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Cover illustration: Cover illustration: The floating plant *Cobbania corrugata* (Lesquereux) Stockey et al. from the Upper Cretaceous of North America inspected by an *Ornithomimus* dinosaur. The quarry in the Dinosaur Provincial Park, Alberta (Canada), produced numerous complete specimens of this plant and the most complete skeleton of the dinosaur (Reconstruction by Marjorie Legin). For details, see Bogner, J.: The free-floating Aroids (Araceae) – living and fossil, pp. 113–128 in this issue.

Umschlagbild: Umschlagbild: Ein *Ornithomimus* Dinosaurier betrachtet die Schwimmpflanze *Cobbania corrugata* (Lesquereux) Stockey et al. aus der Oberkreide Nordamerikas. Im Steinbruch des Dinosaur Provincial Park, Alberta (Kanada), wurden mehrere komplette Exemplare dieser Pflanze und ein nahezu vollständiges Skelett des Dinosauriers gefunden (Rekonstruktion Marjorie Legin). Für weitere Informationen siehe Bogner, J.: The free-floating Aroids (Araceae) – living and fossil, S. 113–128 in diesem Heft.

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This paper is dedicated to the memory of the late Prof. Dr. Volker Fahlbusch

Small and medium-sized Cricetidae (Mammalia, Rodentia) from the Middle Miocene fissure filling Petersbuch 68 (southern Germany)

By
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Abstract

The small and medium-sized Cricetidae (Rodentia, Mammalia) from the fissure filling Petersbuch 68 (Frankonian Alb, southern Germany) are described. The fissure infill is biostratigraphically heterogeneous and probably reflects the result of two successive deposits. The older sample comes from in the middle part of the fissure and contains species characteristic of MN 5. At the top of the fissure, the cricetids represent taxonomically new species for South Germany, which correspond stratigraphically to the late MN 6 or MN 7 faunas of the Swiss sections of the North Alpine Foreland Basin.

Key words: Cricetidae, Mammalia, fissure filling, biostratigraphy, Middle Miocene, North Alpine Foreland Basin

Zusammenfassung

Die kleinen bis mittelgroßen Cricetidae (Rodentia, Mammalia) aus der Spaltenfüllung Petersbuch 68 werden detailliert beschrieben. Die Sedimente der Spalte sind biostratigraphisch heterogen und wurden wahrscheinlich durch zwei sukzessive Füllungen akkumuliert. Eine ältere Fauna ist in dem mittleren Teil der Spalte nachweisbar und entspricht MN 5. Der obere Teil der Spalte enthält eine Hamster-Fauna, welche taxonomisch erstmals in Deutschland dokumentiert ist und den späten MN 6 bis MN 7 Faunen aus der Schweizer Ablagerung des nordalpinen Vorderlandbeckens entspricht.

Schlüsselwörter: Cricetidae, Mammalia, Spaltenfüllung, biostratigraphie, Mittel-Miozän, Nordalpines Vorlandbecken

1. Introduction

The German part of the North Alpine Foreland Basin (NAFB) is delimited to the North-North/West by the kartsified Jura deposits of the Franconian and Swabian alb plateau. These karts may contain rich and well preserved fossil vertebrate faunas, which have been the focus of intensive paleontological studies since the beginning of the last century (see references in Rummel 1993). The karts system of the White Jura- δ of Petersbuch near Eichstätt (Fig. 1) has yielded more than 100 fossil faunas that range in age from the Oligocene to Pleistocene. For an overview, refer to Bolliger & Rummel (1994), (Daxner-Höck 1999: 339), Klembara et al. (manuscript submitted), Prieto (2007), Prieto & Rummel (2009a, b), Rummel (1995, 1997), and Ziegler (2003a, 2003b, 2003c, 2005).

The material analyzed in this study was collected from the top of the fissure Petersbuch 68. In order to test the homogeneity of the infilling, a second sample was collected from a deposit lying around two meters deeper (Fig. 2). This paper presents the Cricetidae from these samples and discusses the biostratigraphical implications.

2. Methods

The material from Petersbuch 68 is stored in the Naturmuseum Augsburg (NMA, upper part of the fissure filling) under accession number 2007-x/2017), and in the Bavarian State Collection for Palaeontology and Geology in Munich (BSPG, middle part of the fissure) under accession number 2008 V. Additional specimens (indicated by CRW) used for comparison are from the private collection of Michael Rum-

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MEL (Weissenburg). Measurements are given in mm, and the terminology used in the description of the molars follows FREUDENTHAL et al. (1994). All teeth illustrated are show in left orientation.

3. Systematic paleontology

Order: Rodentia BOWDICH, 1821
Family: Cricetidae ROCHEBRUNE, 1883
Subfamily: Copemyinae JACOBS & LINDSAY, 1984

Genus: *Democricetodon* FAHLBUSCH, 1964

Diagnosis: see FAHLBUSCH (1964).

Type species: *Democricetodon crassus* FREUDENTHAL, 1969 [= *D. minor* (LARTET, 1851) sensu FAHLBUSCH 1964]

Other species included: *Democricetodon affinis* (SCHAUB, 1925), *D. brevis* (SCHAUB, 1925), *D. gaillardi* (SCHAUB, 1925), *D. vidobonensis* (SCHAUB & ZAPFE, 1953), *D. romieuensis* (FREUDENTHAL, 1963), *D. hispanicus* FREUDENTHAL, 1964, *D. sulcacus* FREUDENTHAL, 1964, *D. mutilus* FAHLBUSCH, 1964, *D. freisingensis* FAHLBUSCH, 1964 (considered to represent junior synonym of *D. gaillardi* by THEOCHAROPOULOS in DE BRUIJN et al. 2003: 60), *D. gracilis* FAHLBUSCH, 1964, *D. franconicus* FAHLBUSCH, 1966, *D. cretesis* BRUIJN & MEULEKAMP, 1972, *D. nemoralis* AGUSTÍ, 1981, *D. kohatensis* WESSELS et al., 1982, *D. haznosensis* KORDOS, 1986, *D. iazygum* RADULESCU & SAMSON, 1988, *D. zarandicus* RADULESCU & SAMSON, 1988, *D. walkeri* TONG & JAEGER, 1993, *D. lindsayi* QIU, 1996, *D. tongi* QIU, 1996, *D. hanniae* AGUILAR et al., 1999, *D. sudrei* AGUILAR et al., 1999, *D. doukasi* THEOCHAROPOULOS, 2000, *D. anatolicus* THEOCHAROPOULOS, 2000, *D. fourensis* MARIDET et al., 2000, *D. moralesi* VAN DER MEULEN et al., 2003.

Note: The taxonomy of the genus *Democricetodon* remains controversial. VAN DER MEULEN et al. (2003) synonymized the genera *Fahlbuschia* MEIN & FREUDENTHAL, 1971 *Pseudofahlbuschia* FREUDENTHAL & DAAMS, 1988 and *Renzimys* LACOMBA, 1983 with *Democricetodon*, as well as several species included in these genera. However, FREUDENTHAL (2005) rejected this proposal. As the main focus of this paper is not to provide a revision of the *Democriceton*-like species, and since the *Democricetodon* species from the samples from Petersbuch 68 correspond to the definition of FREUDENTHAL (2005), we limit the list of species included in *Democricetodon* to FREUDENTHAL's synopsis. The concept of sub-species is not followed.

The North American genus *Copemys* WOOD, 1936 and the Asian *Spanocricetodon* LI, 1977 share morphological features with *Democricetodon* (FAHLBUSCH 1967, ENGESSER 1979, Freudenthal 2005), but not discussed. A comparison with *Collimys* DAXNER-HOECK, 1972 is provided in PRIETO & RUMMEL (2009a and c).

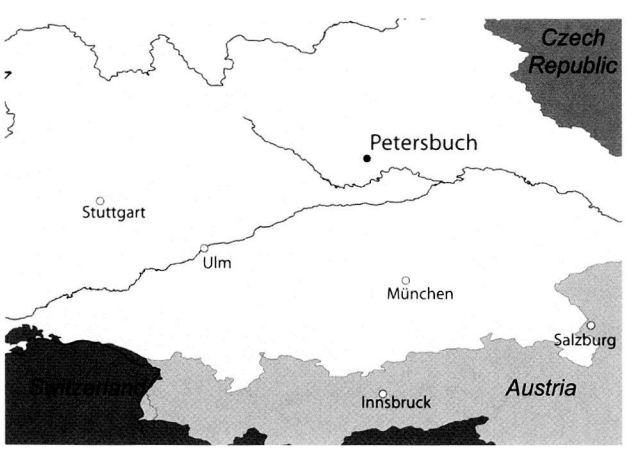

Figure 1: Geographic position of the studied locality

Species: *Democricetodon gracilis* FAHLBUSCH, 1964
Figures 3A, B

? 1993 *Democricetodon brevis*. – KÄLIN: fig. 75b,d.

