauricio Antón.)

size, are minute (Heizmann 1973). The first species to appear is the smallest, *P. turnauensis* (Dehm 1950). However, all three remaining species appear in MN 4 (18–17 Ma). This indicates a rapid radiation of the *Pseudaelurus* grade, suggesting a monophyletic origin of at least European *Pseudaelurus* from a single species of *Proailurus*. *P. lorteti* and *P. romieviensis* become extinct at the end of the Middle Miocene (c. 11.6 Ma), but *P. quadridentatus* and *P. turnauensis* survive into the Late Miocene (MN 9, c. 11.2–9.5 Ma). They thus overlap stratigraphically with the earliest documented Machairodontinae (*Miomachairodus pseudailuroides* from Turkey; Schmidt-Kittler 1976; Viranta and Werdelin 2003) (Fig. 2.2, letter E).

Pseudaelurus is poorly known from Asia, possibly due to a relative dearth of Middle Miocene localities on the continent. Two Chinese species are known. Cao *et al.* (1990) describe *P. guangheensis* from Gansu and Wang *et al.* (1998) describe *P. cuspidatus* from Xinjiang. In addition, Qiu and Gu (1996) describe material referred to *P. lorteti*. All this material is Middle Miocene in age. What the relationship is

between the Chinese and European species has not been determined, nor has their relationship to the North American radiation of the grade.

The fossil record of *Pseudaelurus* in North America was recently reviewed by Rothwell (2003). There are five valid species: *P. validus* (stratigraphic range c. 17.5–16.5 Ma), *P. skinneri* (c. 17.5–17.1 Ma), *P. intrepidus* (c. 17.1–13.3 Ma), *P. stouti* (c. 15.2–12.7 Ma), and *P. marshi* (c. 16.4–12.7 Ma). Thus, *Pseudaelurus* appears later in North America and goes extinct sooner there than in Europe. This, and the cladistic analysis of Rothwell (2003), in which the three younger species (*P. intrepidus*, *P. stouti*, and *P. marshi*) form a clade with the two older species (*P. validus* and *P. skinneri*) as outgroups, are consistent with a single origin for North American *Pseudaelurus*.

Finally, a single record of *P. turnauensis* has been reported from Saudi Arabia (Thomas *et al.* 1982) in deposits now considered to be of MN 5 age (17.0–15.2 Ma). Material from Africa previously referred to *P. africanus* (Andrews 1914) is now referred to *Afrosmilus*, a barbourfelid (see Morales *et al.* [2001] and see below).

The endemic North American genus *Nimravides* undoubtedly originated from one of the above-mentioned North American species of *Pseudaelurus* (Baskin 1981; Beaumont 1990), probably *P. intrepidus* or *P. marshi*, which both have a prominent chin, also seen in *Nimravides* (Fig. 2.2, letter D). *Nimravides* differs from its putative ancestors only in relatively minor features: it has a more prominent chin, more elongated, serrated canines, a more reduced P4 protocone, and more developed P4 ectoparastyle. These are all features pointing towards a sabre-toothed morphology, not dissimilar to that seen in *M. pseudailuroides* and *Machairodus aphanistus* (see below), but evolved in parallel. Four species of *Nimravides* are known: *N. thinobates* (c. 11.0–9.6 Ma), *N. pedionomus* (c. 12.0–11.5 Ma), *N. hibbardi* (c. 7.0–6.4 Ma), and *N. galiani* (c. 11.6–10.7 Ma). Near the end of the Miocene, *Nimravides* became extinct, apparently without leaving descendant lineages. A North American felid of uncertain affinities that may possibly belong here is *Pratifelis martini* from the Late Miocene (c. 7–6 Ma) of Kansas (Hibbard 1934). This species has a distinctively enlarged m1 talonid and does not fit comfortably into any of the larger felid lineages.

Sabretooths

The further evolution of Felidae beyond the *Pseudaelurus* grade begins with *M. pseudailuroides* (Fig. 2.2, letter E). This taxon, which is at present known only from Turkey (Schmidt-Kittler 1976; Viranta and Werdelin 2003), has cheek teeth that are very similar to those of *P. quadridentatus*, but the upper canines are more flattened and have small crenulations on the mesial and distal faces that are not present in *Pseudaelurus* spp. (Schmidt-Kittler 1976, figs. 114a, 1c, 2, and 3, plate 5). In an important contribution, Schmidt-Kittler (1976) discusses the relationship between *M. pseudailuroides* and the *Pseudaelurus*-grade and how the morphological transition may have occurred. However, he does not pinpoint any specific relationships between taxa, nor does he extend his discussion to conical-toothed cats. *M. pseudailuroides* is at present known only from MN 7/8 and MN 9 (c. 12.5–9.5 Ma). The taxonomic status of the species and genus has been discussed several times. Beau-

mont (1978) made *Miomachairodus* a subgenus of *Machairodus*, and included *Machairodus robinsoni* from the early Late Miocene (c. MN 9) of Tunisia (Kurtén 1976) in the subgenus. On the other hand, Ginsburg *et al.* (1981) synonymized *M. pseudailuroides* with *M. aphanistus*, type species of the genus *Machairodus*. Morlo (1997) followed this, but suggested that *M. robinsoni* in that case be considered a separate genus. This discussion is far from settled, but at the very least shows that these forms grade into one another. Another early form about which there is taxonomic disagreement is *M. alberdiae* from MN 9 of Spain. Ginsburg (1999) considers this to be the most primitive *Machairodus*, but Morlo (1997) synonymizes it with *M. aphanistus*.

M. aphanistus was described by Kaup (1833) and was the first Miocene felid to be named. Its cranio-dental morphology was recently reviewed in detail (Antón *et al.* 2004). These authors found that the functional morphology of the killing bite in *M. aphanistus*, and characters related to this behaviour, were considerably more primitive than in later machairodonts from the Eurasian Late Miocene. They concluded that *Machairodus* should be restricted in content to Vallesian (c. 11.2–9.0 Ma) forms, while Turolian (c. 9.0–5.3 Ma) forms should be referred to *Amphimachairodus* (Fig. 2.2, letter F). Morlo and Semenov (2004) objected to this procedure, arguing that the evolution from *Machairodus* to *Amphimachairodus* was gradual and mosaic and that the two could not be generically distinct. However, making the distinction is taxonomically useful and in line with a trend in recent years of trying to restrict the usage of *Machairodus* to something other than a waste-basket taxon for any or all Miocene sabretooths (Beaumont 1978; Ginsburg *et al.* 1981; Ginsburg 1999).

Some time in the Vallesian, *Machairodus* probably migrated to North America, where it gave rise to *M. coloradensis* (c. 9.0–5.3 Ma). This is a fairly generalized species, similar to *M. aphanistus*. It is possible, if unlikely, that it evolved from the North American *Nimravides*. This would require extensive parallelism with *Machairodus*. The possibility has been noted before, however, and the generic name *Heterofelis* (Cook 1922) is available for this taxon.

The next stage in the evolution of the machairodont lineage is the genus *Amphimachairodus* (Fig. 2.2, letter G). This genus includes a number of closely

related species that morphologically lead up to the Plio-Pleistocene tribe Homotheriini (Fig. 2.2, letter H), which includes the genera *Homotherium*, *Dinobastis*, and *Xenosmilus*. *Amphimachairodus* includes the species *A. giganteus* (Eurasia; *c.* 9–5.3 Ma), *A. kurteni* (Kazakhstan; *c.* 7.1–5.3 Ma), *A. kabir* (Chad and Libya; *c.* 7–5.5 Ma), and possibly *A. irtyschensis* (Russia; *c.* 7.1–5.3 Ma), though the latter may be a synonym of *A. giganteus*. Closely related is also *Lokotunjailurus emageritus* (Werdelin 2003b; *c.* 7.4–5.5 Ma), which lacks a number of the derived cranial features of *Amphimachairodus*, but is dentally the most derived of the group. *A. giganteus* is, as the name implies, characterized by very large size, extremely long upper canines and a derived mastoid region relative to that of *Machairodus*, implying modifications to the killing bite. The mastoid region is further evolved in *M. kurteni* and *M. kabir*, but has not yet reached the condition seen in *Homotherium*. Dentally, the upper incisor arcade is modified and the cheek dentition progressively simplified, with reduction of p3/P3, complete loss of the m1 talonid, and nearly complete loss of the P4 protocone. The dentition of *L. emageritus* is very close to that of primitive *Homotherium*, but the skull and skeleton of the former preclude it from the direct ancestry of that genus (Werdelin 2003b). *L. emageritus* has an extremely enlarged dew claw (absolutely and relative to the other claws) on the manus and this feature appears to be present also in *Homotherium* (Ballesio 1963).

