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Presence of the peculiar carnivore *Sivanasua* in Carinthia

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ABSTRACT

A lophocyonid carnivore (Mammalia) is reported for the first time from Miocene (lower Badenian, ca. 16 My) deposits in Austria. A single, lower first molar from Schönweg-"Brüchl" (Lavanttal, Carinthia) is assigned to *Sivanasua viverroides*. The species is also recognised in Germany in few faunas of similar ages.

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Austria; Carnivora; Lophocyonidae; Badenian; Miocene

Introduction

Since their discovery in the early 20th century (Schlosser 1916), lophocyonid carnivores have been a curiosity of the lower and middle Miocene faunas of Europe because of their unusual lophodont dentition linked to a herbivorous diet (Schmidt-Kittler 1999). Their phylogenetic affinity was long debated, with attempts to relate them to the Procyonidae (Schlosser 1916), to the prosimian primates (Gingerich and Sahni 1984), to the Feliformia and closely related to the viverrids (Schmidt-Kittler 1983; Fejfar et al. 1987) or to the Creodonta (Ginsburg and Morales 1999). Today this group of carnivores is linked to the Feliformia under its own family (Schmidt-Kittler 1999; Morales et al. 2019). Four genera are known: the oldest, *Izmirictis* is monospecific and restricted to Anatolia (Morales et al. 2019). Similarly, *Euboictis aliverensis* is restricted to his type locality Aliveri in Greece (Fejfar and Schmidt-Kittler 1984). *Sivanasua* comprises three European species (*S. moravica, S. viverroides. S. antiqua*) that differ in size (Fejfar and Schmidt-Kittler 1984). This is also the case for *Lophocyon*, which is known from Slovakia and Greece (*L. paraskevaidisi, L. carpathicus*; Koufos et al. 1995).

Lophocyonidae remain rare in the fossil record and each new discovery provides crucial information on the evolution of this peculiar family. This is the case of the Miocene molar discovered in Carinthia (southern Austria; found in 2012) and presented in this work.

The locality Schönweg-"Brüchl"

Several Miocene sites are known close to Schönweg (Lavant valley, district Wolfsberg, Carinthia). However, their terrestrial vertebrate content is often limited to few finds (Mottl 1967; Wank 1977, 1991; Rabeder 1984, 1986). Discovered in 2008, the locality Schönweg-"Brüchl" was located about three kilometres southwest of St. Andrä in Lavanttal (14°48′01 "E/46°44′37 "N; Figure 1). The limnic deposits are there strongly influenced by debris flows.

Regarding the published fossils, the freshwater crab *Potamon* sp. has been reported by Klaus and Gross (2010). In addition, Böhme et al. (2012) mentioned the deer *Heteroprox larteti*. A very preliminary faunal list (including all animal groups) was proposed by Dojen and Schmidl (2014), and completed by the study of the small mammals (Prieto et al. 2016, 2019, 2021(in press)), as well as the carnivores (Prieto et al. submitted). These results are summarised in Figure 1 for the mammals.

Prieto et al. (2016) proposed a lower Badenian age (ca. 16 My) for the locality.

Systematic palaeontology

Order: Carnivora Bowdich, 1821
Suborder: Feliformia Kretzoi, 1945
Family:Lophocyonidae Fejfar et al. 1987
Genus: *Sivanasua* Pilgrim, 1932
Species: *Sivanasua viverroides* (Schlosser, 1916)
Fig. 2

