

A new species of *Prosansanosmilus*: implications for the systematic relationships of the family Barbourofelidae new rank (Carnivora, Mammalia)

MICHAEL MORLO¹*, STÉPHANE PEIGNÉ² and DORIS NAGEL³

¹Forschungsinstitut Senckenberg, Abt. Messelforschung, Senckenberganlage 25, 60325 Frankfurt, Germany

²Laboratoire de Géobiologie, Biochronologie et Paléontologie humaine, UMR 6046 CNRS, Université de Poitiers, 40, Avenue du Recteur Pineau, 86022 Poitiers Cedex, France

³Institut für Paläontologie, Geozentrum, Althanstr. 14, 1090 Wien, Austria

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A new barbourofelid species, *Prosansanosmilus eggeri*, is described from the Middle Miocene (MN 5) locality of Sandelzhausen, Germany. It differs from all other European barbourofelid species in being smaller and showing a more plesiomorphic morphology, especially in the relatively less developed sabretooth adaptations, low accessory cusps on the premolars, and the remnant of a very small talonid on the carnassial. The species is, however, stratigraphically later than the more apomorphic *P. peregrinus*, which is known from MN 4 of Germany and France. A phylogenetic analysis based on dental characters of early nimravids, barbourofelids and felids supports previous results on skull morphology of *Barbourofelis* that Barbourofelinae is not closely related to the Late Eocene and Oligocene Nimravinae. Instead, both subfamilies should be treated as separate families, with the Barbourofelidae closely related to the Felidae. The Barbourofelidae differ from the Felidae as well as from the Nimravidae s.s., particularly in the unique morphology of their basicranium. They presumably originated in Africa; *P. eggeri* sp. nov. is interpreted as part of a Miocene immigration of African faunal elements into Europe that took place at the beginning of MN 5. © 2004 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2004, 140, 43–61.

ADDITIONAL KEYWORDS: Felidae – Germany – Miocene – MN 5 – Nimravidae – palaeobiogeography – systematics – taxonomy.

INTRODUCTION

The barbourofelid carnivorans were originally regarded as a separate tribe (Barbourofelini) within Felidae by Schultz, Schultz & Martin (1970), who first recognized these sabretoothed Carnivora as a natural group. Although *Sansanosmilus* was known as early as the middle 19th century from the classical French locality of Sansan (Blainville, 1843), it was not until Tedford's (1978) study that it was realized that the Barbourofelini did not belong to the Felidae, but represented a separate line of evolution towards extreme hypercarnivory in Carnivora. Today, having been elevated to subfamily rank by Bryant (1991), they are usually included within the Nimravidae (e.g. Bryant, 1991; McKenna & Bell, 1997) although the latter's

systematic position within the Carnivora is still debated. While the traditional view places the Nimravidae within the Feliformia (e.g. Tedford, 1978; Baskin, 1981; Hunt, 1987; Bryant, 1991; Martin, 1998), some authors support a relationship to the Caniformia (Flynn & Galiano, 1982, followed by Werdelin, 1996), or as an outgroup to all other Carnivora (Neff, 1983). In fact, the phylogenetic relationships of the Barbourofelinae (as the supposed Miocene radiation of nimravids) to their implied Eocene-Oligocene nimravine relatives have never been resolved. Instead, there is strong support for the monophyly of both subfamilies. In reviewing the group, Bryant (1991) presented numerous anatomical features that demonstrate that the two groups have a long and distinct history. Assuming a sister-group relationship of the Barbourofelinae to the Nimravinae, and given that derived nimravines are recognized as early as the Middle Eocene in China, the phylogenetic analy-

*Corresponding author. E-mail: Michael.Morlo@senckenberg.de

sis of Peigné (2003) suggests a divergence age of these subfamilies of 50–53 Myr. Thus, we must accept that the first 25–30 Myr of the history of the Barbourfelinae provide no fossil record, since the earliest barbourfelid specimens come from the African early Miocene (c. 20 Myr). Such a vast gap has led to questioning of the sister-group relationship of those subfamilies. The idea that the Barbourfelinae are not closely related to Nimravinae has been suggested by earlier authors (e.g. Neff, 1983; Flynn, Neff & Tedford, 1988). More recently, Peigné & de Bonis (2003) described the juvenile anatomy of nimravines and demonstrated that the ontogeny of the auditory bulla and the relationships between the eruption of the upper canines and the development of other sabre-tooth features (especially the mandibular flange) distinguish the Nimravinae and Barbourfelinae (at least *Barbourfelis*). Moreover, Morales *et al.* (2001) described some barbourfelid carnivorans from the African early Miocene and suggested that the Barbourfelinae should be included within the Felidae.

In this paper we report the identification of a new barbourfeline species from the Middle Miocene of Europe, which represents the most plesiomorphic member of the group known from this continent. Based on this evidence, combined with a phylogenetic analysis of the dentition of early nimravids, barbourfelids and felids, and a revision of barbourfelid basi-crania, we demonstrate that the barbourfeline carnivorans should be assigned to their own family, Barbourfelidae, distinct from the Nimravidae and Felidae. Hence, we use this familial name throughout the text. The Barbourfelidae remain poorly known and therefore the discovery of new material assigned to early members is very important for our knowledge of this group. Because this new species sheds light on the origin and dispersal of the Barbourfelidae, which may be more complicated through time than previously thought, we also address more precisely the systematic position, as well as the early evolution and palaeobiogeography, of barbourfelids.

MATERIAL AND METHODS

The specimens described here were found in 1959 in Sandelzhausen (Bavaria) and are housed in the Bayerische Staatssammlung für Paläontologie und historische Geologie, München. For about 40 years, these undescribed specimens were assigned to the felid *Pseudaelurus quadridentatus* (Blainville, 1843) on the specimen labels and by Fahlbusch & Liebreich (1996). Sandelzhausen is one of the richest Middle Miocene localities of Germany, containing a total of 63 mammalian species (V. Fahlbusch, pers. comm.). For details see Fahlbusch *et al.* (1974) or Fahlbusch & Liebreich (1996). All measurements were made with cal-

ipers to the nearest 0.1 mm and are given in mm. Tooth morphology nomenclature follows Van Valen (1994).

PHYLOGENETIC ANALYSIS

To test recent hypotheses regarding the relationship between the Barbourfelidae, Nimravidae and Felidae (e.g. Bryant, 1991; Morales *et al.*, 2001), we performed a phylogenetic analysis of the most primitive or earliest species of each family, with the primary goal to compare the Barbourfelidae to the Felidae and Nimravidae. The fragmented fossil record of earlier barbourfelids meant that we were restricted to dental characters, although postcranial and cranial characters are well documented in some derived taxa, in particular *Barbourfelis*. The character state polarity was based on outgroup comparison. Outgroups included primitive Caniformia: miacids, basal canids (Hesperocyoninae; Wang, 1994) and basal arctoids (*Amphicyonodon* and *Pachycynodon*; Cirot & de Bonis, 1992; Cirot, 1992). The resulting outgroup (hypothetical ancestor) was used to root the tree in the cladistic analysis. The interpretation of anatomical characters was based on the study of original material by at least one of us. For additional specimens or information, we also used bibliographic data from Dehm (1950), Ginsburg (1961), Heizmann (1973), Ginsburg & Bulot (1982), and Rothwell (2001) for early *Pseudaelurus* (from Europe, Mammal European biozones MN 3–4; from North America, Late Hemingfordian); from Andrews (1914), Savage (1965), and Schmidt-Kittler (1987) for *Afrosmilus turkanae*, *A. africanus*, and *Ginsburgsmilus napakensis*. The following taxa were included: the barbourfelids *Syrtsmilus*, *Ginsburgsmilus* and *Afrosmilus* (three species), *Prosanosmilus* (two species), the nimravids *Eofelis edwardsii* and *Nimravus intermedius* and the felids *Proailurus lemanensis* and basal *Pseudaelurus* (specimens from biozones MN 3–4, see below).

PAUP, v. 4.0 b10 (Swofford, 1998) was used to obtain a directed Wagner tree of minimum length. Due to the considerable quantity of missing data (86%), we did not include *Syrtsmilus* in the final analysis presented here; missing data constitute 17.4% of the final matrix. We used the exhaustive search option, which guarantees finding the most parsimonious tree(s), with the following options: initial Maxtree setting = 100, branches collapsed if maximum branch length = 0, Multree option in effect, topological constraints not enforced.

Abbreviations

BSP Bayerisches Museum für Paläontologie und historische Geologie, München (Germany)

MNHN	Muséum National d'Histoire naturelle, Paris (France)
MPZ	Museo de Palaeontologia, Universidad de Zaragoza (Spain)
SMNS	Staatliches Museum für Naturkunde, Stuttgart (Germany)
UF	University of Florida, Gainesville (USA)
UM	Department of Antiquities and Museum, Kampala (Uganda)
UNSM	University of Nebraska State Museum, Lincoln, Nebraska (USA)
UV-BC	Collection from Buñol (C for Carnivora), Departamento de Geología, Universidad de Valencia (Spain)

SYSTEMATIC PALAEONTOLOGY

ORDER CARNIVORA BOWDICH, 1821

FAMILY BARBOUROFELIDAE SCHULTZ, SCHULTZ & MARTIN, 1970 **NEW RANK**

Type genus: Barbourofelis Schultz *et al.*, 1970

Other included genera: *Afrosmilus* Kretzoi, 1929, *Ginsburgsmilus* Morales, Salesa, Pickford & Soria, 2001, *Prosansanosmilus* Heizmann, Ginsburg & Bulot, 1980, *Sansanosmilus* Kretzoi, 1929, *Syrtosmilus* Ginsburg, 1978, *Vampyriictis* Kurtén, 1976.

Emended diagnosis: Barbourofelidae are distinguished by the following: loss of P1/, M2/, P1 and M2/; plesiomorphic tooth formula 3131/3131; apomorphic species additionally lose P2/ and P2/; scimitar-like sabreteeth with crenulations on, at least, the posterior border of upper canines; upper canines markedly compressed with vertical grooves present; strong relationships between the eruption of the upper canines and the development of other sabretooth features, especially the mandibular flange (see Peigné & de Bonis, 2003); no anterior cusp on P3, but distinct and sometimes large posterior accessory cusp on P3–4; protoconid of M1 relatively tall (at least in early taxa); talonid of M1 extremely reduced, and markedly more so than the metaconid; reduction of the talonid before the metaconid on M1; angular chin on mandible (genial flange in the apomorphic genera) and slightly (*Afrosmilus turkanae*) to strongly (other taxa) curved mandibular body; short horizontal proseptum in the anteromedial corner of the auditory bulla; early and complete fusion of elements making up the bulla. In addition to those features, the Barbourofelidae differ from the Nimravidae (primitive taxa) by the following: fully ossified bulla invading the mastoid; thin wall of the caudal entotympanic, not composed of three layers as in Nimravidae; petrosal not deeply recessed in the basicranium; absence of the postglenoid foramen; presence of a parastyle on P4/; protocone on P4/

located further back; bulla more anteriorly located (than in the most primitive felid genera such as *Proailurus* and *Pseudaelurus*) and consequently a more anteriorly placed foramen ovale which is close to the posterior opening of the alisphenoid canal (except *Barbourofelis*); a shortened palate; lateral walls of the nasopharynx converging posteriorly; broad metacarpals (known from *Sansanosmilus palmidens* and *Barbourofelis fricki* only).

GENUS *PROSANSANOSMILUS* HEIZMANN, GINSBURG & BULOT, 1980

Type species: P. peregrinus Heizmann *et al.*, 1980

Other included species: P. eggeri sp. nov.

Emended diagnosis: Relatively short genial flange, well developed P3 presenting a clear posterior cingulid, relative to *Ginsburgsmilus* and *Afrosmilus* large posterior accessory cusp on P4, small preparastyle and well developed protocone on P4/, and P2 vestigial or absent.

