

A new barbourofelid mandible (Carnivora, Mammalia) from the Early Miocene of Grillental-6, Sperrgebiet, Namibia

Jorge MORALES¹ and Martin PICKFORD²

1. Departamento de Paleobiología, Museo Nacional de Ciencias Naturales-CSIC – C/José Gutiérrez Abascal 2, 28006, Madrid, Spain (jorge.morales@mncn.csic.es)
2. Sorbonne Universités – CR2P, MNHN, CNRS, UPMC – Paris VI, 8, rue Buffon, 75005, Paris, France (martin.pickford@mnhn.fr)

Abstract: Prospecting in the continental Miocene deposits at Grillental 6 in the Sperrgebiet, Namibia, has resulted in the discovery of a mandible of a barbourofelid carnivore. Despite the poor preservation of the dentition, the specimen yields important information for understanding the oldest members of the family, classified in the tribe Afrosmilini. The new Grillental mandible and other fossils from the Sperrgebiet (Fiskus and Langental) are currently classified in the species *Ginsburgsmilus napakensis* Morales, Salesa, Pickford & Soria 2001. The tribe Afrosmilini was widespread throughout the African continent in the Early Miocene and at the end of the Burdigalian it dispersed to western Europe.

Key words: Miocene; Namibia; Barbourofelidae; Afrosmilini; Biochronology; Biogeography.

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Introduction

The tribe Afrosmilini (Barbourofelidae, Schultz, Schultz & Martin 1970) was proposed by Morales, Salesa, Pickford & Soria (2001) to include the genera *Ginsburgsmilus* Morales, Salesa, Pickford & Soria 2001, *Afrosmilus* Kretzoi 1929, *Syrtosmilus* Ginsburg 1978 and *Prosansanosmilus* Heizmann, Ginsburg & Bulot 1980, in which the dentition is morphologically primitive compared to that of typical genera of the subfamily Barbourofelinae Schultz, Schultz & Martin 1970 (today included in the tribe Barbourofelini Schultz, Schultz & Martin 1970), *Sansanosmilus* Kretzoi 1929, *Albanosmilus* Kretzoi 1929, *Vampyriactis* Kurten 1970 and *Barbourofelis* Schultz, Schultz & Martin 1970, which possess highly derived machairodont canines (saber tooth cats), including several genera more specialised than Machairodontinae Gill 1872. The systematic position of the Barbourofelinae is still a matter of debate, alternatively sharing a sister group relationship with the Nimravidae Cope 1880 (see for example Bryant 1991; Baskin 2005) or with the Felidae Fischer 1817, either at the subfamily rank (Morales *et al.* 2001) or as an independent family

Barbourofelidae, but more closely related to the felids than to the nimravids (Morlo *et al.* 2004).

A persistent source of uncertainty concerning the systematics of this group of carnivores resides in the unequal knowledge about the fossil record of the Barbourofelini (Middle Miocene-Pliocene) which are rare in Africa but are well-known from Eurasia and North America, and the Afrosmilini (Early-Middle Miocene) known from limited remains in Europe and Africa and generally represented by fragmentary fossils. This means that the origins of the more specialised forms, the Barbourofelini, are obscured by the absence of informative fossils of its possible ancestors. In this context, the discovery of a mandible of Afrosmilini in the Early Miocene of Grillental-6, Namibia, contributes, admittedly modestly, to the knowledge of the early barbourofelids.

The locality of Grillental-6 is located in the northern half of the Sperrgebiet east of Elisabethfeld. The fossiliferous sediments are green clays-silts which overlie Basement gneisses, and are overlain by 1-2 metre thick cross-bedded grits. The fauna from the deposits is

varied, ranging from rodents and macroselidids to suids, anthracotheres and ruminants. Morales *et al.* (2016) described amphicyonids from the site

and Morales & Pickford (2017) published the creodonts from the same deposits.