The evolution of *Machairodus* and *Amphimachairodus* is paralleled in the sabretooth group by the evolution of the genus *Paramachaerodus* (Fig. 2.2, letters J and K). At least two and possibly as many as four species of this genus are known: *P. ogygius* (*c.* 9–7 Ma), *P. orientalis* (*c.* 8–6 Ma), *P. indicus* (age uncertain), and *P. maximiliani* (*c.* 7–5.3 Ma) (Salesa *et al.* 2003). The latter two may be synonymous, with each other and with *P. orientalis*. *Paramachaerodus* is much smaller than *Machairodus* and (especially) *Amphimachairodus* (*Paramachaerodus* is leopard, rather than lion-sized or larger in the case of *Amphimachairodus*). Clearly, this genus and its larger relatives were dividing up the prey-spectrum by size, though the details of this are not yet understood. New material from the early Late Miocene of Spain is doing much to clarify the taxonomic, functional, and ecological

relationships between these Miocene sabretooths (Antón *et al.* 2004; Salesa *et al.* 2005).

A further lineage that is likely to at least in part belong among the sabretooths, despite lacking the typical craniodental attributes of this functional grade, is the tribe Metailurini (Fig. 2.6). This tribe as generally conceived includes the larger genus *Dinofelis* (Fig. 2.6a), with at least ten species (Werdelin and Lewis 2001), *Metailurus* (Fig. 2.6b), with at least four species, and *Stenailurus*, with one species (though the latter may be a synonym of *Metailurus*). *Dinofelis* is in many ways convergent on *Panthera*, but its evolution is not straightforward convergence. Instead, various species of *Dinofelis* are more or less pantherine-like, while the oldest and youngest species are the most sabretooth-like. The Metailurini is essentially a waste-basket for taxa that show some sabretooth features but can not be placed in either the *Machairodus* or the *Paramachaerodus* lineages. It is not clear that *Dinofelis* and *Metailurus* are closely related, nor what their respective antecedents are. Nor is it clear, although it seems likely, that *Metailurus* is a member of the subfamily

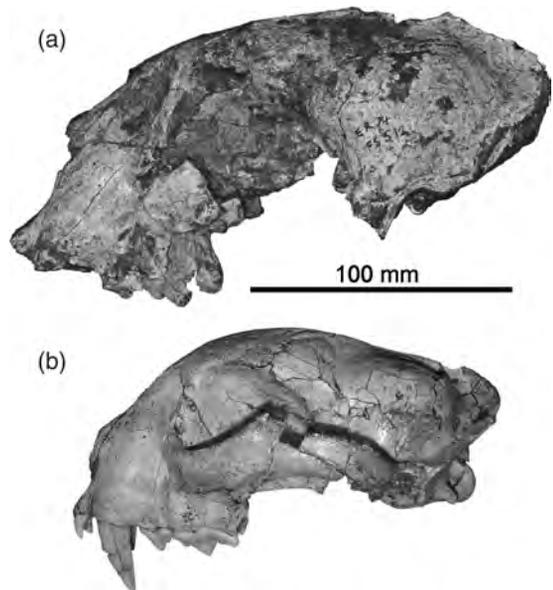


Figure 2.6 (a) Skull of *Dinofelis petteri*, KNM ER 2612 (holotype), Tulu Bor member, Koobi Fora Formation, Kenya; in left lateral view. (b) Skull of *Metailurus parvulus* PIU M3835, Locality 108, Baode Province, China; in left lateral view.

Machairodontinae (sabretooth cats). *Dinofelis*, however, shares several traits with derived sabretooths and can confidently be placed in this subfamily (Werdelin and Lewis 2001). Both of these genera originate in the Miocene and survive into the Plio-Pleistocene; *Metailurus* is mainly a Miocene genus, while *Dinofelis* has its main radiation in the Pliocene.

The Plio-Pleistocene sees the appearance of the two derived sabretooth tribes, Homotheriini and Smilodontini (Fig. 2.2, letters H and L; Fig. 2.7). The Homotheriini includes the genera *Dinobastis* (with at least one species, *D. serus*) and *Xenosmilus* (with one species, *X. hodsonae*) from North America and *Homotherium* (Fig. 2.7b) (with several species, including *H. crenatidens* and *H. problematicum*) from Eurasia

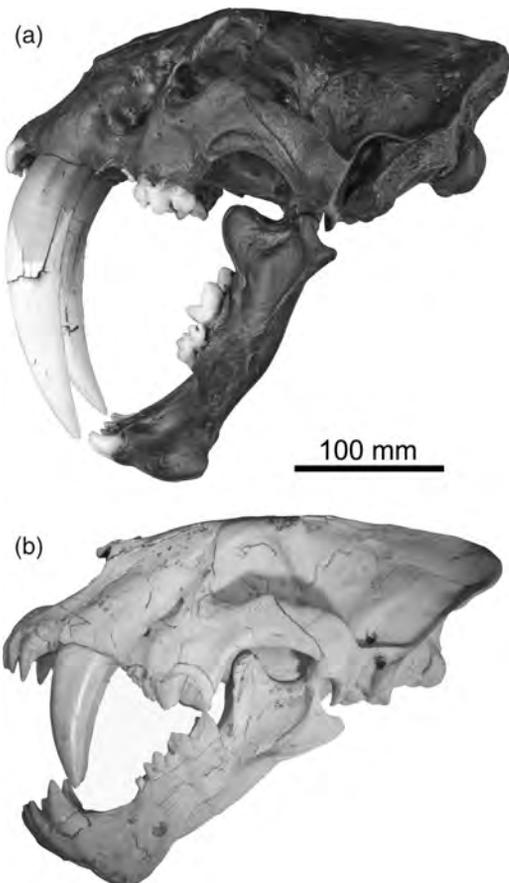


Figure 2.7 (a) Skull (cast) of *Smilodon fatalis* from Rancho La Brea, California, United States; in left lateral view. (b) Skull (cast) of *Homotherium* sp., unknown locality, China; in left lateral view.

and Africa. The relationships between these genera will be discussed below. The Smilodontini includes two genera: *Megantereon* (with at least five species: *M. cultridens*, *M. whitei*, *M. hesperus*, *M. falconeri*, and *M. ekidoit*) from Africa, Eurasia, and North America; and *Smilodon* (with three species: *S. gracilis*, *S. fatalis* [Fig. 2.7a], and *S. populator*) from North, Central, and South America.

Differences between Homotheriini and Smilodontini are substantial, both craniodentally and postcranially. The Homotheriini have relatively short, mediolaterally narrow upper canines with large crenulations on the anterior and posterior edges; their postcranial skeleton shows some adaptations to a cursorial lifestyle (except in *Xenosmilus*), with long, slender limbs and forequarters that are massive but not hyperdeveloped. The cheek dentition of Homotheriini is dominated by very large carnassials, which especially in *Homotherium* become larger in later forms, with the p4 also usurped into the cutting blade. The Smilodontini have very long, broad upper canines with minute serrations (lost in *Megantereon*). Their skeleton is very robust and the forequarters extremely massive. The cheek dentition is reduced, but the carnassials are not elongated to the extent seen in Homotheriini.

Conical-toothed cats

The conical-toothed cats, subfamily Felinae, comprise the common ancestor of all living cats and all of its descendants (Fig. 2.8). As the name implies, conical-toothed cats differ from sabretooths in having a more rounded canine cross-section. They are also united by a few other features, such as the relatively long lower canine. The interrelationships of the living members of this subfamily were discussed above. Their fossil history is much less well known than that of the sabre-toothed cats. This could be for three reasons: (1) they were predominantly adapted to environments in which fossilization is less likely than in the environments inhabited by sabre-toothed cats (i.e. the poor fossil record reflects a taphonomic bias; species that today occur in habitats in which fossilization potential can be considered fair [e.g. cheetahs and lynx], have a reasonably good fossil record, while species that today inhabit

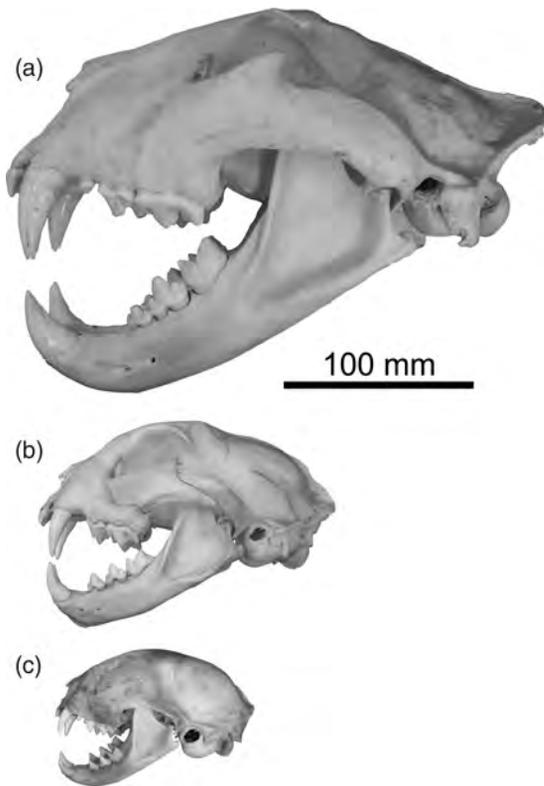


Figure 2.8 Skulls of extant Felidae in left lateral view: (a) Lion, *Panthera leo*; (b) Eurasian lynx, *Lynx lynx*; (c) Domestic cat, *Felis catus*.

