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Cover illustration: Cover illustration: The floating plant *Cobbania corrugata* (LESQUEREAUX) 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 Schwimmmpflanze *Cobbania corrugata* (LESQUEREAUX) STOCKEY et al. aus der Oberkreide Nordamerikas. Im Steinbruch des Dinosaur Provincial Park, Alberta (Kanada), wurden mehrere komplett 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.

The genus *Collimys* DAXNER-HÖCK, 1972 (Rodentia, Cricetidae) in the Middle Miocene fissure fillings of the Frankian Alb (Germany)

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Abstract

New fossil material of the genus *Collimys* (Rodentia, Mammalia) from the fissure fillings of the Frankian Alb (South Germany) is described and the new species *C. gudrunae* is introduced. This species is integrated in the new *C. transversus* / *C. gudrunae* lineage which is restricted to the Middle Miocene (MN 7, base of MN 8?) and contains three distinct evolutionary stages: *C. transversus*-*C. aff. transversus*-*C. gudrunae*. It is independent from the *C. hiri* / *C. dobosi* lineage found around the Middle/Late Miocene (MN9) boundary. The biostratigraphical value of the *C. transversus* / *C. gudrunae* lineage is promising although it has to be confirmed by future findings from stratified deposits.

Key words: Miocene, Cricetidae, *Collimys*, biostratigraphy, Germany, central Europe, fissure filling.

Zusammenfassung

Neues Material der Gattung *Collimys* (Rodentia, Mammalia) aus den Spaltenfüllungen der fränkischen Alb wird beschrieben und die neue Art *C. gudrunae* definiert. Diese Art ist in der neuen Entwicklungslinie *C. transversus* / *C. gudrunae* integriert, die zeitlich auf das Mittelmiozän (MN 7, Basis MN 8?) beschränkt ist. Drei Entwicklungsstadien sind erkennt: *C. transversus*-*C. aff. transversus*-*C. gudrunae*. Diese Entwicklungslinie ist unabhängig einer zweiten Linie *C. hiri* / *C. dobosi* aus dem Mittel-/Obermiozän Grenze (MN 9). Die vielversprechende biostratigraphische Bedeutung der *C. transversus* / *C. gudrunae* Linie muss durch zukünftige, stratifizierte Funde bestätigt werden.

Schlüsselwörter: Miozän, Cricetidae, *Collimys*, Biostratigraphie, Deutschland, Mitteleuropa, Spaltenfüllung

1. Introduction

Collimys was traditionally considered a rare genus and its value in biostratigraphical was negligible. Recently PRIETO & RUMMEL (2009) recognized a new lineage (*C. hiri* sp. nov. / *C. dobosi*) in the German part of the North Alpine Foreland Basin. These authors assign *C. longidens* from the Upper Miocene (MN 9) of the Swiss locality Nebelbergweg (KÄLIN & ENGESSER 2001) and *C. dobosi* from Miocene deposits of Hungary (HÍR 2003, 2005, 2006) to this lineage and prove the great utility of the genus *Collimys* in biostratigraphy.

Since the first description of *Collimys primus* (type species, DAXNER-HÖCK 1972) more than two decades passed before new *Collimys* specimens were discovered in the German fissure fillings of Petersbuch near Eichstätt (BOLLIGER & RUMMEL 1994). These molars are morphologically close to *C. transversus* from Steinheim (HEISSIG 1995). Here we describe new *Collimys* specimens from four South German localities and show that evolutionary lineages within this genus are essential in understanding the late Middle Miocene/Upper Miocene Central European continental biostratigraphy

2. Geological setting and fossil localities

The German part of the NAFB is delimited in the north-north/west by Jurassic deposits of the Franconian and Swabian Alb plateau. During the Middle Miocene (14,88 My Bp, ABDUL-AZIZ et al. 2008) the impact of the Ries and Steinheim meteorites shocked and melted the rocks of the basement at a distance of at least 10 km from the impact center and to a depth of 5000 m, ejecting Jurassic debris into the NAFB, the so called “Brockhorizont” (BÖHME et al. 2001). The meteoritic crater of Steinheim is filled by Middle Miocene lake deposits, which contain an important large and small mammal fauna that indicates MN 7 (TÜTKEN et al. 2006).