Institution Abbreviations

GSN - Geological Survey of Namibia, Windhoek

KNM - Kenya National Museum, Nairobi

MNHN - Muséum National d'Histoire Naturelle, Paris

NHMUK - Natural History Museum, United Kingdom, London

SNSB-BSPG - Bayerische Staatssammlung für Paläontologie und Historische Geologie, München

UM - Uganda Museum, Kampala

Systematic Palaeontology

Order Carnivora Bowdich 1821

Family Barbourfelidae Schultz, Schultz & Martin 1970

Subfamily Barbourfelinae Schultz, Schultz & Martin 1970

Tribe Afrosmilini Morales, Salesa, Pickford & Soria 2001

Genus and species *Ginsburgmilus napakensis* Morales, Salesa, Pickford & Soria 2001

Partial synonymy:

1987 *Afrosmilus turkanae* Schmidt-Kittler pars.

2008 *Afrosmilus africanus* (Andrews 1914); Morales *et al.*

2010 *Afrosmilus africanus* (Andrews 1914); Werdelin & Peigné.

Locality: Grillental-6, Sperrgebiet, Namibia.

Age: Early Miocene.

Material and measurements: GSN GT 1'17 fragment of right mandible (Fig. 1) (L= Length, W= Width, in mm) ; m/1 ca. L= 13, W=5.3, p/4 ca. L=10.4, W= 4.4, p/3 ca. 9.8, W= 4.1, p/2 ca. L= 4.9, W= 2.3, depth of mandible below m/1-p/4= 23.8 mm.

Description and comparisons

GSN GT 1'17 is a right mandible fragment lacking the ascending ramus and the symphysis (Fig. 1, 2). The body of the mandible is deep and robust. The masseteric fossa does not extend as far as the posterior end of the m/1. The dentition is poorly preserved, comprising a part of the buccal wall of the m/1, the roots of p/4 and p/3 and the buccal wall of the p/2, the latter tooth separated from the rest of the cheek teeth by diastemata in front and behind it. The p/2 is two-rooted and is reduced with a small notch in the posterior cristid which separated the main cusp

from the posterior one. The p/3 is quite a bit smaller than the p/4, which is, in its turn, smaller than the m/1. There is no sign of alveoli for an m/2.

The Grillental mandible is comparable in robustness to that of *Diamantofelis ferox* from the Early Miocene of Arrisdrift (Morales *et al.* 1998, 2003) but is clearly distinguished from it by the lesser shortening of the horizontal ramus and the presence of a p/2. In these features it approaches *Namafelis minor*, also defined at Arrisdrift (Morales *et al.* 1998, 2003) but this species

possesses a notably more gracile mandible, and its dentition (taking into account the damaged teeth in the Grillental specimen) would have been more robust. This association of characters : presence of p/2, deep and robust mandible, and gracile dentition, occurs in the holotype of *Afrosmilus africanus* (Andrews 1914), a species defined at the site of Karungu (Kenya) as *Pseudaelurus* (?) *africanus*, and which Schmidt-Kittler (1987) following Kretzoi (1929) reclassified as

Afrosmilus africanus, although in this specimen the p/2 is more reduced and is uniradicate (Fig. 2B). In the mandible of *Afrosmilus turkanae* from Rusinga (Schmidt-Kittler 1987) the depth of the mandible is not as great but it is taller than that of *Namafelis minor*, and as in the case of the holotype of *Afrosmilus africanus* it possesses a vertically oriented symphysis typical of “machairodontine felids”, but with lesser downward projection of the chin (Fig. 2C).