Type species. *Aeluravus viverroides* (Schlosser, 1916)
Other species included in the genus. *Sivanasua antiqua* (Crusafont Pairó, 1959), *S. moravica* (Fejfar and Schmidt-Kittler, 1984)
Material and Measurements. Left first lower molar (m1; 10.3 × 6.15 mm; *Paläontologische Sammlung der Universität Tübingen* GPIT/MA/18610).
Description. The tooth belongs to a young individual. It shows traces of corrosion in the form of punctual and superficial lacks of enamel. The metaconid is broken almost at its base. According to Fejfar and Schmidt-Kittler (1997, p. 98), the first two lower molars are easily distinguished, noting that, in the m2, 'the anterior crest of the hypoconid does not reach the lingual border of the tooth but ends at the base of the posterior wall of the trigonid more or less in the long middle axis of the tooth'. This is not clear here, but the shape of the posterior part of the molar, with little backward projection and no hypoconulid, is rather reminiscent of an m1. The cusps of the trigonid form more or less an equilateral triangle. The cristids are not well individualised from the conids. The carnassial notch is only superficially developed. The lingual cristid of the protoconid is slightly directed backwards. The crista oblica ends on the (damaged) postero

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- Primates (Linnaeus, 1758)
  - Pliopithecidae (Zapfe, 1960)
    - *Pliopithecus* sp. *
- Eulipotyphla Waddell, OkaDa & Hasegawa, 1999
  - Erinaceidae Fischer, 1814
    - Erinaceinae gen. et sp. indet.
  - Talpidae Gray, 1825
    - *Desmanodon* cf. *antiquus* Ziegler, 1985
    - Talpidae gen. et sp. indet.
  - Soricidae Fischer, 1814
    - *Dinosorex* cf. *zapfei* Engesser, 1975
- Chiroptera Blumenbach, 1779
  - Megadermatidae Allen, 1864
    - *Megaderma* cf. *lugdunensis* (Depéret, 1892)
- Rodentia Bowdich, 1821
  - Cricetidae Fischer, 1817
    - *Eumyarion weinfurteri* (Schaub & Zapfe, 1953)-*bifidus* (Fahlbusch, 1964)
    - *Democricetodon mutilus* Fahlbusch, 1964
    - *Democricetodon gracilis* Fahlbusch, 1964
  - Gliridae Thomas, 1897
    - *Seorsumuscardinus* cf. *bolligeri* (Prieto & Böhme, 2007)
    - *Bransatoglis* aff. *cadeoti* Bulot, 1978
    - *Paraglirulus werenfelsi* Engesser, 1972
    - ?*Microdyromys koenigswaldi* De Bruijn, 1966
  - Eomyidae Depéret & Douxami, 1902
    - *Keramidomys* sp.
  - Platacanthomyidae Alston, 1876
    - *Neocometes* aff. *similis* Fahlbusch, 1966
  - Sciuridae Gray, 1821
    - *Palaeosciurus sutteri* Ziegler & Fahlbusch, 1986
    - ?*Spermophilinus besana* Cuenca, 1988
- Carnivora Bowdich, 1821
  - Viverridae Gray, 1821
    - *Forsythictis* cf. *aureliensis* (Schlosser, 1889)
  - Amphicyonidae Kretzoi, 1945
    - *Amphicyon* cf. *major* Blainville, 1841
  - Lophocyonidae Fejfar, Schmidt-Kittler and Zacharov, 1987
    - *Sivanasua viverroides* (Schlosser, 1916)
  - Hyanidae Gray, 1821
    - cf. *Protictitherium* sp.
  - Mustelidae Fischer von Waldheim, 1817
    - *Trocharion* aff. *albanense* Major, 1903
- Proboscidea Illiger, 1811
  - Gomphotheriidae Hay, 1922
    - *Gomphotherium* sp. *
- Perissodactyla Owen, 1848
  - Rhinocerotidae Gray, 1821
    - *Lartetotherium* sp. *
  - Equidae Gray, 1821
    - *Anchitherium* sp. *
- Artiodactyla Owen, 1848
  - Tragulidae Milne-Edwards, 1864
    - *Dorcatherium* sp. *
  - Cervidae Goldfuss, 1820
    - *Heteroprox larteti* (Filhol, 1890)
    - *Stephanocemas* sp. *
  - Suidae Gray, 1821
    - *Hyotherium* sp.*