Diagnosis: see FAHLBUSCH (1964)

Type locality: Sandelzhausen

Age: Middle Miocene (MN 5)

Provenance: Middle and upper parts of the fissure filling

Material and measurements: (Fig. 4) Upper part: 3 m1, 2 m2 (NMA 2007-1 to 5/2017): m1: 1.46 x 1.00; 1.38 x 1.00, 1.34 x 0.98; m2: 1.19 x 0.98, 1.26 x 0.98. Middle part: 1 m1, 1 fragmentary upper jaw with M2-M3 (BSPG 2008 V 3, 4): m1: 1.34 x 0.94; M2: 1.13 x 1.10; M3: 1.10 x 0.93.

Description and discussion: The molars correspond well to *D. gracilis*. The m1 are characterized by a short mesolophid, a posterior part of the teeth somewhat enlarged and a forwards directed, almost closed, protosinusid. The m1 from the upper part of the fissure are isolated from *D.* aff. *crassus* by both morphologie and metric criteria (see below).

Species: *Democricetodon* aff. *crassus* FREUDENTHAL, 1969
Figures 3D–F, K, L

Diagnosis: see FAHLBUSCH (1964)

Type locality: Sansan

Age: Middle Miocene (MN 6)

Provenance: Upper part of the fissure filling

Material and measurements: (Fig. 4; Tab. 1) 7 m1, 13 m2, 2 m3, 9 M1, 3 M2 (NMA 2007-6 to 37, 163 and 164/2017)

Description: m1: the anterior part of the molars rounded and anteroconid diamond-shaped; the labial anterolophid is present and the lingual anterolophid is strongly reduced or lacking; the mesolophid, although very low, reaches the border of the teeth or ends in the cingulum closing the mesosinusid.

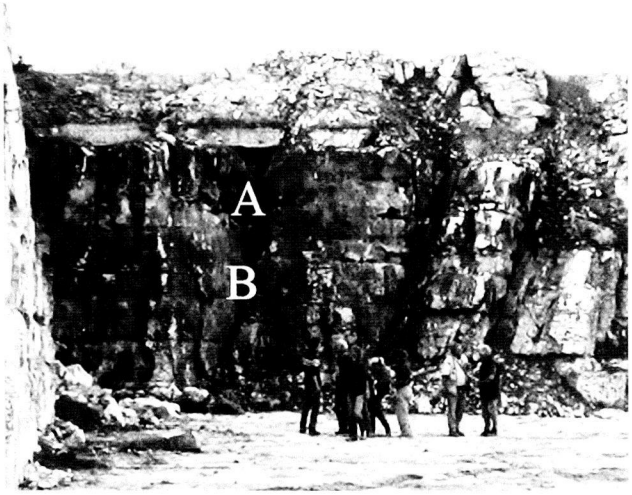

Figure 2: Fissure filling Petersbuch 68. **A**: Upper part of the fissure, Collection NMA; **B:** middle part, Collection BSPG

m2: The massive labial anterolophid closes the anterosinusid; the lingual anterolophid is highly reduced; the mesolophid may reach the border of the m2 or the cingulum closing the mesosinusid (3 out of 13 molars); in most specimens, it is medium-sized; in one molar it is short; the posterolophid may be labially extended (2 m2).

m3: The lingual anterolophid is missing; the labial anterolophid closes the protosinusid but is very low; the entoconid is integrated into a crest connecting the metaconid with the posterolophid, and may extend onto the posterior part of the tooth (Fig. 3F); the mesolophid reaches the border of the molars; a second small crest (second mesolophid?) is developed somewhat parallel to the mesolophid close to the metaconid.

M1: The lingual anteroloph closes the anterosinus; the anterocone is integrated in this crest; the labial anteroloph is missing but a low cingulum closes the sinus; the straight anterolophule connects both anterocone and lingual anteroloph on their junction point; in three of the molars (out of 9) the anterior protolophule ends on the base of the paracone; in one tooth this crest is enlarged and terminates in the anterosinus; the mesoloph is typically medium-sized (in 7 out of 9 molars), or longer, but never reaches the tooth border; the metalophule is directed backwards; posterolophule and metalophule are delimited by a small posterosinus.

M2: The labial anteroloph closes the anterosinus; the lingual anteroloph is variable in shape but always low; the two protolophules are present; the mesoloph is medium-sized (in 2 out of 3 teeth) or long; a double metalophule occurs on two molars, whereas the posterior metalophule is missing on the third.

Discussion: Compared to the teeth of *D. gracilis*, the molars of this *Democricetodon* Sample from Petersbuch 68 have a denser general morphology, low mesolophid reaching the tooth border, and a rounder outline of the anterior teeth; moreover, they tend to be larger.

With regard to outline, general form and arrangement of the various structural elements, the molars from Petersbuch 68 closely correspond to the small *Democricetodon* from Sansan. This species, which has a long and complex taxonomical history (see synonymy in Baudelot 1972, Maridet 2003), was first described by Fahlbusch (1964) as *D. minor* and regarded as the type species of the genus. Baudelot (1972) named the same population *D. crassus*, awaiting the decision by the International Commission for Zoological Nomenclature relative to the synonymy of this species with *D. minor* (Freudenthal & Fahlbusch 1969). Nevertheless, these authors agree in that the species from Sansan is similar to *D. gracilis* (differential diagnosis in Fahlbusch 1964: 98 and Baudelot 1972: 274). More recently, Maridet (2003) reexamined the teeth from Sansan and concluded that the species is related to *D. gracilis*.

Based on the material from Petersbuch 68, the m1 of *D. gracilis* can easily be discriminated from the other small *Democricetodon* teeth. The morphological differences observed by Fahlbusch (1964) are relevant. Thus, we refer the species to *D. crassus*. The main differences are with regard to the slightly larger size and, most important, the length of the mesolophid, which is more often complete in Petersbuch 68. Long mesolophids are also found in forms related to *D. brevis*, but the species from Petersbuch 68 does not possess ectomesolophids. Moreover, the spur on the anterolophule of the M1 is missing. In addition, Prieto (2007) described specimens of *D.* cf. *brevis* from Petersbuch 6 and 18, which usually lack these structures. However, the general outline of the molars and distinctly more backward-directed mesosinusid of the m1 do not correspond with the species from Petersbuch 68. Based on these observations, we decided to assign these specimens to *D.* aff. *crassus*.

Species: *Democricetodon mutilus* Fahlbusch, 1964
Figures 3G–I, M–O

Diagnosis: see Fahlbusch (1964)

Type locality: Langenmoosen

Age: Middle Miocene (MN 5)

Provenance: Middle and upper part of the fissure filling

Material and measurements: (Fig. 4; Tab. 2) Upper part: 7 m1, 4 m2, 1 m3, 3 M1, 3 M2 (NMA 2007-38 to 50, 100 to 103 and 162/2017). Middle part: 3 m1, 3 m2, 1 m3, 4 M1, 3 M2, 1 M3 (BSPG 2008 V 5–19): m1: 1.60 x 1.03; 1.63 x 1.09, 1.68 x 1.09; m2: 1.54 x 1.25, 1.53 x 1.28; m3: 1.31 x 1.09; M1: 1.98 x 1.43, 1.93 x 1.29, 2.06 x 1.43, 1.99 x 1.21; M2: 1.55 x 1.39, 1.35 x 1.26; M3: 1.11 x 1.18.