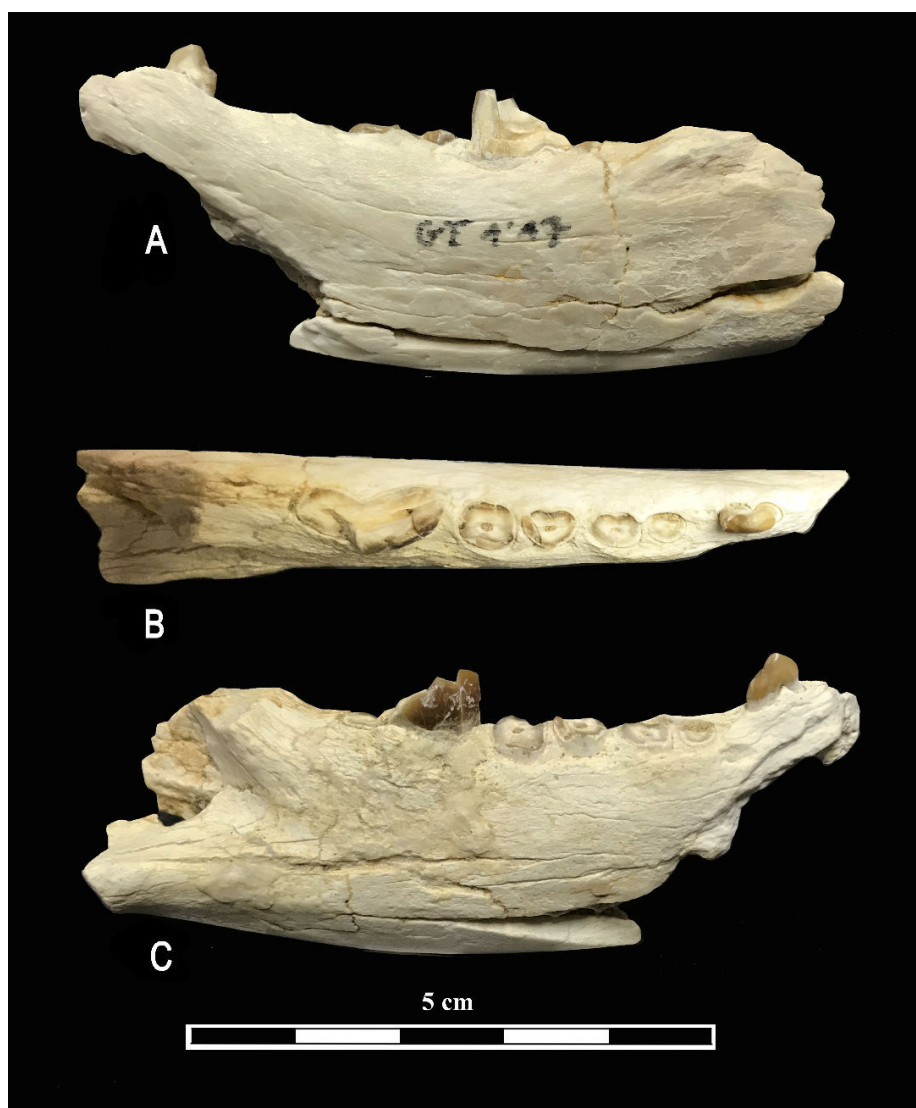


Figure 1. *Ginsburgsmilus napakensis* Morales *et al.* (2001) from Grillental, Namibia. (GSN GT 1'17) right mandible fragment. A) lingual view, B) occlusal view, C) buccal view (scale : 5 cm).

Afrosmilus africanus was described from the localities of Langental, Grillental and Fiskus

in the Sperrgebiet, Namibia. From Fiskus, dentognathic remains have been found : GSN FS 35'93,

fragment of mandible with p/2, fragment of p/3 and anterior part of p/4; GSN FS 30'01, associated fragments of right mandibular symphysis, right p/2, left p/3, right p/4 and anterior part of left p/4 (Morales *et al.* 2008). However, comparisons are quite limited, the p/2 showing similar morphology and dimensions to the Grillental specimen, and in both individuals

the p/2 is separated by a diastema from the p/3. The dimensions of the premolars, p/3 and p/4 and of the m/1, are also similar in the two specimens. The presence of an upright symphysis is well-documented at Fiskus, and there is no reason to think that the Grillental mandible would have been different (Fig. 2D, E).