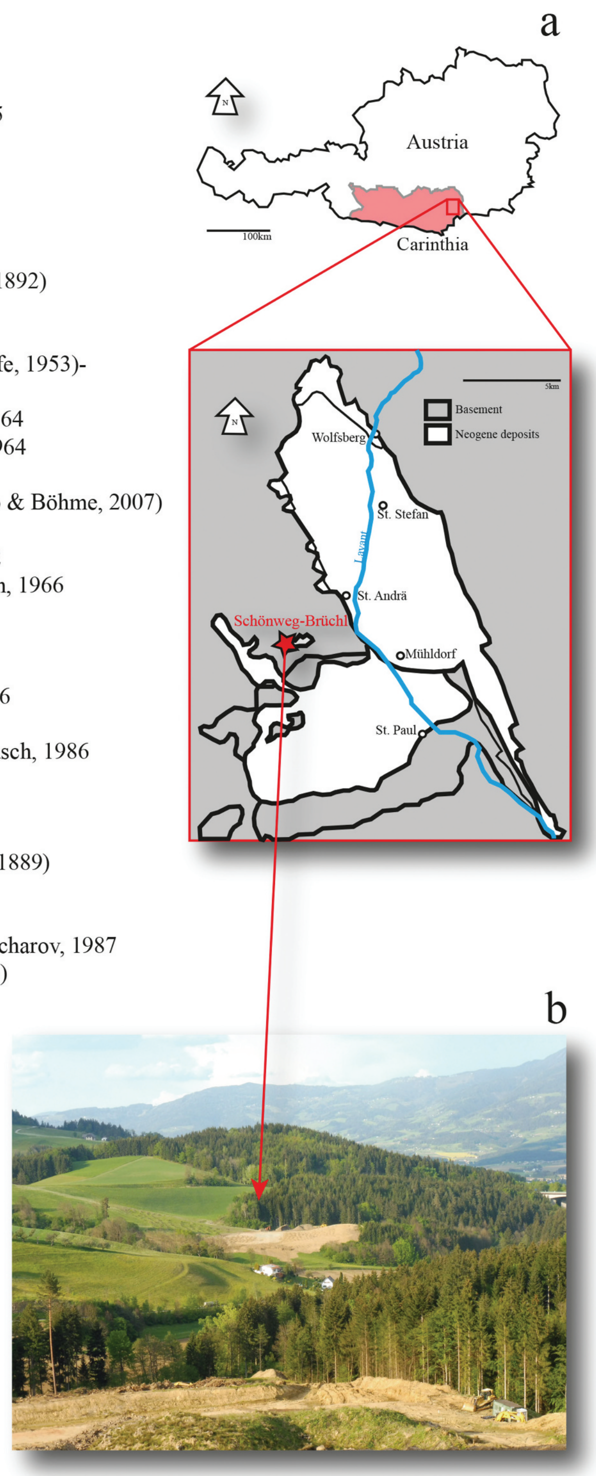

Figure 1. Faunal list of Schönweg-"Brüchl" mammals and geographical location of the Miocene locality. Faunal list according to (Prieto et al. 2016, 2019, 2021, submitted); : unpublished data. a) Map of the study area. Geological map according to Reischenbacher et al. (2007), simplified. b) View of the quarry during its re-cultivation.