Description (upper part of fissure filling): m1: The anterior part of the molars is rounded but the small anteroconid comes off on occlusal view; the labial anterolophid is present, the short lingual anterolophid may almost close the protosinusid; the mesolophid is short to medium-sized, runs parallel to the posterior wall of the metaconid, and it is slightly bent in forward direction.

m2: The massive labial anterolophid closes the anterosinusid; the lingual anterolophid is strongly reduced; the mesolophid is short to medium-sized.

m3: The lingual anterolophid is extremely reduced; the labial anterolophid closes the protosinusid but is very low; the entoconid is integrated in a crest connecting the meta-

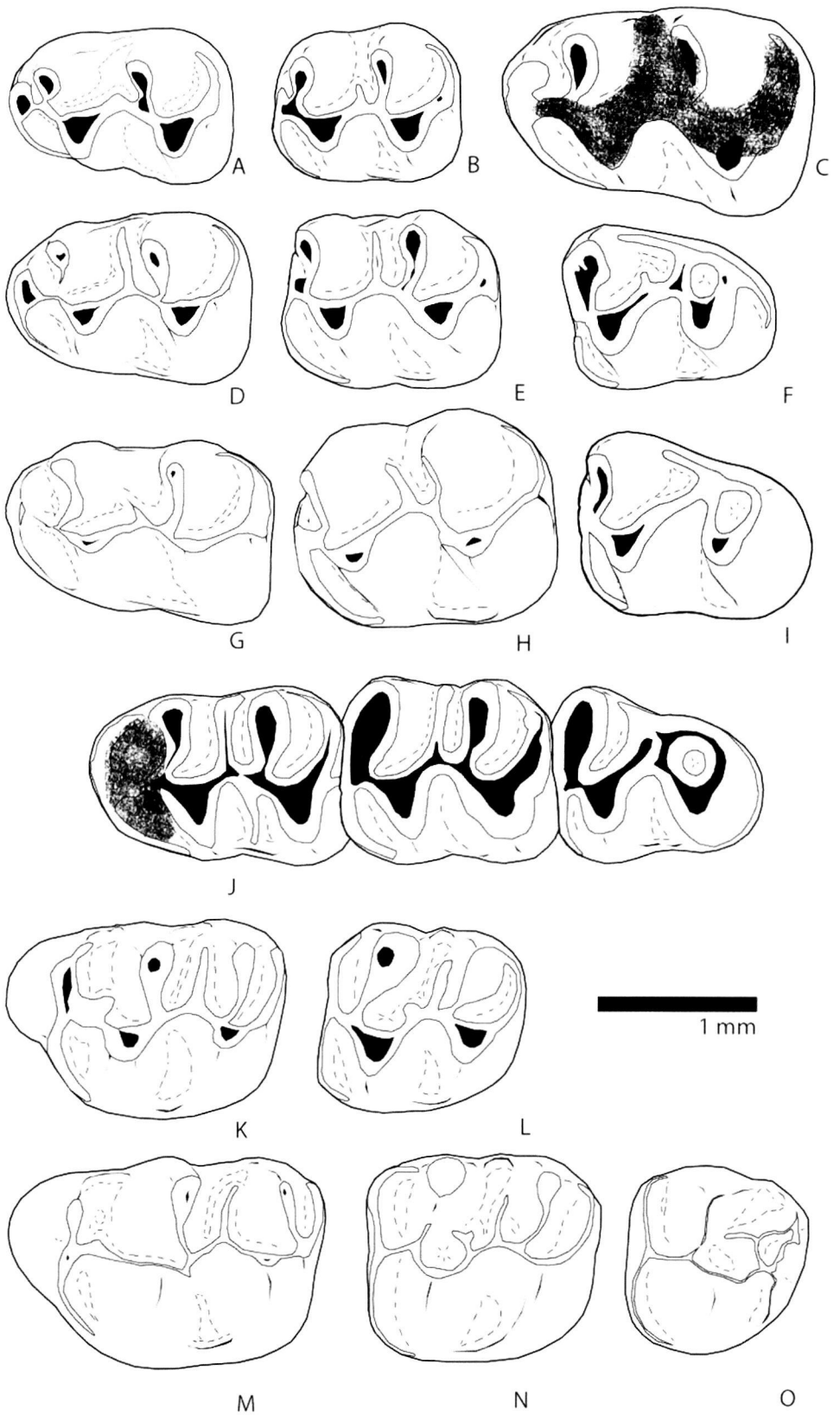

Figure 3: *Democricetodon* Fahlbusch, 1964 from Petersbuch 68. **A, B**: *D. gracilis* Fahlbusch, 1964: A: left m1 (NMA 2007-5/2017), B: right m2 (revers., NMA 2007-2/2017); **C**: *D.* sp., left m1 (BSPG 2008 V 20); **D–F, K, L**:. *D.* aff. *crassus* Freudenthal, 1969: D: left m1 (NMA 2007-19/2017), E: left m2 (NMA 2007-26/2017), F: right m3 (revers., NMA 2007-16/2017), K: left M1 (NMA 2007-6/2017), L: left M2 (NMA 2007-164/2017); **G–I, M–O**: *D. mutilus* Fahlbusch, 1964: G: right m1 (revers., NMA 2007-102/2017), H: right m2 (revers. NMA 2007-39/2017), I: left m3 (NMA 2007-162/2017), M: right M1 (invers., NMA 2007-42/2017), N: left M2 (NMA 2007-45/2017): O: right M3 (invers., BSPG 2008 V 19); **J**: *D.* aff. *freisingensis* Fahlbusch, 1964, left mandible with m1–m3 (CRW 2/68 1).

conid with the posterolophid; the mesolophid reaches the border of the molars and is fused with the posterior part of the entoloph.

M1: The lingual anteroloph closes the anterosinus; the anterocone is integrated in this crest; the labial anteroloph is missing but a low cingulum closes the anterosinus; the short and straight anterolophule connects both anterocone and lingual anteroloph; the anterior arm of the protocone is, compared to the anterolophule, long and slanted; the mesoloph is always long but never reaches the border of the teeth; the metalophule is directed backwards; posterolophule and metalophule are delimited a small posterosinus.

M2: The labial and lingual anterolophs are well developed; the two protolophules are present; the mesoloph is medium-sized (in 2 out of 3 teeth) or short; the anterior metalophule is developed in two of the molars, whereas it joins the hypocone in the third tooth.

Table 1: *Democricetodon* aff. *crassus* Freudenthal, 1969, sample statistics of the molars.

		n	min.-max.	mean
m1	length	6	1.44-1.58	1.53
	width	6	1.01-1.11	1.06
m2	length	12	1.28-1.43	1.37
	width	12	1.00-1.16	1.09
m3	length	2	1.29	
	width	2	1.03-1.06	
M1	length	9	1.65-1.79	1.7
	width	9	1.11-1.24	1.15
M2	length	3	1.25-1.31	1.28
	width	3	1.13-1.18	1.16

Table 2: *Democricetodon mutilus* Fahlbusch, 1964, sample statistics of the molars.

		n	min.-max.	mean
m1	length	4	1.68-1.76	1.71
	width	4	1.10-1.15	1.12
m2	length	4	1.41-1.50	1.54
	width	4	1.23-1.31	1.26
m3	length	1	1.5	
	width	1	1.25	
M1	length	3	1.93-2.13	2.01
	width	3	1.38-1.39	1.39
M2	length	3	1.46-1.54	1.5
	width	3	1.29-1.40	1.33

Discussion: The molars from Petersbuch 68 share features with *Democricetodon mutilus*, a species previously described under the name *D. affinis mutilus* by Fahlbusch (1964). Compared to *D. affinis* from Steinheim (material from the collection of the Museum at Stuttgart), the species from Petersbuch 68 is different in numerous traits, including the general outline of the m1 that is more elongated, and the shorter anteroconid. According to Heissig (1995: 99), the presence of a well-developed lingual anterolophid, together with the presence of an anterior spur of the metaconid, link the species from Petersbuch 68 to *D. mutilus*. The *D. mutilus* populations of the NAFB are not characterized by a regular size increase through time, but rather display repetitive fluctuations (Heissig 1995). Regarding size and morphology, the molars from Petersbuch 68 could easily be included in the reference population from Langenmoosen. The specimens from the middle and upper part of the fissure do not differ from each other.

Species: *Democricetodon* aff. *freisingensis* Fahlbusch, 1964
Figure 3J

1925 *Cricetodon gaillardi*. – Schaub: p. 36–38, pl. 1 fig. 9: pl. 3 figs 10–11.
1972 *Democricetodon gaillardi*. – Baudelot: p. 258.
1993 *Democricetodon gaillardi*. – Kälin: fig. 76c.
1995 *Democricetodon* aff. *freisingensis*. – Heissig: p.95–103, figs 2j, 3i, 3r, 4i, 5i, 5q.
2003 *Democricetodon gaillardi*. – Maridet: p. 84–86; pl. 6 figs 12–25.