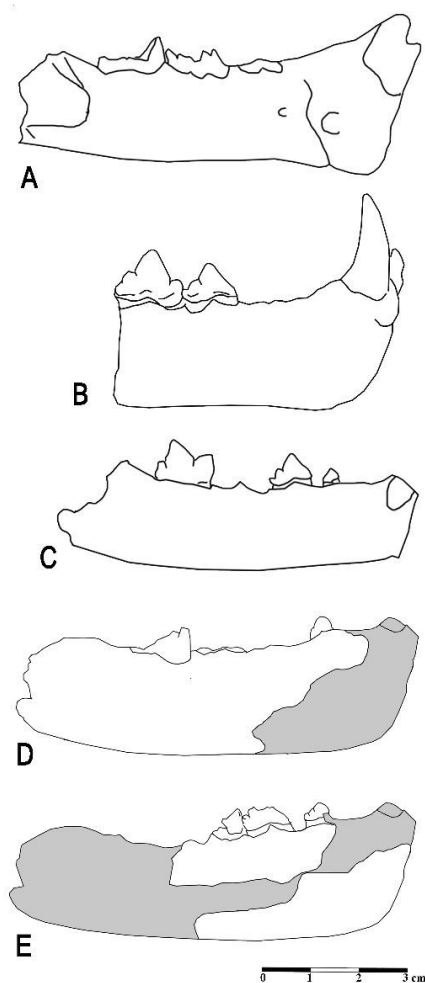


Figure 2. African Afrosmilini mandibles in lingual view. A) *Syrtosmilus syrtensis* Ginsburg 1978 (MNHN-2-1961) holotype right mandible from Gebel Zelten, Libya. B) *Afrosmilus africanus* Andrews (1914) (NHMUK M-10634) holotype left mandible from Karungu, Kenya. C) *Afrosmilus turkanae* Schmidt-Kittler 1987 (KNM MO-15292) holotype left mandible from Muruorot, Kenya. D) *Ginsburgsmilus napakensis* Morales, Salesa, Pickford & Soria 2001 (GSN GT 1'17) right mandible from Grillental, Namibia, the shaded areas are lost in the original. E) *Ginsburgsmilus napakensis* Morales, Salesa, Pickford & Soria 2001 (GSN FS 30'01) mandible from Fiskus, Namibia, figured by Morales *et al.* (2008), the shaded areas are lost in the original (scale : 3 cm).

The presence of Afrosmilini in this locality was already reported on the basis of post-

cranial bones belonging to a species which could correspond to *Afrosmilus africanus*. The new

mandible supports this attribution. However, the identification of these Afrosmilini from the Early Miocene of the Sperrgebiet as *Afrosmilus africanus* needs to be changed to *Ginsburgsmilus napakensis* Morales *et al.* (2001) as discussed below.

In the upper dentition of Afrosmilini from the Early Miocene (Fig. 3) there are two morphological patterns which are clearly distinct; one characterised by *Ginsburgsmilus napakensis* which is close to that observed in *Pseudaelurus quadridentatus* from the locality of Sansan, France (Ginsburg 1961; Peigné 2011) with a quite robust P4/, in which the parastyle is well-developed and the protocone is in an anterior position in front of the parastyle. This morphology indicates that it could be classified as belonging to a Felinae but the association with an upper canine of machairodontid type precludes such a relationship. The maxilla from the locality of Songhor, Kenya, KNM SO-670, identified by Schmidt-Kittler (1987) as *Afrosmilus turkanae*, is almost identical to the maxilla from Napak, Uganda, and was included in the same genus and species by Morales *et al.* (2001). A more derived hypercarnivorous pattern occurs in the maxilla from Rusinga, Kenya (NHMUK M-19076) identified by Savage (1965) as *Metailurus africanus*. The P4/ of this maxilla is clearly more elongated, with the protocone in a more posterior

position. As was the case in *Ginsburgsmilus*, the upper canines, even though they were not preserved, were, on the basis of the alveoli, hyperdeveloped. Likewise, the P3/s in this maxilla are more gracile, a consequence of lengthening of the crown accompanied by a narrowing of the basal postero-lingual cuspid. The correlation between the lower dentition of the holotype of *Afrosmilus africanus* and the maxilla from Rusinga is reasonably solid. A second species, *Afrosmilus turkanae*, was defined by Schmidt-Kittler (1987) at the site of Moruorot (Kenya) on the basis of a mandible which has smaller teeth, a more gracile mandibular ramus and a less developed symphysis than in the type species of the genus. In addition to the maxilla fragment from Songhor, Kenya, included in *G. napakensis* by Morales *et al.* (2001), a second maxilla with P4/ and the alveolus of the P3/ found at Rusinga (KNM RU-13984) were also attributed to *A. turkanae* by the German author. The difference in size between the two P4/s from Rusinga (NHMUK M-19076 and KNM RU-13984) is certainly too great for it to represent sexual dimorphism (difference greater than 30%). However, in the lower dentition from Moruorot, the p/3 is only 17% smaller than that of the holotype of *A. africanus*, which shows a more reduced p/2 with a single alveolus.

