New remains of Barbourofelidae (Mammalia, Carnivora) from the Miocene of Southern Germany: implications for the history of barbourofelid migrations

by

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Abstract

Three new specimens belonging to the rarely preserved carnivoran sabre-toothed family Barbourofelidae are described from different Early to Middle Miocene localities of Bavaria (Southern Germany): a P4 of *Prosansanosmilus peregrinus* from Petersbuch 2 (MN 4a), an upper deciduous canine of *Sansanosmilus jourdani* from Benningen (late MN 6 or early MN 7/8), and a lower jaw fragment of the same species from Massenhausen (late MN 7/8).
In MN 4-5 barbourofelids migrated at least three times from Africa to Europe, presumably via the Iberian Peninsula. In the late Middle Miocene the family reached North America. Comparisons of new and known specimens of *Sansanosmilus* to the earliest North American barbourofelid, *Barbourofelis whitfordi*, reveal a reduced incisor region and a different symphysis shape to be the only morphological differences of apomorphic *S. jourdani* to *B. whitfordi*. The more posteriorly protruding dorsal symphysis of *S. jourdani* is regarded as a diagnostic character to separate the genera *Sansanosmilus* and *Barbourofelis*, because it also occurs in *S. palmidens* and *S. piveteaui*, but is lacking in all species of *Barbourofelis*. The barbourofelid radiation in North America started with the immigration of *S. jourdani* at a time around the MN 6-7/8 transition followed by a rapid evolution towards *B. whitfordi*.

Keywords: Barbourofelidae, morphology, palaeobiogeography, Miocene, Bavaria

Zusammenfassung

Aus dem Unteren und Mittleren Miozän Bayerns werden drei Carnivorenreste beschrieben, die alle der selten überlieferten Familie Barbourofelidae angehören: Ein isolierter P4 von *Prosansanosmilus peregrinus* von Petersbuch 2 (MN 4a) sowie ein oberer Milchcaninus von Benningen (spätes MN 6 oder frühes MN 7/8) und ein Unterkiefer-fragment von Massenhausen (spätes MN 7/8), die beide zu *Sansanosmilus jourdani* gestellt werden.
Von Afrika aus migrierten die Barbourofeliden in MN 4 und MN 5 mindestens dreimal nach Europa, in allen drei Fällen wahrscheinlich über die Iberische Halbinsel. Im oberen Mittelmiozän erreichten sie Nordamerika. Ein Vergleich der neuen wie beschriebener Reste von *Sansanosmilus* mit dem frühesten nordamerikanischen Familienvertreter, *Barbourofelis whitfordi*, zeigt außer einer reduzierten Frontregion und einer unterschiedlichen Symphysenform keine morphologischen Unterschiede apomorpher *S. jourdani* zu dieser urtümlichsten nordamerikanischen Art. Die dorsal etwas längere Symphyse von *S. jourdani* wird als diagnostischer Unterschied zwischen den Gattungen *Sansanosmilus* und *Barbourofelis* gewertet, da dieses Merkmal auch bei *S. palmidens* und *S. piveteaui* auftritt, bei den Arten von *Barbourofelis* aber fehlt. Die Verbreitung der Barbourofeliden in Nordamerika beginnt um die Grenze MN 6-7 mit *S. jourdani*, wobei die Art schnell zu *B. whitfordi* evolvierte.

1. Introduction

Early to Middle Miocene sabre-toothed carnivorans are long known to be present in Europe: the earliest taxonomical record dates back to 1843, when BLAINVILLE described *Felis palmidens* from MN 6 of Sansan. Since then its genus name has been changed into *Sansanosmilus* KRETZOI, 1929, which itself was placed into the Barbourofelidae by MORLO et al. (2004), a family, the systematic position of which greatly varied due to assignments to Nimravidae (starting with TEDFORD, 1978) and Felidae (MORALES et al., 2001). Today, Barbourofelidae consists of seven genera and seventeen species. By placing the family apart from the Nimravidae, it became the third carnivoran lineage which independently evolved sabre-tooth morphology. The other (among Carnivora) are the Nimravidae and the machairodontine felids. With its terminating species, *Barbourofelis fricki*, Barbourofelidae evolved the most adapted sabre-tooth morphology among all known sabre-toothed mam-

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mals ever, including the metatherian *Thylacosmilus* and the creodont Machaeroidinae (THERRIEN, 2005).

Barbourofelidae had a complex migration history with the earliest members occurring in the Early Miocene of Africa, a Eurasian distribution in the late Early to early Late Miocene, and a migration into North America in the late Middle Miocene. The last members of the family occurred in MN 9 of Europe and the late early Hemphillian (Hh2) of North America (SCHULTZ et al., 1970; GERAADS & GÜLEÇ, 1997; MARTIN, 1998; MORALES et al., 2001; WANG et al., 2003; MORLO et al., 2004). Details of the underlying migration events are however unclear, especially concerning the migration of *Sansanosmilus* into North America.

The fossil record of the family, especially in Asia and Africa, is extraordinarily poor. For most species, less than half a dozen specimens are known. Therefore, every newly described specimen adds information to the scarce knowledge of the family, which represented the dominating sabre-toothed carnivorans in the Early and Middle Miocene of Africa and all the Northern continents. In this study, three new barbourofelid specimens are described and the holotype of the earliest North American species, *Barbourofelis whitfordi* (BARBOUR & COOK, 1915), is compared to known and new material of *Sansanosmilus* to clarify which Eurasian taxon started the North American radiation of the family.

