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RELATIONSHIPS OF *BARBOUROFELIS PIVETEAUI* (OZANSOY, 1965), A LATE MIOCENE NIMRAVID (CARNIVORA, MAMMALIA) FROM CENTRAL TURKEY

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ABSTRACT—An incomplete skull and associated mandible of "*Megantereon*" *piveteaui* Ozansoy, 1965, from the Middle Sinap Formation (Vallesian Mammal Age, early late Miocene) of Turkey is one of the best preserved and perhaps the latest known record of the Nimravidae outside North America. It shares many synapomorphies (such as the very specialized carnassials, reduced P3s and lower canine, broad palate, large infraorbital foramen, and large masseter insertion) with North American *Barbourofelis*, and is accordingly referred to this genus, which probably also includes *B. vallesiensis* (Beaumont and Crusafont, 1982) from the late Miocene of Spain. Immigration of this group into North America may have taken place near the middle/late Miocene boundary.

INTRODUCTION

Although rich in Neogene fossiliferous continental deposits, Turkey has received relatively little attention from mammalian paleontologists. For instance, only a handful of papers specifically deal with Carnivora from this country. Schmidt-Kittler's (1976) monograph is the most extensive systematic study of Miocene carnivorans from the region, but shorter descriptions occur in more general accounts. In 1965, Ozansoy published a monograph dealing mainly with mammals from a limited area about 60 km northwest of Ankara, called Sinap Tepe (=Sinap Hill), where he distinguished three sedimentary formations, the Lower, Middle and Upper Sinap; the Middle Sinap, which he thought to be of Pliocene age, was by far the most fossiliferous. The most recent revision of the biostratigraphy of the Middle Sinap (Sen, 1991) shows it to be most probably early late Miocene (Vallesian Mammal Age, equivalent to the North American Clarendonian Mammal Age).

Several localities are known in the Middle Sinap, but Ozansoy did not mention which one yielded the mandible of the saber-toothed cat that he described as *Megantereon piveteaui,* n. sp. This uncertainty has some chronological implications, since our observations on bovid collections from the main localities of Middle Sinap, called SL1 (SL stands for Sinap Locality), SL1a, SL1b, and SL2, suggest that they are not exactly contemporaneous. However, they are not far apart stratigraphically, and all of them are probably slightly older than 10 Ma (Sen, 1991).

Nikolov and Thenius (1967) suggested the removal of Ozansoy's species from *Megantereon,* a Plio-Pleistocene felid, and its inclusion within *Sansanosmilus* Kretzoi, a genus based upon *Felis palmidens* Blainville from the middle Miocene of Sansan, France. "*Megantereon*" *piveteaui* was later doubtfully included in their new genus *Barbourofelis* by Schultz et al. (1970), as ?*Barbourofelis piveteaui,* thus extending the range of the genus outside North America.

The Department of Anthropology of the Faculty of Letters and History in Ankara houses the associated skull and mandible of a saber-toothed carnivoran from SL2, which we refer to "*M.*" *piveteaui* because its mandible displays the same distinctive features as the holotype, such as a small canine, long diastema, extremely reduced p3, high p4, long m1, and because no other dirk-toothed carnivore is known from this formation. The few differences between the two mandibles

are probably age-related, or due to intraspecific variation (see below). This specimen now allows us to confirm the tentative identification of Schultz et al. (1970), to discuss in greater detail the cranial anatomy of this extremely specialized dirk-toothed nimravid, and to try to assess its phylogenetic position.

SYSTEMATIC DESCRIPTION

Family NIMRAVIDAE Cope, 1880

We follow Baskin (1981) and Bryant (1991) in including the genera considered here in this family.