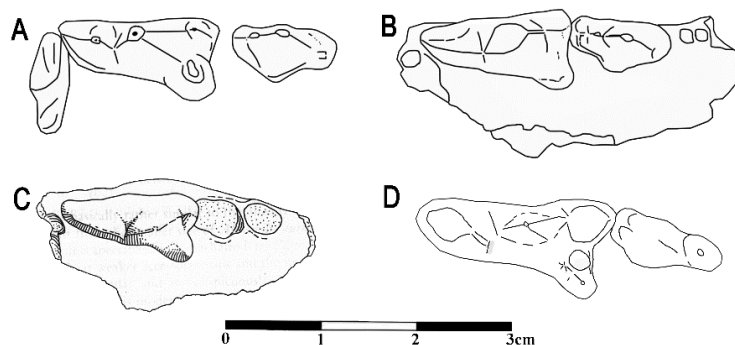


Figure 3. Upper dentition of African Afrosmilini. A) *Ginsburgsmilus napakensis* Morales, Salesa, Pickford & Soria 2001 (UM Nap IX 1966) holotype right maxilla from Napak, Uganda. B) *Ginsburgsmilus napakensis* Morales, Salesa, Pickford & Soria 2001 (KNM SO-5670) left maxilla with P4/-P3/ from Songhor, Kenya, figured as *Afrosmilus turkanae* by Schmidt-Kittler (1987) mirrored. C) *Afrosmilus turkanae* Schmidt-Kittler 1987 (KNM RU-15984) left maxilla with P4/ from Rusinga, Kenya, mirrored. D) *Afrosmilus africanus* Andrews (1914) (NHMUK M-19076) left maxilla with P4/-P3/ from Rusinga, Kenya, mirrored.

The presence of two closely related species at Rusinga is difficult to explain. Yet, considering the scarcity of material and the difficulty of correlating upper and lower dentitions, we opt to retain two species in the hope that new discoveries may clarify the situation. The known mandibles from the Sperrgebiet localities (Fiskus and Grillental) differ from the holotype of *Afrosmilus africanus* by the lesser reduction of the p/2, which is biradicate. The mandibular symphysis, known only from Fiskus, has a minor downward projection of the chin, whereas the horizontal ramus of the Grillental mandible is as deep and as robust as the material from Karungu. As such it seems reasonable to distinguish these jaws from those of *Afrosmilus africanus*. However, in the retention of p/2, which

is quite well-developed, and in the lesser projection of the chin it approaches *A. turkanae*, from which it differs by its greater dimensions and the robustness and depth of the horizontal ramus. With due caution, a correlation between these mandibles and the maxillae from Songhor and Napak attributed to *Ginsburgsmilus napakensis* seems to be a reasonable alternative for the Sperrgebiet fossils. It is noted that the small maxilla from Rusinga classified as *A. turkanae*, shows closer morphology to the other material from Rusinga attributed to *A. africanus*, than to those of *G. napakensis*.

Clearly, the age of the localities is an additional factor that needs to be taken into account with this proposal to change the nomenclature.

Biochronology and Biogeography of the Afrosmilini

The Afrosmilini in Africa, in addition to the species discussed above, includes *Syrto-smilus syrtensis* Ginsburg 1978, from the end of the Early Miocene of Gebel Zelten, Libya (Morales *et al.* 2001). This species is known only by the holotype, an edentulous mandible (Fig. 2A) which differs from *Afrosmilus africanus* by the loss of p/2 and the greater downward projection of the chin. It differs from *Sansanosmilus palmidens* by the greater lengthening of the mandible, the lesser downward projection of the chin and the less reduced p/3 (Ginsburg 1978). After Gebel Zelten there is a long gap in the African fossil record of Barbourfelidae spanning almost all the Middle Miocene. The group is known from the beginning of the Late Miocene in two localities : Bled Douarah, Beglia Formation, Tunisia, represented by a form identified by Kurten (1976) as *Vampyriactis vipera*, which could be close to *Albanosmilus jourdani*. The second form, identified as Machairodontinae gen. et sp. indet. by Tsujikawa (2005) is from the Namurungule Formation, Samburu Hills, Kenya. Werdelin & Peigné (2010) included the latter in the family as Barbourfelidae indet. In Western