2. Material and Methods

All three specimens described here are housed at the Bayerische Staatssammlung für Geologie und Paläontologie, Munich, Germany (BSP). They come from the Bavarian localities Petersbuch 2, Massenhausen, and Benningen near the town Memmingen. The well-known MN 4a locality Petersbuch 2 is described in HEISSIG (1978) and ROTH (1987), information on Massenhausen can be found in FAHLBUSCH (1964). The fauna is interpreted as being late MN 7/8 due to the presence of the proboscidean *Prodeinotherium giganteum*. The fauna of Benningen is poorly known and not yet published. Information is only available from a field book of R. Dehm. All Benningen specimens were unearthed during the excavation of a skeleton of *Prodeinotherium bavaricum* in 1934 which allowed a tentative assignment of the fauna into MN 5-7/8. The *Sansanosmilus* canine described herein restricts the age to MN 6-7/8 (see below). Other remains found (gastropods, turtles, and a tooth of an ochotonid) do not provide further information on the age of the Benningen fauna.

Abbreviations: MNHN – Muséum national d'Histoire naturelle, Paris (F); SMNS – Staatliches Museum für Naturkunde Stuttgart (D); UNSM – University of Nebraska State Museum, Lincoln, NE (U.S.A.).

Measurements are done with callipers to the nearest 0.1 mm and are given in mm. Tooth sizes are given in max. length: max. breadth. Tooth morphology nomenclature follows VAN VALEN (1994). Upper teeth are referred to by capitals, as in "P4", lowers by normal letters, as in "p4" Taxon occurrence in specific MN-zones was mainly taken

out of NOW (http://www.helsinki.fi/science/now) if not otherwise stated.

3. Systematic Paleontology

Carnivora BOWDICH, 1821
Feliformia KRETZOI, 1945
Familia: Barbourofelidae SCHULTZ, SCHULTZ & MARTIN, 1970 (sensu MORLO et al., 2004)

Type genus: *Barbourofelis* SCHULTZ, SCHULTZ & MARTIN, 1970

Other included genera: *Afrosmilus* KRETZOI, 1929; *Ginsburgsmilus* MORALES, SALESA, PICKFORD & SORIA, 2001; *Prosansanosmilus* HEIZMANN, GINSBURG & BULOT 1980; *Sansanosmilus* KRETZOI, 1929; *Syrtosmilus* GINSBURG, 1978; *Vampyrictis* KURTÉN, 1976.

Prosansanosmilus HEIZMANN, GINSBURG & BULOT, 1980

Type species: *Prosansanosmilus peregrinus* HEIZMANN, GINSBURG & BULOT, 1980
Additional species: *P. eggeri* MORLO, PEIGNÉ & NAGEL, 2004

Prosansanosmilus peregrinus HEIZMANN, GINSBURG & BULOT, 1980

Holotype: SMNS 41482, mandible with c-m1.
**Age and distribution**: MN 4-5 of Central and Western Europe.
New material: BSP 1976 XXII 3678 (Fig. 1A-C), isolated right P4 (22.9:10.6) from MN 4a of Petersbuch 2 (ROTH 1987).
Description and comparisons: This isolated tooth shows the typical morphology of P4 of *P. peregrinus*. Its morphology is nearly identical to that of MNHN Be 7212, a P4 from Bézian (HEIZMANN et al., 1980; MORLO et al., 2004: fig. 5D). Both specimens differ in the same way from the other two plesiomorphic barbourofelid species from MN 4-5 of Europe, *Afrosmilus hispanicus* MORALES, SALESA, PICKFORD & SORIA, 2001 and *P. eggeri*. The P4 of *P. peregrinus* differs from that of *P. eggeri* in having a minute preparacone that is lacking in *P. eggeri*. Furthermore, the small preparastyle is protruding anteriad instead of anterolabiad as is typical for *P. eggeri*. The P4 of *P. peregrinus* differs from that of *P. eggeri* and *A. hispanicus* in having the posteriormost point of the anterior tooth border placed lingual to the paracone instead of antero-lingual. From the P4 of *S. palmidens*, known from European MN 5 as *P. peregrinus* and *P. eggeri*, the Petersbuch tooth differs in being smaller, having the protocone much more pronounced, and the preparacone smaller.
Discussion: This isolated P4 was previously described in a dissertation, only (ROTH, 1987). Its morphology is identical to that of the long known P4 of *P. peregrinus* from Bézian

Figure 1: A-C. *Prosansanosmilus peregrinus* Heizmann, Ginsburg & Bulot, 1980. BSP 1976 XXII 3678, isolated right P4 from MN 4a of Petersbuch 2 in A: labial view, B: occlusal view, C: lingual view.