Genus BARBOUROFELIS Schultz, Schultz, and Martin, 1970

Type Species—*B. fricki* Schultz, Schultz, and Martin, 1970.
Generic Diagnosis—Skull with postorbital bar; [infra-orbital foramen very large; palate broad at the level of P3–P4;] canine saberlike, elongated, and flattened, with labial and lingual grooves; [P4 with very high parastyle and preparastyle;] postorbital portion of cranium shortened, resulting in decidedly brachycephalic skull; bullae flattened posteriorly to form part of occipital region; posterior lacerate foramen opening on occipital region; ramus expanding in depth anteriorly, with broad U-shaped flange; symphysis of rami united almost to ventral border of flange; [lower canine small;] pronounced convexity on labial side of ramus in area of cheek teeth with p3–m1 sloping outward and posteriorly; P3 and p3 greatly reduced (mainly from Schultz et al., 1970:2; characters in brackets are further distinctions from more primitive barbourofelines).

BARBOUROFELIS PIVETEAUI (Ozansoy, 1965)

Megantereon piveteaui Ozansoy, 1965:41.
?*Barbourofelis piveteaui* Schultz et al., 1970:22.
Holotype—Mandible with both rami, figured by Ozansoy, 1965:pl. 4, figs. 6, 8, 9. Housed in Muséum National d'Histoire Naturelle, Paris; catalogue no. TRQ 1016 and 1017 (TRQ stands for "Turquie"; the specimens are also labeled YAS 21 a and b, for Yassiören, a village close to Sinap).
Type Locality—Middle Sinap Formation, Kazan District, Ankara, Turkey; precise locality unknown.
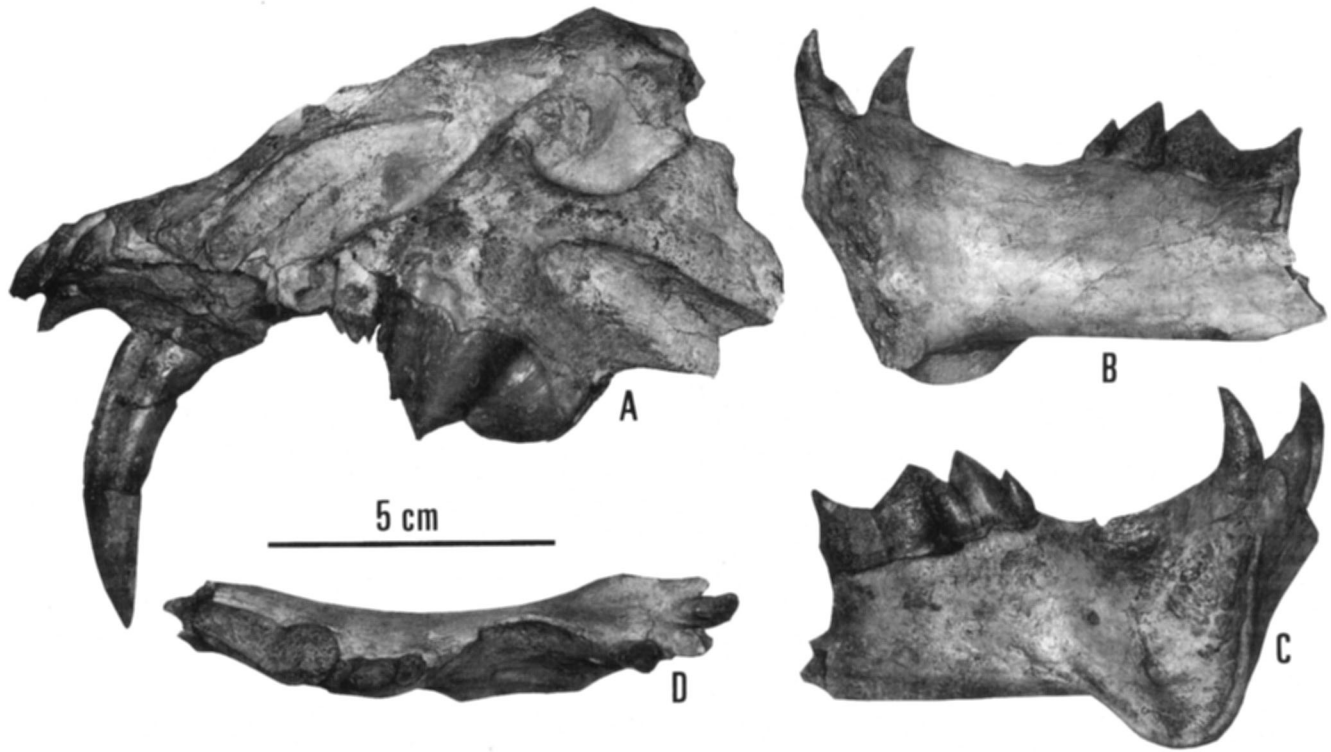**Diagnosis**—Ozansoy (1965) gave no formal diagnosis of his