tropical, wet forests [e.g. golden cats and clouded leopards] tend to have a very poor fossil record); (2) they were less common in the past than sabretoothed cats (i.e. the poor fossil record reflects a true pattern that is an outcome of a consideration of intra-familial competition between sabretoothed and conical-toothed cats); (3) they are more similar to each other in hard-tissue morphology than sabretoothed cats (i.e. the poor fossil record reflects a bias in investigator perception; there are great similarities between all conical-toothed cats in, for example mandibular morphology, a region in which sabretoothed cats exhibit a number of diagnostic differences). All three of these possibilities may be true to some extent. Finally, the poor fossil record of conical-toothed cats may also reflect the interests of researchers. Sabretooth cats are large, spectacular, and to some extent mysterious, at least as far as their feeding behaviour is concerned. Conical-toothed

cats are often small, nondescript and closely similar to living forms that are comparatively well known ecologically and functionally. Hence, the former receive far more attention in the palaeontological literature than the latter.

Only one researcher, Helmut Hemmer, has focused almost exclusively on the fossil record of conical-toothed cats, and it is thus from his work (e.g. Hemmer 1974, 1976; Hemmer *et al.* 2001, 2004) that most of the information on the fossil record of this group is to be gleaned. In the following section, the fossil record of conical-toothed cats will be outlined, following the scheme of eight major lineages as found in the molecular phylogeny (Fig. 2.1). Focus will be on the earliest members of each lineage and/or species.

Some early conical-toothed cats cannot with confidence be included in any of the eight lineages. These include the first '*Felis*', '*F. attica*', known from MN 11–MN 13 (c. 9.0–5.3 Ma) in western Eurasia. This species is a little larger than a wildcat. In morphology it is very similar to smaller species of *Pseudaelurus*, but it has a dentition that is reduced beyond the *Pseudaelurus* grade. It is noteworthy that the stratigraphic range of '*F. attica*' is younger than the estimated age of the base of the radiation of extant Felidae (Fig. 2.1), so that it may belong within that radiation rather than to the stem lineage. The same is true of '*F. christoli*', another primitive cat, known from MN 13–MN 14 (c. 7.1–4.2 Ma) of Spain and France. In addition, there are significant collections of Late Miocene small cats from China that remain undescribed. This material may answer some questions regarding the early evolution of extant cats.

The clade with by far the best fossil record is the *Panthera* lineage. Despite this, it is also the clade with the longest ghost lineage (cladistically inferred lineage undocumented by fossils). According to molecular data (Johnson *et al.* 2006b) this lineage split off from the Felidae stem lineage about 10.8 Ma. However, the oldest fossils unequivocally assigned to the lineage are no older than 3.8 Ma (Barry 1987; Werdelin and Dehghani, in press), leaving a ghost lineage that is nearly twice as long as the documented lineage. The earliest fossil *Panthera* from Laetoli belong to two species: a lion-sized one and a leopard-sized one. They have been suggested to belong to the

extant species (Turner 1990), but in fact differ from them morphologically (Werdelin and Dehghani, in press). The molecular dates suggest that they may belong to the stem lineage of these species and there is nothing in the fossils that would suggest otherwise.

The first definite lions are from Olduvai, Bed 1 (<2 Ma), which is also in line with the molecular data. The subsequent fossil history of lions is well known, with dispersal out of Africa across Eurasia and into North (and possibly South) America. These developments have been discussed by numerous people (Vereshchagin 1971; Hemmer 1974; Burger *et al.* 2004; Yamaguchi *et al.* 2004a). It is not until the middle Pleistocene that lions significantly extend their range outside Africa, and by about 500 ka they are found throughout Europe and parts of Asia north and east of the Black and Caspian Seas. By 300 ka their range had extended to encompass most of northern and eastern Asia except for the south-east and southern China, possibly due to competition with tigers (although this cannot be verified in the fossil record). At about this time, lions probably crossed the Bering Strait into North America, where they are known from Illinoian (<310 ka) and later deposits. In the Sangamonian, after the retreat of the Illinoian glaciers, lions could spread further into North America and, arguably, also northern South America. Lions became extinct in the Americas and large parts of Asia at the end of the latest glaciation. Further range contraction occurred in historic times.

Lion taxonomy has long been controversial. Some authorities place all fossil lions in the modern species, *P. leo*, while others recognize a number of extinct species, for example *P. spelaea*, the cave lion, and *P. atrox*, the North American lion. Burger *et al.* (2004) analysed mtDNA cytochrome *b* sequences of some cave lions and found them to form a monophyletic clade distinct from living lions. Until more data from a broader range of fossil lions have been studied, the question of whether lions conform better to a one-species or a multiple-species model must remain open.

The other members of the *Panthera* lineage are less well known in the fossil record and some aspects of their evolution are at present controversial. The characters linking fossils with extant species are often of

uncertain value and the material commonly limited. The snow leopard, *P. uncia*, and clouded leopard, *N. nebulosa*, are, for example, only known from isolated fossil teeth, and it is doubtful whether this is sufficient for specific attribution.

The jaguar, *P. onca*, has been traced back to the 'European jaguar', *P. gombaszoegensis*, which is considered by some to be a subspecies of the extant species (Hemmer *et al.* 2001). If *P. toscana* can be included in this species, as suggested by Hemmer, it is first known from the latest Pliocene and survived into the Middle Pleistocene. During this time it was mainly distributed across western Eurasia.

The earliest leopards, *P. pardus*, are known from Africa. As noted, Laetoli (c. 3.8–3.4 Ma) includes a leopard-sized pantherine. Hemmer *et al.* (2004) have suggested that these remains should be referred to the *Puma* lineage, but the fossils provide no support for this hypothesis (Werdelin and Dehghani, in press). The oldest unequivocal leopards in Africa are from about 2 Ma, and the first leopards appear in Eurasia about 1 million years later.

Tiger remains are known from the Lower Pleistocene of South-east Asia (Kurtén, 1962). However, the oldest member of the tiger lineage is generally considered to be *P. palaeosinensis* (Fig. 2.9) from (probably) Upper Pliocene sediments in northern China (Zdansky 1924). However, renewed study (Christiansen 2008) indicates that its specific relationship to tigers is tenuous at best. Metrically, the specimen is not particularly close to any extant *Panthera*. It is generally agreed that fossil tigers have not been

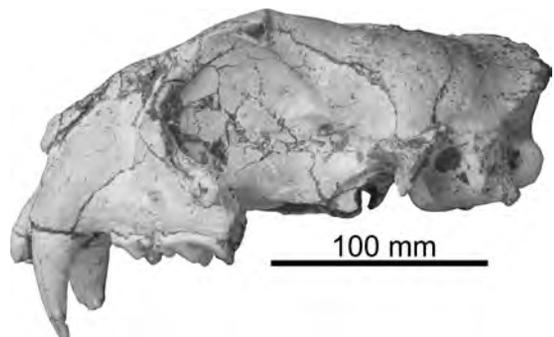


Figure 2.9 Skull of *Panthera palaeosinensis*, PIU M3654 (holotype), one of the earliest fossil *Panthera*, in left lateral view.

recorded outside Asia (but see Herrington 1987; Groiss 1996).

The bay cat lineage is not known with certainty in the fossil record. The *Caracal* lineage is represented in the fossil record by specimens dating back c. 4 Ma. These specimens group into two distinct size classes, large and small. Given the molecular ages of these lineages, these may represent members of the caracal/golden cat stem lineage and serval stem lineage, respectively. Whether any or all of the fossils, which are known from a number of sites in eastern and southern Africa, are conspecific with the extant forms is not determinable on the basis of the available material, which consists mainly of isolated teeth and fragmentary jaws. An intriguing recent suggestion is that '*Felis*' *issiodorensis*, a species generally referred to the genus *Lynx* (Werdelin 1981) should instead be referred to *Caracal* (Morales *et al.* 2003b). This conclusion is based on the observation that the metric analyses of Werdelin (1981) showed that specimens identified as belonging to *L. issiodorensis* were more similar to specimens of *Caracal* than to specimens of *Lynx*. This possibility deserves further study, but it is well to remember that it is just as likely that the similarities between *Caracal* and *L. issiodorensis* are shared ancestral characters.

