Re-Appraisal of 'Felis' pamiri Ozansoy, 1959 (Carnivora, Felidae) from the Upper Miocene of Turkey: the Earliest Pantherin Cat?

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2   Turkey: the earliest pantherin cat?

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8   **Running head**: *'Felis' pamiri* from Turkey

9

10   **Abstract**

11   Although the divergence of the *Panthera* clade from other Felidae might be as old as the

12   earliest middle Miocene, its fossil record before the Pliocene is virtually non-existent. Here we

13   reassess the affinities of a felid from the early upper Miocene of Turkey, known by well-preserved

14   associated upper and lower dentitions. We conclude that it belongs to the same genus

15   (*Miopanthera* Kretzoi, 1938) as the middle Miocene *'Styriofelis' lorteti* (Gaillard, 1899), and that

16   this genus is close to, if not part of, the *Panthera* clade.

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20   **Introduction**

21   The Felidae can be divided in two subfamilies (Johnson et al. 2006; Werdelin et al. 2010)

22   Felinae (= Pantherinae, or big cats, plus Felinae, or smaller cats, in e.g., Wilson and Mittermeier

23   2009) and Machairodontinae, although their monophyly is hard to demonstrate, the second one

24   being extinct. The Neogene fossil record of the Machairodontinae, or saber-toothed felids, is

25   satisfactory, but that of other members of the family, conveniently called conical-toothed felids

26   (although several of them have compressed, flattened canines) is much more patchy. The fossil

27   history of many of the modern genera is poorly documented and, frequently, is not older than the

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Pleistocene (see Werdelin et al. 2010 for details). Among the best known modern Old World genera are *Lynx* Kerr, 1792, *Acinonyx* Brookes, 1828, *Caracal* Gray, 1843, and *Panthera* Linnaeus, 1758, the earliest records of which range from the latest Miocene to the end of the Pliocene (i.e., 6-3 Ma; see, e.g., Morales et al. 2003b; Werdelin et al. 2010; Werdelin and Dehghani 2011; Tseng et al. 2014). The earliest representatives of *Felis* were long thought to date to the early late Miocene (*'Felis' attica* Wagner, 1857), but these have been recently assigned to distinct genera, *Styriofelis* Kretzoi, 1929, and *Pristifelis* Salesa et al., 2012 (Salesa et al. 2012); the earliest published Old World *Felis* is now considered to be *Felis* sp. from the Lower Pliocene of Kanapoi (Werdelin 2003). By contrast with these relatively recent fossil records, divergence time estimates between, for example, the *Panthera* s.l. group (including the clouded leopard *Neofelis nebulosa* [Griffith, 1821]) and other modern Felidae has been dated to c. 10.8 Ma (Johnson et al. 2006), c. 16 Ma (Nyakatura and Bininda-Emonds 2012), and even c. 19 Ma (Tseng et al. 2014). Obviously, there remains a wide gap in the fossil record of large conical-toothed felids during a large part of the Miocene.

Here we intend to show that a large-lynx-sized felid, *'Felis' pamiri* from the late Miocene of Turkey, contributes to filling this gap. The species name *Felis pamiri* was created by Ozansoy (1965) for "un maxillaire avec denture; deux mandibules également bien conservées" (Ozansoy 1965:43), stored in the MNHN, Paris. They were found at Yassiören, a well-known locality in the Sinap region of Turkey, northwest of Ankara, which is presently called Locality 8 and is dated to c. 9.9 Ma, or to latest MN9 in the Neogene European mammal zonation (Kappelman et al. 2003).

Abbreviations: BSP, Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich; CCEC, Centre de Conservation et d'Etude des Collections, Lyon; MCGL: Musée Cantonal de Géologie, Lausanne; MHNT: Muséum d'Histoire naturelle de Toulouse; MNCN: Museo Nacional de Ciencias Naturales, Madrid; MNHN: Muséum national d'Histoire naturelle, Paris; NMB: Naturhistorische Museum Basel; SMNS: Staatliches Museum für Naturkunde, Stuttgart.

1 **Materials and methods**

2 The holotype and single specimen of '*Felis' pamiri*, MNHN.F.TRQ1212, consists of a

3 snout fragment with left I2-C and P3-M1, right I1-C and mesial part of P3, plus left and right

4 mandibles virtually complete except for most of the incisors and the ascending rami

5 (measurements: Table 1).