FIGURE 1. *Barbourofelis piveteaui,* associated skull and mandible, locality SL2, Middle Sinap Formation, Turkey. **A**, skull in left lateral view, showing left P3 and P4, incisors, and right deciduous canine, **B–D**, mandible in lingual, labial and occlusal views. ×¾.

new species, although he stressed some of the important features of the lower jaw. The following diagnosis lists the apomorphic characters of both the skull and mandible:

A species of *Barbourofelis* of medium size, comparable to that of *B. morrisi.* Maxilla very deep vertically, anterior root of zygomatic arch deeply excavated for masseter insertion; blade of P4 very long and high; M1 much reduced, largely hidden by P4 in labial view; mandibular symphysis thin, with deep and low genial fossa; p3 sometimes absent.

Referred Specimen—Associated anterior part of skull and mandible, described below; Sinap Locality 2, Middle Sinap Formation (Figs. 1, 2). Housed in the Department of Anthropology, Faculty of Letters and History, Ankara, Turkey; catalogue no. 06–AKM–0276.

Description—The SL2 specimen consists of the anterior part of a skull, transversely crushed, with the left maxilla, anterior root of zygomatic arch, and most of the left orbit preserved. All of the upper teeth are represented, either from the left or
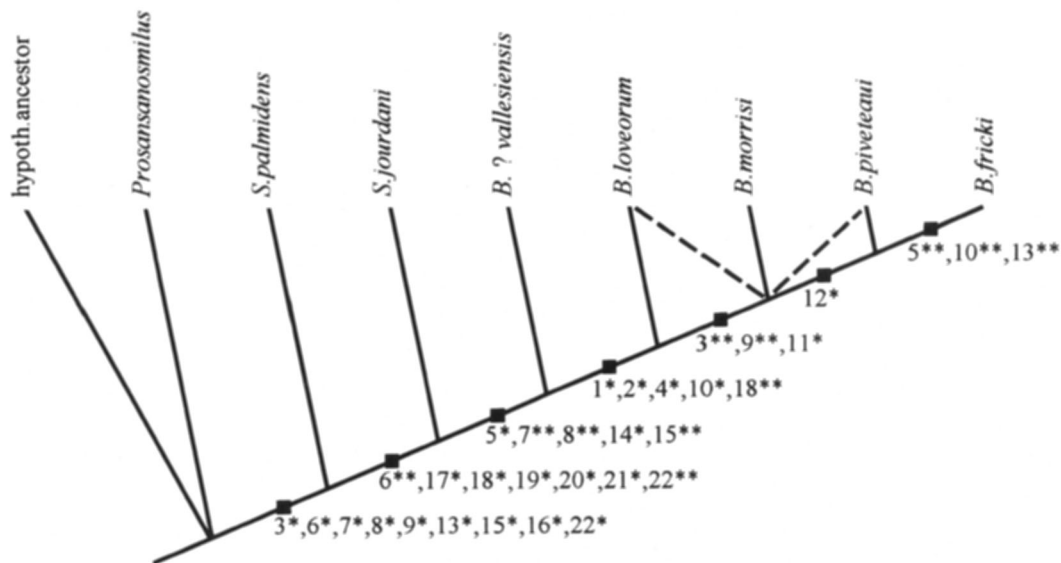

FIGURE 2.   Tentative cladogram of barbourofelines. Numbers refer to characters in Tables 1 and 2. The shortest tree is shown in continuous line, but its higher dichotomies are not strongly supported, and we prefer the unresolved polytomy shown in broken line.

the right side. The anterior part of the right mandible, the more nearly complete, includes i2–m1; smaller fragments of the left mandible are also preserved; i1 is the only unknown tooth.