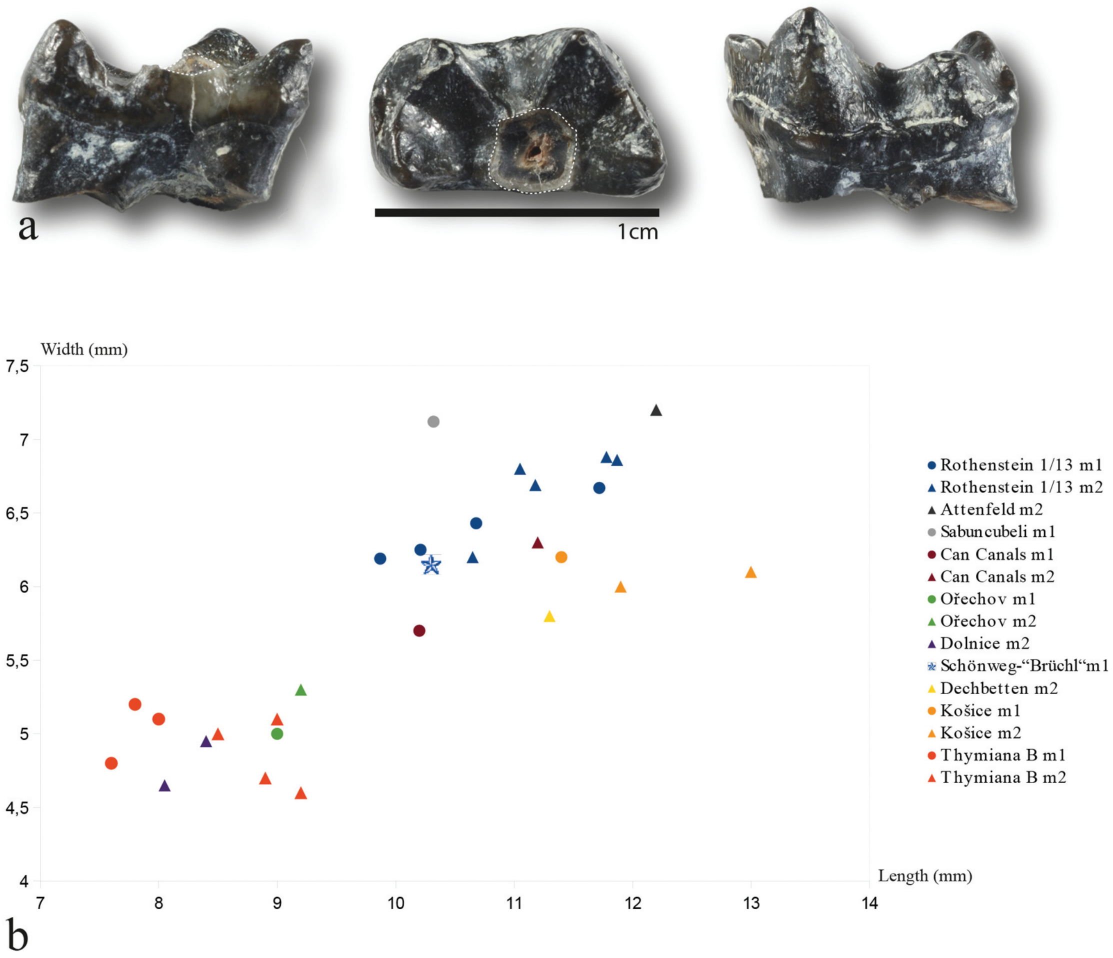

Figure 2. *Sivanasua viverroides* (Schlosser, 1916) from Schönweg-"Brüchl". a) Left m1. From left to right, lingual, occlusal and labial views. b) Size comparison of the first two lower molars of Lophocyonidae. *Sivanasua viverroides*: Attenfeld, Dechbetten, Rothenstein 1/13; *S. antiqua*: Can Canals; *S. moravica*: Ořechov, Dolnice; *Izmirictis cani*: Sabuncubeli; *Lophocyon paraskevaidisi*: Thymiana B; *Lophocyon carpathicus*: Košice-Bankov. See the text for the references.

labial wall of the metaconid. Lingually, there is no cristid developed on the posterior wall of the metaconid, and the anterior cristid of the entoconid ends abruptly. Thus the talonid remains open but a weak cingulid outlines this region. A cingulid continually surrounds the tooth from the anterior basis of the protoconid to the labial-posterior basis of the entoconid. The posterior part of the cingulid is thickened.