D-G. *Sansanosmilus jourdani* (Filhol, 1883). BSP 1936 I 48, isolated deciduous left upper canine from late MN 6 or early MN 7 of Benningen, D: external view of the tip, E: external view, enclosed area marks enlarged detail in Fig. 1D, F: posterior view, G: internal view.
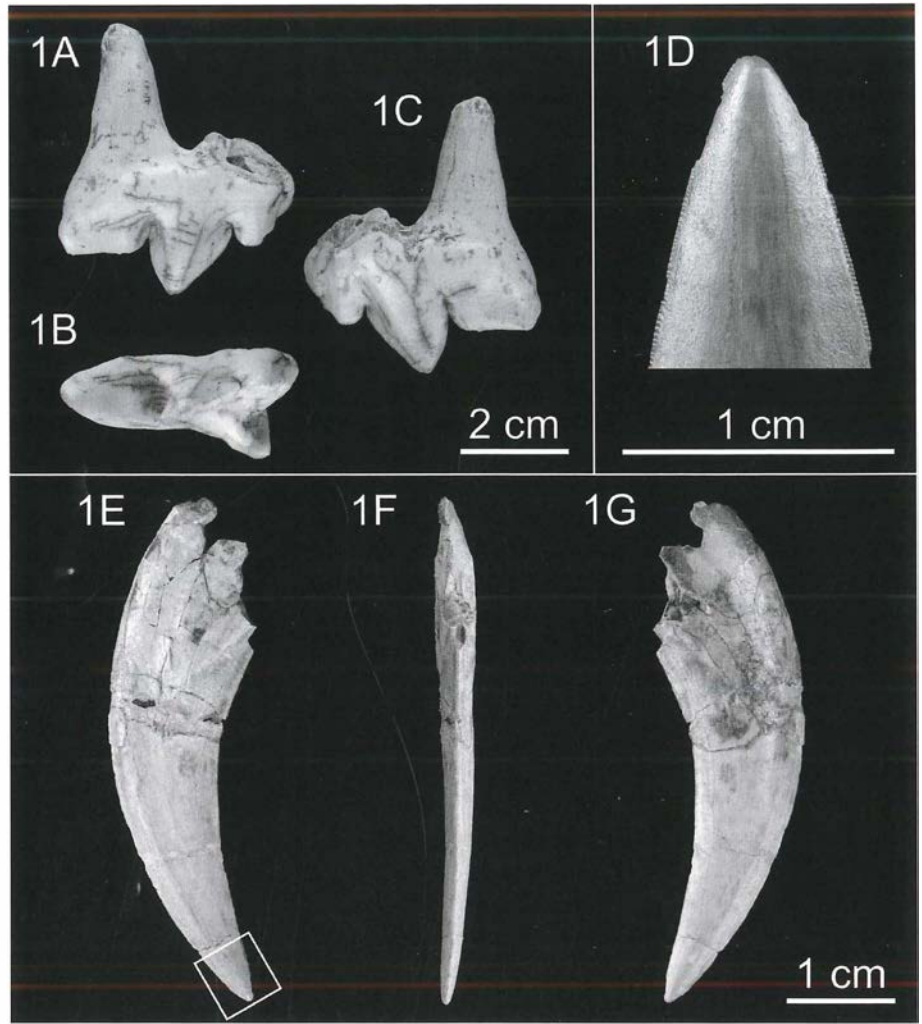
(24.1:11.1), but reaches only 90% of the size of the French specimen. This upper dental size variability is far smaller than known from the lower dentition of *P. eggeri*, in which p4-size varies by about 17% (Morlo et al., 2004: table 1). The consistent morphological differences of these two specimens to P4 of *P. eggeri* and *A. hispanicus* confirm the separation of all three taxa (Morales et al., 2001; Morlo et al., 2004). The Petersbuch specimen, however, sheds no light to the recent discussion on the generic assignment of *A. hispanicus* (Morlo et al., 2004).

Sansanosmilus Kretzoi, 1929

Type species: *S. palmidens* (Blainville, 1843)
Additional species: *S. jourdani* (Filhol, 1883); *S. piveteaui* (Ozansoy, 1965); *S. vallesiensis* Beaumont & Crusafont-Pairo, 1982.

Sansanosmilus jourdani (Filhol, 1883)

Holotype: MNHN 1384 from MN 7/8 of La Grive-St. Alban.
Age and distribution: Middle Miocene of Eurasia (MN 6-7/8).
New material: BSP 1936 I 48 (Fig. 1D-G), isolated left deciduous upper canine fragment (21.0:6.0) from late MN 6 or early MN 7/8 of Benningen. BSP 1951 I 43

(Fig. 2B, C, F), anterior fragment of right mandible with alveolus of i2, root of i3, canine (8.0:5.0), alveolus of p3 (7.2:4.9), and roots of p4 (13.7:7.4) from late MN 7/8 of Massenhausen.

Description and comparisons: The canine is extremely narrow and shows a groove on its internal side (Fig. 1G) as is diagnostic for Barbourofelidae. Anterior and posterior edges were crenulated from the tip (Fig. 1D) down to the enamel base. While gross morphology of the upper canine is fairly uniform in all *Sansanosmilus*, that of *S. palmidens* is clearly smaller than those of the other species. The tooth from Benningen is much larger than that of *S. palmidens* (e.g., Ginsburg, 1961: pl. 14, fig. 2), but is similar in size to the paratype of *S. jourdani* (Filhol, 1883: pl. 4, fig. 3) and the upper canine of *S. vallesiensis* figured by Beaumont & Crusafont-Pairo (1982: pl. 4, fig. 6). The Benningen canine, however, differs from all these specimens in being stronger curved, a character it shares with a canine of a juvenile *Barbourofelis loveorum* (see Bryant, 1988). This specimen therefore is interpreted here as a deciduous upper canine of *S. jourdani*.

The partial right ramus is the first known specimen of *S. jourdani* preserving the anterior mandibular region. In its most dorsal part the symphysis is longer in antero-posterior direction than more ventrally and very similar to that of *S. palmidens*. A large flange is developed which bears three foramina, located beyond the canine and the curved

diastema, respectively. Posteriorly, the flange ends basal to p3. In the incisor region, i1 is completely absent. From i2 only the alveolus is present while i3 is preserved by its root. The lower canine is characterized by a serrated posterior crest. The p1 and p2 are completely absent, p3 was single-rooted. Only the roots are preserved from p4, proving the tooth – as the whole ramus – to be slightly smaller than in the holotype of *B. whitfordi*. The fragment ends with the anterior border of the anterior alveolus of m1.

Discussion: The presence of *Sansanosmilus jourdani* proves the age of the Benningen fauna to be younger than MN 5. Except from MN 7/8, *S. jourdani* is cited to be present in MN 6 of Arroyo del Val and Neudorf-Spalte (see NOW). During this study, it was not possible to check the referenced specimens for correct assignment. Hence, the age of the Benningen fauna remains unclear. Based on the *Sansanosmilus* canine it could be late MN 6 or MN 7/8 if presence of *S. jourdani* in MN 6 is confirmed.