The lower border of the nasal opening is rounded, and the premaxillae extend about as far posteriorly as in *B. morrisi* (Schultz et al., 1970:fig. 1), above the anterior part of P3. The maxilla extends strongly dorsally, because of the very long canine root, which ends only about 1 cm in front of the orbit. Posterior and more or less parallel to the canine root is a long, slitlike opening, which includes the infraorbital foramen, extending from the alveolar border in front of P3 to about half a centimeter in front of the middle of the orbit. *Barbourofelis morrisi* has a similar opening, but it is shorter, both because it does not extend so far dorsally and because the maxilla is less deep vertically (Schultz et al., 1970:fig. 1). *B. fricki* is perhaps less different from *B. morrisi* than the figures in Schultz et al. (1970) suggest (X. Wang, pers.com.). Above the posterior half of P4, the lateral surface of the root of the zygomatic arch is deeply excavated for insertion of the masseter muscle, as in *B. morrisi,* but the jugal is higher than in the latter species. The Sinap skull is broken level with the rear of the orbit, so that it is impossible to ascertain beyond doubt that it was closed posteriorly, as in American barbourofelines, but this was almost certainly the case: the postorbital process of the jugal, although broken at its tip, is still broader and longer than in most carnivorans, and the gap between it and the postorbital process of the frontal, also incomplete, could not have been more than a few mm wide before fossilization, and was probably bridged.

Crushing precludes determination of the detailed morphology of the palate, but the anterior border of the choanae was certainly further forward than the posterior end of P4, as in American barbourofelines. The great width of the palate at the level of the cheek teeth can be deduced from the relative positions of the canine and P3: the latter is much more lateral than the former, and the long axis of the carnassial is much more labial than the canine.

Only the anterior half of the mandible is preserved. The ramus is much deeper anteriorly than below m1, in contrast to *B. whitfordi* of the early Clarendonian (Gregory, 1942; Schultz et al., 1970). The symphysis is more like that of American *Barbourofelis* (Schultz et al., 1970:fig. 6) than that of *Sansanosmilus* in that it is thicker dorsally than ventrally, but the genial fossa is more ventral and anteroposteriorly deeper than in *B. morrisi.* These characters are identical in the type specimen, although it is from a much older individual. The anterior border of the symphysis is a little less inclined than that of *Sansanosmilus jourdani vallesiensis* from the Spanish locality of Santiga, which is of similar age (Beaumont and Crusafont, 1982). The genial (mandibular) flange is shorter ventrally than in both latter taxa, and the mandibular ramus is shallower, but these differences are probably due to the relatively young age of this individual, because they are not found in the holotype. The lingual side of the genial flange, below the level of the lower border of the ramus, is roughened, as if it had given insertion to a muscle. On the holotype which is from an old individual, the presence of a muscular insertion in the same area is not in doubt, and the flange is even recurved inwards, forming a deep groove. In *Sansanosmilus,* which has a smaller flange, the muscle scar on the lingual side is well delimited but much smaller. In the felid *Homotherium,* which has almost no flange, Bonis (1976a) has noted that the anterior lower side of the ramus is roughened and probably gave insertion to the digastric muscle. If this is true, this position is more anterior than in conical-toothed felids, but it seems that it was even more anterior in *B. piveteaui.* This suggests that one of the roles of the genial flange was to provide a larger insertion area for this jaw-opening mus-

cle, rather than just for protecting the upper canines (Emerson and Radinsky, 1980).

All teeth are finely serrated, but this is hardly visible with the naked eye, especially on the upper incisors. All upper and lower incisors include a single cusp with a mesial and a distal crest, but the upper ones are much more slender than the lower ones. None of them is worn. The upper ones increase gradually in size from I1 to I3, the latter being about twice as wide mesiodistally as the former. They are arranged in a curve; the diastema between I3 and C is 7.5 mm.