Diagnosis: see Fahlbusch (1964)

Type locality: Giggenhausen

Age: Middle Miocene (MN 8)

Provenance: Upper part of the fissure filling

Material and measurements: (Fig. 4) 1 mandible with m1–m3 (CRW 2/68 1): m1: 1.63 x 1.11; m2: 1.40 x 1.16; m3: 1.34 x 1.09.

Description and discussion: Characteristic features of this taxon are the long mesolophids that are present in all teeth and the ectomesolophid that occurs in the m1. Moreover, the broad anteroconid of the m1 differs from that seen in the other *Democricetodon* species from Petersbuch 68: the anterolophids and anteroconid form a nearly perfect arc; as a result, the anterosinusid is almost closed. As the tooth is worn and its anterior part covered by sediment, it cannot be determined if many crests are joining the posterior wall of the anteroconid, but we believe that this is likely. The teeth from Petersbuch 68 can easily be referred to the large *Democricetodon* species from Sansan originally described as *D. gaillardi*. Heissig (1995) reinterpreted this population as representing an ancestor of *D. freisingensis* from the MN 8 fauna of the NAFB, and regards the population of Steinheim as the true *D. gaillardi*. This interpretation is not generally followed, and some authors consider *D. freisingensis* and *D. gaillardi* synonymous (de Bruijn et al. 2003: 60). The single specimen from Petersbuch 68 does not provide new information, and thus the interpretation in Heissig (1995) is followed.

Species: *Democricetodon* sp.
Figure 3C

Provenance: Middle part of the fissure filling

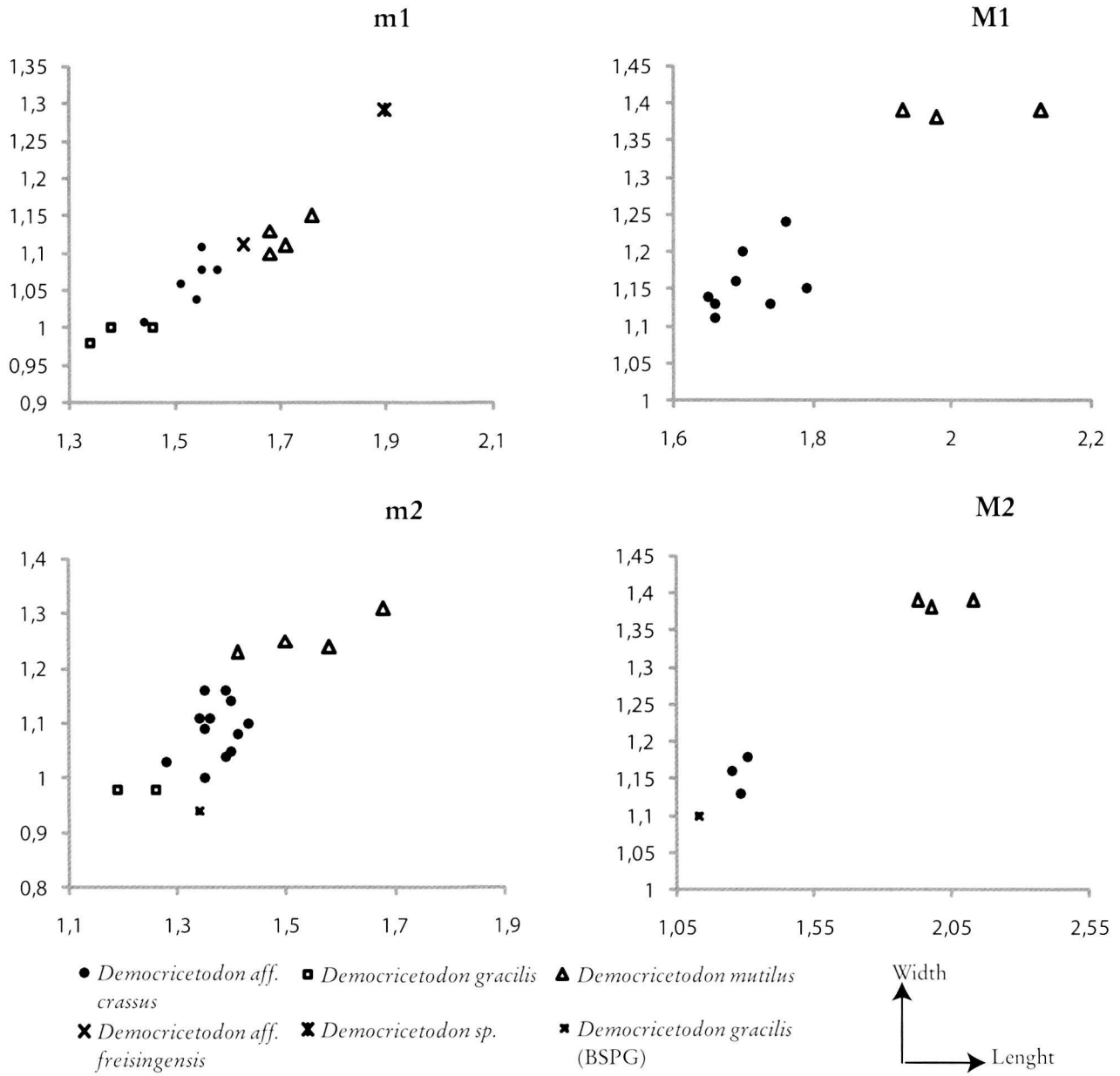

Figure 4: Scatter diagram of the *Democricetodon* FAHLBUSCH, 1964 molars from Petersbuch 68.

Material and measurements: (Fig. 4) 1 m1 (BSPG 2008 V 20): 1.9 x 1.29

Description and discussion: This rare species is characterized by its exceptional size. The strong labial anterolophid is a prolongation of the rounded anteroconid. The lingual anterolophid is missing. The mesolophid is not discernible because it is covered by sediment, but it is obvious that this structure does not reach the border of the tooth. Attribution of the m1 to *Karydomys* THEOCHAROPOULOS, 2000 is unlikely based on the form of the anteroconid and anterolophids. The specimen is not sufficiently well preserved to allow for a more detailed discussion of its taxonomic position, and hence is assigned to *Democricetodon* sp.

Subfamily: Megacricetodontinae MEIN & FREUDENTHAL, 1971

Genus: *Megacricetodon* FAHLBUSCH, 1964

Diagnosis: see FAHLBUSCH (1964).

Type species: *Megacricetodon gregarius* (SCHAUB, 1925).

Other species included: *M. minor* (LARTET, 1851); *M. bourgeoisi* (SCHAUB, 1925); *M. gregarius* (SCHAUB, 1925); *M. ibericus* (SCHAUB, 1944); *M. collongensis* (MEIN, 1958); *M. lappi* (MEIN, 1958); *M. crusafonti* (FREUDENTHAL, 1963); *M.*

primitivus (Freudenthal, 1963); *M. bavaricus* Fahlbusch, 1964; *M. similis* Fahlbusch, 1964; *M. minutus* Daxner, 1967; *M. debruijni* Freudenthal, 1968; *M. bezianensis* Bulot, 1980; *M. germanicus* Aguilar, 1980; *M. gersii* Aguilar, 1980; *M. sinensis* Qiu et al., 1981; *M. lopezae* Garcia Moreno, 1986; *M. roussilonensis* Aguilar et al., 1986; *M. crisiensis* Radulescu & Samson, 1988; *M. rafaeli* Daams & Freudenthal, 1988; *M. fournasi* Aguilar, 1995; *M. lemartinelli* Aguilar, 1995; *M. pusillus* Qiu, 1996; *M. fahlbuschi*, Aguilar et al., 1999; *M. wuae* Aguilar et al., 1999; *M. lalai* Aguilar et al., 1999; *M. andrewsi* Pelaez-Campomanez & Daams 2002; *M. tautavelensis* Lazzari & Aguilar, 2007; *M. aunayi* Lazzari & Aguilar, 2007; *M. yei* Bi et al., 2008.

M. aguilari Lindsay, 1988, *M. sivalensis* Lindsay, 1988, *M. daamsi* Lindsay, 1988 and *M. mythikos* Lindsay, 1988 are excluded from *Megacricetodon* by Wessels (1996).

Species: *Megacricetodon minor* (Lartet, 1851)
Figures 5C–E

1993 *Megacricetodon minor* – Kälin: 107, fig. 68h.