Additionally, and beside its larger size, *Prosansanosmilus* differs from *Ginsburgsmilus* in having a much more specialized sabretooth adaptation: upper canines transversely more compressed; P3/ with the lingual lobe and the posterior accessory cusp more reduced; P4/ with a preparastyle, a taller paracone, and more reduced protocone, about the same size as the parastyle; M1/ transversely more reduced with more reduced metacone; if the assignment of the material from Songhor is correct (described in Schmidt-Kittler, 1987; but see Morales *et al.*, 2001 and discussion below), P3 lacking an anterior cusp, P2 vestigial or absent. *Prosansanosmilus* differs from African *Afrosmilus* by the additional features: P2/ still present (at least in *P. eggeri*), P3/ wider due to a distinct lingual lobe and lacking an anterior cusp, P4/ with a larger parastyle (at least compared to the most primitive *Afrosmilus* species, *A. turkanae*), P2 vestigial or absent, P3 more reduced, P3–4 more specialized towards the sabretooth adaptation (e.g. posteriorly orientated), M1 talonid less reduced; more developed genial flange. *Prosansanosmilus* differs from *Sansanosmilus* in having a less developed mandibular flange, a taller protocone on M1, a smaller and lower preparastyle and parastyle on P4/; a larger P3 which lacks an anterior cusp but has a distinct, prominent posterior cingulid.

PROSANSANOSMILUS EGGERI SP. NOV.

pars 1974 *Pseudailurus quadridentatus*. Dehm in Fahlbusch *et al.* 121, 125.

1996 *Pseudailurus quadridentatus*. Fahlbusch & Liebreich: fig. 34b.

Holotype: BSP 1959 II 8051 (Figs 1, 3A, Fahlbusch & Liebreich, 1996: fig. 34b), right mandible with C/1, P/3–M/1.

Paratype: BSP 1959 II 8055 (Figs 2, 3E), fragment of left maxilla with alveoli of P2/, complete P3/–M1/.

Additional material: BSP 1959 II 8053 (Fig. 3B), fragment of right mandible with posterior part of P/3, P/4–M/1. BSP 1959 II 8054 (Fig. 3D), fragment of left mandible with fragment of P/4, M/1. BSP 1959 II 8057 (Fig. 3G), isolated fragment of left P/4. BSP 1959 II 8058 (Fig. 3F), isolated right P/4. BSP 1959 II 9041 (Fig. 3C), fragment of left mandible.

Type locality: Sandelzhausen, Bavaria, Germany.

Age and distribution: Hitherto solely known from MN 5 of Sandelzhausen.

Etymology: Named in honour of J. Egger, mayor of the village of Sandelzhausen, who has supported the excavation of Middle Miocene fossils on municipal land since 1993.

Diagnosis: *Prosansanosmilus eggeri* sp. nov. is the smallest known European barbourfelid, about 20% smaller than the type species of the genus, *P. peregrinus*. The single possible apomorphy which distinguishes *P. eggeri* from *P. peregrinus* is the slightly more elongated M/1. *P. eggeri* mostly differs from *P. peregrinus* by more primitive features: genial mandibular flange smaller; postcanine diastema on the mandible much shorter; P/3 larger relative to M/1, with posterior accessory cusp lower and relatively smaller and posterior cingulid shorter; P/4 larger in proportion to M/1, with an anterior cusp lower and a main cusp less posteriorly orientated; M/1 with a carnassial blade less open, protoconid slightly taller relative to total length of M/1, metaconid less reduced and posterior cingulid stronger; preparastyle of P4/ smaller, located anterolabially to the parastyle which is shorter and lower, protocone of P4/ slightly larger and more anteriorly placed relative to the anterior face of the parastyle, due to the lacking elongation of this cusp as in *P. peregrinus*. Moreover, *P. eggeri* retains a double-rooted P2/ and a well developed P3/ with a small lingual lobe.

Description

Holotype (Figs 1, 3A): The mandible is laterally compressed due to the taphonomic process and therefore the curvature typical for barbourfelids is not obvious. However, this character can be observed in the other mandibular remains (e.g. BSP 1959 II 8053, see below). A genial flange was present, but is now partially broken. The only visible mental foramen is

beneath the third quarter of the diastema, directly above the flange. C/1 shows medial abrasion and is laterally compressed, as is also seen in *P. peregrinus*. The tip slopes slightly backwards and the lingual and posterior crests are crenulated. P/1–2 are lacking. Instead, a diastema 17.85 mm long is present. P/3 consists of a slightly retracted protoconid, the preprotoconid, which extends to a small anterolingual basal swelling of the cingulid, an accessory posterior cusp, and a basal posterior cusp. The posterior accessory cusp and basal cusp are much less prominent than in P/4. The protoconid of P/4 is only slightly retracted, the anterior basal cusp points lingually and is lower than the posterior basal one. The cristids of the protoconid are crenulated. M/1 has a well defined metaconid that is stronger than that of *P. peregrinus* and a very small talonid which consists only of the posterior cingulid. The preprotocristid of the holotype is broken, but the carnassial notch is visible. It is about 25%

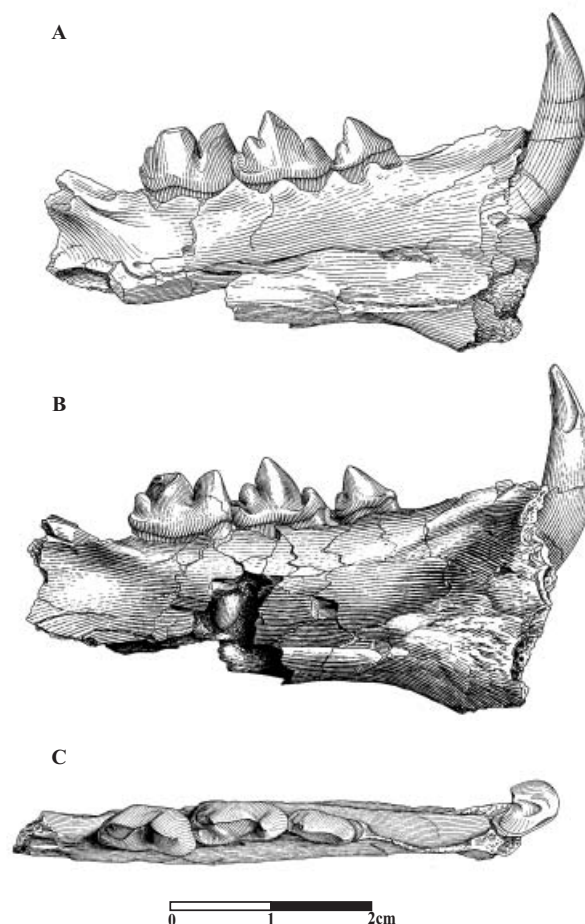


Figure 1. *Prosansanosmilus eggeri* sp. nov. Holotype (BSP 1959 II 8051) in (A) labial, (B) lingual and (C) occlusal views. Note its lateral compression, which obscures the curvature of the mandible visible in Fig. 3C.

lower than the tip of the paraconid. In common with all other Barbouriidae, there is no M/2.

Paratype (Figs 2, 3E): In this maxillary fragment, the posterior border of the alveolus of C1/ is visible, as well as the alveoli of P2/. P3/ to M1/ are completely preserved. Looking from the carnassial blade on P4/ towards the canine, the tooth row curves labially by about 30° between P3/ and P2/. This corresponds to the curved mandibular body to get space for the enlarged C1/. C1/ and P2/ are therefore orientated obliquely with respect to the carnassial blade. The fragment does not allow an estimate of the size of C1/. The alveolus, however, runs far dorsally to the root tips of P3/. It can therefore be assumed that the root of C1/ lies dorso-labially to the roots of the cheek teeth, as is the case in other sabretoothed carnivores. P1/ is completely lacking and there is very little room between the alveolus of C1/ and the anterior alveolus of the small P2/. That one P2/ was present and not two

single-rooted premolars is verified by a small bony elevation between the alveoli. This is typical for the bone between two alveoli of the same tooth. P3/ is relatively large compared to P4/ and much broader than that of *Sansanosmilus palmidens* (see Table 1). Moreover, it has a large posterior accessory cusp and a small cutting edge on the posterior basal platform. The post-paraacrista, including the posterior accessory cusp, is crenulated. The distorted lingual preparacrista extends anterolingually to a small basal cusp. The third root is placed directly under the main cusp, carrying a small swelling which is interpreted as the remains of the protocone. The paracone of P4/ is relatively low. A protocone, a parastyle cusp, and a preparastyle are well developed. The latter points anterolabially, a probable plesiomorphic character due to the antero-labial position of the preparacrista in carnivorans. In its anteriormost part, it bears a small swelling of the cingulum. In more advanced species this swelling is developed to a preparastyle cusp. The lingual part of the paracone-metastyle blade is more curved lingually. A weak lingual cingulum is developed at the metastyle. Lingual to the metastyle and anterior to M1/ a well marked, deep depression into the maxilla is developed which corresponds to the high protoconid of M/1. M1/ is probably double-rooted. Labially, a crest runs from the labialmost point to a very reduced paracone and then to the posteriormost point of the tooth which is situated about midway on the posterior border. Lingually, a strong, crest-like protocone is developed. The tooth is relatively large, since it is only 10% smaller in breadth than M1/ of *S. palmidens* while P3–4/ are 20–25% smaller.

Additional material: In addition to the holotype and the paratype, five other specimens are preserved. The mandibular fragments BSP 1959 II 8053 (Fig. 3B) and 8054 (Fig. 3D) show the typical barbourioid curvature of the mandibular ramus. M/1 (8053, 8054) has a protoconid, which does not slope backwards. Except for this detail they do not reveal any additional information regarding the dental morphology of the species and the same is true for the two additional isolated P/4 (Fig. 3F, G). However, these specimens suggest that there was little size variation in *P. eggeri* (Table 1). The uncompressed, proximal mandibular fragment BSP 1959 II 9041 (Fig. 3C) shows a complete flange, which is delicate but pronounced (broken in the holotype). It additionally presents alveoli for P/3 and C/1, no alveolus for P/2 and two tiny alveoli for I/3 and I/2. There was obviously little space for the incisors.

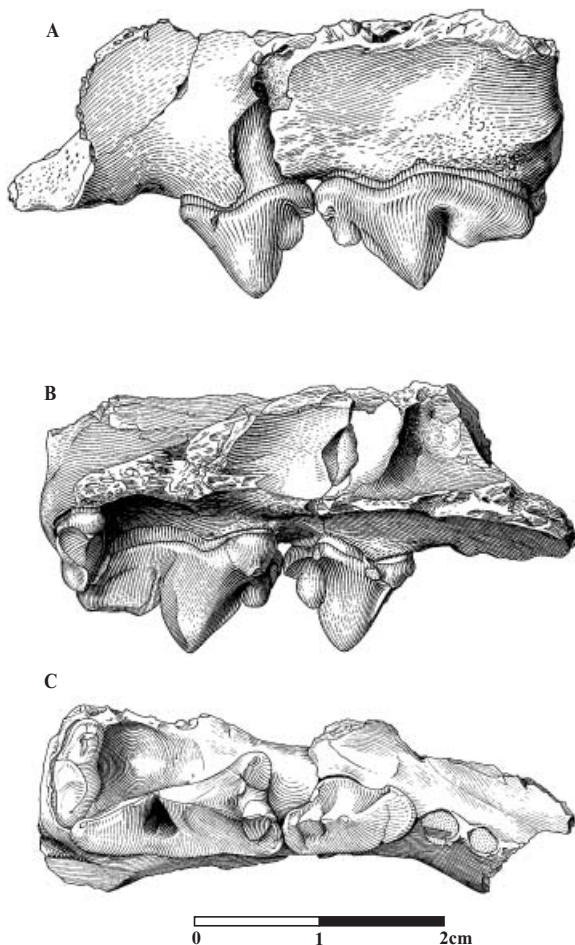


Figure 2. *Prosansanosmilus eggeri* sp. nov. Paratype (BSP 1959 II 8055) in (A) labial, (B) lingual and (C) occlusal views. Note anterolabial pointing and low preparastyle of P4/.