The fossil record of the ocelot lineage is relatively poor. This record has recently been reviewed by Seymour (1999) with updates by Prevosti (2006). The South American record of the group is limited, and with the exception of some remains of *Leopardus colocolo* from Argentina in sediments dating as far back as c. 0.5–1 Ma, and the enigmatic '*Felis*' *vorohuensis* of about the same age, all records are latest Pleistocene in age. North American fossils unequivocally referable to this lineage are also from the Late Pleistocene (Werdelin 1985). The inferred age of the radiation of the extant taxa at c. 2.9 Ma (Fig. 2.1) is younger than previous estimates and compatible with a radiation from a single immigration event into South America (Werdelin 1989). However, this leaves a long ghost lineage back to the reconstructed age of the node leading to this group at c. 8.0 Ma. A number of North American taxa have been proposed at one time or another as members of this ghost lineage, including '*F.*' *lacustris*, '*F.*' *rexroadensis*, '*F.*' *longignathus*, and '*F.*' *proterolyncis* (e.g. Werdelin 1985; Seymour 1999). The first of these is likely to belong to the

Puma lineage, but the relationships of the others are unclear. They may belong to the *Lynx* or ocelot lineages, or be on the backbone of the phylogeny between them. The earliest members of several of these taxa are Late Miocene (c. 7–6 Ma) in age.

The short phylogenetic distance between the ocelot and *Lynx* lineages may explain why several taxa mentioned above could be assigned to either. The genus *Lynx* is well represented in the fossil record, both in Eurasia and North America (Werdelin 1981). In light of the above, it is likely that the earliest fossil members of the lineage are Late Miocene in age. The earliest record of unequivocal *Lynx* in the fossil record has been considered to be *L. issiodorensis* from the Pliocene and Pleistocene of western Europe (but see the opinion of Morales *et al.* [2003a], as discussed above). This species is not, however, found on the African continent as previously suggested (Hendey 1974; Werdelin 1981). The only record of the genus on that continent is the Pleistocene *L. thomasi* from Morocco (Geraads 1980).

The *Puma* lineage has a long, if uneven, fossil record. The oldest fossils unequivocally belonging to this lineage are specimens referred to *Acinonyx* sp. from Laetoli (c. 3.8–3.4 Ma) (Barry 1987; Werdelin and Dehghani, in press). These specimens are about the size of the modern species but differ slightly in morphology. The cheetah subsequently has a continuous though sparse fossil record in Africa. The genus *Acinonyx* has a long history in Eurasia. The 'giant' species *A. pardinensis* appeared in western Europe a little over 3 Ma. This form is also found in China (as *A. pleistocaenicus*) and India (as *A. brachygnathus*). It was about the size of a small lion, though considerably lighter. In most other respects it displayed typical characters of *Acinonyx*, though the skull does not show the extreme vaulting seen in *A. jubatus*. During the later Pliocene there is a marked size reduction in Eurasian cheetahs, leading Thenius (1953) to describe the younger form as a separate species, *A. intermedius*. However, some Pleistocene specimens are as large as the Pliocene ones and we agree with Viret (1954) and Kurtén (1968) that the difference probably does not warrant specific separation. The Eurasian cheetah became extinct in the early Middle Pleistocene. The North American 'cheetah', *Miracinonyx*, with two species, *M. inexpectatus* and *M. studei* (Adams 1979; Van Valkenburgh *et al.* 1990), is not the sister taxon to *Acinonyx* (Barnett *et al.* 2005).

Instead, it apparently evolved its cheetah-like features independently, from puma-like ancestors. The oldest members of this lineage are *c.* 2.5 Ma. However, the oldest '*F. lacustris*' is somewhat older than this. An interesting specimen of about the same age is the *Felis* sp. of Gustafson (1978) from the Blancan of Oregon, which may also belong to this lineage. The presence of *Puma* in Europe has also been suggested, in the form of *P. pardoides* (Hemmer *et al.* 2004). The oldest of this material is of Pliocene age and may be the oldest material of *Puma* on record. The suggestion that *Puma* is present at Laetoli is hardly tenable, however (Werdelin and Dehghani, in press). The oldest fossil jaguarundi is less than 0.5 Ma.

The leopard cat lineage is very poorly known in the fossil record. A few fossils probably pertaining to this lineage and possibly to *Prionailurus bengalensis* have been found in Middle Pleistocene sites in South-east Asia (Hemmer 1976). In addition, fossils tentatively referred to *O. manul* have been recorded from Kamyk, Poland (Kurtén 1968). These may be more than 1 Ma.

The fossil record of the domestic cat lineage is not poor, but much of it is hidden beneath the general designation of *Felis* sp., since the species are all but indistinguishable on the basis of incomplete remains. The oldest '*Felis* sp.' that definitely belongs to this lineage is from Kanapoi, Kenya, dated to >4 Ma (Werdelin 2003a). If the molecular dates are correct, this material belongs to a member of the stem lineage of *Felis*. Further specimens belonging to this lineage occur intermittently in the African fossil record. A species of some interest that may be the oldest member of the *F. silvestris* group is *F. lunensis* from Europe. This species goes back at least to the Early Pleistocene and possibly to the Late Pliocene. Specimens referable to *F. chaus* have been found in Holocene strata of Java (outside the modern range of the species; Hemmer 1976). No specimens definitely referable to *F. nigripes* or *F. margarita* have been found in the fossil record.

Barbourofelidae

Finally, we must touch upon the family (or subfamily) Barbourofelidae (Fig. 2.2, letter N), which consists of a number of derived sabre-toothed forms (though not all may be sabre-toothed—see below). Traditionally, they have been seen as Neogene members of the

Nimravidae, a group that itself has been the subject of much phylogenetic discussion. The nimravids were once known as 'paleo-felids' because of their felid-like craniodental morphology. They are known from the Late Eocene to Late Oligocene of North America and Europe and include genera such as *Nimravus*, *Hoplophoneus*, and *Eusmilus*. Studies of basicranial morphology have, however, clearly shown that nimravids are not felids (Neff 1983; Hunt 1987). They are therefore placed in the family Nimravidae. In its original conception, Nimravidae also included the barbourofelids, Miocene sabretooths with representatives both in North America and Europe (Schultz *et al.* 1970). These, however, have a basicranial morphology, including an ossified bulla, that differs from those in both Nimravidae and Felidae. Therefore, Morales *et al.* (2001) proposed removing them from the Nimravidae and placing them as the subfamily Barbourofelinae within the Felidae. This proposal was amended by Morlo *et al.* (2004), who proposed raising Barbourofelinae to full family status as the Barbourofelidae, which is the path followed here. The Nimravidae are likely to be basal Carnivora, while the Barbourofelidae are either the sister-group to Felidae or the sister-group to other Aeluroidea (Fig. 2.2, letter N). Because of their phylogenetic and ecomorphological closeness to Felidae, their fossil record is outlined here.

In Africa, the likely centre of origin of Barbourofelidae, the family is known from a number of genera (Morales *et al.* 2001; Morlo *et al.* 2004). *Afrosmilus* has two east African species, *A. africanus* (Fig. 2.10) and *A. turkanae*, both *c.* 18–17 Ma. *Ginsburgsmilus*, the most primitive member of the family, has a single

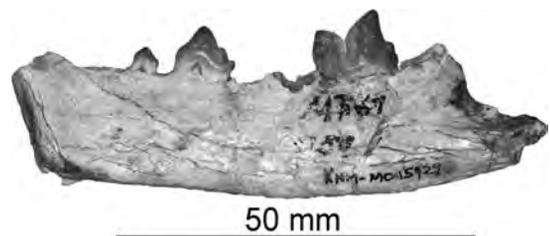


Figure 2.10 Left horizontal mandibular ramus of *Afrosmilus turkanae*, KNM MO 15929, Moruorot, Kenya, a barbourofelid. Note the well-developed metaconid at the posterior end of the tooth—a diagnostic difference between Barbourofelidae and Felidae (Morlo *et al.* 2004).

east African species, *G. napakensis* (c. 20.5–17 Ma). *Syrtosmilus* with one species, *S. syrtensis* (c. 19–15 Ma), and *Vampyrictis* with one, *V. vipera* (c. 12.5–9.5 Ma), are North African representatives of the family.

In Europe, Barbourofelidae is known from several genera, *Prosansanosmilus*, with two species, *P. peregrinus* (MN 4, c. 18–17 Ma) and *P. eggeri* (MN 5, c. 17–15.2 Ma), *Sansanosmilus* with two species, *S. palmidens* (Fig. 2.11) (MN 5–MN 7/8, c. 17–11.2 Ma) and *S. jourdani* (MN 6–MN 9, c. 15.2–9.5 Ma), and *Afrosmilus* with one European species, *A. hispanicus* (MN 5, c. 17–15.2 Ma). These show a temporal progression towards larger and more sabretooth forms, though they are generally less extreme in their adaptations than the North American *Barbourofelis* spp. *Sansanosmilus* is also known from the Middle Miocene of China, though it is less common there than in Europe.