Comparison of Middle Miocene *Sansanosmilus* and *Barbourofelis whitfordi*:

Sansanosmilus palmidens represents the most plesiomorphic species of the genus. It was said to be extremely similar to *B. whitfordi* (SCHULTZ et al., 1970), but ,in fact, it differs from that species in being much smaller, having the dorsal symphysis reaching more posteriorly, a double-rooted and less reduced p3, a p4, which is larger relative to m1, and an m1, which bears a minute metaconid. Moreover, i1 is always present in *S. palmidens*, but is only occasionally found in *B. whitfordi*, e.g., is lacking in the holotype (SCHULTZ et al., 1970). *S. palmidens* resembles the North American taxon in having a similarly broad incisor region, with the anterior crest of the flange running more anteriorly than in *S. jourdani*.

Sansanosmilus jourdani from Massenhausen resembles the holotype of *B. whitfordi* in all characters except for it being slightly smaller in overall size, having a narrower incisor region, and the dorsal symphysis extending more to posterior. The incisor region is more reduced due to stronger reduction of the incisors and because the anterior crest of the flange runs more posteriorly in the Massenhausen specimen (Fig. 2E-F). Both characters could be interpreted as representing apomorphic states and also separate *S. jourdani* from *S. palmidens*. In contrast, *S. jourdani* shares the more to posteriad extending dorsal symphysis with *S. palmidens* (GINSBURG, 1961: pl. 15, fig. 2b) and *S. piveteaui* (GERAADS & GÜLEÇ, 1997: fig. 1), but not with *B. whitfordi* (Fig. 2A) and the other *Barbourofelis* species (SCHULTZ et al., 1970). Because other specimens of *S. jourdani* do not reveal any other difference to *B. whitfordi*, the different morphology of the symphysis is interpreted as the only known character that clearly separates the genera *Sansanosmilus* and *Barbourofelis*.

4. The history of barbourofelid migrations

The origin of Barbourofelidae, sister-group of Felidae (MORLO et al., 2004), is unknown. Its most plesiomorphic member occurred in Africa contemporary to biozone MN

2 with the genus *Ginsburgsmilus* (Fig. 3). Corresponding to MN 4, the more evolved genera *Afrosmilus*, present with two species in East Africa (MORALES et al., 2001; MORLO et al., 2004), and *Syrtosmilus*, known from a single specimen from Libya, occurred in Africa. *Afrosmilus* was said to be part of an early Miocene carnivoran immigration event at MN 3 (VAN DER MADE, 1999) during which several carnivoran taxa migrated from a yet unknown Asian fauna to Africa. More probably, this arrival took place earlier, in the latest Oligocene (MORALES et al., 2000; MORLO et al., in print). The existence of a land bridge between western Asia and Africa at that time is supported by 1) studies on the foraminiferan fauna of the Paratethys (e.g., DROOGER, 1979, 1993), 2) the presence of a Eurasian tragulid contemporary to MN 2 in Meswa Bridge, Kenya (PICKFORD, 1986; SANDERS et al., 2004), and 3) the occurrence of a possible elephantoid taxon in the latest Oligocene of Pakistan (ANTOINE et al., 2003).

In MN 4 the Barbourofelidae reached Europe with *Prosansanosmilus peregrinus* and *Afrosmilus hispanicus*. Probably, these species migrated to Europe on a western route via the Iberian Peninsula, because they are known from Germany, France, and Spain, only, with *A. hispanicus* known solely from Spain (MORALES et al., 2001; MORLO et al., 2004). Both species are lacking in more eastern faunas.

In MN 5 European barbourofelid diversity is further enhanced by *Prosansanosmilus eggeri* and *Sansanosmilus palmidens*, while *P. peregrinus* persists. The plesiomorphic *P. eggeri* is known from MN 5 localities only and thus represents the third European immigrant from Africa in MN 4-5 (MORLO et al., 2004). The ancestry of *S. palmidens* (and thus of *Sansanosmilus*) and the provenience of its ancestor are unknown. The big differences to known *Prosansanosmilus* specimens from MN 5 presumably exclude an evolution of the genus in Western Europe. More probably, the origin of *Sansanosmilus* roots in an independent barbourofelid migration out of Africa into Western Asia (even if it is not yet documented from Asia prior to MN 6, see WANG et al., 2003). Through time, the genus shows an ongoing adaptation by increasing its body mass and by evolving its sabre-tooth functional complex.

In the last review of Middle to Late Miocene barbourofelids (GERAADS & GÜLEÇ, 1997), four species of *Sansanosmilus* were distinguished (but were partly placed into *Barbourofelis*). *Sansanosmilus palmidens* (MN 5-6) is best known from the French localities Savigné-sur-Lathan (MN 5) and Sansan (MN 6). *Sansanosmilus jourdani* occurs in MN 6-7/8 of Eurasia. *Sansanosmilus vallesiensis* is known from MN 9 of Spain (BEAUMONT & CRUSAFONT-PAIRO, 1982) and the Ukraine (MORLO & SEMENOV, 2004). It may occur in Bled Douarah, Tunisia, as well, from where the contemporary *Vampyrictis vipera* KURTÉN, 1976 is described. This taxon is based on a single, highly derived m1 and a fragment of the upper canine, both of which largely resemble *S. vallesiensis* except for the presence of a tiny cuspid in m1 of *Vampyrictis* that could be interpreted as the last remain of a reduced metaconid. The material, however, is too fragmentary to allow a final

Figure 2: A, D-E. *Barbourofelis whitfordi* (BARBOUR & COOK, 1915). Cast of holotype UNSM 25546 in A: lingual view, D: labial view, E: occlusal view. In this cast, tooth sizes are slightly exaggerated compared to the original while ramus size matches well (pers. comm. B. Hunt). Note dorsal symphysis to reach less far to posterior than in *S. jourdani* (Fig. 2B), an apomorphy of *Barbourofelis*.