Diagnosis: see Fahlbusch (1964)

Type locality: Sansan

Age: Middle Miocene (MN 6)

Provenance: Upper part of the fissure filling

Material and measurements: (Fig. 6; Tab. 3) 3 m1, 4 M1, 1 M2, 2 lower jaws with m1, 2 upper jaws with M1 (NMA 2007-104 to 114 and 116/2017)

Description: m1: The anteroconid is simple, ovaloid, and extends on the labial side into the strong anterolophid, which closes the anterosinusid; there is no lingual anterolophid, and a delicate cingulum may close the protosinusid or is absent; the straight anterolophulid connects to the anteroconid; the mesolophid is most often long (in 3 out of 5 teeth), but may also be medium-sized or very short.

M1: The anterocone consists of two well defined cusps connected with one another by a transverse ridge; the labial cusp is somewhat enlarged; a valley separates the two cusps on the anterior wall of the anterocone; this valley may be closed interiorly by a low crest (in 2 out of 6 M1); in two specimens (out of 6), this valley is deep, separating the two cusps more clearly, but it never descends to more than the half of the anterocone heigth; the anterolophule connects the lingual cusp; two low cinguli are closing the anterosinus; anterior and posterior protolophules are developed in all molars; the mesoloph is most often long and connects the paracone spur, which extends to the molar border (in 4 out of 6); in the two other M1 the paracone spur is missing and the mesoloph medium-sized.

M2: The two anterolophs are well developed; only the anterior protolophule is present; the mesoloph is long and connects the paracone spur, which extends to the molar border; the metalophule is transversal.

Discussion: The lack of diagnostic characters makes it difficult to provide a taxonomical attribution for this small *Megacricetodon* species. Most of the molars from Switzerland and southern Germany are referred to *M.* (cf. or aff.) *minor* based principally on size compared to that seen in the teeth of the reference population from Sansan. Heissig (1989, 1990, 1997) noticed that this large size is not attained prior to MN 6 in southern Germany. On the other hand, the variability in size may be dependant on the localities and/or the size of the sample. Regarding the considerable size variation seen in the *M. minor* molars from Mohrenhausen (Boon 1991), the evolutionary trend in *M. minor* is hard to follow with precision. Furthermore, the variation of the *M. minor* molars given by Baudelot (1972) slightly differs from the data provided in Heissig (op. cit.), Fahlbusch (1964), and Engesser (1972) based on the collection of the museum at Basel.

The teeth from P68 are larger than those from the Sandelzhausen (Fahlbusch 1964) and Untereichen-Altenstadt 565m (Prieto et al. 2008) localities, which are older than the Ries event, traditionally correlated in local biostratigraphy with MN 5. They are somewhat smaller than the teeth from Laimering 3 and Goldberg (MN 6). Based on the morphology and correspondences in size with the reference species from Sansan, we assign the molars from Petersbuch 68 to *M. minor*.

Species: *Megacricetodon* aff. *similis* Fahlbusch, 1964
Figures 5A,B

1992 *Megacricetodon similis* – Bolliger: fig. 73.
? 1993 *Megacricetodon* aff. *minor* – Kälin: fig. 66b.
Part 1994 *Megacricetodon similis* – Bolliger: p. 113.
2007 *Megacricetodon* aff. *similis* – Prieto: p. 82, fig. 38D.

Diagnosis: see Fahlbusch (1964)

Type locality: Giggenhausen

Age: Middle Miocene (MN 8)

Provenance: Upper part of the fissure filling

Material und measurements: (Fig. 6) 2 m1, 1 M1(?) (NMA 2007-117 to 119/2017); m1: 1.50 x 0.96, 1.53 x 0.70; M1: 1.55 x 0.94.

Description and discussion: The m1 are larger than the m1 of *M. minor* from Petersbuch 68. With regard to morphology they do not differ from *M.* aff. *similis* from Petersbuch 48 (Prieto 2007). In this fissure filling, this species represents the only *Megacricetodon* taxon present; it differs from *M. similis* in the following features: (1) a smaller size; (2) the posterior wall of the anteroconid which is more profoundly divided in m1; (3) The anterocone of the M1 which is deeper fissured; and (4) the somewhat longer mesoloph in M1.

M. aff. *similis* also occurs in the fissures fillings Petersbuch 6 and 18, together with two other small *Megacricetodon* species. The identification of the teeth from Petersbuch 68 is based exclusively on the m1. Attribution of the single M1 to the species aff. *similis* remains uncertain since this molar may also belong to *M. minor*. However, it differs from the *M. minor* M1 from Petersbuch 68 by the broader anterocone and deeper anterior

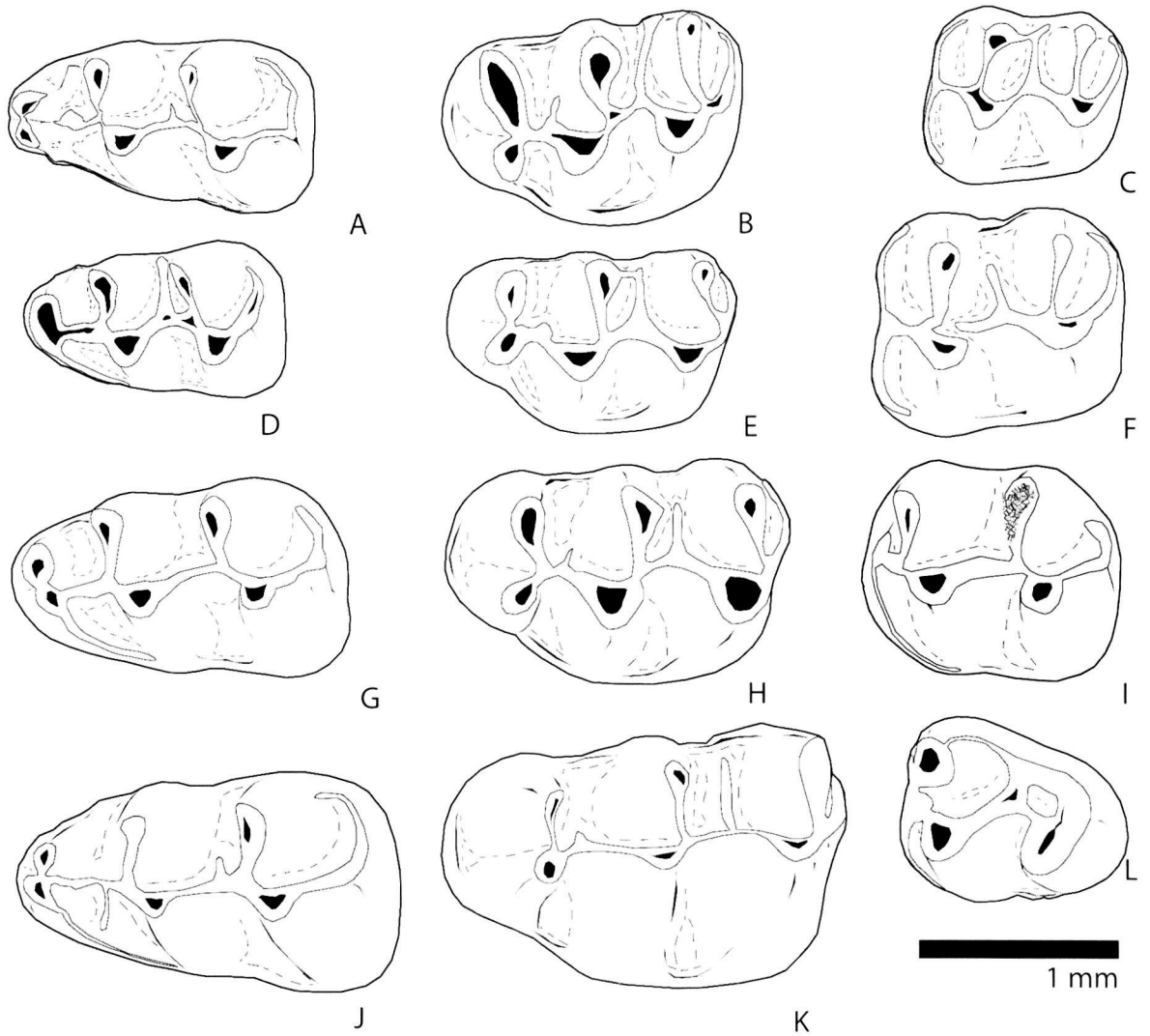

Figure 5: The *Megacricetodon* Fahlbusch, 1964 from Petersbuch 68. **A, B**: *M.* aff. *similis* Fahlbusch, 1964: A: right m1 (revers., NMA 2007-118/2017), B: left M1 (NMA 2007-117/2017); **C–E**: *M. minor* (Lartet, 1851): C: right M2 (revers., NMA 2007-116/2017), D: left m1 (NMA 2007-104/2017), E: right M1 (NMA 2007-111/2017); **F–I, L**: *M.* aff. *germanicus* Aguilar, 1980: F: right M2 (revers., NMA 2007-165/2017), G:left m1 (NMA 2007-121/2017), H: left maxillary with M1 (NMA 2007-135/2017), I: right m2 (revers., NMA 2007-130/2017), L: right m3 (revers., NMA 2007-133/2017); **J, K**: *M.* aff. *bavaricus* Fahlbusch, 1964: J: m1 (BSPG 2008 V 21), K: M1 (BSPG 2008 V 23).

valley, but, at the same time, does not correspond exactly to the morphology of the *M.* aff. *similis* M1 from Petersbuch 48.