6 We have compared *'Felis' pamiri* to most species of modern Felidae housed in MNHN

7 (see Supplementary Data 1), and to a number of early felids from the Miocene of Europe and

8 western Asia, housed in BSP, CCEC, MCGL, MHNT, MNCN, MNHN, NMB, SMNS (see

9 Supplementary Data 1): *Pristifelis attica* from the Turolian (late Miocene) of Pikermi,

10 Vathylakkos, and Samos, Greece; *Styriofelis vallesiensis* from the Vallesian of Cerro de los

11 Batallones, Spain and perhaps Maragha, Iran; *S. turnauensis*, *'S'. lorteti*, and *Pseudaelurus*

12 *quadridentatus* from the middle Miocene of France. Data on North American forms come from

13 Rothwell (2001, 2003) but, unfortunately, he provided very few measurements and paid little

14 attention to the canines.

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16 **Description**

17 First, it must be mentioned that Ozansoy incorrectly reconstructed the left maxilla that he

18 illustrated (Ozansoy 1965: pl. 4, fig. 5): in fact, as shown by the right maxilla, the canine is not so

19 close to P3, because he used the alveolus of the anteriormost premolar to insert the left canine.

20 Fig. 1A,E show the rectified position of these teeth.

21 Not much is preserved of the bones of the snout, so that few observations are possible. The

22 premaxillae are broader than in similar-sized modern *Panthera*; the orbit and infra-orbital foramen

23 were probably rather rostrally located (the latter opens above the distal end of P3), but more

24 precise estimates are impossible. The premaxillae are long and the incisors are distinctly more

25 rostrally inserted than the canines. The incisive foramina are rostrally located, their caudal border

26 being more rostral than that of the canines. The jugal is shallow below the orbit.

The difference in size between I3 and the other incisors is quite marked, this tooth being longer than the diastema that separates it from the canine, but I1 and I2 are not very small; they bear lingual accessory cusps.

The upper canines are well preserved and nearly unworn. The crown is only slightly taller than P4 is long (22 mm vs. 20.6 mm). The root is not much longer than the crown, but its distal border, in lateral view, is only slightly concave, while that of the crown is more distinctly concave; the mesial outline of the whole tooth forms a regular, strongly convex curve. There are two longitudinal, smooth crests: one is straight and runs along the distal border, the other is located mesially and slightly lingually near the tip, but turns more lingually towards the base, so that at the base of the crown it is mesio-lingual. The basal cross-section of the crown is ovoid, with a strongly convex mesial part that narrows distally to the distal crest; between the two crests, the lingual surface is only slightly less convex than the labial one; there are no labial furrows.

The distance between the canine and P3 is proportionally longer than in modern *Panthera*, and a (now missing) P2 was inserted at mid-length between them; it was not vestigial, but single-rooted. P3 is a long, low tooth, with only a slight tendency to distal broadening. It bears only a hint of a mesiolingual accessory cusp, from which a crest, slightly convex in lateral view, ascends to the top of the main cusp, which is followed by strong distal accessory cusp, and an inflated cingulum that circles the distal part of the tooth, where it reaches its greatest width.

The carnassial is not much worn, but an imperfectly repaired crack between the paracone and parastyle has slightly increased its apparent length. The inflated cingulum forms an incipient, indistinct ectostyle; the parastyle, paracone, and metacone-metastyle have roughly the same proportions as in large modern felines, although the distal blade may be somewhat longer. The moderate-sized protocone is located slightly more distally than the parastyle; its size and position fall within the variation range of the modern Pantherini (here, the clade *Neofelis-Panthera*).

The paracone of M1 is worn off, but this tooth was clearly short and broad, being about as broad as P4, and much broader than in modern Felidae.

The dentaries suffered some crushing, as shown by the differences in curvature of the left and right ones, but their general shape can be described with good confidence (Fig. 1B-D). The rostral border of the symphysis is rather upright, straight, and long; in lateral view, it is rather clearly demarcated from the ventral border on the left corpus, but less so in the right one, suggesting some distortion. In rostral view, the symphysis itself is thick in its central part, but narrows ventrally to a point, so that the fusion of the two branches did not quite extend to the ventral borders. The ventral border of the corpus is convex below p4-m1, with slight concavities rostrally and caudally. The masseteric fossa is deep ventrally, but does not reach the ventral border of the dentary; rostrally it ends gradually below the level of the m1 protoconid.