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The Franconian and Swabian Albs are karstified by a highly complicated system where the fissure fillings may contain rich and well-preserved fossils (RUMMEL 1993). In the karst system of the White Jura-δ of Petersbuch (Pet) near Eichstätt (Fig. 1), more than 100 fossil faunas have been discovered, ranging in time from Oligocene to Pleistocene. We describe here the Middle Miocene *Collimys* populations from five fissure fillings (Petersbuch 6, 10, 18, 26 and 48). The localities and faunas are surveyed in BOLLIGER & RUMMEL (1994), RUMMEL (1995, 1997, 2000, 2001) and ZIEGLER (2003a, 2003b, 2003c, 2005).

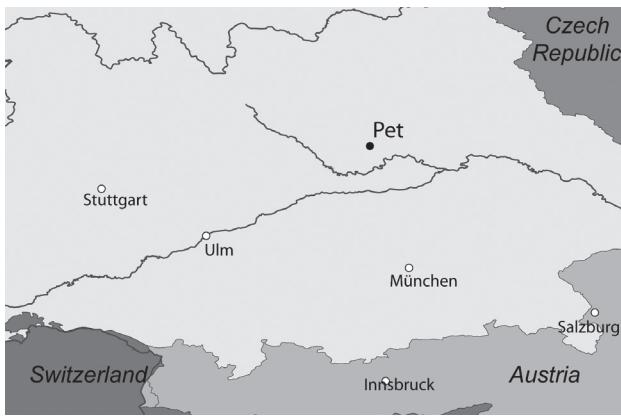


Figure 1: Geographical map of southern Germany showing the positions of the studied localities. Pet: Petersbuch.

3. Material and methods

The Petersbuch 6 and 48 samples are stored in the Bavarian State Collection for Palaeontology and Geology in Munich (BSP). The type specimen of *C. gudrunae* is kept in the Naturmuseum Augsburg (NMA). The other specimens are from the private collection of Michael Rummel (Weissenburg), abbreviated CRW. Measurements are taken with an ocular micrometer and indicated in mm. The terminology used in the description of the molars follows FREUDENTHAL et al. (1994). In addition we use the term anterior arm of the protocone. The spur of the anterolophid of m1 is considered a branch of a multibranched anterolophid. All teeth in the figures are shown in left orientation.

4. Systematic paleontology

Order: Rodentia BOWDICH, 1821

Family: Cricetidae ROCHEBRUNE, 1883

Subfamily: Cricetidae incertae sedis

Genus: *Collimys* DAXNER-HÖCK, 1972

Type species: *Collimys primus* DAXNER-HÖCK, 1972

Other species included in *Collimys*: *C. transversus* HEISSIG, 1995, *C. longidens* KÄLIN & ENGESSER, 2001, *C. dobosi* HÍR, 2005, *C. hiri* sp. nov. PRIETO & RUMMEL, 2009, *C. gudrunae* sp. nov. (this paper).

Emended diagnosis: PRIETO & RUMMEL (2009).

Note: Because some doubts remain as to the taxonomical attribution of the species *Collimys* sp. 1 and sp. 2 (see paragraph discussion on these two species), the above cited diagnosis does not include these molar samples. As a result, the form of the valleys is considered an important characteristic.

Differential diagnosis: PRIETO & RUMMEL (2009). Complementary comments are given in the Discussion.

Species: *Collimys transversus* HEISSIG, 1995

- | | |
|------|--|
| 1995 | <i>Collimys transversus</i> n. sp. – HEISSIG: p. 93, pl. 1. |
| 2001 | <i>Collimys transversus</i> . – KÄLIN & ENGESSER: p. 42–45, figs 36, 37. |
| 2005 | <i>Collimys transversus</i> . – HÍR: p. 15. |

Emended diagnosis: PRIETO & RUMMEL (2009).