Species: *Megacricetodon* aff. *germanicus* Aguilar, 1980
Figure 5F–I, L

Pars	1993	*Megacricetodon germanicus* – Kälin: fig. 72a, d, e.
	1997	*Megacricetodon germanicus* – Kälin: fig. 11.
	2001	*Megacricetodon germanicus* – Kälin et al.: tab. 1.

Diagnosis: see Aguilar (1980)

Type locality: Anwil

Age: Middle Miocene (MN 8)

Provenance: Upper part of the fissure filling

Material und measurements: (Fig. 6; Tab. 4) 5 m1, 3 m2, 2 m3, 3 M1, 1 M2, 3 lower jaws with m1, 2 upper jaws with M1 (NMA 2007-115, 120 to 137 and 165/2017).

Description: m1: The anteroconid is simple (in 2 out of 5 molars) or shares two abutted cusps; in the latter case, a very short furrow on the anterior wall of the anteroconid may be present; the labial anterolophid is complete, whereas the lingual anterolophid is missing; the anterolophulid may connect the anteroconid between the two cusps; the mesolophid is highly reduced to short.

m2: The labial anterolophid closes the anterosinusid; the lingual anterolophid is highly reduced; the ectolophid is straight; the mesolophid is missing (in 2 out of 3 m2) or short.

m3: The labial anterolophid closes the anterosinusid; the lingual anterolophid is highly reduced; the mesolophid reaches the border of the molar; the entoconid is integrated in a crest connecting the metaconid with the posterolophid.

M1: The anterocone consists of two well defined cusps, which are interconnected by a transversal ridge; the labial cusp is more prominent; a valley consistently separates the two cusps on the anterior wall of the anterocone; this valley is usually closed interiorly by a low crest (in 4 out of 5 molars); in one molar, however, the valley is, in comparison with the other specimens, reduced; the anterolophule connects the lingual cusp or the crest joining the two cusps; two low cinguli close the anterosinus; anterior and posterior protolophules are developed in all molars; the mesoloph is medium-sized or slightly longer and connects to the paracone spur in two teeth.

M2: The labial anteroloph is more prominent than the lingual anteroloph; the protolophule transversally connects the paracone with the protocone; the anterior part of the entoloph is interrupted; the mesoloph is directed forwardly and medium-sized; the metalophule is transversal.

Discussion: The overall morphology and size of the teeth place *Megacricetodon* from the upper part of Petersbuch 68 near the molars from the Swiss locality Zegligen that have been described as *M. germanicus* (KÄLIN 1993, 1997). On the other hand, AGUILAR (1995) describes the lineage *M. collongensis**-*M. roussillonensis* from southern France, in which *M. lemartinelli* shows strong affinities to the species from Petersbuch 68. This species differs from the Petersbuch 68 specimens in that it generally has a simple anteroconid on the m1 (in 79–100% of the specimens; see AGUILAR 1995: fig. 2). Moreover, AGUILAR et al. (1999) described *M.* aff. *bavaricus* from the Digne area, a species that is also characterized by a mostly simple or 8-shaped anteroconid and by the absence or low heights of the mesolophids on m1.

M. bavaricus from the NAFB can be excluded because (1) the general outline of M1 in *M.* aff. *germanicus* is different and the anterocone is broader; (2) a spur on the anterolophid is lacking in the m1 from Petersbuch 68 (this has been observed by KÄLIN 1997: 108); and (3) the paracone spur is more prominent in the M1 from Petersbuch 68.

The filiation *M. bavaricus-M. germanicus,* as proposed by AGUILAR (1995), among others, is not supported in the NAFB (HEISSIG 1990, 1997, 2006; BÖHME et al. 2001; REICHENBACHER et al. 2004; ABDUL AZIZ et al. 2008 in press; PRIETO et al. 2008) where the lineage that includes *M. bavaricus* terminates with a large *Megacricetodon* species that has previously been described as *M. lappi* (BOON 1991; KÄLIN 1997;). In this proposal, *M. germanicus* from Anwil is not equivalent to the similarly sized *Megacricetodon* aff. *bavaricus* from the MN 5 localities of the NAFB; however, a revision of these *Megacricetodon*-populations has not yet been published, and thus a more detailed comparison of the teeth from Petersbuch 68 with the French material is impossible at present. As a consequence, identification of the teeth from the Frankian Alb follows KÄLIN (1997, *M.* aff. *germanicus*), but we refrain from proposing a new species.

*LAZZARI & AGUILAR (2007) propose that the populations previously attributed to *M. collongensis* from the Languedoc-Roussillon have to be renamed because they apparently differ from the type population from Vieux-Collonges.

Table 3: *Megacricetodon minor* (LARTET, 1851), sample statistics of the molars.

		n	min.-max.	mean
m1	length	5	1.30-1.36	1.34
	width	5	0.79-0.86	0.81
M1	length	6	1.40-1.58	1.46
	width	6	0.85-0.95	0.91
M2	length	1	0.99	
	width	1	0.9	

Species: *Megacricetodon* aff. *bavaricus* FAHLBUSCH, 1964
Figure 5J, K

Diagnosis: see FAHLBUSCH (1964)

Type locality: Langenmoosen

Age: Middle Miocene (MN 5)

Provenance: Middle part of the fissure filling

Material and measurements: (Fig. 6) 2 m1, 1 M1 (BSPG 2008 V 21–23): m1: 1.83 x 1.15; 1.79 x 1.15; M1: 2.06 x 1.25.

Description and discussion: The teeth do not differ from *M.* aff. *bavaricus*, a common species in MN 5 faunas of the NAFB. They can be distinguished from *M.* aff. *germanicus* from the upper part of the fissure filling by the characteristics mentioned above.

Subfamily: Eumyarioninae ÜNAY, 1989

Genus: *Eumyarion* THALER, 1966

Diagnosis (emended): see MEIN & FREUDENTHAL (1971)

Type species: *Eumyarion medius* (LARTET, 1851) (=*Eumyarion helveticus* (SCHAUB, 1925))

Other species included: *E. latior* (SCHAUB & ZAPFE, 1953), *E. weinfurteri* (SCHAUB & ZAPFE, 1953), *E. bifidus* (FAHLBUSCH, 1964), *E.leemanni* (HARTENBERGER, 1965), *E. valencianum* DAAMS & FREUDENTHAL, 1974 (Nomen dubium in DE BRUIJN & SARAÇ 1991: 14), *Eumyarion montanus* DE BRUIJN & SARAÇ, 1991, *E. intercentralis* DE BRUIJN & SARAÇ, 1991, *E. microps* DE BRUIJN & SARAÇ, 1991, *E. carbonicus* DE BRUIJN & SARAÇ, 1991, *E. kowalskii* LINDSAY, 1996, *E. orhani* DE BRUIJN et al., 2006.