The incisors are incompletely and imperfectly preserved; they are small and transversely compressed, but arranged in a straight transverse line, none being lingually displaced. Only the crowns of the left i2 and i3 are nearly fully preserved. The crown of i2 is very small and widens apically; its tip is both worn and damaged. The i3 is much larger and caniniform; its distal rim bears a vestigial accessory cuspid. The lower canines are almost as large as the upper ones both in diameters and height, but their crown is more curved and the keels closer to each other, resulting in a lingual surface clearly less convex than the labial surface; they also lack crenulations and labial furrows.

No tooth is preserved between the canines and p3, but on both sides, an alveolus shows that a monoradiculated tooth, much smaller than the P2, was present about midway between these teeth. The p3 is long and low, with a distinct mesial accessory cuspid, quite a small distal one, and an inflated distal cingulid where the tooth is broadest. The p4 is in line with p3, with a large, lanceolate main cuspid, large mesial and distal accessory cuspids, followed by a moderate distal cingulid.

The carnassial is moderately worn and was certainly taller than p4 in its unworn state. It is also much longer, in contrast to most modern Felidae. The protoconid is longer than the paraconid and ends distally into a small ledge (talonid) bearing only a minute tubercle in line with the main blade; no metaconid can be discerned. There is no m2.

Comparisons

Ozansoy (1965) compared his fossil with a number of Miocene to Pleistocene Felidae, but this was mainly aimed at demonstrating that he was dealing with a new species. Since then, *'Felis' pamiri* has received little attention, and was not even mentioned by Viranta and Werdelin (2003) in their study of the Sinap Carnivora. A few previous studies mention the species, considering it either as a Metailurini (Lungu 1978; Bonis et al. 2008) or as a close relative of *Panthera* (Spassov and Geraads 2015); in both cases, however, *'Felis' pamiri* was used in a comparative perspective and was not the central topic. The only author who paid some attention to it was Ginsburg (1983) who considered that it could be descended from the European *'Pseudaelurus' lorteti* Gaillard, 1899; he also surmised that European *Pseudaelurus* (in its former comprehensive conception) could be close to the ancestry of *Felis*, *Lynx*, and *Panthera*. Indeed, there are not many Miocene Felidae with which *'Felis' pamiri* can be compared; only some species of *Pseudaelurus* and some machairodont forms are of similar size but the comparison can be extended to smaller forms.

Machairodontinae:

The machairodonts are probably the Carnivora that received the most attention (Peigné et al. 2005; Salesa et al. 2010; Antón et al. 2014, and refs therein). They used to be characterized by their enlarged, compressed upper canines with sharp keels, but Christiansen (2013) concluded that they are better defined by their small lower canines, small M1s, and large P3 parastyle. *'Felis' pamiri* definitely lacks all these four characters and is clearly not a member of this group. Machairodonts also have a straight rostral border of the symphysis, but the symphysis itself is much thicker in its ventral part (e.g., Salesa et al. 2010: fig. 8) than in '*F*'. *pamiri*. The area of insertion of the masseter muscle does not extend so far ventrally as it does in some machairodonts (e.g., *Homotherium crenatidens*: Ballésio 1963: fig. 13; *Homotherium nestianus*: Bonis, 1976: fig. 5; *Promegantereon ogygia*: Salesa et al. 2010: fig. 11). Some other late Miocene to Pleistocene machairodontines, often called Metailurini, display less clear machairodont characters. The most

commonly cited late Miocene form is *Metailurus*, but Spassov and Geraads (2015) showed that the contents of this genus is heterogeneous, and added a second genus, *Yoshi*. Both genera sharply differ from '*F*'. *pamiri* in: 1) their shorter snout with a short C-P3 diastema; 2) a significantly larger upper canine, which is both longer (mesio-distally) and taller relative to the other teeth, and more transversely compressed; 3) a more reduced M1. A cladogram (Spassov and Geraads 2015) made *Yoshi* the sister-group of *Acinonyx*, but these authors regarded this conclusion with much caution, and the systematic position of this genus remains uncertain. In any case, it is clear that '*F*'. *pamiri* cannot be assigned to the Machairodontinae.

Felinae:

We will focus our comparisons on the Miocene Old World forms, such as *Pseudaelurus* spp., *Styriofelis* spp., *Pristifelis attica*, and on modern felids and their close fossil relatives.