PHYLOGENETIC ANALYSIS

The character analysis is presented in the Appendix and the character matrix in Table 2. Using exhaustive

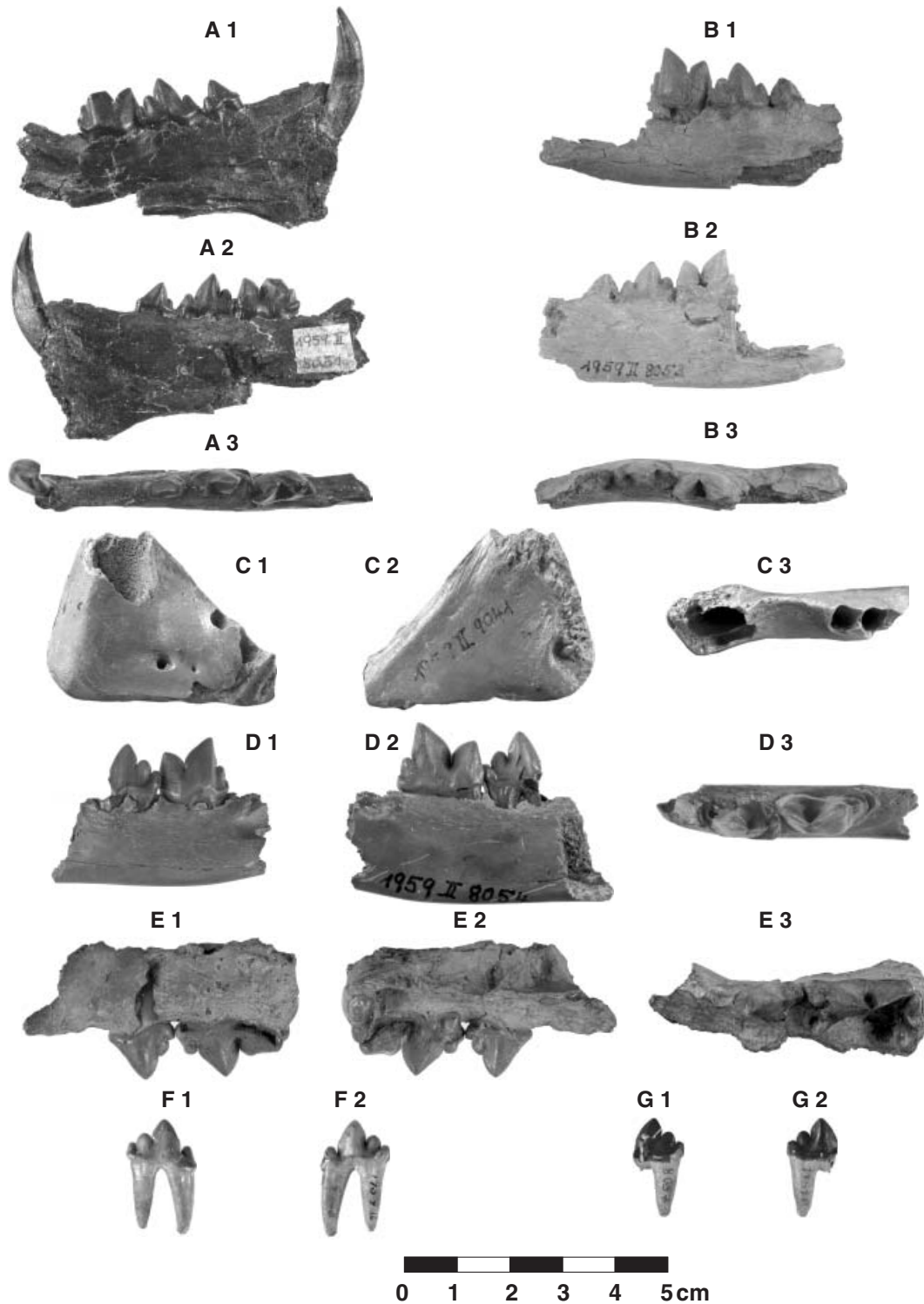


Figure 3. *Prosansanosmilus eggeri* sp. nov.: (1) labial, (2) lingual and (3) occlusal views. A, BSP 1959 II 8051, holotype. B, BSP 1959 II 8053, fragment of right mandible. C, BSP 1959 II 9041, fragment of left mandible. D, BSP 1959 II 8054, fragment of left mandible. E, BSP 1959 II 8055, paratype. F, BSP 1959 II 8058, isolated fragment of left P/4. G, BSP 1959 II 8057, right P/4.

Table 1. Measurements of European barbourufelid dentitions (in mm). †After Morales *et al.* (2001); *estimated; – not preserved

	C/1	P/2	P/3	P/4	M/1	P3/	P4/	M1/
<i>P. eggeri</i> sp. nov.								
BSP 1959 II 8051, holotype			7.4:2.0	11.3:5.9	11.7:4.2			
BSP1959 II 8055, paratype						11.2:6.2	18.0:9.0	4.1:10.9
BSP 1959 II 8053				10.8:4.1	11.4:4.2			
BSP 1959 II 8054				–:5.0	13.6:5.8			
BSP 1959 II 8057				–:5.1				
BSP 1959 II 8058				13.0:5.1				
<i>P. peregrinus</i>								
SMNS 41482, holotype	8:5.5	1.2:1.2	9.2:4	15.2:5.7	16.6:7.5			
MNHN Be 7212							24.1:11.1	
<i>G. napakensis</i>								
UM Nap IX 1966, holotype						11.0:5.8	16.8:8.9	4.4:11.2
SO-5670†						10.1:5.7	15.8:8.5	3.5:–
<i>A. hispanicus</i>								
MPZ 16506, 16409, holotype						–:5.0	21.3:9.3	
UV-BC 23					16.0:6.8			
<i>S. palmidens</i>								
MNHN-Sa 453, holotype			5.5:3.3	14.7*:6.1				
MNHN-Sa 451						10.7:4.8	24.5:7.5	3.5:8.7
MNHN-Sa 458				16.8:6.3	19.4:7.8			
MNHN-Sa 460					18:7.7			
MNHN-Sa 468							28.7:8	

Table 2. Distribution of states of the characters used in the analysis. '?' character state unknown; 'early *Pseudaelurus*' mainly corresponds to *P. turnauensis* from Europe and *P. validus* from North America. Species are not indicated for monospecific genera

Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Syrtosmilus</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	2	2	?	?	?	?	?	2
<i>Ginsburgsmilus</i>	1	?	1	1	?	0	0	1	1	0	1	2	1	1	?	0	1	?	?	?	?	?
<i>Afrosmilus turkanae</i>	?	?	?	?	2	2	?	0	1	0	2	2	?	?	2	0	1	1	2	2	3	2
<i>A. africanus</i>	1	?	2	?	2	2	1	0	2	0	3	3	?	?	2	0	1	?	?	?	?	?
<i>A. hispanicus</i>	1	?	2	?	2	2	?	0	2	1	3	2	?	?	?	?	?	1	2	2	3	?
<i>Prosansanosmilus eggeri</i> sp. nov.	1	?	?	?	2	0	0	1	1	1	2	2	2	2	2	2	1	1	2	2	2	2
<i>P. peregrinus</i>	1	?	2	?	?	?	?	?	2	1	3	3	?	?	2	2	1	1	2	2	2	2
<i>Eofelis edwardsii</i>	1	?	1	0	1	0	0	1	0	0	1	0	1	2	1	0	2	0	1	3	1	1
<i>Nimravus intermedius</i>	1	1	1	0	1	0	0	0	0	0	4	1	3	3	1	0	2	0	1	3	1	0
<i>Proailurus lemanensis</i>	0	0	0	0	0	0	0	1	1	0	1	2	1	1	1	0	1	0	0	2	1	0
early <i>Pseudaelurus</i>	0	?	0	0	0	0	0	0	1	0	1	2	1	2	1	1	1	0	0	3	1	1

search, the cladistic analysis of the ten taxa (all but *Syrtosmilus*) and outgroup using unweighted and unordered characters yielded eight most parsimonious trees of 52 steps with a consistency index (CI) of 0.808 (after excluding uninformative characters #2, 4, 7, 13 of 0.783), and a retention index (RI) of 0.773. Table 3 provides character support for one of these trees, which is the basis of the discussion. The tree (Fig. 4),

which shows enhanced distinction of *Prosansanosmilus* and *Afrosmilus* spp., was selected because it implies far fewer reversals (3) than the other seven (5–8). We find this difference significant because most of the reversals imply incongruities in character distribution, such as the reappearance of teeth (P2/ or P/2) or cusps (parastyle or preparastyle on P4/, metaconid on M/1). In addition, the distinction between *Prosan-*

Table 3. Distribution of character states for internal nodes on one of the eight most parsimonious trees (see Fig. 4). Reversals are indicated in italic

Clade/taxa	Character state
All genera	11:1, 13:1, 14:2, 15:1, 17:1, 20:3, 21:1
Nimravidae	1:1, 2:1, 3:1, 5:1, 17:2, 19:1
Felidae–Barbourofelidae	9:1, 12:2
Barbourofelidae– <i>Proailurus</i>	8:1, <i>14:1</i> , 20:2
Barbourofelidae	1:1, 3:1, 4:1, 5:2, 15:2, 18:1, 19:2, 21:2, 22:2
<i>Prosansanosmilus</i> – <i>Afrosmilus</i>	3:2, 11:2, 13:2, 14:2
<i>Prosansanosmilus</i>	10:1, 16:2
<i>Afrosmilus</i>	6:2, 7:1, 8:0, 21:3
<i>Afrosmilus africanus</i> – <i>A. hispanicus</i>	9:2, 11:3
<i>E. edwardsii</i>	8:1, 22:1
<i>N. intermedius</i>	11:4, 12:1, 13:3, 14:3
<i>Pseudaelurus</i>	16:1, 22:1
<i>A. africanus</i>	12:3
<i>A. hispanicus</i>	10:1
<i>P. peregrinus</i>	9:2, 11:3, 12:3

sanosmilus and *Afrosmilus* is supported by characters not included in the cladistic analysis (e.g. mandibular flange present in *Prosansanosmilus* spp.).

With the exception of *Ginsburgsmilus* (see Discussion below), the monophyly of barbourofelids is well supported by dental characters (Table 3). The paraphyly of the Felidae, represented here by *Proailurus* and *Pseudaelurus*, seems to be insignificant for several reasons. First, we concentrated our analysis on early barbourofelids and therefore did not include mandibular or cranial characters, which clearly distinguish these two families (see Comparisons and discussion). Second, the lack of resolution of the relationship between basal felids and barbourofelids was expected given the great similarity of the dentition in these taxa. Third, major dental differences exist between the Felidae and Barbourofelidae concerning the lower tooth row (especially M/1). The paraphyly of the Felidae is thus also partly due to the lack of information on the lower dentition of *Ginsburgsmilus*. Nevertheless, the latter appears to be the most primitive barbourofelid in the hypothesis presented in Figure 4, which is consistent with previous studies (Morales *et al.*, 2001).

Although the use of dental characters provides only moderate support for a separation of Barbourofelidae from Felidae, a clade Felidae + Barbourofelidae (or Felinae + Barbourofelinae inside Felidae, *sensu* Morales *et al.*, 2001) is much more supported than any other relationship, especially that between the Nimravidae and Barbourofelidae.

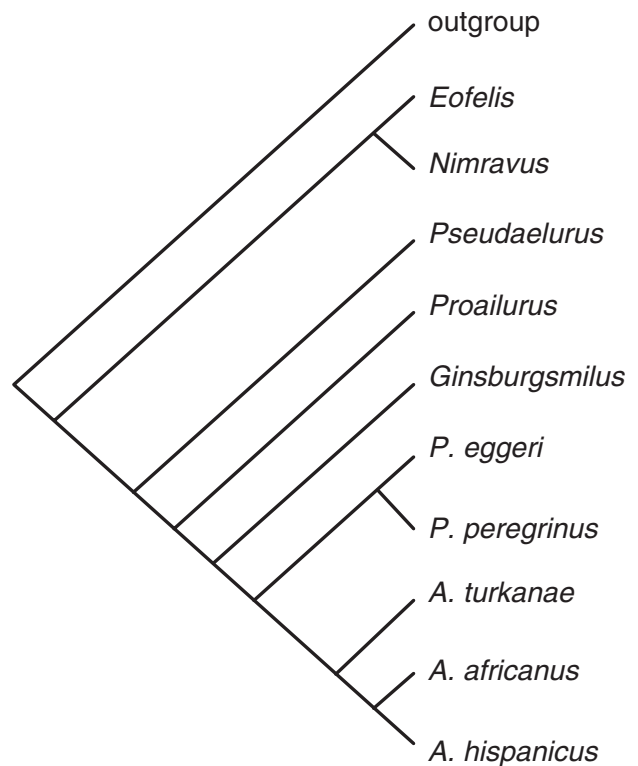


Figure 4. One of eight most parsimonious trees obtained from the cladistic analysis. See text for discussion and Table 3 for character support.