Species: *Eumyarion* cf. *medius* (LARTET, 1851)
Figure 7

Diagnosis (*E. medius*): see BAUDELOT (1972)

Type locality: Sansan

Age: Middle Miocene (MN 6)

Provenance: Upper part of the fissure filling

Material and measurements: (Fig. 8; Tab. 5) 6 m1, 2

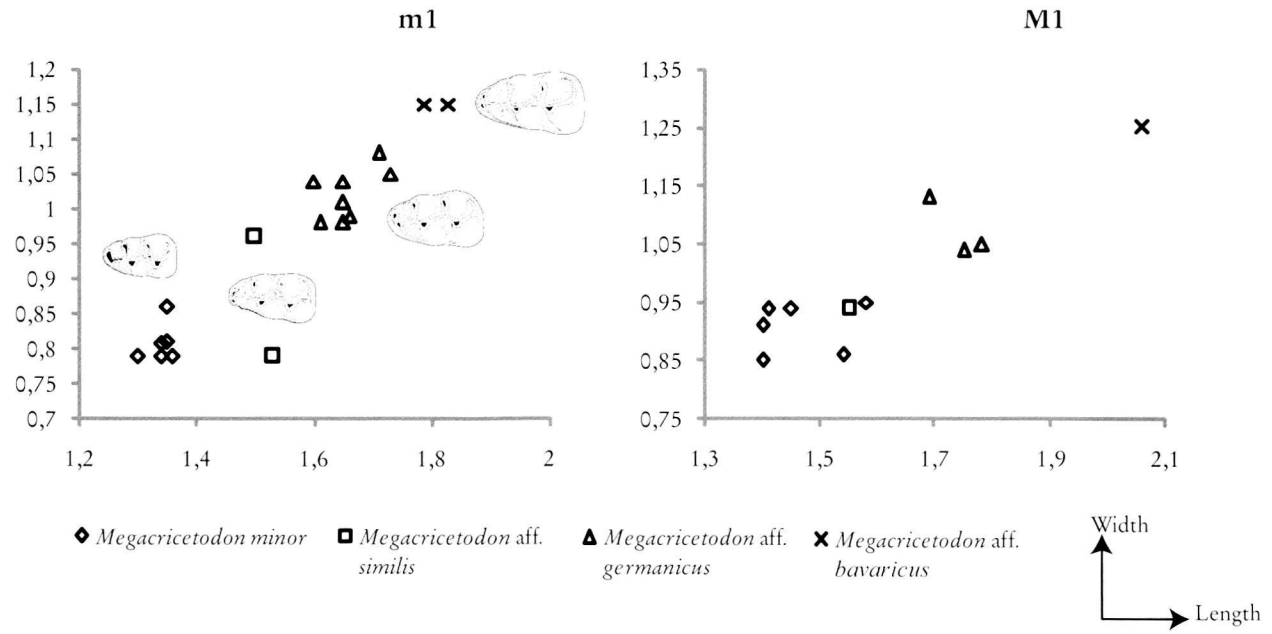

Figure 6: Scatter diagram of the *Megacricetodon* FAHLBUSCH, 1964 molars from Petersbuch 68

m2, 3 m3, 2 M1, 7 M2, 1 M3 (NMA 2007-138 to 161/2017).

Description: m1: Three of the four smaller m1 are either worn or damaged; in one specimen (Fig. 7D), the anteroconid is situated more labially; the labial anterolophid closes the protosinusid; the anterolophulid is missing; metalophulid and anterior arm of the protoconid are not connected; the broad mesolophid occupies the whole mesosinusid; a very low ectomesolophid is present as an extension of the cingulid, which closes the sinusid; the posterolophid occurs as a strong crest extending to the top of the entoconid; two larger m1 (Fig. 7A) differ from the other specimens by their broader anteroconid; the anterolophid are complete and connected to the meta- and protoconid; the mesolophid and metaconid are connected by a short supplementary longitudinal crest; the posterolophid is enlarged (reduced hypoconid branch?).

m2: In the first specimen (Fig. 7B), the labial anterolophid occurs as a strong crest that closes the protosinusid; the reduced lingual anterolophid is fused with the anterior wall of the metaconid; the long mesolophid extends into a crest reaching the top of the metaconid; the posterolophid extends to the posterior wall of the entoconid; the second m2 is damaged but differs from the others by having a "double mesolophid": the protoconid hind arm connects the mesolophid.

m3: The labial anterolophid closes the narrow protosinusid; the reduced lingual anterolophid is abutted to the metaconid;

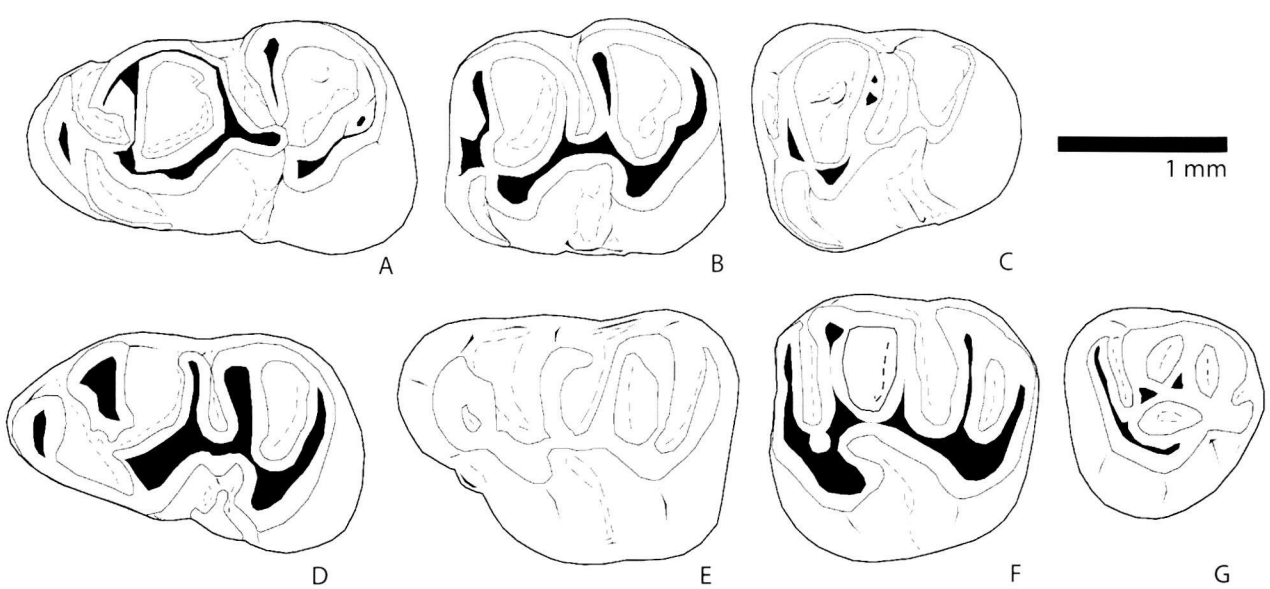

Figure 7: *Eumyarion* cf. *medius* (LARTET, 1851) from Petersbuch 68. **A:** right m1 (revers., NMA 2007-142/2017), **B:** right m2 (revers., NMA 2007-144/2017), **C:** right m3 (revers., NMA 2007-146/2017), **D:** right m1 (revers., NMA 2007-143/2017), **E:** right M1 (revers., NMA 2007-149/2017), **F:** right M2 (revers., NMA 2007-151/2017), **G:** left M3 (NMA 2007-161/2017).

Table 4: *Megacricetodon* aff. *germanicus* AGUILAR, 1980 , sample statistics of the molars.

		n	min.-max.	mean
m1	length	8	1.60-1.73	1.66
	width	8	0.98-1.08	1.02
m2	length	3	1.31-1.33	1.32
	width	3	1.04-1.09	1.06
m3	length	2	1.15-1.2	
	width	2	0.90-0.94	
M1	length	3	1.69-1.78	1.74
	width	3	1.04-1.13	1.07
M2	length	1	1.28	
	width	1	1.14	

protoconid hind arm (?), hypolophulid and hypolophid are transversal and somewhat parallel; the entoconid occurs as an enlargement of the lingual crest joining metaconid to posterolophid.

M1: The straight anterolophule connects the lingual part of the anterocone to the protocone; a transversal labial spur of the anterolophule connects the lingual part of the anterocone; the mesoloph is medium-sized or long and connects the top of the metacone.

M2: The strong labial anteroloph delimits the anterosinus; in one tooth (out of 7), a very small cingulum is present on the anterior wall of the protocone; the mesoloph is always long, connecting the paracone (4 molars), the metacone (1 M2) or is isolated.

M3: The molar is rounded; protocone and paracone are present, the other cusps are integrated in a crest surrounding the M3; the axioloph extends to the posterior part of the molar; the mesoloph reaches the border of the tooth.

Discussion: See Discussion section on the *Eumyarion* species from Petersbuch 68 below.

Species: *Eumyarion* sp.