The genus *Pseudaelurus* Gervais, 1850, was erected for *Felis quadridentata* Blainville, 1843, from the middle Miocene (MN 6) of Sansan. Some other European species were later included in the same genus, namely *Felis turnauensis* Hoernes, 1882 (type locality: Göriach, Germany, MN 5), *Pseudaelurus lorteti* Gaillard, 1899 (type locality: La Grive Saint Alban, France, MN 7/8), *Pseudaelurus transitorius* Depéret, 1892 (type locality: La Grive Saint Alban, France, MN 7/8), and *Pseudaelurus romieviensis* Roman and Viret, 1934 (type locality: La Romieu, France, MN 4). The first three species are now often included in *Styriofelis* Kretzoi, 1929 (Peigné 2012; Salesa et al. 2012), together with *S. vallesiensis* Salesa et al., 2012 (type locality: Batallones-3, Spain, MN 10), so that this would leave only *Ps. romieviensis* and *Ps. quadridentatus* in European *Pseudaelurus*. *Pseudaelurus transitorius* is usually regarded as a synonym of *Ps. turnauensis* (Beaumont 1961; Rothwell 2001; Peigné 2012), and indeed Thenius (1949) designated as neotype of the latter species the holotype of the former.

The poorly known *Pseudaelurus cuspidatus* from China (Wang et al. 1998) differs much in its tall, narrow premolars, and minute P4 protocone, and is perhaps not of this genus. Early to middle Miocene American forms have been assigned to six species by Rothwell (2003), thus showing a similar radiation as in Europe. The stratigraphic range of these European species is still

uncertain, probably because their definitions are in need of revision; for instance, it is hard to

believe that *S. turnauensis* could range from MN 2 to MN 8 (Robles et al. 2013: fig. 1). *Styriofelis*

vallesiensis and *Ps. quadridentatus* are the only species known in the late Miocene, being

recorded from the Vallesian of Spain (Villalta and Crusafont 1943; Fraile et al. 1997; Salesa et al.

2012; Morales et al. 2015).

The African fossil record is poor, consisting only of the mandibular remains of

Diamantofelis ferox Morales et al., 1998, *Namafelis minor* (Morales et al., 1998) Morales et al.,

2003a (perhaps not a felid, according to Werdelin 2011), and *Asilifelis coteae* Werdelin, 2011.

Skull: Cranial differences are few, especially because cranial remains are rare. The

comparison of *'Felis' pamiri* with similar-sized modern Felidae does not show prominent

morphological differences, except perhaps a broader incisor arch than in most of them, and a

shallower jugal than in *Panthera*. Of the fossil Pantherini, both the early Pleistocene *Panthera*

zdanskyi Mazák et al., 2011, and the early Pliocene *Pa. blytheae* Tseng et al., 2014, have a deep

jugal and narrow incisors, like modern forms.

Mandible: There are some differences in the curvature of the ventral border of the

mandibular corpus, but they are probably not very significant (especially in regard of the variation

in *Panthera*). The chin looks less rounded than in the few available Miocene non-machairodont

felids, and the rostral border of the symphysis looks straighter and more vertical, but we believe

that the rounded chin of the fossil forms often results in part from the imperfect preservation of

the symphysis, the difference being accentuated by the slight transverse crushing of the Yassiören

fossil. The shape of the symphysis is variable in modern felids, with *Pa. pardus* being closest in

its deep symphysis and front teeth inserted at a higher level than the cheek-teeth.

Upper teeth: The upper incisors have about the same size and proportions as in modern

large Felidae. The central incisors I1 and I2 are much less reduced than in *S. lorteti* (MHNT

San879) and *Ps. quadridentatus* (MNHN.F.Sa612, Sa963, Sa964, Sa9768). They are also less

reduced than in the similar-sized *Ps. marshi* (Thorpe, 1922), from North America (Rothwell 2003:

figs. 52, 55).

The upper canine is the tooth that most differs from that of *Ps. quadridentatus*. Ginsburg (1961) described those from Sansan as long, slender, transversely compressed, and with clear keels, and noted a clear machairodont tendency; Peigné (2012) added that the crown is high, with a straight distal border and two sharp keels. Several maxillae show that its mesio-distal length is significantly greater than half that of P4. These machairodont features sharply differ from those of *'Felis' pamiri*, whose upper canines are distinctly less compressed, and smaller. Allometry alone can explain the differences in canine compression index (L / W) between the various species of *Styriofelis* and *Pseudaelurus*, larger forms having more compressed canines, but *'F.' pamiri* (Fig. 2) plots above their regression lines, between medium-sized representatives of this group and the modern Felidae. In addition, and although sample size (associated Cs and P4s) is much smaller, the canine of *'F.' pamiri* is distinctly smaller relative to P4 than in *Pseudaelurus* and *S. lorteti* but again, more similar to modern large Felidae (Fig. 3). In addition, the crowns of the upper canines of *Ps. quadridentatus* are much taller, the mean height being more than 3/2 the mean of the upper carnassial length, whereas it is only a bit taller at Yassiören. *Panthera blytheae* also had a relatively large, but conical, upper canine (Tseng et al. 2014).