In North America, the Barbourofelidae consists of the single genus *Barbourofelis*, with five species, *B. fricki* (c. 10 Ma), *B. loveorum* (c. 11–9.8 Ma), *B. morrisi* (c. 11.5 Ma), *B. osborni* (c. 11.5 Ma), and *B. whitfordi* (c. 12–11.5 Ma). They are all extreme sabretooth ecomorphs, with long sabres, large mental flanges and short, stout limbs (where known).

Finally, two species from southern Africa must be mentioned, *Diamantofelis ferox* (the size of a small puma) and *Namafelis minor* (lynx-sized) (Morales *et al.* 1998, 2003a). Both are from the late Early–

earliest Middle Miocene of Arrisdrift, Namibia (c. 17–15.2 Ma). These species are not, as far as is known, sabre-toothed in morphology, as neither has a squared-off symphyseal region, but they do share other mandibular and dental features with species of *Afrosmilus*. *D. ferox* has a short and deep mandible, while that of *N. minor* is longer and more slender. The oldest true felid from Africa is a small specimen from Songhor, Kenya (c. 18–17 Ma), probably referable to *Pseudaelurus sensu lato*. Thus, since Felidae is rare or non-existent in Africa at this time, whereas Barbourofelidae is known from a number of sites and regions, and given the morphological similarities between them, it should at least be considered whether the Arrisdrift species might be ‘conical-toothed’ barbourofelids.

The Barbourofelidae was a relatively short-lived group (c. 20.5–9.5 Ma), within which the vast majority of species were specialized sabretooths. Their extinction in the early Late Miocene may be tied to the spread of sabre-toothed Felidae at this time.

Discussion

In this section, we will attempt to draw some conclusions from the review above. We advocate the use of generic names for fossils that maximizes the number of monophyletic taxa by splitting up at least those genus-level groups that are obviously para- or polyphyletic. In so doing we hope to create a more consistent framework for future studies. Unfortunately, many of the assertions made in the following discussion are at present untested, though we hope that it will be possible to test them in the future. We aim to erect a series of hypotheses to establish the basic level of understanding of felid evolution, that of interrelationships. When the interrelationships of fossil felids have been better established, a foundation for the understanding of the ecological, biogeographical, and functional patterns of felid evolution will have been laid, in much the same way as the current phylogeny of living felids provides such a foundation for study of their radiation.

We will also point out areas where we know too little, which is especially true of the fossil record of the living felids, which at present has not much to contribute to an understanding of the modern



Figure 2.11 Artist's reconstruction of the head of *Sansanosmilus palmidens*, a barbourofelid. (Illustration courtesy of Mauricio Antón.)

radiation. Johnson *et al.* (2006b) estimate that fossil representation in the modern cat radiation is about 24%, leaving large areas unknown (cf. Fig. 2.1). Fig. 2.2 provides a graphical summary of the discussion in the following section.

Early cats

The origins of the family Felidae are relatively uncontroversial, though that may merely be because the gap between the earliest unequivocal felids and their ancestors among Carnivoramorphia is relatively substantial. Thus, *Proailurus* is unquestionably a felid and *Stenogale* and *Haplogale* are likely to belong to this family as well. All of these genera are undoubtedly closer to crown group Felidae than is the extant sister taxon, *Prionodon*. Aspects of this early evolution are covered by Hunt (1998) and Peigné (1999) and require no further elaboration here.

The subsequent radiation of Felidae in the Early–Middle Miocene is far more complex, however. The genus *Pseudaelurus* comprises 11 named species, 4 from Europe and Arabia, 2 from China, and 5 from North America. Unanswered questions surrounding this radiation include: Does *Pseudaelurus* have a single origin? What are the interrelationships of the European species to each other? What is the relationship between Chinese and European species? From which species did North American *Pseudaelurus* originate? Which species of *Pseudaelurus* belong to which lineages of later, more derived felids?

Answers to some of these questions have been proposed in the past, whereas some have rarely been discussed, if at all. An example of the latter is the first question raised above: Does *Pseudaelurus* have a single origin? This has tacitly been assumed in discussions of felid evolution in the past. However, the data in favour of this hypothesis are largely circumstantial. The presumed ancestor, *Proailurus*, has a limited geographic distribution and *Pseudaelurus* from Europe is older than *Pseudaelurus* on other continents, arguing for a single origin and subsequent dispersal. There is, on the other hand, no phylogenetic framework in which this has been demonstrated to be the most parsimonious hypothesis. It is certainly also possible that different species of *Proailurus* or related genera gave rise to different

species of *Pseudaelurus*, rendering the latter polyphyletic. The Ginn Quarry felid discussed above (Hunt 1998) makes such a scenario more plausible. At present, there does not seem to be any way to resolve this issue definitively and the monophyletic origin of *Pseudaelurus* is assumed here as a working hypothesis.

On the other hand, *Pseudaelurus* is undoubtedly paraphyletic, with different species groups giving rise to different descendant taxa. The paraphyletic nature of *Pseudaelurus* has been recognized for a long time, though perhaps the first to do so explicitly was Kretzoi (1929b), and this was also implicitly acknowledged by Viret (1951) before being elaborated on by Beaumont (1964, 1978). Beaumont (1964), like Kretzoi before him, split *Pseudaelurus* into a number of genera at the bases of several subsequent radiations. Though Beaumont (1978) reduced these to subgenera, his Figure 2 remains the fullest envisioning of felid evolution to this day. If we ignore the subgenera, he split *Pseudaelurus* into three genera: *Pseudaelurus* (Gervais 1850, type species *P. quadridentatus*), *Schizailurus* (Viret 1951, type species *P. lorteti*), and *Hyperailurictis* (Kretzoi 1929b, type species *P. intrepidus*). The first-mentioned includes only the type species, while the second includes *P. turnauensis* in addition to *P. lorteti*. The third includes all North American species of *Pseudaelurus* listed above. However, it should be noted that *Schizailurus* is an objective junior synonym of *Miopanthera* Kretzoi (1938) (based on the same type species), and this, in turn is a subjective junior synonym of *Styriofelis* Kretzoi (1929a; type species *F. turnauensis*). Thus, the latter name is the senior valid synonym and is used here.

Beaumont (1978) places *Pseudaelurus* at the base of the radiation of sabre-toothed cats, *Styriofelis* at the base of the radiation of conical-toothed cats, and *Hyperailurictis* at the base of the North American radiation, as well as the radiation of ‘intermediate’ forms such as *Metailurus*, *Stenailurus*, and *Dinofelis*. The radiation of these three genera takes place at letter B in Fig. 2.2. The evidence for this scenario is not particularly strong, as it is based mainly on the somewhat more sabretooth-like characteristics of *P. quadridentatus*, as opposed to the clearly conical-toothed features of *Styriofelis lorteti* and *Styriofelis turnauensis*. Although the generic separation between

these taxa has generally not been considered in reviews of *Pseudaelurus*, (Heizmann 1973; Ginsburg 1983), the separation has been implicitly acknowledged by several other workers (e.g. Morlo 1997). The status of the North American pseudaelurines (*Hyperailurictis*) as a distinct, generic-level clade is somewhat more secure, as these species are relatively derived, very similar to each other, and also very similar to their presumed descendant *Nimravides*.

This scenario provides possible answers to several of the questions posed above, apart from the question of the relationship of *Pseudaelurus* to later, more derived felids. Among European 'Pseudaelurus', *S. lorteti* and *S. turnauensis* are closely related and more distant from *P. quadridentatus* (the status of *P. romieviensis* is unclear). The North American *Hyperailurictis* did not evolve from any of them, though it may be related to one or both of the Chinese species. It is more likely, however, that *Hyperailurictis* descended from a felid similar to the Ginn Quarry felid described by Hunt (1998). The wholly unanswered question is the relationship between European and Chinese pseudaelurines.

A reasonable consensus, however, is that *Styriofelis* gave rise to the radiation of modern cats (Fig. 2.2, letter C). Aside from *S. lorteti* and *S. turnauensis*, no species definitely belonging to the stem lineage are known (but see *Felis attica* and see below).

In North America there is little doubt that *Hyperailurictis* gave rise to *Nimravides* (Fig. 2.2, letter D). Whether the former is mono- or paraphyletic is not known at this time. If it is paraphyletic, further nomenclatural complications may arise, but these need not concern us here. *Nimravides* seems to have gone extinct without leaving descendants, though it is just possible that *M. coloradensis* evolved from this genus rather than being an immigrant from Eurasia. The close similarity between *M. coloradensis* and the Eurasian early Late Miocene *M. aphanistus* argues against this, however.

The relationship between *Hyperailurictis* and *Dinofelis*, *Metailurus* and *Stenailurus* is far less well established and is not followed here. These genera are usually grouped together as the Metailurini, though the monophyly of this tribe has not been satisfactorily demonstrated. This is clearly an Old World group, with the evolution of *Metailurus* centred in Eurasia and that of *Dinofelis* in Africa. This presents

some biogeographic problems for an origin from *Hyperailurictis* in North America as suggested by Beaumont (1964, 1978). It is very tempting instead to associate this group with the Chinese pseudaelurines, though these are so poorly known that this remains pure speculation at present. Here we will consider the Metailurini to belong to the sabretooth cats (but see below), and thus a part of the radiation at letter E of Fig. 2.2.