Europe the fossil record of the Afrosmilini starts at the end of the Burdigalian, during MN4, with *Prosansanosmilus peregrinus* Heizmann *et al.* 1980 (Morlo 2006). The holotype of *Prosansanosmilus peregrinus* is an exquisitely preserved mandible from Langenau 1, Germany, which appears to be very close to *Sansanosmilus palmidens* Blainville 1843, from the locality of Sansan, France. It is somewhat smaller, and the dentition differs from it by the presence of a metaconid and a small talonid in the m/1 and by the lower cusps in the premolars (p/4 and p/3), which are however less reduced. The upper teeth are unknown from the type locality, but Heizmann & Ginsburg (1978) attributed a P4/ from Bézian, France, to this species (Fig. 5D), and subsequently Morlo (2006) included another P4/ from Petersbuch-2, Germany, in the species (Fig. 5C). Both of these P4/s differ notably from their homologues in *Sansanosmilus palmidens* from Sansan (Ginsburg 1961) by the reduction of the protocone, which almost disappears and the strong transverse compression of the tooth, which is converted into a continuous cutting blade (Fig. 5E).

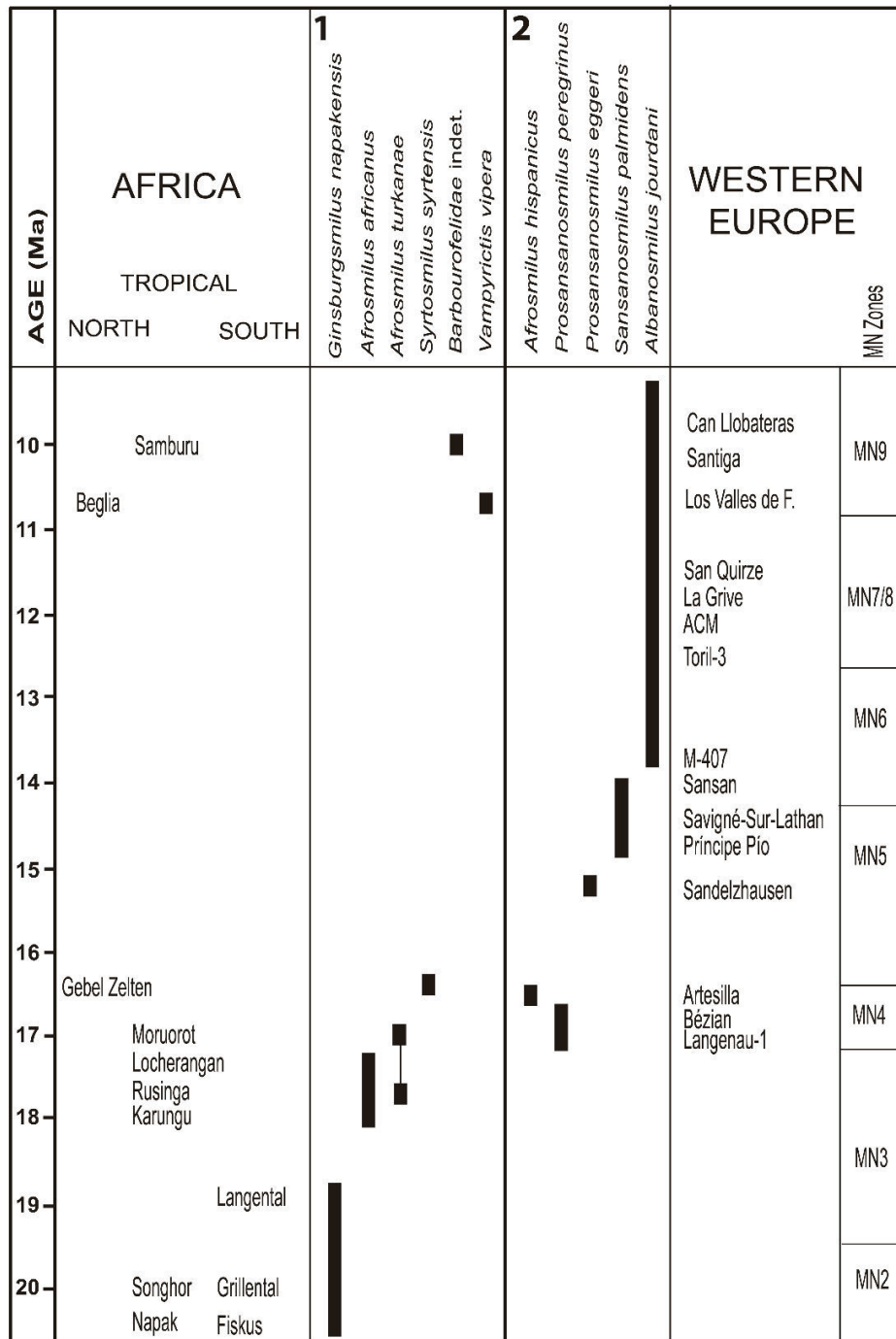


Figure 4. Biostratigraphy of African and Western European Miocene localities, with the temporal ranges of the diverse species of Barbourofelidae found therein. See Morlo (2006), Pickford (1986), Pickford & Senut (2003) Werdelin (2010) and Werdelin & Peigné (2010) for African localities; Azanza *et al.* (1993), Van Dam *et al.* (2006), Ginsburg (2001), Ginsburg *et al.* (1981), Hernández-Ballarín & Peláez-Campomanes (2017), Hilgen *et al.* (2012), Morales *et al.* (2001), Morlo (2006), Reichenbacher *et al.* (2013) and Robles *et al.* (2013) for European localities. Petersbuch-2, Germany with *Prosansanosmilus peregrinus* (Morlo 2006) and Buñol, Spain, with *Afrosmilus africanus* (Belinchón & Morales 1989; Morales *et al.* 2001) are not included in the figure, the two localities being correlated to zone MN4. 1, African species. 2, European species.