Labial grooves on the canines are present in most Felidae, several Viverridae, Procyonidae, Ailuridae, and some Mustelidae (pers. observation); they are absent in machairodonts, *Pseudaelurus*, large *Styriofelis*, and *'F.' pamiri*, but also poorly indicated or absent in some other Felidae, mostly with short canines, such as *Pu. concolor*, *A. jubatus* (Schreber, 1775), *C. caracal* (Schreber, 1776), and seemingly *Pa. blytheae* (Tseng et al. 2014, fig. S3, although these authors mention their presence).

The distance between C and P3 is about relatively as long as in *S. lorteti* and *Ps. quadridentatus*. There are usually two minute (deciduous?) teeth between them in these species, but sometimes only a larger one, as in *'F.' pamiri*. The presence of a P2 is variable in modern forms, but follows no obvious pattern and is probably irrelevant above species level. The P3s of *Ps. quadridentatus* from Sansan, La Grive, Vieux-Collonges, Los Valles de Fuentidueña (Mein 1958; Ginsburg 1961; Ginsburg et al. 1981; Peigné 2012) do not much differ from those of

'*F.' pamiri*, but are consistently broader, like those of American *Pseudaelurus* (Rothwell 2003: figs. 13, 28, 32, 53) and *Pa. blytheae*. *'Felis' pamiri*, instead, plots close to the regression lines of modern similar-sized felids (Fig. 4).

The protocone of P4 in *'F.' pamiri* is more reduced than that of *Ps. romieviensis* and *S. lorteti*, *Ps. marshi*, and probably also than that of *Ps. quadridentatus*, although it may also be reduced in the last species. In *'F.' pamiri* it is perhaps also located more distally, but the location of this cusp displays some variation, as in modern forms, so that these characters are of limited significance. The parastyle is longer than in the *Ps. quadridentatus* from Sansan and probably also than in *S. lorteti,* although this is hard to quantify precisely; it is more similar in size in *Ps. romieviensis* or *Ps. quadridentatus* from La Grive. Similar-sized modern felids have long parastyles.

By contrast, the M1 is distinctly larger than in modern felids, but about as large as in *Ps. quadridentatus*; it is larger still in *S. turnauensis* from Wintershof-West (Dehm 1951), and there is little doubt that the size of this tooth decreased with time.

Lower teeth: Both Ginsburg (1961) and Heizmann (1973) described the peculiar arrangement of the lower incisors of *Ps. quadridentatus*, which are not transversely aligned, as in *'F.' pamiri*, the machairodonts, and modern felids, but are instead closely appressed against the canine, i2 being located more lingually This arrangement is unique in Neogene felids but Beaumont (1978) thought that it could reverse to the normal, transverse one.

The size of the lower canine (relative to m1) is less variable than that of the upper one. It is about as large in *Styriofelis* as in most modern Pantherini; *'F.' pamiri* seemingly has a smaller canine, like *Ps. quadridentatus* and the Machairodontinae (and *Acinonyx*), but this is due to its long m1. Labial furrows of the lower canines show the same distribution as the upper ones, i.e., they are absent in *'F.' pamiri*, the machairodonts, *Ps. quadridentatus*, *S. lorteti*, *Pu. concolor*, *A. jubatus*, and *C. caracal*.

The presence of a small tooth between the canine and p3 seems to be the rule in Miocene forms, although there are some exceptions (Heizmann 1973; Morales et al. 2003a; Koufos 2008);

this tooth is vestigial in '*F.' pamiri*, and its disappearance in modern forms is the endpoint of a general trend.

In *Pseudaelurus* and middle Miocene forms of the genus *Styriofelis*, the mesial accessory cuspid of p3 is absent or weaker than in '*F.' pamiri*; it is usually large in modern large felids. Variations in the size of the mesial cuspid of p4 are less marked. In most forms this tooth is intermediate in length between p3 and m1; its lengthening relative to these teeth is peculiar to *Panthera*. African forms plot close to the regression line for *Styriofelis* s.l.