Upper Miocene to Pleistocene cats

Pseudaelurus, sensu stricto, gave rise to the radiation of sabretooth cats that first appeared in the late Middle Miocene of Eurasia (and possibly Africa) and spread across the world in the Late Miocene (Fig. 2.2, letter E). There has been much controversy surrounding sabretooths (subfamily Machairodontinae) and considerable confusion regarding taxonomy and the allocation of specimens ever since Cuvier (1824) placed the first sabretooth specimens in the genus *Ursus*. Numerous genera and species have been named over the years and the course of evolution of the group has been poorly understood. Part of the problem has been the focus on *Smilodon*, a late and highly derived sabretooth, as the exemplar species in discussions of the functional morphology and evolution of the group (e.g. Bohlin 1940; Simpson 1941; Miller 1969; Akersten 1985). However, considerable progress in understanding these issues has come in recent years with the study of the excellently preserved material from the carnivore trap site of Batallones-1 in the Cerro de Batallones, Spain (e.g. Antón *et al.* 2004; Salesa *et al.* 2005). These studies show that the functional morphology of sabretooths was not uniform across taxa, evolved over time, and is compatible with a gradual origin from *Pseudaelurus*-grade forms.

Nevertheless, numerous questions regarding the systematics and evolution of sabretooth cats remain. Some of these are: What is the relationship of *Dinofelis* and *Metailurus* to Machairodontinae? What are the evolutionary patterns within the paraphyletic *Amphimachairodus* group? What is the relationship between *Homotherium* and *Dinobastis*? How did the Smilodontini evolve and which taxa are their

ancestors? What did sabretooths feed on and how? How and why did sabretooths become extinct?

The relationship of *Dinofelis* and *Metailurus* to Machairodontinae (and to each other) has always been controversial. Some authors, (e.g. Beaumont 1978; Werdelin and Lewis 2001), have considered them to be members of the Machairodontinae with slight to moderate sabretooth adaptations, while others (Kretzoi 1929b; Hendey 1974) have considered them to be conical-toothed cats with a tendency to develop sabretooth adaptations. The main feature they share with Machairodontinae is a reduced lower canine relative to the upper canine. *Dinofelis* further shares with Machairodontinae a deep groove or pit supero-medial to the trochlear notch of the ulna (Werdelin and Lewis 2001). This feature seems not to be present in *Metailurus* (Roussiakis *et al.* 2006). Thus, it appears likely that *Dinofelis* belongs in the Machairodontinae, but the position of *Metailurus* is equivocal. This also, of course, makes the relationship between the two genera uncertain. Thus, the position of this group at letter J of Fig. 2.2 is problematic, as is the placement, even existence, of the node at letter M.

Amphimachairodus is clearly paraphyletic, as *Homotherium* evolved from within this species group. This is reflected in the intermediate position of letter G (Fig. 2.2), between letter F where *Amphimachairodus* splits off from a similarly paraphyletic *Machairodus*, and letter H, at the base of the monophyletic Homotheriini. What is not clear is exactly which species gave rise to Homotheriini (Fig. 2.2, letter H). *L. emageritus* from Kenya has a more derived dentition than any species currently assigned to *Amphimachairodus*, but is too primitive in other respects and too derived in a few to be the ancestral taxon. Of the species of *Amphimachairodus*, *A. kurteni* seems the most derived dentally, but *A. kabir* (if the material from Sahabi belongs there; cf. Sardella and Werdelin 2007) has the most derived mastoid region. Whichever of these (or some as yet unknown taxon) is ancestral to *Homotherium*, *Amphimachairodus* as presently conceived becomes paraphyletic. To resolve this issue, the detailed relationships of *Amphimachairodus* spp. need to be better understood.

The relationship between *Homotherium* and *Dinobastis* (and *Xenosmilus*) is particularly interesting (Fig. 2.2, letter I). Traditionally, they are synonymized in the genus *Homotherium* (Turner and Antón

1997). However, early North American homotheriines such as that from the Delmont Local Fauna, South Dakota (Martin and Harksen 1974) (c. 2.9–2.6 Ma) differ considerably from contemporary forms in Eurasia (see, e.g., Ficarelli 1979), suggesting a long, separate evolution. In addition, *Homotherium* and *Dinobastis* differ in a number of aspects of their morphology. As an example, the upper canine of *Dinobastis* is smaller than that of *Homotherium* in specimens of approximately equal skull size (Werdelin and Sardella 2006, plate 1, fig. 1). This is an area that deserves further in-depth study.

Regardless of which species in the *Amphimachairodus* group is closest to *Homotherium*, it is nearly universally acknowledged that there is, broadly conceived, an ancestor–descendant relationship between the two genera. However, the origins of the other major Plio-Pleistocene sabretooth lineage, the Smilodontini (Fig. 2.2, letter L), is much less clear. This group consists of the genera *Megantereon* and *Smilodon*, which share features such as reduced or absent serrations on the teeth and extremely long and relatively mediolaterally broad upper canines compared to Homotheriini (the latter probably a plesiomorphic feature). It is tempting to associate them with the other Miocene sabretooth lineage, *Paramachaerodus* (Turner and Antón 1997) (Fig. 2.2, letter K), but the morphological distance between that genus and Plio-Pleistocene Smilodontini is considerable and the hypothesized relationship is not based on any clear synapomorphies. Another question germane to this issue is the difference between Smilodontini and Homotheriini: why is it there and what does it mean for the functional morphology and ecology of the respective groups? One answer would be that the former were closed-habitat taxa and the latter open-habitat taxa, but can such a simplistic view be maintained? Martin (1980) and Martin *et al.* (2000) discuss some of these questions, but more research needs to be done on the functional differences between Homotheriini and Smilodontini, and in particular on the latest Miocene species of *Paramachaerodus* (*P. orientalis* and *P. maximiliani*), to understand their ecology and feeding behaviour, and whether these can be directly related to those of Smilodontini.

The extinction of Homotheriini and Smilodontini occurs at different times on different continents. In

Africa, both *Homotherium* and *Megantereon* became extinct some time before 1.4 Ma (with *Dinofelis* lingering on another 500 ka). In Europe, *Homotherium* became extinct at c. 0.5 Ma (the recent record of a Late Pleistocene *Homotherium* from North Sea sediments [Reumer *et al.* 2003] needs to be corroborated by further material before its implications can be fully assessed) and *Megantereon* at c. 1 Ma. In North America, on the other hand, both tribes survive into the latest Pleistocene, with the last occurrence of *Dinobastis* from Friesenhahn Cave (Texas) at c. 11,000 BP and the last occurrence of *Smilodon* from Rancho La Brea (California) at c. 13,000 BP. We don't fully understand why these dates differ so much between continents. The differences may reflect the different first appearance datums on each continent of advanced hominid competitors in sufficient numbers to affect the populations of sabretooths, through direct or indirect competition for resources. Or they could be the result of major faunal changes on each continent brought about by human interference, climatic change, or a combination of the two. In building and testing these scenarios, it is also important to consider the conical-toothed cats and their impact on their sabretooth competitors, for example, the relatively rapid range expansion of lions from Africa through Eurasia during the Middle–Late Pleistocene (Yamaguchi *et al.* 2004a), understanding of which has been hampered by the poor fossil record of the conical-toothed cats.

Possibly no subject in mammal palaeontology has been more debated than that of sabretooth feeding adaptations. How did they use their canines? What did they feed on? What was their killing behaviour like? Questions like these have been posed and answered numerous times since sabretooths were first discovered (see Kitchener *et al.*, Chapter 3, this volume). To answer these questions, it is important to realize that this ecomorphology is not restricted to felids and their carnivoran relatives among nimravids and barbourfelids. The package (with variations) is also present in some creodonts, an extinct order of mammals that lived from the Paleocene to the Miocene (genera *Apataelurus* and *Machaeroides*, Early–Middle Eocene of North America), in marsupials (genus *Thylacosmilus*; Miocene–Early Pleistocene of South America) and in various groups of synapsid 'reptiles' of the Late Palaeozoic, for example, Gorgo-

nopsia (Kemp 2004). Despite this, it is among felids, nimravids, and barbourfelids that the adaptation appears to have been most successful. Recent work on early felid sabretooths (Salesa *et al.* 2003; Antón *et al.* 2004; Salesa *et al.* 2005) has begun to close the functional gap between sabre-toothed and conical-toothed cats. This and other lines of evidence, such as the meandering evolutionary history of *Dinofelis* from more sabretooth to less sabretooth and back (Werdelin and Lewis 2001), suggest that the ecomorphology of the feeding apparatus in felids is more of a continuum than a dichotomy. The implications of this for understanding the ecology of sabretooths and competition between sabretooths and conical-toothed cats are in need of detailed investigation.