Also from MN4 there is *Afrosmilus hispanicus* Morales, Salesa, Pickford & Soria 2001, the holotype of the species being a maxilla fragment with the base of the canine, the partly broken P3/ and the P4/ found at Artesilla, Spain. The P4/ of *Afrosmilus hispanicus* (Fig. 5A) is close to that of *A. africanus* from Rusinga (Savage 1965) but differs from it by the presence of an ectostyle aligned with the parastyle. In this character it is close to the P4/s from Bézian and Petersbuch-2, although differing from them by their lower cusps and the anterior position of the protocone, which in *Prosansanosmilus* is displaced posteriorly, in a position homologous to the reduced protocone of *Sansanosmilus palmidens*. A third species of Afrosmilini *Prosansanosmilus eggeri* Morlo, Peigné & Nagel 2006, was defined in the MN5 locality of Sandelzhausen, Germany. The holotype of the species is a right mandible with the ascending ramus broken off, containing the canine and p/3-m/1 and without alveoli for the p/2 (SNSB-BSPG 1959 II 8051). It is smaller than *Prosansanosmilus peregrinus* (ca 20%), and its dentition is clearly plesiomorphic with respect

to the type species of the genus; in particular by the lesser reduction of the metaconid of the m/1 and the more vertical main cusp (protoconid) of the p/3 and p/4, slightly inclined backwards (Morlo *et al.* 2004). The morphology of the paratype maxilla (SNSB-BSPG 1959 II 8055) attributed to this species (Morlo *et al.* 2004) is characterised by the presence of large alveoli for the P2/, P3/-M1/ (Fig 5B) and is also clearly plesiomorphic with respect to the upper dentition attributed to *Prosansanosmilus peregrinus*. As such, it is close to the upper dentition attributed to *Pseudaelurus romieviensis* from the same site at Sandelzhausen (Nagel *et al.* 2009) or to those of *Pseudaelurus quadridentatus* from Sansan (Peigné 2011). Morlo (2006) resolved the contradiction of the presence of a primitive species with a more derived one by proposing several dispersals of barbourofelids from Africa; two during MN4 (*Afrosmilus* and *Prosansanosmilus*), and a third during MN5 with *Prosansanosmilus eggeri*, which, if it proves to be correct, would imply a change in the generic attribution of this species.