Smaller carnassial teeth look on the average relatively taller, but there seem to be no clear correlation between geological age and reduction of the metaconid, as it is still present in *S. vallesiensis* from the Vallesian of Batallones (Spain). However, the talonid of '*F.' pamiri* is as reduced as that of many modern felids. The m2 may still be present at Bézian (Ginsburg and Bulot 1982) and Artenay (Ginsburg 1983), in species respectively identified as *Ps. transitorius* and *Ps. (Miopanthera) lorteti* by these authors, but it disappears in the middle Miocene.

Parsimony analysis

A matrix of the main cranial and dental characters, in part modified from Salesa et al. (2012) is given in Supplementary Data 2A. A parsimony analysis conducted with TNT (Goloboff et al. 2008) with default options yields 80 most parsimonious trees. The strict consensus tree is poorly resolved, but the 50% majority rule consensus tree is shown in Supplementary Data 2B. This result should certainly not be taken at face value, especially because it is based almost exclusively upon dental characters, because many of the characters are hard to score precisely, because of the high degree of homoplasy so that small changes in the data matrix result in significant changes in the trees, because many branches are poorly supported, because the choice of the outgroup has a major impact on the topology, and because the arrangement of the living species differs from the supertree obtained by Nyakatura and Bininda-Emonds (2012), especially concerning some widely accepted clades, such as, e.g., (modern *Panthera* + *Neofelis*) to the exclusion of (*Puma concolor* [Linnaeus, 1771] + *Acinonyx jubatus*). Still, it correctly displays

some modern clades and, also correctly in our opinion, the grouping of machairodonts with *Ps. quadridentatus* as their sister taxon, as suggested by Beaumont (1964, 1975) and Salesa et al. (2010); whether they are really connected to the pantherin group is debatable. The issue of the position of *'Felis' pamiri* and *Panthera blytheae* will be discussed further below.

Discussion

The machairodont lineage is first documented in the late Miocene by *Promegantereon* Kretzoi, 1938, *Paramachaerodus* Pilgrim, 1913, *Metailurus*, *Yoshi*, and *Pseudaelurus quadridentatus*, which display clear machairodont features. The origin of the conical-toothed felids is usually placed in what is now called *Styriofelis* (Beaumont 1978; Werdelin 2010; Salesa et al. 2012), but the issue of the relationships within this genus has never been seriously addressed. Even though they considered only two species (*S. turnauensis* and *S. vallesiensis*), Salesa et al. (2012) found the genus to be paraphyletic, and we may observe that no diagnosis of *Styriofelis* has recently been provided. That of Kretzoi (1929) applies only to the type species *S. turnauensis* and its only really diagnostic features refer to a P4 (Hofmann 1893: pl.3, fig. 13) that is either pathological, improperly illustrated, or not felid. In fact, this genus is mainly based upon the concept (Beaumont 1978) that there must have existed in the middle Miocene, along with the lineage leading to the machairodonts, a branch leading to conical-toothed felids. At La Grive (MN7) and Sansan (MN6), a medium-sized species, usually called *Styriofelis lorteti*, is present alongside *Ps. quadridentatus*, and clearly belongs to a different lineage. However, we may assume that the distinctive features dwindle in earlier sites, and assigning earlier forms to either of these two lineages is more difficult, if not impossible. It might prove convenient to restrict the generic name *Styriofelis* to this early and middle Miocene paraphyletic group including *romieviensis*, *turnauensis* (including *transitorius*), from which later felids probably arose. By contrast, we believe that assigning '*Pseudaelurus*' *lorteti* to the genus *Styriofelis*, which is based upon a species from the MN5 locality of Göriach whose holotype is lost, is misleading. Still, generic distinction of *'Ps.' lorteti* from *Ps. quadridentatus* is certainly warranted (Peigné 2012);

fortunately, another generic name is available for it, *Miopanthera* Kretzoi, 1938, of which it is the

type species. Ginsburg (1983) came to the same conclusions (but we question his assignment of

the MN4 Artenay material to this species, because it displays a lot of more primitive features:

smaller size, bi-rooted p2, metaconid occasionally present on m1, m2 present, and the Artenay

material is better left in *Styriofelis*).