One possible implication of the feeding apparatus of sabre-toothed and conical-toothed cats being on a continuum is that there may have been more direct competition between the two groups than previously thought. Previous models tend to emphasize the difference, with sabretooths specializing in larger prey than similar-sized conical-toothed cats. However, more recent analyses suggest that perhaps the two groups focused on very similar prey. In Africa, sabretooths are fairly common fossils and conical-toothed cats rare until around the time when the number of fossils of sabretooths decreases (Werdelin and Lewis 2005). This can be explained if sabretooths were dominant in the most commonly sampled habitats and competitively excluded conical-toothed cats. Support for such an idea can be found at Laetoli. This site (or at least the Laetolil Member, Upper Beds) is unique among eastern African sites in not being near a large body of standing water. It is also unique among sites in having a large number of fossils of conical-toothed cats and very few fossils of sabretooths. Further research on competition between sabretooths and conical-toothed cats is needed, as is research on the competitive structure of the carnivore guild as a whole.

The single most important issue impeding an increased understanding of the evolution of conical-toothed cats is the extensive ghost lineage between the oldest fossil members of the *Panthera* lineage and the common ancestor of all Felinae. Two explanations for this gap in the fossil record immediately spring to mind: a poor fossil record in the earliest Pliocene and the possibility that the

Panthera lineage (and the Felinae as a whole) evolved in an environment that is not conducive to the process of fossilization. Both of these factors are undoubtedly in play, but it is hard to escape the impression that pantherines are present in the fossil record prior to 4 Ma, but that they are misidentified for as yet unknown reasons. To either identify these fossils or explain why they have not been found is the most pressing issue in felid palaeontology and evolution and without progress here it will not be possible to move towards a fuller reconciliation of the fossil record with the molecular evidence for felid evolution as presented by Johnson *et al.* (2006b).

The position of Barbourfelidae is, of course, very uncertain, since there is no consensus at present on how closely related it is to the Felidae. Here, we have opted for the view that it split off from the stem lineage leading to Felidae after *Prionodon* but before the evolution of *Proailurus* (Fig. 2.2, letter N). This leaves an extensive barbourfelid stem lineage that is at present entirely unknown.

Evolutionary patterns

The availability of a phylogeny of extant Felidae makes it possible to consider evolutionary patterns within the family in the absence of fossils. Such studies have been attempted in the past (Ortolani and Caro 1996; Werdelin and Olsson 1997; Ortolani 1999; Mattern and McLennan 2000), but given that the current phylogeny (Fig. 2.1) is fully resolved and, we believe, better corroborated than older hypotheses, this work is worth reconsidering. Further, since the current hypothesis is based on molecular data, it is possible to study morphological character evolution without the need to discuss possible circularity in the results. Some such uses of the phylogeny were presented by Johnson *et al.* (2006b) and O'Brien and Johnson (2007) (intercontinental migrations, ghost lineage analysis), and we will only briefly present two further examples of the sort of work that can and should be done on felid evolution using the phylogeny as a baseline. For other examples based on previously proposed phylogenetic hypotheses, see in particular Mattern and McLennan (2000).

Werdelin and Olsson (1997) presented a phylogenetic study of coat patterns in Felidae using a selection

of then-current phylogenetic hypotheses as the baseline. Their conclusion was that 'most transformations of coat pattern originate from the flecked pattern, which we consider to be primitive for the Felidae as a whole' (Werdelin and Olsson 1997, p. 399). The current phylogeny has some substantial differences from the phylogenies used in that study, so the question arises whether the conclusions hold up. Fig. 2.12 shows coat pattern mapped on the current phylogeny. The data are identical to those in Werdelin and Olsson (1997) except for *P. tigris*, which has been recoded from vertical stripes to rosettes, as we believe that what appear to be vertical stripes in the tiger's coat in reality are enormously vertically elongated rosettes. This is indicated through examination of various coat pattern anomalies in tigers and can be more simply seen by holding up an image of a tiger pelt nearly parallel to one's line of sight. One difference from the previous results is immediately obvious: under the current phylogeny, the primitive coat pattern for Felidae as a whole is large blotches. This coat pattern is present in only two genera: *Neofelis*, clouded leopards and *Pardofelis*, marbled cat. Both are basal within their clades, and these clades are basal within the family and hence the primitive condition is reconstructed as large blotches. Above the node leading to *Pardofelis*, however, flecks are primitive as they were in the previous study. If we consider the number and direction of the state changes in the cladogram (Fig. 2.13), we can also see that changes to and from flecks are still the dominant transformations, though not quite as dominant as previously thought. Thus, the new phylogeny corroborates the main thrust of the results of Werdelin and Olsson (1997), but also leads to some modifications of specific parts of their conclusions.

In a second demonstration of possible phylogenetic reconstructions, we mapped habitat (as open or closed), activity pattern (diurnal or nocturnal), and pupil shape (slit-like or rounded in the contracted state) in all felids. The data are partly from Mattern and McLennan (2000) and partly original. Many species occur in both open and closed habitats and the mapping reflects this, not showing any clear phylogenetic associations of open- or closed-habitat specialists (Fig. 2.14), although the *Panthera* and domestic cat lineages are dominated by open-habitat taxa and have this habitat reconstructed as primitive for the

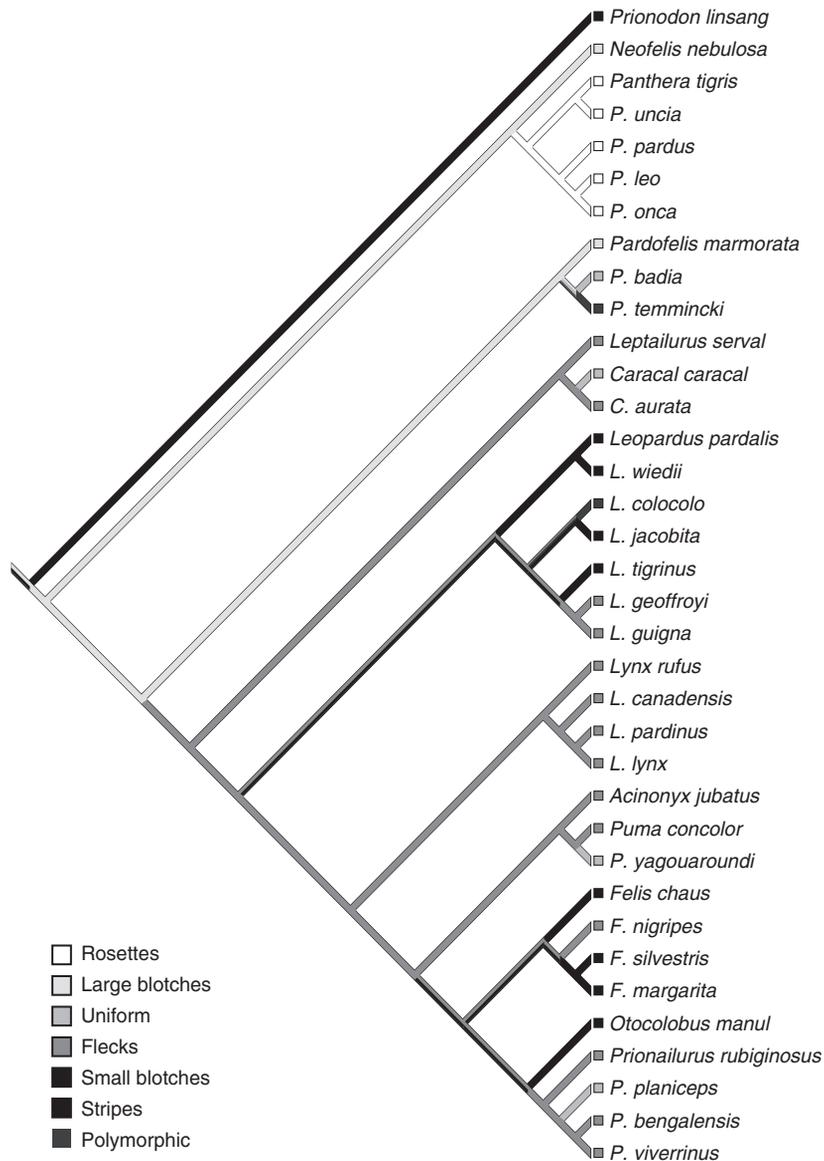


Figure 2.12 Coat patterns (as labelled) mapped on the phylogeny of extant Felidae.

respective clades. Likewise, there are no clear phylogenetic patterns underlying activity patterns in modern felids (mapping not shown). Rounded pupils, on the other hand, only occur in three clades, the *Panthera*-lineage, where all species except the two *Neofelis* (A. Kitchener, personal communication) have rounded pupils, the *Puma*-lineage, where all three species have rounded pupils, and the leopard cat lineage, where the single species *O. manul* has rounded pupils.