The comparisons below include results of the cladistic analysis. The discussion is based on the most parsimonious tree illustrated in Figure 4, with character supports presented in Table 3. We also discuss other morphological characters not included in the cladistic analysis, especially of the cranium and postcranium.

COMPARISONS AND DISCUSSION

COMPARISON WITH *PSEUDAEELURUS*

The material discussed herein was previously assigned to the co-occurring felid *Pseudaelurus quadridentatus* (Blainville, 1843) on the specimen labels and by Fahlbusch & Liebreich (1996). Only this felid is mentioned in lists of the Sandelzhausen fauna (e.g. Fahlbusch *et al.*, 1974; Fahlbusch & Liebreich, 1996). We thus compare the new material with this taxon first, as it is the only felid species of similar size in the Middle Miocene of Europe. *P. quadridentatus* lacks a flange as well as a curved mandibular body. The misidentification of the holotype is mainly due to the fact that the latter character is not visible because of lateral com-

pression. The other specimens never received detailed investigation. *P. quadridentatus* is on average approximately 20% larger than *P. eggeri*. The posterior cusp on P/3 is less prominent, and the protoconid does not slope backwards. In P/4, the anterior and posterior cusps are less developed and the protoconid does not slope backwards. In M/1, the metaconid is absent or relatively smaller and placed lower at the lingual protoconid wall. In occlusal view, the angle between proto- and paraconid is about 110° in *P. quadridentatus*, while it ranges from only 105° to 98° in *P. eggeri*. The protoconid is also much taller in the barbourufelid than in the felid (relative to the total length of M/1); in labial view, the preproto- and postparacristids are therefore at right angles, instead of forming obtuse angles as in *Pseudaelurus*. Finally, the lower canine and M/1 in the holotype of *P. eggeri* preserve crenulations, which are absent in the felid.

COMPARISON WITH OTHER BARBOUROFELIDS

Prosansanosmilus peregrinus

Prosansanosmilus eggeri is clearly distinct from *P. peregrinus*, although most of its diagnostic features are plesiomorphic, implying that it is less specialized. Only two characters of *P. eggeri* could be interpreted as apomorphic relative to *P. peregrinus*: the lack of P/2 (cf. Heizmann *et al.*, 1980: pl. 1) and the relatively elongated M/1 (length/width ratio higher in *P. eggeri*). It is known from living Carnivora that additional teeth may occasionally be present and, if so, are highly variable (Hell, 1966; Dayan, Wool & Simberloff, 2002). We therefore interpret the presence of a vestigial P/2 in *P. peregrinus* as a very minor difference from *P. eggeri*. The relatively more elongated M/1 is hence the only autapomorphy of the new species. The primitive morphology of *P. eggeri* relative to that of *P. peregrinus* (e.g. P4/: Fig. 5D) is especially remark-

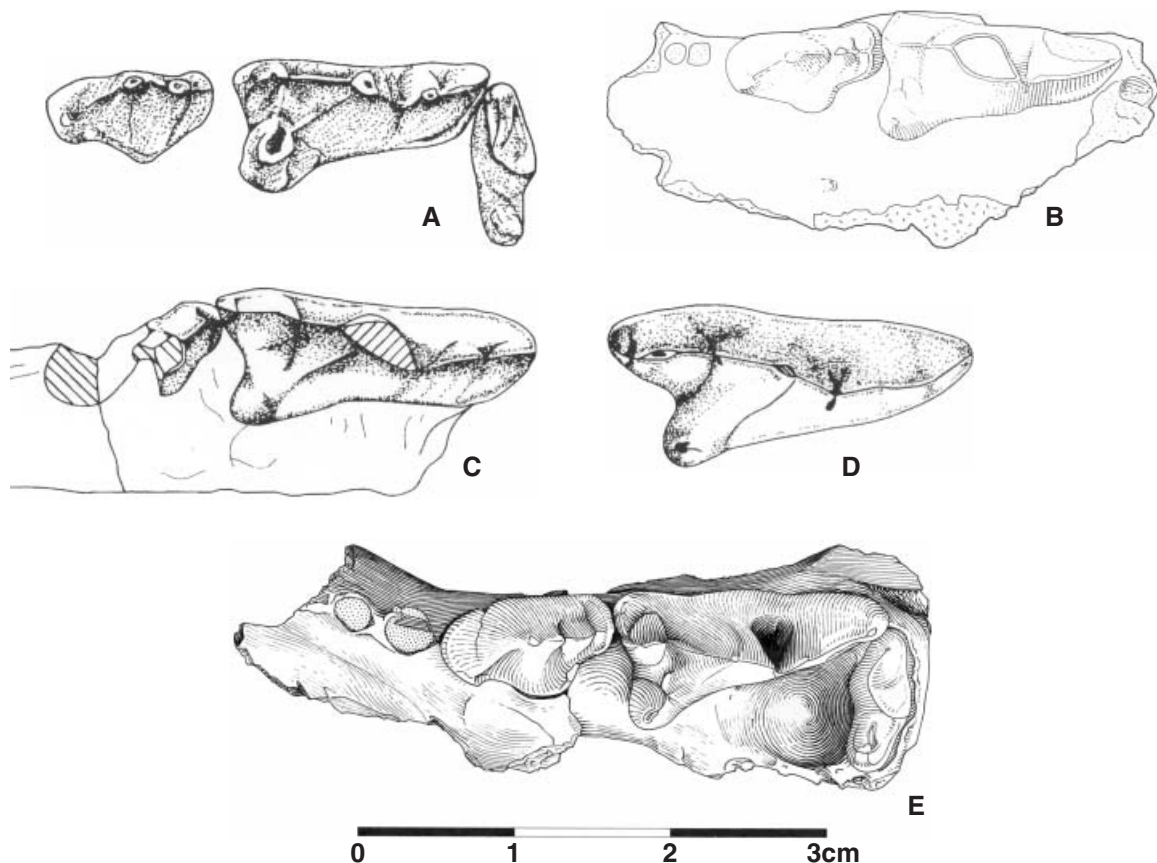


Figure 5. P4/ of different primitive Barbourufelidae. A, *Ginsburgsmilus napakensis* Morales, Salesa, Pickford & Soria, 2001, holotype, maxilla from Napak (UM Nap IX 1966), mirrored. B, maxilla from Songhor (SO-5670), originally described as '*Afrosmilus turkanae*' (Schmidt-Kittler, 1987). C, *Afrosmilus hispanicus* Morales, Salesa, Pickford & Soria, 2001, holotype maxilla from La Artesilla (MPZ-16506), mirrored. D, *Prosansanosmilus peregrinus* Heizmann, Ginsburg & Bulot, 1980 (MNHN Be 7212) P4/ from Bézian. E, *Prosansanosmilus eggeri* sp. nov., paratype, maxilla from Sandelzhausen (BSP 1959 II 8055). All occlusal views.

able, because the latter species is so far known only from MN 4 (Heizmann *et al.*, 1980). *P. eggeri*, from MN 5, therefore cannot be ancestral to *P. peregrinus*. Moreover, it is nearly as plesiomorphic as the older genera *Syrtosmilus*, *Afrosmilus* and *Ginsburgsmilus* and smaller than any other barbourofelid except *A. turkanae*.

The position of *P. eggeri*, and of the genus *Prosansanosmilus* itself, can only be inferred from comparison with other Old World barbourofelid genera.

Syrtosmilus

This genus is only represented by its type species *S. syrtensis* Ginsburg, 1978, from the locality of Gebel Zelten, Libya. This locality is still not precisely dated. An Orleanian age is generally accepted, although the best estimates range from late MN 3 (Savage, 1989) to late MN 4 (Mein, 1989: table 1). The holotype and only specimen is a mandible with tooth fragments (MNHN not numbered). Its poor state of preservation prevents us including this taxon in the cladistic analysis of early barbourofelids, nimravids and felids. Nevertheless, it displays a small mandibular flange and a curved body, which are diagnostic of advanced barbourofelids. The lack of P/1, P/2 and M/2 are additional characters which support this relationship. The type individual is slightly larger than *P. eggeri* and has a smaller flange. No comparisons are possible concerning the dental morphology.

Ginsburgsmilus

The diagnoses of the genera *Ginsburgsmilus* and *Afrosmilus* are not simple and depend on the assignment of remains, which are often fragmentary. *Ginsburgsmilus* Morales *et al.*, 2001 was erected based on dental material from the Early Miocene of Napak, Uganda (c. 19–20 Myr, corresponding to the European biozone MN 3) and Songhor, Kenya (c. 19.6 Myr). The latter material was originally described as *Afrosmilus turkanae* (Schmidt-Kittler, 1987) and assigned to *G. napakensis* by Morales *et al.* (2001). If these dates are correct, *G. napakensis* may be the oldest known barbourofelid. All comparisons of *Ginsburgsmilus* and *Prosansanosmilus* clearly show that *G. napakensis* is more plesiomorphic than *Prosansanosmilus* spp., making it the most primitive barbourofelid. As a result of the lack of derived characters from the upper dentition (Fig. 5A,B), the systematic relationships of *Ginsburgsmilus* as interpreted here have yet to be confirmed by mandibular and lower dentition characters.

Afrosmilus

As suggested by the cladistic analysis, there is some support for the sister-group relationship between *Afrosmilus* and *Prosansanosmilus* (Fig. 4, Table 3).

Afrosmilus differs from other barbourofelids by the lack of P2/, narrowed P3/ with an anterior cusp present, and M/1 with a talonid vestigial or absent. It contains three species, all of which are known from a few specimens only (see Schmidt-Kittler, 1987; Morales *et al.*, 2001): *A. africanus* (Andrews, 1914) and *A. turkanae* Schmidt-Kittler, 1987 from Kenya, and *A. hispanicus* Morales *et al.*, 2001 from Spain. The relatively moderate robustness of the sister-group relationship was therefore expected. The hypothesis discussed here (Fig. 4) suggests that *A. turkanae* is the most primitive species of the genus; it is represented by the holotype, a mandibular fragment from Morurot, and some maxillar fragments from Rusinga. In the morphology of the mandible and lower premolars, both African species are distinctly more primitive than *Prosansanosmilus*: P/3–4 are less typical for a sabretoothed carnivore in being less posteriorly orientated, P/3 is still large with a tall posterior accessory cusp, and there is no (*A. turkanae*) or only a very small (*A. africanus*) mandibular flange. Despite these primitive features, *A. turkanae* displays a lower carnassial that may be more derived than in species of *Prosansanosmilus* (the tooth is not known in *A. africanus*). The hypothesis is based on interpretation of the third cusp of this tooth. Interpreted as a talonid by previous authors (e.g. Schmidt-Kittler, 1987; Morales *et al.*, 2001), the cusp is actually very similar in placement and size to the metaconid of other barbourofelid species, such as *P. eggeri*. We therefore regard it as homologous to the metaconid present in *Prosansanosmilus*. This is supported by the type (Schmidt-Kittler, 1987: pl. 4, fig. 1a), which demonstrates that a vestigial posterior cingulid is still present but less strong than in *Prosansanosmilus*. The reduction of the talonid and posterior cingulid in *Afrosmilus* is more advanced than in *Prosansanosmilus*, suggesting that *Afrosmilus* may represent a distinct line of evolution. The upper dentition confirms the distinction between the two genera: *A. africanus* and *A. turkanae* lack a P2/ but have a more primitive P4/, with a parastyle but no preparastyle present (Savage, 1965: figs 61, 62; pl. 5, fig. 4; Schmidt-Kittler, 1987: text-figs 3 and 5B). *A. africanus* differs from *A. turkanae* by an enlarged parastyle on P4/ and a narrow P3/ with an anterior cusp. The African *Afrosmilus* seem to follow a line of evolution distinct from that of *Prosansanosmilus* as early as the early Miocene.