The dirklike canine, preserved on the right side, is extremely long and slender, and regularly curved. It is also strongly compressed, its mesiodistal diameter at the base of crown being about three times greater than the transverse one. It has anterior and posterior crests, the former being lingually recurved near the base, and a shallow longitudinal groove on the lingual side, but little more than a slight indication of a labial one.

The radiograph shows that a permanent canine, not visible externally, is still enclosed in the maxilla, and the saber-tooth is therefore a deciduous canine. Delayed eruption of the canines is the rule in nimravids, because of the large size of the deciduous tooth (Brunet, 1972; Bryant, 1988).

P3 is much reduced, but less so than in *B. fricki.* It has two roots and three aligned cusps of which the central one is the highest; they are all unworn.

P4 is by far the largest of all of the cheek teeth. There is no protocone. The blade consists of a short but high preparastyle, with a straight anterior border, a strongly asymmetrical parastyle with long anterior cutting edge, and a tip close to the paracone. The latter is taller and much longer than the two preceding cusps, and the metacone is about as long as the paracone. The tooth is extremely hypsodont, with the pillars of all four cusps strongly convergent downwards: it seems, thus, that they are especially well designed to withstand stresses during shearing. The posterior two-thirds of the tooth are well worn, but the preparastyle and parastyle are almost unworn.

M1 is a small tooth, broader than long, only partly visible behind P4 in labial view. It is recurved forward so as to wear against the posterior side of m1, in an almost vertical plane.

The lower incisors and canines are arranged in a smooth curve. The i1, as indicated by its alveolus, was the smallest and i3 the largest, the lower canine being slightly smaller than i3. They are high and slender, without accessory cusps, but with mesial and distal crests, and are unworn.

There is no p3. On the right ramus, a minute alveolus, about 1 mm in diameter, located well forward of p4, could have been left by dp3, but it is absent on the left ramus. The radiograph shows that no tooth is concealed in bone. The p3, although sometimes much reduced, is almost always present in other Nimravidae, including the type specimen of *B. piveteaui,* and this mandible displays thus an extreme case of reduction of this tooth, comparable only to *Eusmilus,* some *Hoplophoneus* specimens and a few individuals of *B. loveorum.*

The p4 consists of four cusps, all inclined posteriorly. The anterior one is the lowest and is unworn. The main cusp is much longer than the other three and is as high as the paraconid of m1. The last cusp, which is not cingular according to Baskin (1981), is very short. The cusps are arranged in a straight line, and the posterior part of the tooth, together with m1, forms a single, uninterrupted shearing blade. These teeth strongly overlap, a derived character also found in American barbourofelines (Martin, 1984).

The lower carnassial, which is much longer than p4, has an anterior crest forming a kind of "preparaconid"; even so, the paraconid is shorter than the protoconid; they are less clearly individualized than in the Felidae, and there is almost no notch

TABLE 1. Character states.

Matrix, Table 2: Cladogram, Fig. 2:	0	1 *	2 **
1. Orbit	open	closed	
2. Infraorbital foramen	medium-sized	very large	
3. Masseter insertion	normal	enlarged	excavated
4. Palate at level of P3/P4	normal	very broad	
5. P3	4 cusps	3 cusps	2 cusps
6. Protocone of P4	large	reduced	vestigial/absent
7. Preparastyle of P4	present	high	very high
8. Parastyle of P4	low	high	very high
9. P4	low	hypsodont	very hypsodont
10. M1	small	very small	minute
11. Position of M1	distal to P4	medial to P4	
12. Mandibular symphysis	low and thick	high and thin	
13. Genial flange	small	long	very long
14. Lower canine	larger than i3	same size	
15. p3	normal	small	minute/absent
16. p4	low	hypsodont	
17. Anterior cusp of p4	high	lower	
18. Length P4/Length p4	<1.85	1.95–2.1	>2.25
19. Length p4/Length m1	>0.85	<0.72	
20. Paraconid of m1	normal	expanded	
21. Notch of m1	deep	attenuated	
22. Metaconid of m1	strong	weak	absent

between them. There is no metaconid or talonid, but the posterior side wears against M1.