B-C, F. *Sansanosmilus jourdani* (FILHOL, 1883). BSP 1951 I 43. Anterior fragment of right mandible with alveolus of i2, root of i3, canine, alveolus of p3, and roots of p4 from MN 7/8 of Massenhausen in B: lingual view, C: labial view, and F: occlusal view. Note incisor region to be less broad in the Massenhausen specimen than in *B. whitfordi*, because the anterior crest of the flange runs more posteriorly than in the North American taxon. Also note the dorsal part of the symphysis extending to posterior more far, a plesiomorphic character of *Sansanosmilus palmidens* persisting in all *Sansanosmilus* species. Finally note the length of diastema, flange size, and size of p3 alveolus equally developed in both specimens.
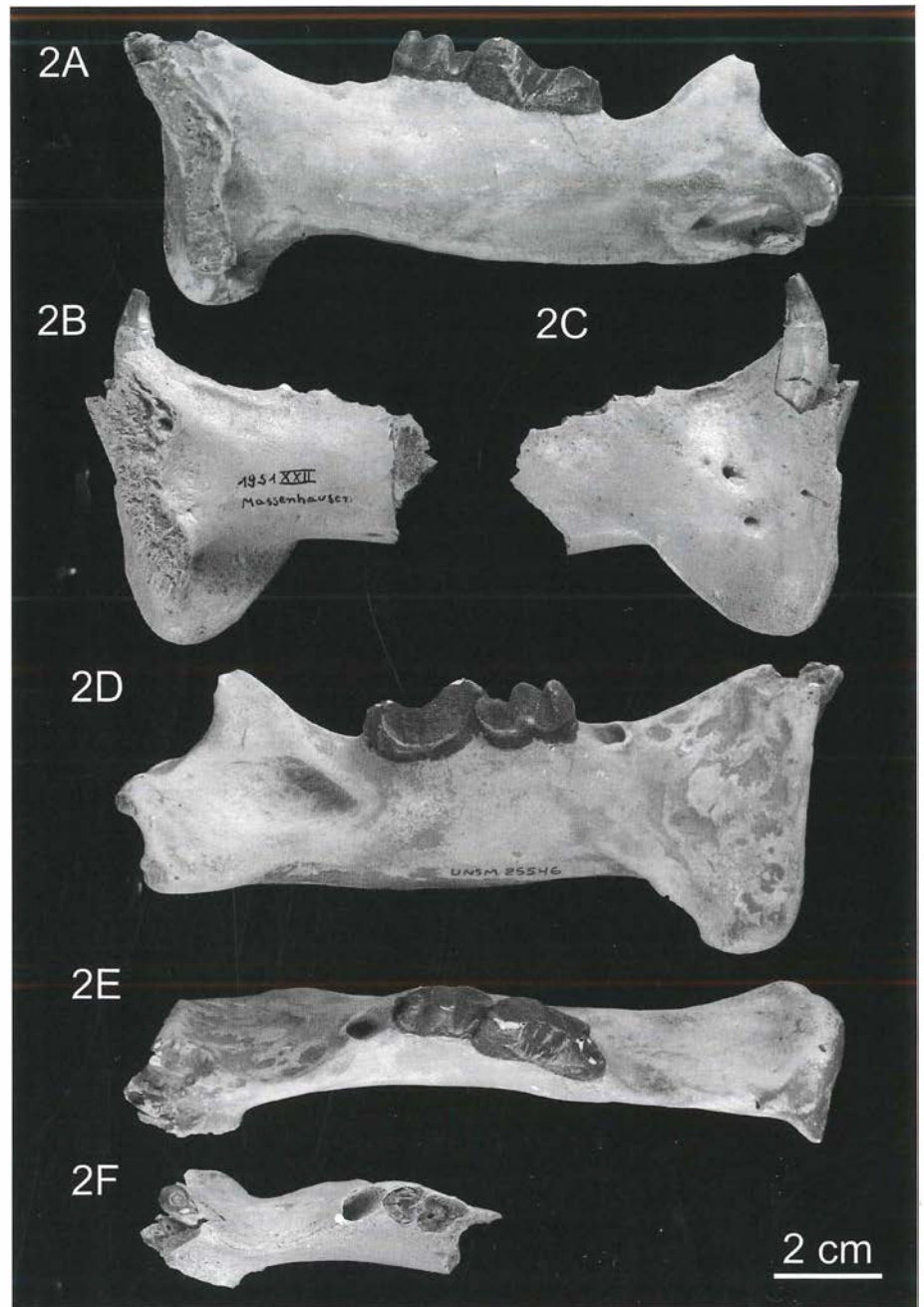
decision whether it should be assigned to *S. vallesiensis* or not. Finally, *S. piveteaui* is recorded from MN 9 of Turkey (OZANSOY, 1965; GERAADS & GÜLEÇ, 1997; VIRANTA & WERDELIN, 2003) and Moldavia (LUNGU, 1978). Based on their advanced morphology, *S. vallesiensis* and *S. piveteaui* were tentatively assigned to the North American genus *Barbourofelis* (SCHULTZ et al., 1970; GERAADS & GÜLEÇ, 1997). Following the latter authors, '?*B.*' *vallesiensis* differs from '*B.*' *piveteaui* in having relatively larger M1 and p4. It depends on how the migration of Barbourofelidae into North America is interpreted, whether or not these two species should be placed into *Barbourofelis*.