The European species *A. hispanicus* was recently described by Morales *et al.* (2001) from material originally included in *P. peregrinus* by Belichón & Morales (1989) and Azanza *et al.* (1993). The holotype specimen is a right maxillar fragment with C1/, posterior fragment of P3/, and complete P4/ from La Artesilla, Spain (c. 16.7 Myr; Morales *et al.*, 2001). These authors also assign an isolated lower carnassial from

Buñol, Spain (c. 16 Myr), to the same species. The relationships of this species are less clear due to the mixture of primitive and derived characters displayed by the material. Like the African *Afrosmilus*, *A. hispanicus* lacks P2/. However, the P3/ is too poorly preserved to identify an anterior cusp and P4/ has a distinct preparastyle, an apomorphy of *Prosansanosmilus* (Fig. 5C). Thus, the upper carnassial of *A. hispanicus* suggests a close relationship with *P. peregrinus*, although it retains a relatively larger and more anteriorly placed protocone (as mentioned by Morales *et al.*, 2001), the size of which is much smaller than illustrated by their drawing. The lower carnassial from Buñol was initially described and illustrated by Belichón & Morales (1989: pl. 1, fig. 11) as belonging to *P. peregrinus*. However, we agree with Morales *et al.* (2001) that this specimen markedly differs from *P. peregrinus* (and also from *P. eggeri*) by having a lower and less posteriorly orientated protoconid and no distinct posterior cingulid (again, we interpret the third cuspid of this M/1 as a metaconid instead of a talonid as in Schmidt-Kittler, 1987 and Morales *et al.*, 2001). The morphology of the lower carnassial from Buñol is therefore consistent with that of African *Afrosmilus* and represents a slightly more derived state with a completely reduced talonid. The reduction of the metaconid in the African species of *Afrosmilus* and the complete reduction of the talonid in *A. hispanicus* thus exclude *Afrosmilus* as an ancestor of *Prosansanosmilus*, as already mentioned.

Two interpretations of *A. hispanicus* appear to be equally valid. Both specimens might belong to one taxon, which is interpreted as close to *Afrosmilus* (Morales *et al.*, 2001). Alternatively, they could belong to different taxa, with the lower carnassial from Buñol close to *Afrosmilus*, and the La Artesilla specimen representing a species of *Prosansanosmilus*, tentatively named *P. hispanicus*. The relationships between species of *Afrosmilus* and *Prosansanosmilus* are still not well resolved. Consequently, in our view the very fragmentary nature of the material prevents any definitive taxonomic changes, and we continue to use *A. hispanicus sensu* Morales *et al.* (2001). Additional material, of the lower jaw in particular, will help to clarify the assignments of these specimens.

Vampyriictis

This genus may be, based on the stratigraphy, the latest African barbourufelid. It was described by Kurtén (1976) and is only known from a single M/1 and a fragment of an upper canine from the Late Miocene (corresponding to European biozone MN 9; Mein, 1989: table 1) of Bled Douarah, Tunisia. Both specimens are assigned to the type and only species *V. vipera*. As a result of the fragmentary nature of the material, the status of this species is still unclear. It was originally

assigned to the Machairodontinae (Felidae). However, following previous workers (Bryant, 1991; McKenna & Bell, 1997), we place it in the Barbourufelidae because it is much more derived than the contemporary machairodontine *Machairodus aphanistus* Kaup, 1832 from Eppelsheim: the M/1 retains a vestigial metaconid but lacks the talonid. As has been shown, reduction of the talonid before the metaconid is typical for barbourufelid M/1. The lower carnassial of *Vampyriictis* attains a similar evolutionary grade of sabretooth characters as the latest European *Sansanosmilus*, and surpasses *Prosansanosmilus* in being more than twice as long as that in, for example, *P. eggeri*.

Sansanosmilus

This Middle to Late Miocene Eurasian genus is markedly more specialized than *Prosansanosmilus*. The species are: *S. palmidens* (Blainville, 1843), best known from the French localities Savigné-sur-Lathan (MN 5) and Sansan (MN 6); *S. jourdani* (Filhol, 1883), best known from MN 7/8 of La Grive; *S. vallesiensis* Beaumont & Crusafont-Pairó 1982 from MN 9 of Santiga and other Vallesian localities, and '*Barbourufelis*' *piveteaui* (Ozansoy, 1965; placed in *Barbourufelis* by Geraads & Güleç, 1997) from the Sinap Formation, Turkey. All four are clearly larger and display many differences: flange much more pronounced; P/3 reduced to absent; additional cusps of P/4 larger and M/1 with a vestigial or absent metaconid; completely reduced posterior cingulid; P/4/ more hypsodont with a lingual lobe but no protocone and an anteriorly pointing preparastyle.

PALAEOBIOGEOGRAPHY

The origin of the Barbourufelidae remains unresolved. That the early evolution of this family took place in the early Miocene of Africa is supported by the presence of *Syrtosmilus*, *Ginsburgsmilus* and *Afrosmilus* (Morales *et al.*, 2001). *P. eggeri* sp. nov. from MN 5 of Sandelzhausen not only serves as a morphological example of how plesiomorphic European barbourufelids may have appeared, but also reveals that the evolution and palaeobiogeography of the early barbourufelids was more complicated than previously thought.

Prosansanosmilus peregrinus and *A. hispanicus* are the oldest known European members of the family. They arrived in Europe in MN 4 with other immigrants such as *Hyainailouros* and *Gomphotherium* during the so-called Creodont event (Van der Made, 1999). As already stated, however, they are more apomorphic than the slightly younger *P. eggeri* from MN 5. Other African immigrants such as the pliopithecoid primates (Köhler, Moyà-Solà & Andrews, 1999)

and the tayassuid *Sanitherium* (Hünemann, 1999), also appear in Europe in MN 5. Of course, *P. eggeri* might have been present in Europe before MN 5. This, however, seems unlikely given the extremely well-known carnivoran fauna of the Central and Western European Early Miocene (see e.g. Ginsburg, 1999; Alba, Agustí & Moyà-Solà, 2001; Morlo, 1996; for comparisons of European MN 1–MN 4a carnivorans). Additionally, barbourufelids are now known to be present in the early Miocene of Africa. It thus seems much more likely that the early evolution of *Prosanosmilus* occurred in Africa rather than in Europe and that *P. eggeri* was a part of the MN 5 immigration, the so-called *Conohyus/Pliopithecus* event (Van der Made, 1999) rather than being present in Europe before MN 5.

RELATIONSHIPS OF BARBOUROFELIDAE TO NIMRAVIDAE

The most detailed analysis placing the Barbourufelidae as a subfamily in Nimravidae *s.l.* was made by Bryant (1991: table 1, appendix I). His cladistic analysis of almost all morphological characters regarded as diagnostic by previous authors supported the sister-group relationship of Nimravinae to Barbourufelinae with 14 synapomorphies. However, nine of these are not exclusive to Nimravidae, but are also present in other carnivoran groups. Thus, these characters (skull catlike with shortened rostrum and mesocranium, short palate, cerebrum with continuous ectosylvian sulcus, distinct angle between the anterior and lateral surface of the mandible, loss or reduction of the anterior premolars and the posterior molars, incisors with reduced lingual cingula, C1/ significantly larger than C/1, C1/ eruption delayed, hourglass-shaped crenulations on C/1) do not contain phylogenetic information by themselves, but can be interpreted as synapomorphies only after the sister-group relationship has been established based on other, autapomorphic, characters. We therefore do not discuss these characters here, with the exception of the hourglass-shaped crenulations on C/1. Only five characters used by Bryant (1991) may indeed be unique to the Nimravidae (*sensu* Bryant, 1991). To facilitate character analysis, we discuss dental (based on the cladistic analysis presented above), basicranial, and other characters (cranium and postcranium) separately for barbourufelid–nimravid and barbourufelid–felid comparisons.

Among the dental features used by Bryant (1991), the moderately to extremely enlarged dC1/ is the only character known from both Nimravidae and Barbourufelidae, but not from other taxa. According to Bryant (1991: 69), the particular shape of the crenulations is unique for the Nimravidae *s.l.* However, this statement is refuted by illustrations of the crenulation

shape on upper canines of felids like *Nimravides* (see Baskin, 1981: fig. 6B) or *Machairodus* (see Pons-Moya, 1989–90: fig. 1; M. Morlo, unpubl. data) which display crenulations very similar to those in Nimravidae *s.s.* Our cladistic analysis supports the view that crenulations appeared independently in Nimravidae and Barbourufelidae. In our analysis of early species of nimravids, barbourufelids and felids, the relative size of dC1/ compared to C1/ is a character unknown in all taxa but *Nimravus* (see cladistic analysis), in which it is of moderate size. Within barbourufelids, an extremely large dC1/ is currently known only in *Barbourufelis*, the most apomorphic genus of the family. This character must therefore be considered as uninformative when comparing the Barbourufelidae to other carnivoran families. As with this character, previous comparisons between the Barbourufelidae and Nimravidae were mainly based on the most apomorphic (and stratigraphically latest) North American genus, *Barbourufelis*. However, comparison of the dentition of the most primitive barbourufelids (and especially *P. eggeri* as the most plesiomorphic European barbourufelid) with that of the most plesiomorphic nimravids, *Eofelis* and *Nimravus* (see Peigné, 2000, 2001, 2003) from the Oligocene of Quercy provides a very different interpretation (see cladistic analysis presented above; Fig. 4; Table 3). It reveals extremely poor support for a Nimravidae–Barbourufelidae sister-group relationship. Barbourufelidae differs from Nimravidae *s.s.* by the following dental characters (see also Table 3): vertical grooves present on upper canines (autapomorphy); P1/, P/1 and M/2 lost; M/1 with a relatively tall protoconid; an extremely reduced talonid which only forms a posterior bulge and is markedly more reduced than the relatively large metaconid. In addition, the lower premolars of the Barbourufelidae retain posterior accessory cusps (consistently lacking in Nimravidae) and, as in early felids, the upper carnassial has a parastyle and a more posteriorly located protocone (at least primitively).