Type locality: Steinheim am Aalbuch (Germany)

Type level: late Middle Miocene (MN 7)

Occurrence: Steinheim am Aalbuch.

Species: *Collimys aff. transversus* HEISSIG, 1995

Figures 2 and 8b

Occurrence: Petersbuch 26, Le-Locle-Sous-le-Stand 11.

Material: 24 isolated teeth, 5 mandibles and 1 maxillary from Petersbuch 26 (CRW P26-00001 to 00030).

Measurements: see Table 1 and Figure 3

Description: M1: The high lingual anteroloph descends from the broad anterocone and is not connected to the protocone; the labial anteroloph is absent (3 out of 4 molars) or developed as a longitudinal spur, which is connected to the labial spur of the anterolophule; this spur is long (3 out of 4) or reaches the labial border of the molar; the narrow sinus is transversal; the mesoloph is small to medium-sized; highly reduced posteroloph; metalophule directed backward; three roots.

M2: High and long labial anteroloph; lingual anteroloph may be developed (2 out of 4) or extremely reduced; the narrow sinus is transversal; the mesoloph is medium-sized (3 out of 4) or long; posteroloph reduced; the metalophule is directed backward; three roots.

M3: The four main cusps are present but the metacone is reduced; the lingual anteroloph is absent; the mesoloph always reaches the labial border of the molar; the metacone is isolated (2 out of 5) or the metalophule is present and directed forwards; the posteroloph is well delimited and reaches the base of the metacone; three roots.

Mandible: see description and discussion of *Collimys* mandibles.

m1: Broad and unsplit anteroconid, typically developed as a transversal ridge with widening of its lingual and labial parts (6 out of 8) or composed of two directly adjacent cuspids; the lingual anterolophid is missing; the labial