The question of the occurrence and causes behind slit-like or rounded pupils has been intermittently discussed in the literature without a consensus being reached (see Kitchener *et al.*, Chapter 3, this volume, for a discussion of some recent research). One suggestion that has been considered is that slit-like pupils allow the pupil to be more completely closed than rounded pupils (Walls 1942). This would suggest that the former would be more useful in the

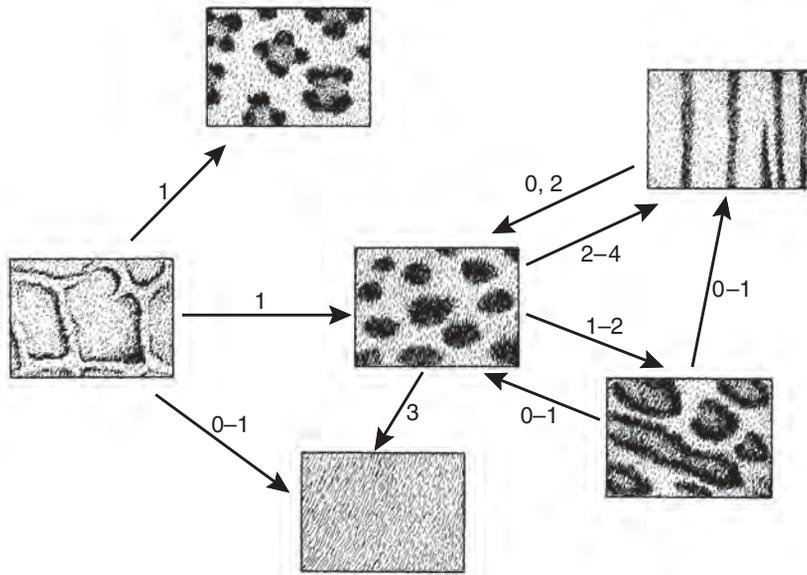


Figure 2.13 The coat pattern transformations implied by the mapping in Fig. 2.12. The majority of transformations involve flecks (centre pattern). Thus, clockwise from bottom, there are three transformations from flecks to uniform, one transformation from large blotches to flecks, two to four transformations from flecks to stripes, zero or two (no reconstruction allows for one) transformations from striped to flecks, one to two transformations from flecks to small blotches, and zero to one transformations from small blotches to flecks. Remaining reconstructed transformations are zero to one transformation from large blotches to uniform, one transformation from large blotches to rosettes, and zero or one transformations from small blotches to stripes. No other transformations are allowed by the phylogeny of extant Felidae.

brighter light of day: that is, slit-like pupils should be preferentially present in diurnal species. However, a comparison between the patterns does not corroborate this idea (not shown). There seems to be no correlation at all between pupil shape and activity pattern. However, if we compare habitat and pupil shape (Fig. 2.14), we find that with the exception of *Puma yagouaroundi*, which, if the fossil record of this clade is taken into account, must be considered secondarily adapted to closed habitats, rounded pupils never occur in closed-habitat specialist species. All the taxa with rounded pupils are either open-habitat species or occur in a variety of habitats. Further, all three nodes where there is a change from slit-like to rounded pupils are also nodes where there is a shift from closed-to open-habitat preference. What this means in functional terms is beyond the scope of this chapter, but the results point to a fruitful avenue of research. These very tentative results must be corroborated by more in-depth study and statistical test-

ing. More generally, phylogenetically based studies such as the ones discussed above can direct future research and provide tests of functional hypotheses that could otherwise not be investigated due to a lack of independent data. The existence of a well-corroborated phylogeny such as that in Fig. 2.1 is a powerful tool for future research on felid evolution.

Final words

This chapter presents one possible scenario for the evolution and interrelationships of cats. Some of this work, such as that which has led to the phylogeny of Johnson *et al.* (2006b), is strongly corroborated by and based on considerable amounts of data. The fossil record of Felidae is uneven. Some groups, such as parts of the Machairodontinae, have a fairly extensive fossil record, while others, such as the lineage leading to the extant radiation, are much more

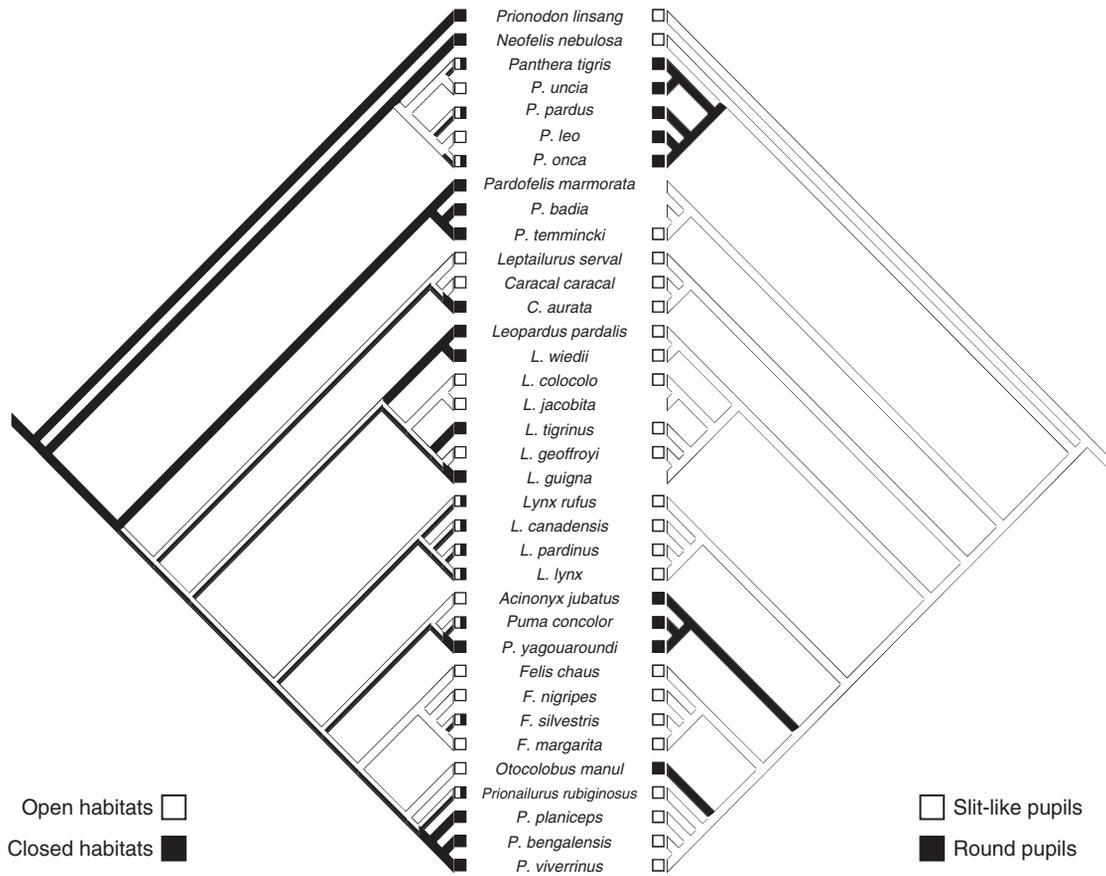


Figure 2.14 Habitat type preference and pupil shape mapped on the phylogeny of extant Felidae.

poorly documented. In no case, however, can the fossil record be said to be adequate, either in quantity or quality. Nor can the fossil record of Felidae be said to have been adequately studied. Some areas, such as the functional morphology of sabretooths, have been investigated over and over, while others, such as the stem lineage of modern cats, have been relatively neglected. Overall, the phylogeny and evolution of fossil Felidae have been neglected in favour of studies of their functional morphology and ecology. Given the limited resources available for this work, this is understandable, as the latter topics have proven more tractable and have yielded interesting and significant results. But if our understanding of the group is to progress, we must try to address such pressing issues as the fossil record of living cats, the origins of Smilodontini, and the relationship of Barboourofelidae to Felidae. This will require extending

the work of Johnson *et al.* (2006b) into the realm of fossils, by comparing the fossil record with the results obtained from the phylogeny of extant cats on aspects such as continental migration (O'Brien and Johnson 2007), to see if the timing of intercontinental migrations of fossil cat groups can be matched up with those postulated for the extant cats based on phylogeny and geology.

It must be understood that developing a phylogeny, or even the simpler task of testing some aspect of the scenario developed herein, requires more than a superficial glance at the record and doing a phylogenetic analysis of the first few characters that come to mind. It will require developing new characters and looking at the fossil record in new ways. If the fossil record and phylogeny of extant Felidae can be better integrated, we can expect to develop a significantly better understanding of the evolution of this

fascinating group and its conditions for existing, thereby not only enhancing current knowledge, but also building a better platform for the conservation of the many endangered species of Felidae today.

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