Remarks.The size comparison of the first two lower molars of several Lophocyonidae species is presented in Figure 2. Compared to the *Lophocyon* species, the Austrian m1 is more brachyodont. It is also significantly larger than *L. paraskevaidisi*. The m1 of *Izmirictis cani* from Sabuncubeli (Morales et al. 2019: Figure 2 V–X) has a clear hypoconulid and no posterior cingulid. In addition, entoconid and metaconid are stronger in Schönweg-"Brüchl". Finally, the trigonid forms a larger angle in the Turkish species. There are no known m1 or m2 of *Euboictis aliverensis*. The Schönweg-"Brüchl" tooth is larger than *Sivanasua moravica* and morphometrically corresponds to *S. viverroides*. The Spanish form *S. antiqua*, originally described as a subspecies of *S. viverroides* by Crusafont Pairó (1959; *Schlossericyon viverroides antiquus*), differs only in minor details of size and morphology of the p4 (Ginsburg and Morales 1999). The Iberian lower molars are slightly narrower. In conclusion, the Carinthian tooth is most consistent with *S. viverroides*.

Discussion

Fejfar and Schmidt-Kittler (1984) proposed two hypotheses in which the extra-European origin of forms belonging to the *Sivanasua-Euboictis* Group is clear. The first proposal implies a general dispersal wave at the end of the lower Miocene (MN 4) where the species arrived more or less simultaneously, like the small mammals of that time (Mein 1999). The second hypothesis assumes the arrival of a single ancestral form (unknown in the 1980's), which then evolved rapidly to give the species of the European fossil record. They note the absence of this hypothetical ancestor in the older deposits (MN3) and thus consider this hypothesis unlikely.

But, recently, Morales et al. (2019) described *Izmirictis* in the Turkish Sabuncubeli deposits (MN 3, de et al. 2006; Bilgin et al. 2019; older than 17.7 My, Uzel et al. 2020; possibly 19 My in Figure 3). This genus retains primitive traits compared to other Lophocyonidae. Fejfar and Schmidt-Kittler's second hypothesis then seems more likely.

Euboictis is considered by Fejfar and Schmidt-Kittler (1997, p. 106) to be an ancestor of *Lophocyon*, and resembles *Sivanasua* by parallel evolution. The age of Aliveri, the Greek type locality of *Euboictis*, has often been discussed because the fauna resembles the Anatolian MN 3 faunas, but also includes typically European