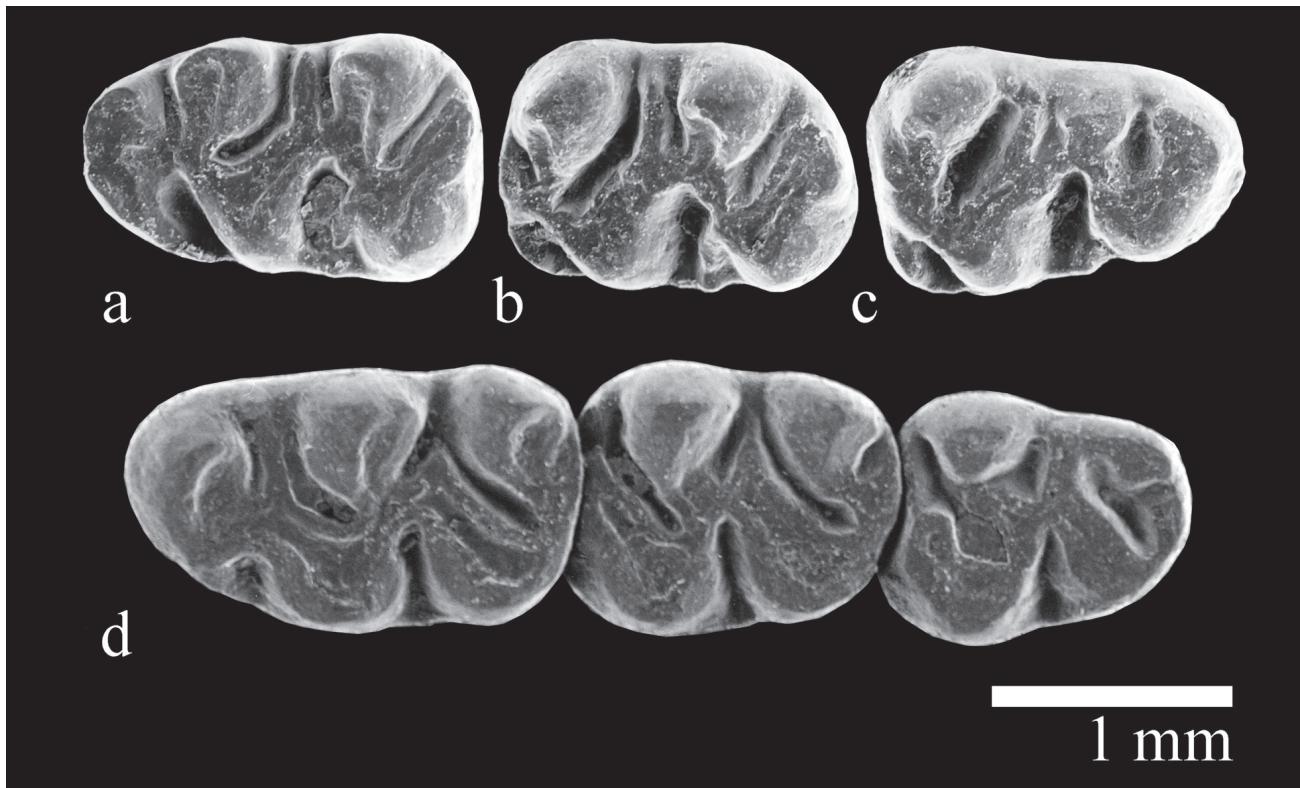


Figure 2: *Collimys* aff *transversus* HEISSIG, 1995 from Petersbuch 26. All teeth are shown in occlusal and left view. a. Right m1 (CRW P26-00001). b. Right m2 (CRW P26-00002). c. right m3 (CRW P26-00003). d. Left maxillary with M1-M3 (CRW P26-00004).

anterolophid reaches the base of the protoconid; narrow protosinusid; the disposition of the double anterolophid is hardly observable after light wearing; the lingual branch of the double anterolophid reaches the lingual part of the anteroconid, whereas the labial branch reaches most often the labial anterolophid near the anteroconid; it may also be connected to the anteroconid (Fig. 2a); the long mesolophid either ends in a mesostyloid or reaches the border of the tooth; the ectomesolophid may be absent (2 out of 8) or curved and ends in the ectostyloid; it is connected to the ectolophid near the hypoconid; the posterolophid is often broadest the near the hypoconid; two roots.

m2: The lingual anterolophid is reduced; the labial anterolophid reaches the base of the protoconid; the mesolophid always reaches the border of the tooth; ectomesolophid absent (5 out of 8) or complete; broad posterolophid; two roots.

m3: The lingual anterolophid is reduced; the labial anterolophid is long but more isolated from the anteroconid than in the m2; mesolophid always complete; entoconid developed as a crest; valley between these two structures variable in development; an ectomesolophid-shaped stylid may close the labial sinusid; two roots.

Discussion: The description of *C. transversus* is based on 14 specimens from the type locality. As a result, the intraspecific variability of the species remains poorly known. The population from Petersbuch 26 shows clear morphologic relations with *C. transversus*, although the teeth are larger than the specimens from Steinheim (see Tab. 1 and Fig. 3). Based on the comparison of the variability in size of *Collimys lon-*

gidens (KÄLIN & ENGESSER 2001), we refrain from describing this population as a new species. The size of the single M1 from Le-Locle-Sous-le-Stand (KÄLIN et al 2001: pl. 1, fig. 5) corresponds to Petersbuch 26.

Species: *Collimys gudrunae* sp. nov.
Figure 4

1997 *Collimys transversus*. – RUMMEL: p. 90.

Etymology: In honour of Gudrun DAXNER-HÖCK (Vienna) for her intensive work on Miocene mammals and *Collimys* in particular.

Holotype: Right fragmentary maxillary with M1 (NMA 2007/1/2017); measurements; 2.06 x 1.32; Fig. 4, b1 and b2.

Type locality: Petersbuch 31, Petersbuch near Eichstätt, Germany.

Type level: late Middle Miocene, MN 7.

Diagnosis: Brachydont *Collimys* species; upper molars with transversal and narrow sinus and most often complete mesoloph.

Differential diagnosis: The degree of hypsodonty of the molars of *C. hiri*, *C. longidens*, *C. dobosi* and *C. primus* is higher than in *C. gudrunae*. *C. transversus* is smaller and the mesolophs of M1 and M2 are less developed (see Tab. 2).