In this study European *Sansanosmilus jourdani* is directly compared with *Barbourofelis whitfordi* (for unknown reasons, GERAADS & GÜLEÇ (1997) omitted *B. whitfordi* from their phylogenetic analysis, but included it into their discussion). The comparison reveals no relevant differences between the two taxa except a more reduced incisor region and an antero-posteriorly longer dorsal symphysis in *S. jourdani* from MN 7/8 of Massenhausen. In the past, North American authors already considered this similarity by placing *B. whitfordi* as a separate species into *Albanosmilus* – and thus close to *S. jourdani* – (KITTS, 1957) or into *Sansanosmilus* (MAWBY, 1965). Even SCHULTZ et al. (1970) implied the assignment of the species to *Barbourofelis* to be questionable by citing it as ?*Barbourofelis whitfordi* and by stressing its similarity to *S. palmidens* (which in fact is less than to *S. jourdani* as has been demonstrated above). However, the longer dorsal symphysis is constantly present in all *Sansanosmilus* species (unfortunately, no specimen of *S. vallesiensis* is known with the symphysis preserved), but absent in *B. whitfordi* and all other *Barbourofelis* species. This apomorphic symphysis reduction clearly allows an assignment of the earliest North American species into *Barbourofelis*. *Sansanosmilus jourdani* is interpreted as the migrating taxon, thereby corroborating the results ob-
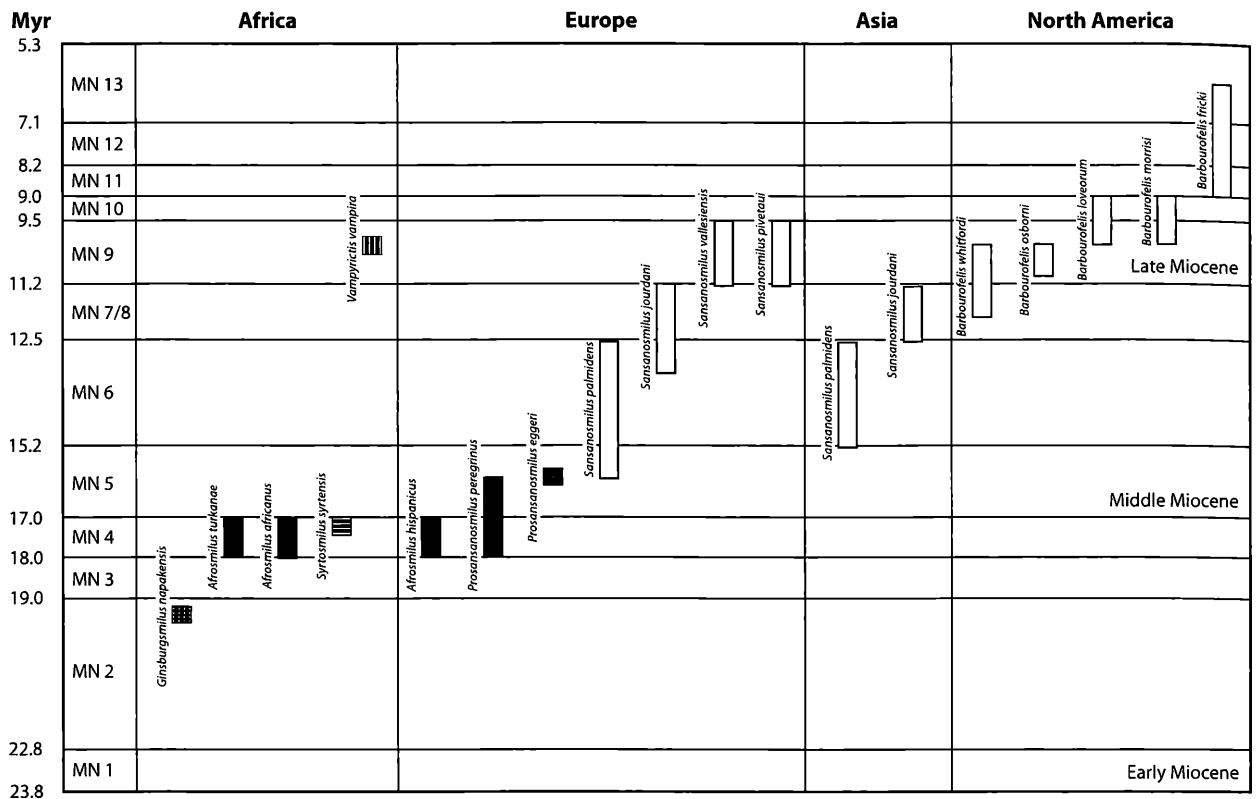
Figure 3: Gross temporal and geographical distribution of barbourofelid species.

tained from the analysis of an isolated P4 from the Chinese Tunggur area (MN 6 or 7/8) which is morphologically less advanced than '?B.' *vallesiensis* and 'B.' *piveteaui*, but similar to *S. jourdani* (WANG et al., 2003). Due to the more reduced incisor region, however, European *S. jourdani* from late MN 7/8 was slightly more apomorphic than *B. whitfordi*, inferring that the migration event happened at a time corresponding to late MN 6 or early MN 7/8 (see also QIU, 2003) very shortly before the first record of *Barbourofelis*. This again is consistent with the observation that "the Tunggur *Sansanosmilus* is comparable in stage of evolution to that of early Clarendonian *B. whitfordi*" (WANG et al., 2003:26). The barbourofelid radiation in North America following this immigration gave rise to the genus *Barbourofelis* and resulted in extremely derived species such as *B. morrisi* and *B. fricki* (SCHULTZ et al., 1970; GERAADS & GÜLEÇ, 1997).

Placing the two most apomorphic European taxa into *Barbourofelis* (GERAADS & GÜLEÇ, 1997) implies their origin in North America instead of in Europe and thus a re-migration of *Barbourofelis* into Eurasia, a scenario GERAADS & GÜLEÇ (1997) themselves did not believe in. They instead followed SCHULTZ et al. (1970) in proposing a Eurasian evolution towards more apomorphic sabre-tooth conditions parallel to that in North America. This interpretation is also followed here. In doing so, however, '?B.' *vallesiensis* and 'B.' *piveteaui* cannot be placed into *Barbourofelis*, because they obviously would not belong to the North American clade. Therefore, both species are placed into *Sansanosmilus*. This genus, consequently, is paraphyletic (see also GERAADS & GÜLEÇ, 1997): Eu-

ropean *S. jourdani* probably gave rise to *S. vallesiensis* and *S. piveteaui* (a clade not yet named with no old name available, because *Albanosmilus* KRETZOI, 1929 as well as *Grivasmilus* VILLALTA & CRUSAFONT-PAIRO, 1952, both were erected on *S. jourdani* as type species) while East Asian *S. jourdani* migrated to North America to evolve soon to *B. whitfordi*.