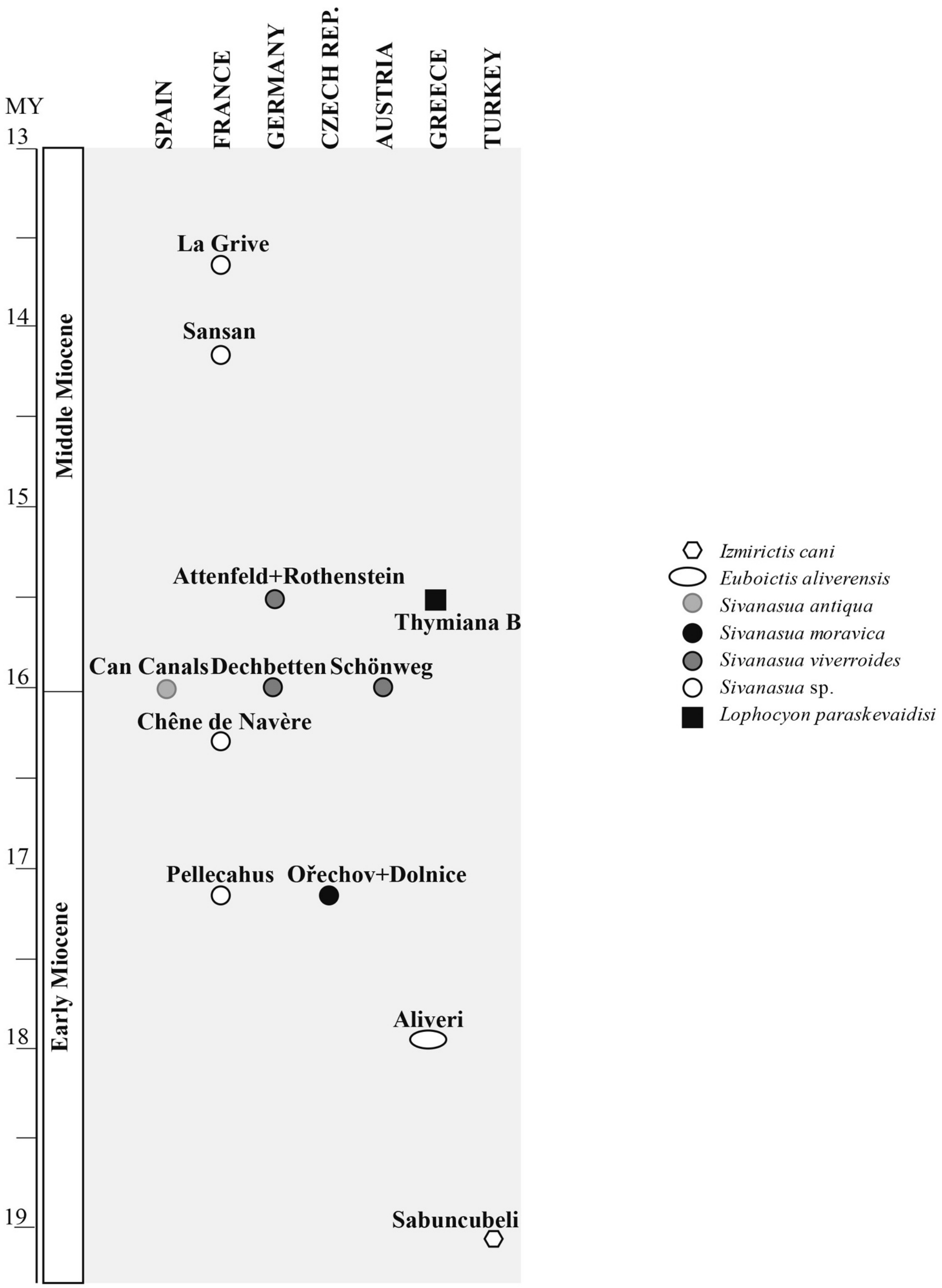

Figure 3. Geographic and stratigraphic distribution of lophocyonid carnivores. *Lophocyon carpathicus* (Fejfar, Schmidt-Kittler and Zacharov, 1987) has been excluded because the locality Košice-Bankov cannot be dated. Note that the species from Pellecahus, Chêne de Navère and La Grive are assigned herein to *Sivanasua* sp.

elements. Recently, Hoek Ostende et al. (2015) came to the conclusion that the fauna is correlated to the MN 4 but remains older than the European faunas of this 'biozone' (approximation to 18 My).

The Greek *Lophocyon* is younger: *L. paraskevaidisi* from Thymiana B (Island of Chios) is close to 15.5 My in age (MN 5, Koufos 2006; Kondopoulou et al. 2011).

The Spanish (Can Canals) species *Sivanasua antiqua* is seen as a biogeographically separated species from *S. viverroides* by Fejfar and Schmidt-Kittler (1997), with *S. moravica* being their common ancestor (Ginsburg and Morales 1999). The Can Canals type locality has not yielded micromammals, but the stratigraphic position of the site and new studies of nearby localities indicate that an age near 16 My is plausible (Alba et al. 2018; Jovells-Vaqué and Casanovas-Vilar 2021, Casanovas-Vilar pers. comm.).