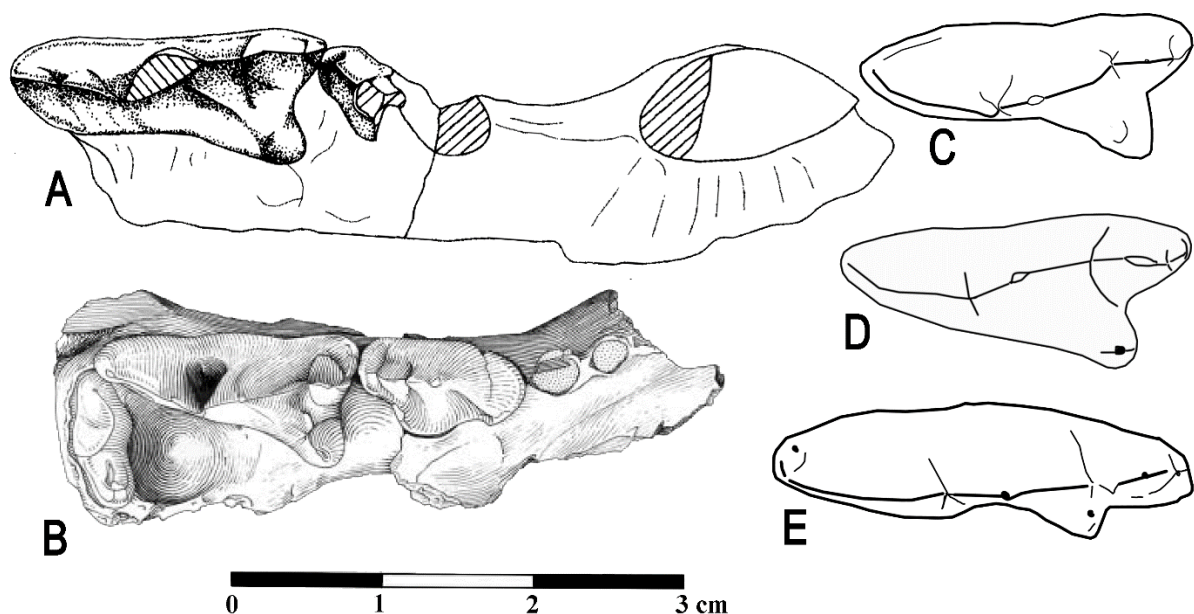


Figure 5. Upper dentitions of Western European Afrosmilini and Barbourofelini. A) *Afrosmilus hispanicus* Morales, Salesa, Pickford & Soria (2001) (MPZ-16506) holotype right maxilla with P4/-P3/ from Artesilla, Spain. B) *Prosansanosmilus eggeri* Morlo, Peigné & Nagel (2004) (SNSB-BSPG 1959 II 8055) paratype left maxilla with P2/ alveoli, P3/-M1/ from Sandelzhausen, Germany, mirrored. C) *Prosansanosmilus peregrinus* Heizmann, Ginsburg & Bulot (1980) (SNSB-BSPG 1976 XXII 3678) right P4/ from Petersbuch-2, Germany. D) *Prosansanosmilus peregrinus* Heizmann, Ginsburg & Bulot (1980) (MNHN Be 7212) left P4/ from Bézian, France, mirrored. E) *Sansanosmilus palmidens* Blainville (1843) (MNHN Sa 468) right P4/ from Sansan, France.

Conclusions

The Barbourofelidae appear in the fossil record for the first time in the Early Miocene of Africa, with species classified in the tribe Afrosmilini Morales *et al.* (2001). Although they are represented over large parts of the continent, their fossil record is nevertheless scarce, which renders it difficult to establish a clear systematic scenario. On the basis of the discovery of a new mandible from Grillental-6, Namibia, we revise the classification of the Barbourofelidae of the Sperrgebiet hitherto included in *Afrosmilus africanus* Andrews (1914) by Morales *et al.* (2008) as *Ginsburgsmilus napakensis* Morales

et al. (2001). The Afrosmilini appeared in Western Europe at the end of the Burdigalian (MN4) with forms which are clearly rooted in the African species of the genus *Afrosmilus*. In Western Europe the transition of the Afrosmilini to the Barbourofelini occurred during MN5 with *Sansanosmilus palmidens*, the record of the family was continuous until its disappearance during the Late Vallesian. In contrast, in Africa, there is a long hiatus spanning the entire Middle Miocene, with the Barbourofelini appearing only at the beginning of the Late Miocene.

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