Dimensions (mesiodistal × labiolingual):

I1	I2	I3	C	P3	P4	M1
Upper						
4.7×5.3	7.5×6.2	9.3×7.2	17.4×6.0*	8×4.3	40.3×9.5	3.5×6.5
Lower						
	4.7×6.7	8.3×5.5	7.3×5.5		17.7×7.2	26.6×10.8**

* dC
** minimum width near mid-length = 8.0

RELATIONSHIPS

Eurasian Miocene nimravids are characterized by a short muzzle, high zygomatic root, choanae well forward of the rear of P4, the upper canine with at least a lingual groove, P4 with a preparastyle, M1 reduced, the mandible with a genial flange, a low coronoid process, m1 without a talonid and with a protoconid longer than the paraconid. Although they have been referred to at least three different genera (*Prosansanosmilus* Heizmann, Ginsburg, and Bulot, *Sansanosmilus* Filhol, and *Albanosmilus* Filhol), Eurasian Miocene nimravids remain poorly known, with the only previously known skulls being those referred to *Sansanosmilus* from Sansan (Ginsburg, 1961); other localities have yielded only teeth and fragmentary jaws, referred to the following taxa:

1) *Prosansanosmilus peregrinus* Heizmann, Ginsburg and Bulot, 1980 is known from the lower Miocene of Langenau and other sites in western Europe. It was regarded by its authors as an ancestor of *Sansanosmilus*;

2) *S. palmidens* Blainville, mainly known from Sansan (Ginsburg, 1961), has also been found in China (Chen and Wu, 1976).

3) *Albanosmilus jourdani* Filhol is based upon a fragment of mandible and upper canine from the late middle Miocene of La Grive-Saint Alban in France (Filhol, 1981; Viret, 1951). It has also been described from the roughly contemporaneous localities of Steinheim in Germany (Heizmann, 1973) and San Quirico in Spain (Villalta and Crusafont, 1943), and given the new subspecific name of *andresi*.

4) *S. jourdani vallesiensis* Beaumont and Crusafont (1982)

comes from the early late Miocene (Vallesian) of Santiga in Spain. The specimens of *S. jourdani* from Los Valles de Fuentidueña, also in Spain, of similar age (Ginsburg et al., 1981) should probably be referred to the same subspecies. Nimravids are unknown in Eurasia after the Vallesian, probably being replaced by felid saber toothed cats.

We have compared the characters displayed by the Old World species with those published for the North American *Barbourofelis*, the best known species of which are *B. fricki*, *B. morrisi* (Schultz et al., 1970), and *B. loveorum* (Baskin, 1981; Bryant, 1988; the specific name has been amended from *B. lovei* by Hulbert, 1992). These characters, some of which were listed by Bonis (1976b), Heizmann et al. (1980), Martin (1980, 1984), and Beaumont and Crusafont (1982), are listed in Tables 1 and 2.

This matrix was submitted to parsimony analysis (program Hennig86) with all characters treated as additive (state 1 being intermediate between 0 and 2), and rooted with a hypothetical ancestor that differs from *Nimravus* by two characters only:

1) P3 has 4 cusps instead of only 2, but the polarity of this change, towards the reduction of this tooth, is obvious; and

2) its index length p4/length m1 is supposed to be greater than 0.85, while it is smaller in *Nimravus*, but m1 is long in this genus because there is a long talonid. Here also, the polarity, towards lengthening of the blade, is not in doubt.

The shortest cladogram (Fig. 2) has 33 steps and no homoplasy. The main results of the analysis are the following:

1) "*Albanosmilus*" *jourdani* is undoubtedly distinct from *Sansanosmilus palmidens*, but a genus *Albanosmilus* is either mono-specific (if it includes only *jourdani*) or paraphyletic (if *vallesiensis* is included). Alternatively, *Sansanosmilus*, with at least two species, could be retained as a paraphyletic genus.