Even if major differences in the dental pattern occur, the basicranial structure is more important for analyses of high rank relationships within the Carnivora. As a result some authors have paid particularly attention to that region to pinpoint the systematic position of Nimravidae *s.l.* Most of these contributions (e.g. Baskin, 1981; Neff, 1983; Hunt, 1987) conclude that the Nimravidae *s.l.* have a distinctive basicranial structure, but this conclusion has mainly been based on the Oligocene taxa (Nimravidae *s.s.*). Two of the remaining five characters of Bryant (1991) belong to the auditory region: the anterior limb of the ectotympanic is long and more anteriorly articulated with the squamosal; a short septum, composed of the rostral and caudal entotympanics, lies antero-medial in the bulla. In our view, these studies have not

provided strong evidence that Nimravidae s.s. and Barbourfelidae share a similar basicranial configuration. The anterior ectotympanic crus is long and applied against the squamosal in *Barbourfelis*, but somewhat more slender in *Sansanosmilus palmidens* (see Ginsburg, 1961: fig. 65, pl. 13, fig. 1) and thus more plesiomorphic than in the Nimravidae s.s. This supports an interpretation that the feature may have appeared in Barbourfelidae and Nimravidae s.s. separately. The presence of an unusually short septum (proseptum) made up of the rostral and caudal entotympanics in the anteromedial corner of the auditory bulla has so far only been demonstrated in *Dinictis* (Hunt, 1987). Given that all Nimravidae s.s. share a very similar configuration of the auditory bulla throughout their stratigraphic distribution (Joeckel *et al.*, 2002), inferring the presence of a similar septum in all Palaeogene nimravids is reasonable. However, the presence of a similarly placed and constructed proseptum in the bulla of the much later Barbourfelidae has not yet been demonstrated, though such a short septum may be present in some *Barbourfelis* specimens (Baskin, 1981: UF 24432, fig. 2; Hunt, 1987: UF 55859, fig. 9). In additional North American specimens (but excluding UF 55859), Neff (1983: 306) identified a crista in the anteromedial corner of the bulla, which she identified as a septum; the dorsal edge is vertical, but the ventral edge “curves mediad to form a horizontal septum”. According to Neff (1983: 306), the dorsal part of the crista is similar to the anterior end of the entotympanic in *Dinictis* while “the horizontal orientation of the ventral part is unlike the condition in *Dinictis*”. We observed the same low, horizontally orientated crest in *Sansanosmilus palmidens* (MNHN-Sa 472, Ginsburg, 1961: fig. 65; MNHN-Sa 3384, Fig. 6D) from Sansan, which may indicate a relative uniformity of the barbourfelid bulla. It is important to note that it is not possible to separate an ectotympanic from an entotympanic portion on the surface of the ossified bulla in *Barbourfelis* and *Sansanosmilus* as is clearly the case in the Nimravidae s.s. As a result, the relationships, origin and composition of the proseptum of *B. loveorum* (Hunt, 1987: fig 9; Fig. 6B herein) and *S. palmidens* (e.g. MNHN-Sa 472, MNHN-Sa 3384; Fig. 6D) cannot be considered as identical to those of the proseptum described in *Dinictis* (Hunt, 1987; Fig. 6A), nor to those of any other auditory separation observable in mammals. Among the features listed in Bryant (1991), the presence of an external auditory meatus that is wider than the auditory notch may be the only basicranial character the Nimravidae and Barbourfelidae have in common (Neff, 1983; Bryant, 1991). In contrast, the auditory bullae of *Barbourfelis* and *Sansanosmilus* present further basicranial differences to the Palaeogene taxa which were not included

in Bryant's analysis: a fully ossified bulla which invades the mastoid and a thinner wall of the entotympanic which is not composed of three distinct layers in Barbourfelidae as in some Nimravidae (Neff, 1983). Even if these barbourfelid characters may have been derived from the nimravid condition, as argued by Hunt (1987), this is not the case for the deep recessing of the auditory region, especially the petrosal, into the basicranium, resulting in a less dorsal placement in the Nimravidae.

One of the remaining five characters of Bryant (1991) uniting the Nimravidae and Barbourfelidae concerns the skull: the posteriorly converging lateral walls of the nasopharynx. This character occurs in the most specialized genera *Hoplophoneus*, *Eusmilus*, *Barbourfelis*, *Nimravus*, *Dinictis* and *Sansanosmilus*. It is uninformative in the cladistic analysis presented above and has to be confirmed in the earliest and/or most primitive members (nimravids: *Eofelis*, *Dinaelurictis*, *Quercylurus*, *Dinaelurus*; barbourfelids: *Ginsburgsmilus*, *Syrtsosmilus*, *Afrosmilus*, *Prosansanosmilus*). The structure of the frontal sinus shows the plesiomorphic condition of Carnivora even in the highly evolved *Barbourfelis morrisoni*, but extends over the brain cavity in the nimravids *Hoplophoneus* and *Dinictis*. Among barbourfelids, only *B. fricki*, as the most apomorphic taxon, shows such an extended frontal sinus (see Joeckel & Stavas, 1996). It can thus be stated, that the consecutive occurrence of converging lateral walls of the nasopharynx and an extended frontal sinus is not unique to Nimravidae s.l. and/or reflects an increasing specialization towards the sabretooth bauplan. In Barbourfelidae, the most apomorphic condition shows up in *B. fricki* – that is, not before the latest Miocene and about 30 Myr later than in the apomorphic Oligocene Nimravidae s.s. Because *Sansanosmilus* and *B. morrisoni* verify that the less apomorphic character states were also present in Barbourfelidae, we interpret both characters as sympleisomorphies rather than as synapomorphies.

Among the postcranial characters, some authors (Bryant, 1991; Joeckel & Stavas, 1996; see Ginsburg, 1961: 162, fig. 68/5) have also noted the morphological similarity of the metacarpus in Nimravidae and Barbourfelidae. It must be understood, however, that the postcranial anatomy of nimravid and barbourfelid genera is far from well known, due to the poor fossil record. The manus (and thus the morphology of the metacarpus) plays an important role in grasping prey in all scimitar-toothed carnivorans and assists in avoiding canine breakage, as these teeth are highly vulnerable to lateral forces (e.g. Bohlin, 1940; Gonyea, 1976; Van Valkenburgh & Ruff, 1987; Van Valkenburgh & Hertel, 1993). Manus morphology is correlated both to use of the forepaw and to locomotion (Ivaniuk *et al.*, 2001), and thus has great functional

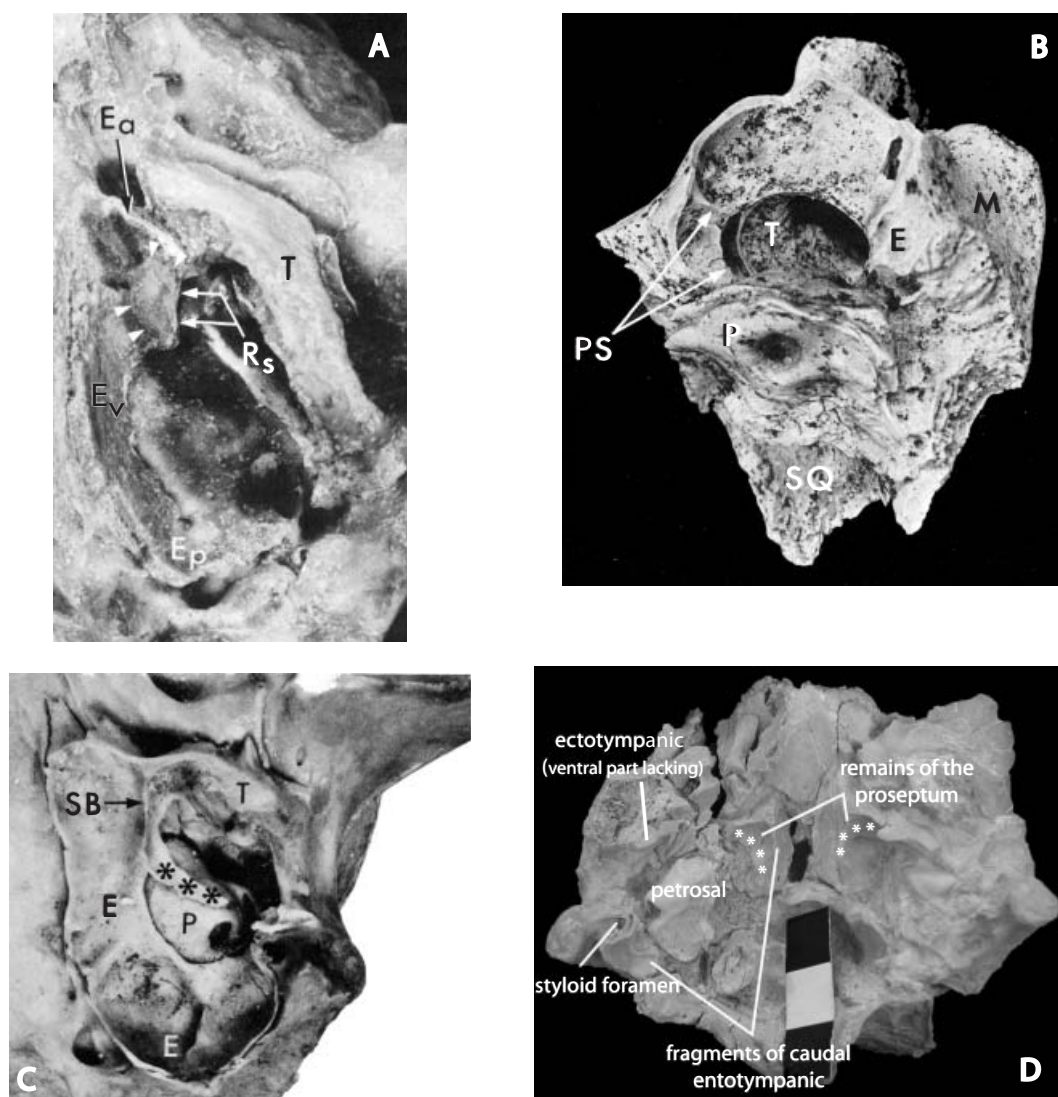


Figure 6. Auditory region of Nimravidae, Barbourfelidae and Felidae. A, auditory region in juvenile *Dinictis* (UNSM 4051–81) from Nebraska (Hunt, 1987: fig. 5A). B, auditory bulla of *Barbourfelis lovei* (UF 55859) from Love bone bed, Florida (Hunt, 1987: fig. 9B). C, auditory bulla of *Lynx rufus* (UNSM 33–67) from Nebraska (Hunt, 1987: fig. 10B). D, auditory region of *Sansanosmilus palmidens* (MNHN Sa 3384) from Sansan, France. Abbreviations after Hunt (1987). E, ossified caudal entotympanic – Ea, anterior lamina, Ep, posterior lamina, Ev, vertical lamina; P, petrosal; PS, nimravid proseptum; Rs, septate lateral margin of rostral entotympanic; SB, septum bullae; SQ, squamosal; T, ectotympanic.

influence. If the postcranial anatomy of nimravids is usually regarded as plesiomorphic within Carnivora (Tedford, 1978; Bryant, 1991), the obvious similarities may be interpreted as symplesiomorphies based on similar functional necessities.

The previous discussion and cladistic analysis of dental characters of early barbourfelids, nimravids and felids show that there is little support for a sister-group relationship of the Barbourfelidae to the Nimravidae. As a result, we exclude the Barbourfelidae from Nimravidae. An alternative approach is to make the Barbourfelidae a subfam-

ily of the Felidae (Morales *et al.*, 2001); this is discussed below.

RELATIONSHIPS OF BARBOURFELIDAE TO FELIDAE

Reasons for excluding the Barbourfelidae from the Nimravidae have been provided by previous authors (Neff, 1983; Morales *et al.*, 2001). The differences between Barbourfelidae and Felidae are less obvious. Following Tedford (1978), the barbourfelids have been excluded from the Felidae mainly due to their peculiar auditory structure. Their assignment has,

however, recently been reaffirmed (Morales *et al.*, 2001). As a result, we address the anatomical characters involved in this relationship in greater detail.

While *Sansanosmilus* and *Barbourofelis* are easy to distinguish from Felidae by dental anatomy, the earliest barbourofelids (*Prosansanosmilus*, *Afrosmilus*, *Ginsburgsmilus*) are similar to Felidae in this respect, as shown by the cladistic analysis. Some dental characters shared by Barbourofelidae and Felidae (e.g. the presence of accessory cusps on the premolars) are, however, also present in early aeluroids such as *Stenoplesictis*, *Stenogale* or *Vireticteis* (Hunt, 1998a; de Bonis, Peigné & Hugueney, 1999; Peigné & de Bonis, 1999). These may therefore be common aeluroid characters rather than evidence for the placement of barbourofelids within Felidae. An upper carnassial with a parastyle and a posteriorly located protocone are common to Barbourofelidae and Felidae, although not exclusive to these two families. Other dental apomorphies of the Barbourofelidae are not present in Felidae and show an early trend towards a different adaptation, in particular, the markedly transversely compressed upper canines with crenulations and vertical grooves; the absence of P1/, P/1 and M/2; a lower carnassial with a tall protoconid, and an extremely small talonid which is markedly more reduced than the metaconid.