The faunas of central and partially western Europe (except Austria) can be biostratigraphically dated using a well-known lineage of the cricetid rodent *Megacricetodon* ('*M. bavaricus*' group; e.g., Kälin and Kempf 2009; Oliver Pérez and Peláez-Campomanes 2014; Prieto and Rummel 2016). Thus, Ořechov and Dolnice contain, beside *Sivanasua moravica*, a very small (primitive) chronospecies of this lineage (Fejfar 1974; Abdul Aziz et al. 2010) and is of an age close to 17.2 My (Reichenbacher et al. 2013).

A similar dating is proposed for the French locality Pellecahus which contains the rodent association *Megacricetodon* aff. *bezia-*

nensis/*Ligerimys florancei*/*Melissiodon* sp. (Ginsburg and Bulot 2000). In this locality, *Sivanasua* cf. *viverroides* is documented only by one calcaneus, which makes determination challenging (Ginsburg and Morales 1999; *Sivanasua* sp. in Figure 3).

Similarly, it is not possible to determine precisely the astragalus of Sansan (ca 14.5–14 My), the only fossil of Lophocyonidae from this French locality although very rich in fossil material.

Sivanuasa is also documented in the La Grive karst infilling (age roughly estimated at ca. 13.8 My) by a single tooth. Originally described as the fourth upper premolar (P4) of *S. viverroides* by Viret (1951), this fossil is seen as *S. moravica* M2 by Ginsburg and Morales (1999). The French specimen resembles the P4s figured by Fejfar and Schmidt-Kittler (1997). A similar remark is made for the two teeth from Chêne de Navère (France). While Ginsburg and Morales (1999) see them as M1-M2 from the same individual, these two are also resembling premolars (Morales et al. 2019, p. 2). Hence, these teeth are considered herein as *Sivanasua* sp. The fauna Chêne de Navère has no *Ligerimys* and yields *Megacricetodon bezianensis* (Bulot 1981). Therefore, this locality is just a little older than Schönweg-"Brüchl".

Rothenstein 1/13 delivered, next to *Sivanuasa viverroides.* a more evolved species of *Megacricetodon*, but also the Eomyidae rodent *Keramidomys* (Fejfar and Schmidt-Kittler 1997). The age of the karstic deposit can be approximated at 15.5 My (Prieto and Rummel 2016).

The Attenfeld karstic fauna is more delicate to date and many correlations have been proposed in the literature (e.g., MN 4 in Morales et al. 2019; MN 5? in Schmidt-Kittler 1999, MN 6 in Göhlich 2002, unknown in, 2017). It can be assumed that the fauna precedes the appearance of *Cricetodon* s. str. in Germany. Indeed, the tribe of cricetodontini, which includes large species, is present in large numbers in the karst infillings and should be represented at Attenfeld. The fauna is reminiscent of that of Rothenstein 1/13 (Rummel 1993) and we cautiously propose a close age for Attenfeld.

Similarly, Dechbetten is difficult to date with precision and is best known for its avifauna, although a mammalian fauna has been discovered there (Dehm 1949). We follow Mayr et al. (2020) who propose an age of about 16 Ma for this locality.

Finally, *Lophocyon carpathicus* is the only known taxon from the Košice-Bankov locality (Slovakia), if we omit some fragments of a mastodon tusk (Fejfar et al. 1987). The age of the locality is therefore uncertain, probably Sarmatian (see also Sabol et al. 2021), and may thus documents the youngest occurrence of a Lophocyonidae.

Conclusions

Although the fossil record of lophocyonid carnivores remains fragmentary, the presence of *Sivanasua viverroides* at Schönweg-"Brüchl" is consistent with the current knowledge of the stratigraphic distribution of the species. The species is recognised in faunas of close age in Germany at around 16 My. At this time a certain diversification of the Lophocyonidae is observed as two other species (*S. moravica* and *Lophocyon paraskevaidisi)* are recognised in Eurasia but they remain geographically separated.

This is the first time that a Lophocyonidae has been documented in Austria, which emphasises the importance of the Schönweg-"Brüchl" locality in understanding the evolution of the central European Miocene faunas.

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