In the Late Miocene, the history of Barbourofelidae ended. Reasons for that are unclear, even though it was long speculated that the rising of the felid Machairodontinae may have played a major role (e.g., GERAADS & GÜLEÇ, 1997). However, the earliest known Eurasian machairodontine *Miomachairodus* co-occurred with *S. jourdani* in the MN 7/8 Sinap Formation (VIRANTA & WERDELIN, 2003), the latest known European barbourofelid, *Sansanosmilus piveteaui*, co-existed with the about similar sized *Machairodus aphanistus* in the MN 9 fauna of the Moldavian Kalfa (LUNGU, 1978), and different species of *Barbourofelis* co-occurred with similar sized species of the machairodontine felid *Nimravides* in the late Middle and early Late Miocene of North America (MARTIN, 1998). Barbourofelids hence where not simply out-competed by machairodontines. Instead, the last and extremely specialized members of the family disappeared during larger faunal turnovers: in Europe at the end of MN 9 and in North America at the end of the early Hemphillian (Hh2). For whatever reason, Machairodontinae, especially *Machairodus* in Europe and *Nimravides* in North America, survived these faunal turnovers without big morphological changes.

The most important centres of barbourofelid diversification moved geographically during time from Africa via Eurasia

to North America (Fig. 3). The number of evolving species during every phase of diversification, however, decreased through time. Barbourofelid diversity is highest in MN 4 with three contemporary species occurring in Africa and two in Europe, while the evolution among the advanced genera *Sansanosmilus* and *Barbourofelis* mostly is anagenetic with maximally two contemporary species occurring on a continent. This decreasing capability of diversification is probably correlated to the increasing morphological and biological specialization of the whole family from the Early to the Late Miocene (see HOLLIDAY & STEPPAN, 2004 for an analysis of such a pattern).

5. Acknowledgements

6. References

ANTOINE, P.-O., WELCOMME, J.-L., MARIVAUX, L., BALOUCH, I., BENAMMI, M. & TASSY, P., 2003. Elephantoidea in the late Oligocene of Pakistan. — Journal of Vertebrate Paleontology, **23** (4):977–980.

BARBOUR, E.H. & COOK, H.J., 1915. A new saber-toothed cat from Nebraska. — Nebraska Geology Survey, **4** (17):235–238.

BEAUMONT, G. de & CRUSAFONT PAIRO,M., 1982. Les Félidés (Mammifères, Carnivores) du Vallésien du Vallès, Catalogne, Espagne. — Archives des Sciences Genève **35** (1):41–64, Genève.

BLAINVILLE, H.M.D., 1843. Ostéographie ou description iconographique comparée du squelette et du système dentaire des cinq classes d'animaux vertébrés récents et fossiles pour servir de base à la zoologie et à la géologie. Mammifères. Carnassiers: des Felis. — (J. B. Baillière & Fils), Paris.

BOWDICH, T.E., 1821. An analysis of the natural classifications of Mammalia, for the use of students and travellers. — 1-115, (J. Smith), Paris.

BRYANT, H.N., 1988. Delayed eruption of the deciduous upper canine in the sabertoothed carnivore *Barbourofelis lovei* (Carnivora, Nimravidae). — Journal of Vertebrate Paleontology, **8** (3):295–306.

DROOGER, C.W., 1979. Marine connections of the Neogene Mediterranean, deduced from the evolution and distribution of larger foraminifera. — Annales Géologiques des Pays Helléniques, **1**:361–369.

DROOGER, C.W., 1993. Radial foraminifera; morphometrics and evolution. — Verhandelingen der Koninklijke Nederlandse Akademie van Wetenschappen, Afdeling Natuurkunde, Eerste Reeks, **41**:1–242.

FAHLBUSCH, V., 1964. Die Cricetiden (Mamm.) der Oberen Süsswasser-Molasse Bayerns. — Abhandlungen der Bayerischen Akademie der Wissenschaften, **118**: 1–136.

FILHOL, M.H., 1883. Notes sur quelques mammifères fossiles de l'epoque miocène. — Archives du Muséum d'Histoire Naturelle de Lyon, **3**:1–69.

GERAADS, D. & GÜLEÇ, E., 1997. Relationships of *Barbourofelis piveteaui* (OZANSOY, 1965), a Late Miocene nimravid (Carnivora, Mammalia) from Central Turkey. — Journal of Vertebrate Paleontology, **17** (2):370–375.

GINSBURG, L., 1961. La faune des carnivores miocènes de Sansan (Gers). — Mémoires du Muséum National d'Histoire naturelle, ns C, **9**:1–190.

GINSBURG, L., 1978. *Syrtosmilus syrtensis*, n. gen., n. sp., Félidé machairodontiforme du Burdigalien de Libye. — Compte Rendu Sommaire de la Société géologique de France, **2**:73–74.

HEISSIG, K., 1978. Fossilführende Spaltenfüllungen Süddeutschlands und die Ökologie ihrer oligozänen Huftiere. — Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie, **18**:237–288.

HEIZMANN, E.P.J., GINSBURG, L. & BULOT, C., 1980. *Prosansanosmilus peregrinus*, ein neuer machairodontider Felide aus dem Miocän Deutschlands und Frankreichs. — Stuttgarter Beiträge zur Naturkunde, Serie B, **58**:1–27.

HOLLIDAY, J.A. & STEPPAN, S.J., 2004. Evolution of hypercarnivory: the effect of specialization on morphological and taxonomic diversity. — Paleobiology, **30** (1):108–128.