'*Felis*' *pamiri* differs from *M. lorteti* in some features that are more derived (larger size,

presence of only one tooth between C and P3), as well as in its slightly smaller upper canine and

large central incisors, a character also found in modern felines. In its low, narrow P3 '*F.*' *pamiri* is

also more similar to modern *Panthera*. Still, most of the differences from *M. lorteti* can be

explained by the younger age of the Sinap form, and we assign it to the paraphyletic genus

Miopanthera.

The recently described *Panthera blytheae* Tseng et al., 2014, was regarded by its

describers as the earliest large conical-toothed felid. Its type locality has an estimated age of 4.42

Ma; other material assigned to the same species (Tseng et al. 2014: fig. S4G-J) is 5.95 Ma but is,

in our opinion, undiagnostic at genus level and could well belong to *Metailurus* or a related (i.e.,

machairodontin) form. On the material from the type locality, grooves are said to be present on

upper canines, although they are not clearly visible (Tseng et al. 2014: figs. S3A-B, F). If they are

indeed present, the *Panthera* + *Miopanthera* group is poorly resolved (Supplementary Data 2B),

but their absence creates a clade consisting of modern *Panthera* + *Neofelis* (Supplementary Data

2C). Pending detailed analysis or illustration of the characters said by Tseng et al. (2014) to

support inclusion of this species in *Panthera*, we prefer to leave the issue of its position open.

In addition, nearly all the shared and unique characters of *Pa. blytheae* supporting a close

relationships with *Panthera* in Tseng et al. (2014) are not supported by our observations. Tseng et

al. (2014) used the same taxonomic sampling as Christiansen (2008); it is almost restricted to

Pantherini, as it includes only two non-pantherin species (*Leopardus pardalis* [Linnaeus, 1758]

and *Puma concolor*). However, whereas the work of Christiansen was focused on the phylogeny

of great cats, that of Tseng et al. (2014) aimed to demonstrate that *Pa. blytheae* is a *Panthera*. The

too-narrow taxonomic sampling used in their study is clearly not pertinent in the context of their objective and may have biased their conclusions. Thus, the position of the frontoparietal suture in *Pa. blytheae* is like in many Felidae, not especially like in *Panthera*. The lack of projection of the dorsal border of the infraorbital canal (character previously used by Salles (1992) as 'jugal anterior process' or by Christiansen (2008: character 14)) is not only common to *Panthera* but also to *A. jubatus* and *Lynx* spp. (see Salles 1992: 37); some fossil species such as the earliest felid *Proailurus lemanensis* Filhol, 1879, also present this morphology, which suggests that this is a primitive state. The morphology of "the border between the dorsal tongue of the maxilla with the frontal," as far as we understand this character, is not different in non-pantherin felids. The shape of the parasagittal crests (i.e., the temporal lines or orbitotemporal crests; Evans 1993) shows exactly the same pattern in many cats (for example in *Felis* spp.). Patterns of the mandibular symphysis are, as mentioned above, extremely variable in modern felids. Finally, features that support a close relationships between *Pa. blytheae* and *Pa. uncia* are debatable due to their poor state of preservation in the fossil species, especially the basicranium and the rostrum. Based on figures S4I-J in Tseng et al. (2014), we consider the similarity in the pattern of p4 cuspids of *Pa. blytheae* and *Pa. uncia* as undiagnostic, because we observed the same pattern in many specimens of other *Panthera* species. The shape of the premaxilla-maxilla border adjacent to the canines seems diagnostic for *Pa. blytheae*; however, we did not observe the same pattern in the *Pa. uncia* used in our comparison (MNHN-ZM-MO-2006-429, MNHN-ZM-AC-A14527).

Conclusions

Based on our analysis we propose the following systematics:

CARNIVORA Bowdich, 1821

FELIFORMIA Kretzoi, 1945

FELIDAE Fischer, 1817

MIOPANTHERA Kretzoi, 1938

Type species−Pseudaelurus lorteti Gaillard, 1899

Diagnosis−A feline ranging in size from that of a large caracal to that of a small leopard. Canines

without grooves. Upper canines conical, moderately compressed. P4 with small protocone; M1

short but broad; p2 vestigial or absent; p3 low; m1 without metaconid, m2 absent.

Other species assigned to the genus: *Felis pamiri* Ozansoy, 1965.

MIOPANTHERA PAMIRI (Ozansoy, 1965)

'Felis' pamiri Ozansoy, 1965: 43; pl. 4, figs. 5, 7.