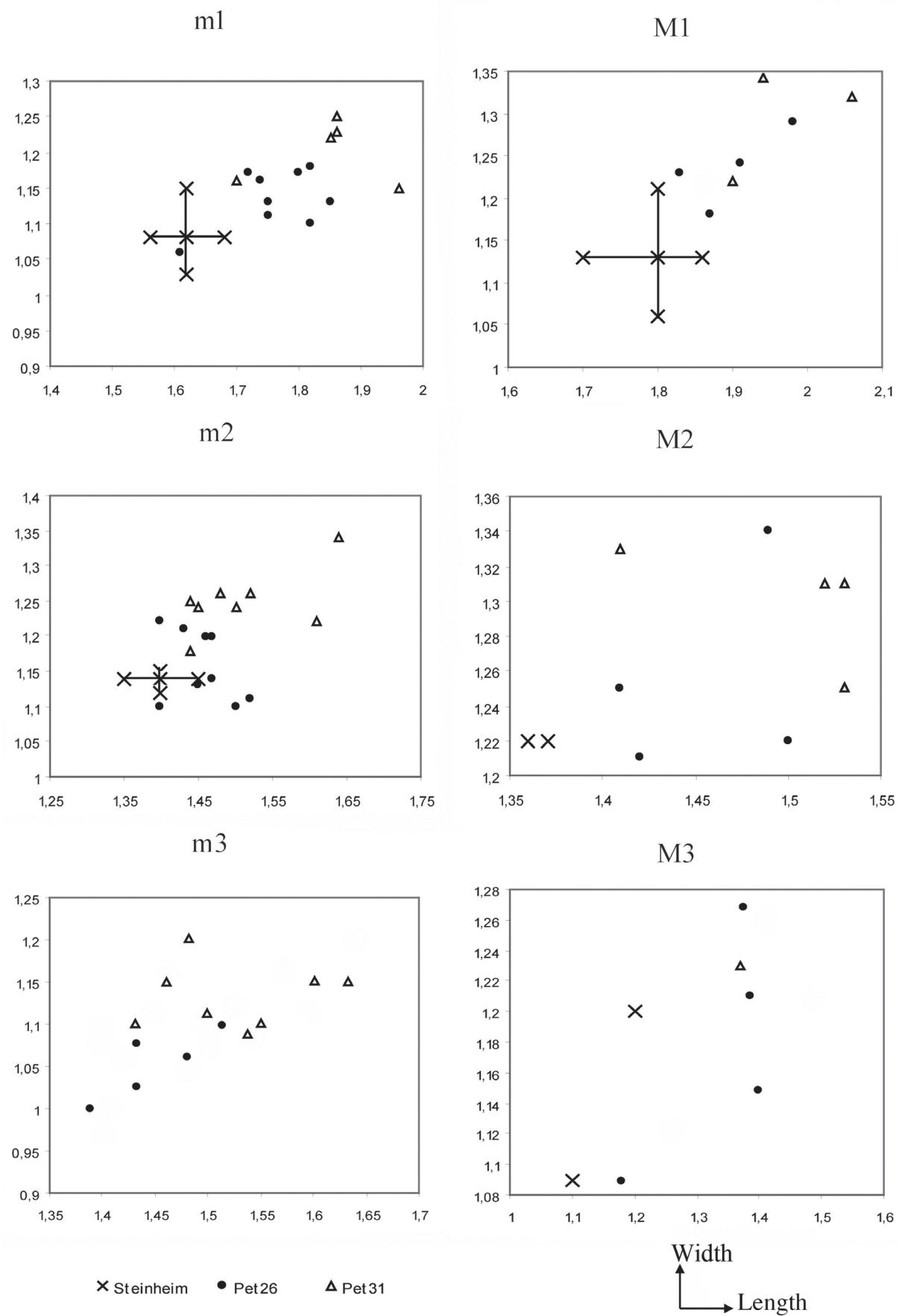


Figure 3: Scatter diagram of the *Collimys* molars in the lineage *transversus* / *gudrunae* sp. nov. The data of Steinheim are taken from HEISSIG (1995).