KITTS, D.B., 1957. A Pliocene vertebrate fauna from Ellis County, Oklahoma. — Oklahoma Geological Survey, Circular, **45**:1–24.

KRETZOI, M., 1929. Materialien zur phylogenetischen Klassifikation der Aeluroideen. — 10. Congres international de Zoologie Budapest, 1927:1293–1355.

KRETZOI, M., 1945. Bemerkungen über das Raubtiersystem. — Annales Historico-Naturales Musei Nationales Hugarici, **38**:59–83.

KURTÉN, B., 1976. Fossil Carnivora from the late Tertiary of Bled Douarah and Cherichira, Tunisia. — Notes du Service Géologique de Tunisie, **42**:177–214.

LUNGU, A.N., 1978. Gipparionovaya fauna srednego sarmata Moldavii (khishchnye mlekopitayushchie. — 1-131, (Izdatel'stvo Shtiintsa), Kishinev. [in Russian]

MADE, J. VAN DER, 1999. Intercontinental relationship Europe – Africa and the Indian subcontinent. — [in:] RÖSSNER, G.E. & HEISSIG, K. (eds.). The Miocene Land Mammals of Europe:457-472, (Dr. Friedrich Pfeil Verlag), München.

MARTIN, L.D., 1998. Nimravidae. — [in:] JANIS, C.M., SCOTT, K.M. & JACOBS, L.L. (eds.). Evolution of Tertiary Mammals of North America. Volume 1: Terrestrial Carnivores, Ungulates, and ungulatelike Mammals: 228-235, (Cambridge University Press) New York.

MAWBY, J.E., 1965. Machairodonts from the late cenozoic of the Panhandle of Texas. — Journal of Mammalogy, **46** (4):573–587.

MORALES, J., PICKFORD, M., SALESA, M.J. & SORIA, D., 2000. The systematic status of *Kelba*, SAVAGE, 1965, *Kenyalutra* SCHMIDT-KITTLER, 1987 and *Ndamathaia*, JACOBS et al., 1987 (Viverridae, Mammalia), and a review of Early Miocene mongoose-like carnivores of Africa. — Annales de Paléontologie, **86** (4):243–251.

MORALES, J., SALESA, M.J., PICKFORD, M. & SORIA, D., 2001. A new tribe, new genus and two new species of Barbourofelinae (Felidae, Carnivora, Mammalia) from the Early Miocene of East Africa and Spain. — Transactions of the Royal Society of Edinburgh: Earth Sciences, **92**:97–102.

MORLO, M., MILLER, E.R. & EL-BARKOOKY, A. Creodonta and Carnivora from Wadi Moghra, Egypt. — Journal of Vertebrate Paleontology. [in print]

MORLO, M., PEIGNÉ, S. & NAGEL, D. 2004. A new species of *Prosansanosmilus*: Implications for the systematic relationships of the family Barbourofelidae new rank (Carnivora, Mammalia). — Zoological Journal of the Linnean Society London, **104** (1):43–61.

MORLO, M. & SEMENOV, Y.A., 2004. New Carnivora (Mammalia) from the Early Vallesian (Late Miocene, MN 9) of Ukraine. — Journal of Vertebrate Paleontology, **24** (3), Supplement: 96A.

OZANSOY, F. 1965. Étude des gisements continentaux et des Mammifères du Cénozoique de Turquie. — Mémoires de Société géologique de France, n.s., **44**:1–92.

PICKFORD, M., 1986. Cainozoic paleontological sites of Western Kenya. — Münchner Geowissenschaftliche Abhandlungen, A, **8**:1–151.

QIU, Z., 2003. Dispersals of Neogene carnivorans between Asia and North America. — Bulletin of the American Museum of Natural History, **279**:18–31.

ROTH, C., 1987. Die Raubtierfauna der miozänen Spaltenfüllungen Petersbuch 2 und Erkertshofen 2. Taxonomie, Stratigraphie, Ökologie. — 1-252; Ph.D. thesis (Univ. Mainz).

SANDERS, W.J., KAPPELMAN, J. & RASMUSSEN, D.T., 2004. New large-bodied mammals from the late Oligocene site of Chilga, Ethiopia. — Acta Palaeontologica Polonica, **49** (3):365–392.

SCHULTZ, C.B., SCHULTZ, M.R. & MARTIN, L.D., 1970. A new tribe of saber-toothed cats (Barbourofelini) from the Pliocene of North America. — Bulletin of the University of Nebraska State Museum, **9**:1–31.

TEDFORD, R.H., 1978. History of dogs and cats. A view from the fossil record. — [in:] Nutrition and management of dogs and cats, (Ralston Purina Co.), St. Louis, MI.

THERRIEN, F., 2005. Feeding behaviour and bite force of sabretoothed predators. — Zoological Journal of the Linnean Society, **145**:393–426.

VAN VALEN, L.M., 1994. Serial homology: the crests and cusps of mammalian teeth. — Acta Palaeontologica Polonica, **38** (3/4):145–158.

VILLALTA COMELLA, J.F. & CRUSAFONT PAIRO, M., 1952. *Grivasmilus* remplaçant *Albanosmilus* (=*Sansanosmilus*). — Compte rendu de Société géologique de France, **14**:308–309.

VIRANTA, S. & WERDELIN, L., 2003. 8. Carnivora. — [in:] FORTELIUS, M., KAPPELMAN, J., BERNOR, R.L. & SEN, S., (eds.). Geology and Paleontology of the Miocene Sinap Formation, Turkey: 178-193, (Columbia Univ. Press), New York.

WANG, X., QIU, Z. & OPDYKE, N.D., 2003. Litho-, Bio-, and Magnetostratigraphy and Paleoenvironment of Tunggur Formation (Middle Miocene) in Central Inner Mongolia, China. — American Museum Novitates, **3411**:1–31.