Although dental characters are consistent with the hypothesis that Barbourofelidae may be included in Felidae, fundamental differences in the mandible, such as the angular chin or the curved mandibular body, and, in particular, the auditory region provide strong support for not doing so. The basicranial anatomy of the Barbourofelidae is documented in *S. palmidens* (MN 6, ~13.5 Myr) and *Barbourofelis*. It differs not only from that of the first true felid *Proailurus*, but also from that of other early aeluroids such as *Stenoplesictis*. In barbourofelids, the external auditory meatus is wider than the auditory notch. The fusion of the elements making up the bulla has obviously proceeded further in barbourofelids, since it is not possible to distinguish the contribution of each element. The presence of a horizontal proseptum in the anteromedial corner of the bulla is unique among Carnivora and can be regarded as an autapomorphy of the Barbourofelidae.

Two other skull characters, both symplesiomorphies with respect to Nimravidae s.s. (see above), may distinguish the Barbourofelidae from the Felidae, although they remain to be confirmed in early barbourofelids: the shortening of the palate and the posteriorly converging lateral walls of the nasopharynx.

Due to the lack of basicrania, dental evidence alone places the plesiomorphic genera *Prosansanosmilus*, *Ginsburgsmilus*, *Afrosmilus* and *Syrtosmilus* in the Barbourofelidae. The similarity to the dentition of

early felids, as demonstrated by, for example, the previous assignment of *Afrosmilus* to Felidae (Schmidt-Kittler, 1987) or the misinterpretation of *P. eggeri* as *Pseudaelurus*, is supported by the cladistic analysis. As a result, dental evidence alone would allow inclusion of Barbourofelidae as a subfamily in Felidae, as has been done by Morales *et al.* (2001), but doing so clearly falsifies the hypothesis that Barbourofelidae are included in Nimravidae s.l. The other anatomical differences, especially the unique basicranial morphology of barbourofelids, however, warrant the distinction of a separate family Barbourofelidae, sister group to Felidae and separate from Nimravidae s.s.

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REFERENCES

- Alba DM, Agustí J, Moyà-Solà S. 2001.** Completeness of the mammalian fossil record in the Iberian Neogene. *Paleobiology* **27** (1): 79–83.
- Andrews CW. 1914.** On the lower Miocene Vertebrates from British East Africa, collected by Dr Felix Oswald. *Quarterly Journal of the Geological Society of London* **70**: 163–186.
- Azanza B, Cerdeño E, Ginsburg L, Van der Made J, Morales J, Tassy P. 1993.** Les grands mammifères du Miocène inférieur d'Artesilla, bassin de Calatayud-Teruel (province de Saragosse, Espagne). *Bulletin du Muséum national d'histoire Naturelle Series 4* **15C**: 105–153.
- Baskin JA. 1981.** *Barbourofelis* and *Nimravides* with a description of two new species from the late Miocene of Florida. *Journal of Mammalogy* **62**: 122–139.
- Beaumont G, Crusafont-Pairó M. 1982.** Les félidés (Mammifères, Carnivores) du Vallésien du Vallès, Catalogne, Espagne. *Archives des Sciences, Genève* **35** (1): 41–64.
- Belichón M, Morales J. 1989.** Los Carnívoros del Mioceno inferior de Buñol (Valencia, España). *Revista Española de Paleontología* **4**: 3–8.
- Blainville HMD. 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. Paris: J. B. Baillière & Fils.
- Bohlin B. 1940.** Food habit of the machaerodonts, with special regard to *Smilodon*. *Bulletin of the Geological Institute of Uppsala* **28**: 156–174.
- de Bonis L, Peigné S, Hugueney M. 1999.** Carnivores féloïdes de l'Oligocène supérieur de Coderet-Bransat (Allier, France). *Bulletin de la Société Géologique de France* **170**: 939–949.
- Bryant HN. 1991.** Phylogenetic relationships and systematics of the Nimravidae (Carnivora). *Journal of Mammalogy* **72**: 56–78.
- Cirot E. 1992.** Etude phylogénétique de quelques genres d'Arctoidea de l'Oligocène eurasiatique. Comparaison des données morphologiques et moléculaires. Unpublished PhD Thesis, University of Poitiers.
- Cirot E, de Bonis L. 1992.** Révision du genre *Amphicyonodon*, carnivore de l'Oligocène. *Palaeontographica A* **220**: 103–130.
- Dayan T, Wool D, Simberloff D. 2002.** Variation and covariation of skulls and teeth: modern carnivores and the interpretation of fossil mammals. *Paleobiology* **28** (4): 508–526.
- Dehm R. 1950.** Die Raubtiere aus dem Mittel-Miocän (Burdigalium) von Wintershof-West bei Eichstätt in Bayern. *Abhandlungen der Bayerischen Akademie der Wissenschaften, mathematisch-naturwissenschaftliche Klasse, N. F.* **58**: 1–141.
- Fahlbusch V, Gall H, Schmidt-Kittler N, Dehm R. 1974.** Die obermiozäne Fossil-Lagerstätte Sandelzhausen. 10. Die Grabungen 1970–73, Beiträge zur Sedimentologie und Fauna. *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und Historische Geologie* **14**: 103–128.
- Fahlbusch V, Liebreich R. 1996.** *Hasenhirsch und Hundebär. Chronik der Tertiären Fossil-Lagerstätte Sandelzhausen bei Mainburg*. München: Verlag Dr. Friedrich Pfeil.
- Filhol H. 1883.** Notes sur quelques mammifères fossiles de l'époque miocène. *Archives du Muséum d'Histoire Naturelle de Lyon* **3**: 1–69.
- Flynn JJ, Galiano H. 1982.** Phylogeny of early Tertiary Carnivora, with a description of a new species of *Protictis* from the middle Eocene of northwestern Wyoming. *American Museum Novitates* **2725**: 1–64.
- Flynn JJ, Neff NA, Tedford RH. 1988.** Phylogeny of the Carnivora. In: Benton MJ, ed. *The phylogeny and classification of the tetrapods*, Vol. 2: *Mammals*. Oxford: Clarendon Press, Systematics Association Special Volume **35B**: 73–116.
- 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, N. S. 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.
- Ginsburg L. 1999.** Order Carnivora. In: Rössner GE, Heissig K, eds. *The Miocene land mammals of Europe*. München: Verlag Dr. Friedrich Pfeil, 109–148.
- Ginsburg L, Bulot C. 1982.** Les carnivores du miocène de Bézian près de la Romieu (Gers, France). *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen B* **85**: 53–76.
- Gonyea WJ. 1976.** Behavioral implications of saber-toothed felid morphology. *Paleobiology* **2**: 332–342.
- Heizmann EPJ. 1973.** Die tertiären Wirbeltiere des Steinheimer Beckens. Teil 5. Die Carnivoren des Steinheimer Beckens. B. Ursidae, Felidae, Viverridae sowie Ergänzungen und Nachträge zu den Mustelidae. *Palaeontographica (supplement)* **8**: 1–95.
- Heizmann EPJ, Ginsburg L, Bulot C. 1980.** *Prosanosmilus peregrinus*, ein neuer machairodontider Felide aus dem Miocän Deutschlands und Frankreichs. *Stuttgarter Beiträge zur Naturkunde B* **58**: 1–27.
- Hell P. 1966.** Polydontie beim europäischen Luchs (*Lynx lynx* L.). *Zeitschrift für Säugetierkunde* **31**: 392–393.
- Hünemann KA. 1999.** Superfamily Suoidea. In: Rössner GE, Heissig K, eds. *The Miocene land mammals of Europe*. München: Verlag Dr. Friedrich Pfeil, 209–216.
- Hunt RM Jr. 1987.** Evolution of the aeluroid Carnivora: significance of the auditory structure in the nimravid cat *Dinictis*. *American Museum Novitates* **2886**: 1–74.
- Hunt RM Jr. 1998a.** Evolution of the aeluroid Carnivora: Diversity of the earliest aeluroids from Eurasia (Quercy, Hsanda-Gol) and the origin of felids. *American Museum Novitates* **3252**: 1–65.
- Hunt RM Jr. 1998b.** Ursidae. In: Janis CM, Scott KM, Jacobs LL, eds. *Evolution of Tertiary mammals of North America, Vol. 1: Terrestrial carnivores, ungulates, and ungulatelike mammals*. New York: Cambridge University Press, 174–195.
- Ivaniuk AN, Pellis SM, Whishaw IQ. 2001.** Are long digits correlated with high forepaw dexterity? A comparative test in terrestrial carnivores (Carnivora). *Canadian Journal of Zoology* **79** (5): 900–906.
- Joeckel RM, Peigné S, Hunt RM Jr, Skolnick RI. 2002.** The auditory region and nasal cavity of Oligocene Nimravidae (Mammalia: Carnivora). *Journal of Vertebrate Paleontology* **22** (4): 830–847.
- Joeckel RM, Stavas JM. 1996.** New insights into the cranial anatomy of *Barbourofelis fricki* (Mammalia, Carnivora). *Journal of Vertebrate Paleontology* **16** (3): 585–591.
- Kaup JJ. 1832.** Vier urweltliche Raubtiere, welche im zoologischen Museum zu Darmstadt aufbewahrt werden. *Archiv für Mineralogie, Geognosie, Bergbau- und Hüttenkunde* **5** (1): 150–158.
- Köhler M, Moyà-Solà S, Andrews P. 1999.** Order Primates. In: Rössner GE, Heissig K, eds. *The Miocene land mammals of Europe*. München: Verlag Dr. Friedrich Pfeil, 91–104.
- Kretzoi M. 1929.** Materialien zur phylogenetischen Klassifikation der Aeluroideen. *X^e Congrès International de Zoologie*, 1293–1355.
- Kurtén B. 1976.** Fossil Carnivora from the late Tertiary of Bled Douarah and Cherichira, Tunisia. *Notes du Service Géologique de Tunisie* **42**: 177–214.