2) "*Sansanosmilus jourdani*" *vallesiensis* Beaumont and Crusafont from the Vallesian of Spain is distinct from *S. jourdani* at the species level. However, it retains a relatively large M1 (Ginsburg et al., 1981) and perhaps large p4 (ratios derived from isolated teeth), and it is very incompletely known, so that many of the synapomorphies that define the highest nodes of the cladogram are not observable in this species. It might in fact be closely related to *B. piveteaui*.

TABLE 2. Data matrix.

Character numbers	B. piveteaui	S. palmidens	S. jourdani	B(?). valle-siensis	B. morrisi	B. loveorum	B. fricki	P. peregrinus	Hypothetical ancestor
1	1	0	?	?	1	1	1	?	0
2	1	0	?	?	1	1	1	?	0
3	2	1	?	?	2	?	2	?	0
4	1	0	?	?	1	1	1	?	0
5	1	0	0	1	?	1	2	?	0
6	2	1	2	2	2	2	2	0	0
7	2	1	1	2	2	2	?	0	0
8	2	1	?	2	2	2	?	0	0
9	2	1	1	?	2	1	?	0	0
10	1	0	?	0	1	1	2	?	0
11	1	0	?	?	1	0	1	?	0
12	1	0	?	?	0	?	1	0	0
13	1	1	?	1	1	1	2	0	0
14	1	0	?	1	1	1	1	0	0
15	2	1	1	2	2	2	2	0	0
16	1	1	1	1	1	1	?	0	0
17	1	0	1	1	1	?	?	0	0
18	2	0	1	1	2	2	2	0	0
19	1	0	1	1	1	1	1	0	0
20	1	0	1	1	?	1	?	0	0
21	1	0	1	1	1	1	1	0	0
22	2	1	2	2	2	2	2	0	0

The highest nodes of the cladogram are poorly supported:

1) the group *piveteaui-fricki* rests only upon the morphology of the symphysis;
2) the group *morrisi-piveteaui-fricki* is supported by the excavated masseter insertion, very high P4, and M1 not visible in labial view. However, the states of the first and second characters are not available from descriptions of *B. loveorum* or *B. fricki*, respectively, and the third character alone is perhaps not of prime significance. Since we have not seen the American material, and pending recovery of more complete material of *B. piveteaui* and especially of *B. ? vallesiensis*, we think it wiser to keep all four higher taxa as an unresolved polytomy, for which we use the generic name *Barbourofelis* until its internal relationships are deciphered. *B. piveteaui* is at the same evolutionary grade as *B. morrisi*, and their specific distinction may even be questioned. The former differs from the latter by its thin symphysis, especially in the lower part, and the higher maxilla; both characters make it more like *B. fricki*, but it lacks the extreme specializations of this species.

The shortest tree would imply that, while *Barbourofelis* is an immigrant from the Old World, *B. piveteaui* followed the reverse route. However, the absence of major morphological differences between *B. ? vallesiensis* and *B. piveteaui* suggests regional continuity, and rather than following strict parsimony, one might consider all American *Barbourofelis* as forming a monophyletic group. In this hypothesis, the similarities between *B. piveteaui* and some American species would result from parallel evolution, because the Turkish species is more evolved than the earliest North American one, *B. whitfordi* of the early Clarendonian. This evolutionary scenario, which we favor, has the advantage of implying only one migration, into North America, probably close to the middle/late Miocene boundary, but no good geographic intermediate is known. *Sansanosmilus* (?) *serratus* Pilgrim, 1932, from the Siwaliks, is too poorly known to be formally included in *Barbourofelis*; in any case, it belongs to the Indian faunal realm, off to one side of any direct Eurasian–American pathway. "*S. palmidens*" from Jiulongkou (Chen and Wu, 1976) has only a small preparastyle on P4, and is thus too primitive to be intermediate. This leaves only the "*Machairodus*" from Tung Gur (Colbert, 1939), known by a single worn P4, as a possible link.

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