Provenance: Middle part of the fissure filling

Material und measurements: 1 M1, 1M2, 1M3 (BSPG 2008 V 24–26): M1: 2.04 x 1.43; M2: 1.58 x 1.55; M3: 1.05 x 1.44.

Discussion of the *Eumyarion* species from Petersbuch 68: The m1 sample from the upper part of the fissure filling may, on first approximation, be subdivided into two species. The smaller species (Fig. 7D) is characterized by a small anteroconid and reduced or absent lingual anterolophid, whereas the second (Fig. 7A) is larger and characterized by a broad anteroconid extending into two well-developed anterolophids on both sides of the molar. The co-occurrence of different *Eumyarion* species has been reported repeatedly in the literature. The most impressive example comes from the Early Miocene locality Sabuncubeli (Turkey), in which three species co-occur (DE BRUIJN et al. 2006). On the other hand, the morphological variability is generally high in the genus *Eumyarion*, and the two morphotyps from Petersbuch 68 are also known to occur in the *Eumyarion medius* molar sample from the Swiss locality Schwamendingen (ENGESSER 1972: fig. 107(2)). However, a clear subdivision of the molar sample from Petersbuch 68 is impossible for the other teeth positions. Based on literature data and the material from Petersbuch, we suggest that all molars from the upper part of the fissure belong to a single species. According to WU (1982: tab. 3), who detailed the molars from Sansan, the anterolophulid is most often complete in the French m1. A comparison with the material from the CRW reveals that the absence of the anterolophulid, as reported for the molars from the NMA, cannot be regarded as a consistent characteristic of the teeth from Petersbuch 68. WU (1982) noted that the morphotype with a "single mesolophid" (="Protoconid-Hinterarm" in tab. 2) is distinctly more abundant (i.e. in 56 out of 100 m1). This morphotype is also represented in 56% of the m1 from Petersbuch 68 stored in the collection of M. RUMMEL. In the NAFB, *Eumyarion* molars assignable to *E. medius* comprise populations of great morphological variability. For example, the development of a "double mesolophid" is, although often incomplete, dominant in the *E. medius* population from Laimering 3 kept in the BSPG (BOLLIGER 1994; HEISSIG 2006). Lacking a detailed revision of these forms, we can only refer to these populations as *E.* aff. *medius*. The size of the molars from Petersbuch 68 (upper part) partially exceeds the size variation present in the type sample from Sansan (BAUDELOT 1972), and thus this population can be referred to *E.* cf. *medius*.

The small *Eumyarion* molar sample (3 teeth) from the middle part of the fissure filling consists exclusively of upper molars. The M1 and M3 cannot be clearly distinguished from *E. medius*. The M2 shows a small crest joining protolophule to anterolophule. This crest is apparently not equivalent to the double protolophule in *E. bifidus*, and may be interpreted as a variant morphotype of *E. medius*. Nevertheless, we cannot completely rule out other *Eumyarion* species as well. Based on a comparison of these molars with the *Eumyarion* samples from the MN 5 faunas of the NAFB (e.g., BOON 1991), we suggest that they are within the morphological variation of these populations. As a consequence, we refrain from proposing a species level identification of these teeth.

4. Discussion

Most of the species in the fossil assemblage allow for a correlation of Petersbuch 68 with the MN 6: *Democricetodon gracilis* and *Democricetodon mutilus* are not known from deposits younger than MN 6. *Democricetodon* aff. *crassus* is first reported in the NAFB and can be related to the species of Sansan. *Eumyarion medius* is mostly known from MN 6 localities in Switzerland and Germany (BOLLIGER 1997; HEISSIG 1997). With regard to the age of the assemblage, *Megacricetodon* aff. *germanicus* represents the most significant biostratigraphic indicator. The taxon has been reported from the top of MN 6 in the Swiss localities Zeglingen (KÄLIN 1997) and Combes Girard 39 (KÄLIN et al 2001). Its presence in MN 7, as the ancestor of the typical *M. germanicus* from Anwil and Kleineisenbach, continues to be uncertain (PRIETO 2007). On the other hand *Megacricetodon*

Table 5: *Eumyarion* cf. *medius* (LARTET, 1851), sample statistics of the molars.

		n	min.-max.	mean
m1	length	3	2.10-2.43	2.26
	width	3	1.25-1.56	1.4
m2	length	1	1.63	
	width	1	1.44	
m3	length	3	1.39-1.59	1.5
	width	3	1.19-1.39	1.29
M1	length	2	2.01-2.15	
	width	2	1.53-1.59	
M2	length	7	1.48-1.65	1.58
	width	7	1.44-1.59	1.6
M3	length	1	1.19	
	width	1	1.3	

aff. *bavaricus* is clearly indicative of MN 5. In the NAFB, the lineage *M." collongensis"-M. bavaricus-M. "lappi"* is characterized by a size increase that formed the basis for a detailed local biostratigraphy for the faunas from the upper part of MN 4 and MN 5 (e.g., HEISSIG 1997; ABDUL AZIZ et al. 2008; PRIETO et al. in press). The *M.* aff. *bavaricus* from the middle part of the fissure filling Petersbuch 68 can be plotted on this biostratigraphy in the unit OSM C+D, which is comprised of the well-known fossil localities Puttenhausen and Sandelzhausen.

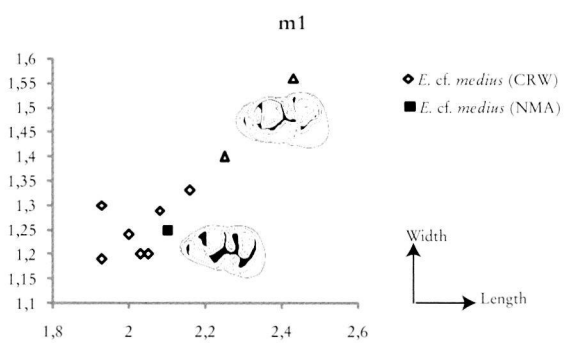

Figure 8: Scatter diagram of *Eumyarion* cf. *medius* (LARTET, 1851) from Petersbuch 68

The differences in faunal composition between the middle and upper parts of the fissure filling can be explained by a postdated deposit of fossils at the top of the fissure. Such multiple origins of the filling in karst systems have frequently been reported in the literature, and are readily detectable based on the presence of species belonging to distinct evolutionary levels (e.g., RUMMEL 1993; BOLLIGER & RUMMEL 1994; LAUDET 2000; PRIETO 2007), the coloration of the karst sediments (DEHM 1935), and sediment stratification (MARIDET et al. 2000; GINSBURG et al. 2001). Interpretation of the samples is more complicated if successive infillings are closed in time or continuous on a large time scale (BOLLIGER & RUMMEL 1994: 260). To some extent, this is the case in Petersbuch 68 where equivalent species are found in MN 5 and MN 6. As a result, it can be hypothesized that the *M.* aff. *bavaricus* specimens – the only molars indicative of MN 5 – perhaps represent a third infilling. However, arguing against this hypothesis is the species composition of the Erinaceidae from Petersbuch 68 (PRIETO & RUMMEL, 2009b).

5. Conclusions

The two hamster samples can be interpreted as follows: During a first infilling (MN 5) a fauna dominated by *Democricetodon mutilus* has accumulated. A few rare specimens such as *D. gracilis* and *D.* sp. also occur, together with *Megacricetodon* aff. *bavaricus* and *Eumyarion* sp.

A second rapid and dense accumulation (MN 6) occurs at the top of the fissure. This fauna is characterized by *Megacricetodon* aff. *germanicus*, *M. minor*, *Democricetodon* aff. *crassus*, *D.* aff. *freisingensis*. The homogeneity of the *D. mutilus* and *Eumyarion* cf. *medius* samples remains uncertain, but the species are common and most molars likely belong to the MN 6 assemblage. The presence of *D. gracilis* in this assemblage can only be hypothesized. *M.* aff. *similis* is found in the fissures fillings Petersbuch 6, 18 (base of MN 8?), Petersbuch 48 (MN 8), as well as in Grat 930 m (MN 8). As the species probably occurs in the MN 7 faunas from the Switzerland (PRIETO 2007), the specimens from Petersbuch 68 can be interpreted as the oldest known occurrence of this species, and not as a result of a mixture of faunal elements from different stratigraphic levels. Moreover, the presence of an abundant population of *Parasorex socialis* (PRIETO & RUMMEL, 2009b) at the top of the fissure filling strongly suggests that the assemblage belongs to MN 7.

Acknowledgements

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