- Martin LD. 1998.** Nimravidae. In: Janis CM, Scott KM, Jacobs LL, eds. *Evolution of Tertiary mammals of North America*, Vol. 1: *Terrestrial carnivores, ungulates, and ungulate-like mammals*. New York: Cambridge University Press, 228–235.
- McKenna MC, Bell SK. 1997.** *Classification of mammals above the species level*. New York: Columbia University Press.
- Mein P. 1989.** Updating of MN zones. In: Lindsay EH, Fahlbusch V, Mein P, eds. *European Neogene mammal chronology*. NATO ASI Series A 180. New York: Plenum, 73–90.
- Morales J, Salesa MJ, Pickford M, Soria D. 2001.** A new tribe, new genus and two new species of Barbourfelinae (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. 1996.** Carnivoren aus dem Unter-Miozän des Mainzer Beckens (2. Mustelida, Pinnipedia, Feliformia, Palaeogale). *Senckenbergiana lethaea* **76** (1/2): 193–249.
- Neff NA. 1983.** The basicranial anatomy of the Nimravidae (Mammalia: Carnivora): character analysis and phylogenetic inferences. Unpublished PhD Thesis, City University of New York.
- Ozansoy F. 1965.** Études gisements continentaux et des Mammifères du Cénozoïque de Turquie. *Mémoires de la Société Géologique de France, N. S.* **44**: 1–92.
- Peigné S. 2000.** A new species of *Eofelis* (Carnivora: Nimravidae) from the Phosphorites of Quercy, France. *Comptes Rendus de l'Académie des Sciences, Paris, Sciences de la Terre et des Planètes* **330**: 653–658.
- Peigné S. 2001.** A primitive nimravine skull from the Quercy fissures, France: implications for the origin and evolution of Nimravidae (Carnivora). *Zoological Journal of the Linnean Society* **132** (4): 401–410.
- Peigné S. 2003.** Systematic review of European Nimravinae (Mammalia, Carnivora, Nimravidae) and the phylogenetic relationships of Palaeogene Nimravidae. *Zoologica Scripta* **32** (3): 199–229.
- Peigné S, de Bonis L. 1999.** The genus *Stenoplesictis* Filhol (Mammalia, Carnivora) from the Oligocene deposits of the Phosphorites of Quercy, France. *Journal of Vertebrate Paleontology* **19**: 566–575.
- Peigné S, de Bonis L. 2003.** Juvenile cranial anatomy of Nimravidae (Mammalia, Carnivora): biological and phylogenetic implications. *Zoological Journal of the Linnean Society* **138**: 477–493.
- Pons-Moya J. 1989–90.** Presencia de carnívoros Turolenses en el Vallesien terminal (MN 10) de Terrassa (Catalunya). *Paleontologia i Evolució* **23**: 199–203.
- Rothwell T. 2001.** A partial skeleton of *Pseudaelurus* (Carnivora: Felidae) from the Nambé Member of the Tesuque Formation, Española Basin, New Mexico. *American Museum Novitates* **3342**: 1–31.
- Savage RJG. 1965.** Fossil mammals of Africa: 19. The Miocene Carnivora of East Africa. *Bulletin of the British Museum (Natural History), Geology* **10** (8): 239–316.
- Savage RJG. 1989.** The African dimension in European Early Miocene Mammal Faunas. In: Lindsay EH, Fahlbusch V, Mein P, eds. *European Neogene mammal chronology*. NATO ASI Series A 180. New York: Plenum, 587–599.
- Schmidt-Kittler N. 1987.** The Carnivora (Fissipedia) from the Lower Miocene of East Africa. *Palaentographica A* **197**: 85–126.
- Schultz CB, Schultz MR, Martin LD. 1970.** A new tribe of saber-toothed cats (Barbourfelini) from the Pliocene of North America. *Bulletin of the University of Nebraska State Museum* **9**: 1–31.
- Swofford DL. 1998.** *PAUP – phylogenetic analysis using parsimony (and other methods)*, Version 4. beta 10. Sunderland, MA: Sinauer Associates.
- Tedford RH. 1978.** History of dogs and cats. A view from the fossil record. In: *Nutrition and management of dogs and cats*. St. Louis, MI: Ralston Purina Co.
- Van der Made J. 1999.** Intercontinental relationship Europe – Africa and the Indian subcontinent. In: Rössner GE, Heissig K, eds. *The Miocene land mammals of Europe*. München: Verlag Dr. Friedrich Pfeil, 457–472.
- Van Valen LM. 1994.** Serial homology: the crests and cusps of mammalian teeth. *Acta Palaeontologica Polonica* **38** (3/4): 145–158.
- Van Valkenburgh B, Hertel F. 1993.** Tough times at La Brea: tooth breakage in large carnivores of the Late Pleistocene. *Science* **261**: 456–459.
- Van Valkenburgh B, Ruff CB. 1987.** Canine tooth strength and killing behaviour in large carnivores. *Journal of Zoology, London* **212**: 379–397.
- Wang X. 1994.** Phylogenetic systematics of the Hesperocyoninae (Carnivora: Canidae). *Bulletin of the American Museum of Natural History* **221**: 1–207.
- Werdelin L. 1996.** Carnivoran ecomorphology: A phylogenetic perspective. In: Gittleman JL, ed. *Carnivore behavior, ecology, and evolution*, Vol. 2. Ithaca: Cornell University Press, 582–624.

APPENDIX

CHARACTER ANALYSIS

- (1) Crenulations. These are well documented in *Ginsburgsmilus napakensis* and *Afrosmilus hispanicus*. In *A. africanus* and *P. eggeri* sp. nov., they are documented on the posterior border of the lower canine only. However, by extension, we consider that the upper canine was probably serrated as well. It is important to note that crenulations may vary within congeneric species. For example, the sabretooth felid *Paramachaerodus ogygius* presents none while the genotype *P. orientalis* does. Polarity: (0) no crenulations on dentition; (1) present, at least on the posterior border on the upper canines.
- (2) Size of dC/ relative to that of C/ (see Bryant, 1991: table 1, character 23). Polarity: (0) dC/ much smaller than C/ (1) dC/ moderately smaller than or nearly the size of C/.

- (3) Transversal compression of the upper canine. This tooth is not preserved in the only known upper dentition of *A. africanus* (Savage, 1965: pl. 5, fig. 4), but the ratio L/W is about 1.8 at the alveolus (data from Savage, 1965). Given that the upper canine tends to be even more compressed at the enamel–dentine boundary, this species probably had an upper canine more compressed than in *Ginsburgsmilus*, *Eofelis* and *Nimravus*. Polarity: (0) very slightly compressed, ratio L/W smaller than 1.5; (1) markedly compressed, L/W between 1.5 and 1.8; (2) very compressed, ratio >1.8.
- (4) Vertical grooves on upper canines. In both *Ginsburgsmilus* and *Sansanosmilus palmidens* deep vertical grooves are present on both faces of the upper canines. Their presence may represent an autapomorphy of barbourofelids, although it remains to be confirmed in taxa where the upper canines have not yet been documented. Polarity: (0) absent; (1) present.
- (5) P1/. Polarity: (0) present and reduced relative to P2/ (1) very reduced, sometimes absent; (2) absent.
- (6) P2/. Polarity: (0) present and reduced relative to P3/ (1) very reduced, sometimes absent; (2) absent.
- (7) P3/, anterior cingulum cusp. Within canids, Wang (1994: 162) considered the acquisition of accessory cusps, associated with better development of the cingulum cusps, to be a derived state. There are neither accessory cusps nor developed cingulum cusps on P3/ in miacids (*Miacis*) and amphicyonodontids (*sensu* Hunt, 1998b). Within Barbourofelidae, Geraads & Güleç (1997) observed reverse evolution from the earliest species of *Sansanosmilus*, with a four-cusp P3/ (main, anterior and posterior accessory and posterior cingulum cusps), to *Barbourofelis fricki* with a two-cusp P3/ (absence of anterior accessory and posterior cingulum cusps). Within taxa included in the analysis, the character state is not known in *P. peregrinus* and in other early barbourofelid genera. P3/ in *Ginsburgsmilus* and *Afrosmilus* (the anterior part is not known in *A. hispanicus*) has three cusps (main, posterior accessory and cingulum). In contrast, the maxillary of *A. africanus* from Rusinga (see Savage, 1965) has a P3/ with four cusps, as in *Sansanosmilus*. In early felids (*Proailurus*) and early canids, P3/ has a developed posterior accessory cusp. P3/ is very simple, with only the main cusp, in *Amphicyonodon* and *Pachycynodon*. It has no anterior cingulum cusp in nimravines (*Eofelis*, *Nimravus*). Polarity: (0) absent; (1) present.
- (8) P3/, lingual development. P3/ is primitively narrow. It widens in some taxa by developing a lingual and posterior bulge which may support a small third cusp; a third root is hence present, more or less separate from the posterior root. Polarity: (0) absent or nearly absent; (1) developed, the third root more or less clearly separate from the others.
- (9) P4/, parastyle. Polarity: (0) absent; (1) present and developed; (2) distinctly more developed than in state 1.
- (10) P4/, preparastyle. Polarity: (0) absent; (1) present and small; (2) distinctly more developed than in state 1.
- (11) P4/, protocone size. The size of the protocone is reduced in catlike carnivorans in comparison with the situation in early canids (e.g. *Prohesperocyon*) and amphicyonodontids (*sensu* Hunt, 1998b). Polarity: (0) large; (1) reduced compared to outgroups (state 0), i.e. still distinctly larger than the parastyle when this cusp is present; (2) about the size of the parastyle; (3) reduced, distinctly smaller than the parastyle; (4) markedly reduced, crest-like, no basin between proto- and paracone; (5) markedly reduced and applied against the paracone lingual wall.
- (12) P4/, location of the protocone anterior border relative to the anterior border of the paracone/parastyle complex. Within early nimravids, the protocone is more anteriorly located than in felids or early barbourofelids, although this is partly due to the development of a parastyle and preparastyle in the two latter groups (characters 11 and 12). We consider four character states. In *Eofelis* and often in *Nimravus*, the protocone remains anteriorly located (state 0). In some *Nimravus* specimens and in most genera, the protocone is across the paracone anterior border or slightly posterior to it, as in, e.g. *A. turkanae* and *A. hispanicus* (state 2). Actually, the difference between the two latter species is not sufficiently great to separate them into two different character states. In *A. africanus* and *P. peregrinus*, the protocone is markedly posterior to the paracone anterior border (state 3). Polarity: (0) protocone anteriorly located; (1) protocone location variable, from state 0–1; (2) protocone anterior border across or slightly posterior to the paracone border; (3) protocone distinctly posterior to the paracone border.
- (13) M1/. Tends to be reduced in size, especially transversely, in catlike carnivorans. The transverse reduction of this tooth is, however, more pronounced in *P. eggeri* and especially in *Nimravus* than in other genera preserving this tooth. The ratio length of P4/ to width of M1/ is used to sep-

- arate the character states. Polarity: (0) large size, with ratio LP4//WM1/ much less than 1.5; (1) reduced and transversely elongated, ratio LP4//WM1/ about 1.5; (2) more reduced, ratio LP4//WM1/ between 1.6 and 1.8; (3) extremely reduced, ratio LP4//WM1 more than 1.8.
- (14) M1/, development of protocone and metacone. In all taxa, the paracone is very reduced and crest-like, which is a derived trait relative to outgroups in which this is clearly distinct with a prominent cusp. The metacone and protocone may be prominent in some taxa, completely reduced in others. Polarity: (0) metacone and protocone large; (1) the two cusps strongly reduced but with protocone still prominent and metacone projected posteriorly; (2) protocone markedly reduced but still prominent, metacone completely reduced and not projected posteriorly; (3) protocone extremely reduced and not prominent, metacone reduced but still projected posteriorly.
- (15) P/1. Polarity: (0) present and reduced; (1) very reduced, sometimes absent; (2) absent.
- (16) P/2. Due to its minute size and location on the postcanine diastema, the P/2 in *P. peregrinus* is considered to be vestigial. Polarity: (0) present and reduced; (1) very reduced, sometimes absent; (2) vestigial or absent.
- (17) P/3–4, posterior accessory cusp. An accessory cusp clearly distinct from the posterior cingulid is present on P/4 only in amphi-cynodontids (*sensu* Hunt, 1998b), on P/3–4 in early canids, felids and early barbourfelids. In advanced barbourfelids as *Sansanosmilus palmidens*, there is no clear distinction between the posterior accessory and cingulid cusps. It is absent in Nimravidae s.s., where it is considered as derived by Bryant (1991). Polarity: (0) present on P/4 only; (1) present on P/3–4; (2) absent.
- (18) Height of M/1 protoconid. *Prosansanosmilus* and *Afrosmilus* have a protoconid which is very tall in comparison with the tooth length. The deep fossa present in the maxillary of *Ginsburgsmilus* also suggests that this species has a pointed protoconid. In *Eofelis*, *Nimravus* (M/1 is very elongated in this genus), *Proailurus*, and *Pseudaelurus*, the protoconid is dominant but relatively lower than in *Prosansanosmilus* and *Afrosmilus*. In comparison with the outgroups, which also have a protoconid low relative to the tooth length, the tall protoconid of *Prosansanosmilus* and *Afrosmilus* is considered as derived. Polarity: (0) protoconid relatively low; (1) protoconid relatively tall.
- (19) Reduction of M/1 talonid compared to that of metaconid. The evolution of the talonid and metaconid is well documented in early barbourfelids, nimravids and felids. As discussed in text, the reduction of the talonid and metaconid distinguishes barbourfelids from the two latter groups. Within canids, the metaconid tends to be reduced before the talonid (see Wang, 1994). In *Amphicynodon* (see Cirot & de Bonis, 1992) and *Pachycynodon*, the reduction of the talonid does not seem to precede that of the metaconid. Polarity: (0) no clear trend, metaconid and talonid display a similar reduction; (1) metaconid markedly more reduced than talonid; (2) talonid markedly more reduced than metaconid.
- (20) M/1 metaconid. The reduction of the metaconid is a derived character. It is absent in basal nimravids, very reduced in early barbourfelids. Polarity: (0) metaconid large and little reduced compared to the paraconid; (1) markedly reduced compared to the paraconid; (2) very small; (3) vestigial or absent.
- (21) M/1 reduction of talonid. Polarity: (0) talonid long, distinctly more than 20% of the total M/1 length; (1) talonid short, between 10 and 20% of the total M/1 length; (2) extremely reduced, forming only a small posterior bulge; (3) vestigial or absent.
- (22) M/2. Polarity: (0) present and reduced; (1) very reduced, sometimes absent; (2) absent.