Metailurus pamiri (Ozansoy, 1965): Lungu 1978:110.

Holotype by monotypy−MNHN.F.TRQ1212, snout fragment with left I2-C and P3-M1, right I1-C

and mesial part of P3, plus left and right mandibles virtually complete except for most of the

incisors and the ascending rami. Although Ozansoy did not mention this, there is no doubt that all

these pieces belong to one and the same individual.

Type locality−Locality 8, Yassiören, Sinap, Turkey.

Age and distribution−Known with certainty from the type locality only, but a mandible AS.95.406

from the slightly younger Sinap Loc. 12 has similar measurements (Viranta and Werdelin 2003);

dated to c. 9.9 Ma; transition MN9-MN10, late Miocene.

Diagnosis−A feline about the size of a large lynx or small puma. Unreduced central incisors;

upper canine of moderate size; P2 present; P3 low, long, and narrow; P4 with long parastyle; p2

vestigial; m1 long (in this and in the following comparisons, statements regarding the tooth

lengths and proportions are relative).

Differs from the earlier *Miopanthera lorteti* in its slightly larger size, larger central

incisors, smaller upper and lower canines, presence of only one tooth between C and P3, long,

low, and narrow P3.

Differs from the similar-sized and contemporaneous *Pseudaelurus quadridentatus*

(Blainville, 1843) in its much larger central incisors, smaller, lower, and less compressed upper

canine, longer P3, m1 without metaconid.

Differs from the contemporaneous *Styriofelis vallesiensis* Salesa et al., 2012, in its much larger size, absence of canine grooves, presence of only three upper premolars, long and narrow P3, larger P4 parastyle, shorter M1, less tall premolar cuspids.

Differs from *Panthera blytheae* Tseng et al., 2014, in its larger central incisors, smaller upper canine, narrower P3 with a smaller mesial cusp, P4 with larger parastyle but no ectostyle. Differs from modern *Panthera* species in the absence of canine grooves, longer distance between C and P3, less reduced M1, and long m1 relative to p4.

Precisely branching *Miopanthera pamiri* onto the tree of the Felinae can only be tentative at present. The major discrepancies between the tree of Salles (1992), based on careful analysis of morphological characters, and the supertree of Nyakatura and Bininda-Emonds (2012) demonstrate that dental characters alone are unable to predict relationships. In addition, the divergence date estimates of the various lineages greatly vary with authors (cf. the example of *Panthera* in the Introduction). Anyhow, if, as assumed by Nyakatura and Bininda-Emonds (2012), the *Panthera*/*Neofelis* clade was the first to diverge from that of the remaining modern Felinae, *M. pamiri* post-dates this split, and probably belongs to either of them rather than to a more basal group. We favor its inclusion in the pantherin clade, because of its relatively large size, low p3, and large incisors, all characters that are more advanced towards this group than those of *M. lorteti*. Still, if the radiation of the modern Pantherini really dates from the late Miocene (Nyakatura and Bininda-Emonds 2012: fig. 10), *M. pamiri* might pre-date it. This is not in full agreement with the results of the parsimony analysis, but would explain retention of primitive features such as the lack of canine grooves (but the polarity of this character is debatable), or long m1 relative to p4.

In any case, the late middle Miocene *Miopanthera lorteti* and the late Miocene *M. pamiri* contribute to filling the wide gap in pantherin history between the estimated age of their origin and *Pa. blytheae*. It would probably be a step too far to regard them as ancestors of *Panthera*, although no character definitely forbids this, but they were certainly close to them.

Acknowledgments

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Figure captions

Figure 1. *Miopanthera pamiri*, holotype, MNHN-F-TRQ-1212. A: occlusal view of the maxilla (stereo); B: occlusal view of left mandible (stereo); C: right mandible, lateral view; D: left mandible, medial view; E; left maxilla, lateral view. Scale bar = 5 cm. [intended for page width – do not reduce]

Figure 2. Plot of upper canine width (bucco-lingual) vs. upper canine length (mesio-distal) in some fossil and modern Felidae, with reduced major axis regression lines and equations.

Figure 3. Plot of upper P4 length vs. upper canine length (mesio-distal) in some fossil and modern Felidae, with reduced major axis regression lines and equations.

Figure 4. Plot of upper P3 width vs. upper P3 length in some fossil and modern Felidae, with reduced major axis regression lines and equations.