Table 1: Sample statistics of the *Collimys* molars. The data of *C. transversus* are from HEISSIG (1995), *C. longidens* from KÄLIN & ENGESSER (2001), *C. dobosi* from Felsőtárkány 3/2 (FT 3/2), Felsőtárkány-Felnémet (FF) from HÍR (2005, 2006), *C. hiri* from Hammerschmiede and *C. dobosi* from Hillenloh from PRIETO & RUMMEL (2009) and *C. primus* from DAXNER-HÖCK (1972).

	Length				Width			
	n	min.	mean	max.	n	min.	mean	max.
	M1							
<i>C. transversus</i>	4	1.7	1.8	1.86	4	1.06	1.13	1.26
<i>C. aff. transversus</i>	4	1.83	1.9	1.98	4	1.18	1.24	1.29
<i>C. gudrunae</i>	3	1.9	1.97	2.06	3	1.22	1.29	1.34
<i>C. sp. 1 (Pet10)</i>	2	1.87	1.94	2.01	2	1.18	1.18	1.18
<i>C. hiri (Ham1)</i>	1		1.82		1		1.19	
<i>C. bin (Ham3)</i>	8	1.92	1.97	2.04	8	1.09	1.16	1.25
<i>C. longidens</i>	4	1.9	1.98	2.12	4	1.04	1.16	1.28
<i>C. dobosi (FF2/3)</i>	0				0			
<i>C. dobosi (FF2/7)</i>	2	1.96	1.96	1.96	2	1.2	1.27	1.34
<i>C. dobosi (FT3/2)</i>	76	1.85	2	2.21	79	1.15	1.28	1.41
<i>C. dobosi (Hil)</i>	9	2	2.09	2.21	9	1.27	1.31	1.37
<i>C. primus</i>	1		1.96		1		1.28	
M2								
<i>C. transversus</i>	2	1.36	1.37	1.37	2	1.22	1.22	1.22
<i>C. aff. transversus</i>	4	1.41	1.46	1.5	4	1.21	1.26	1.34
<i>C. gudrunae</i>	4	1.41	1.5	1.53	4	1.25	1.3	1.33
<i>C. sp. 1 (Pet10)</i>	6	1.31	1.38	1.49	6	1.1	1.2	1.31
<i>C. hiri (Ham1)</i>	1		1.41		1		1.15	
<i>C. hiri (Ham3)</i>	12	1.26	1.4	1.53	12	1.16	1.2	1.28
<i>C. longidens</i>	5	1.32	1.42	1.48	5	1.2	1.24	1.28
<i>C. dobosi (FF2/3)</i>	4	1.33	1.43	1.53	4	1.19	1.23	1.26
<i>C. dobosi (FF2/7)</i>	3	1.47	1.53	1.58	3	1.26	1.33	1.4
<i>C. dobosi (FT3/2)</i>	82	1.4	1.53	1.67	82	1.18	1.29	1.4
<i>C. dobosi (Hil)</i>	5	1.45	1.55	1.7	5	1.26	1.36	1.54
<i>C. primus</i>	1		1.28		1		1.16	
M3								
<i>C. transversus</i>	2	1.1	1.15	1.2	2	1.09	1.15	1.2
<i>C. aff. transversus</i>	4	1.18	1.33	1.4	4	1.09	1.18	1.28
<i>C. gudrunae</i>	1		1.37		1		1.23	
<i>C. sp. 1 (Pet10)</i>	1		1.1		1		1.01	
<i>C. hiri (Ham1)</i>	1		1.23		1		1.15	
<i>C. hiri (Ham3)</i>	0				0			
<i>C. longidens</i>	4	1.08	1.12	1.16	4	1.08	1.12	1.18
<i>C. dobosi (FF2/3)</i>	1		1.33		1		1.22	
<i>C. dobosi (FF2/7)</i>	2	1.33	1.34	1.34	2	1.18	1.19	1.2
<i>C. dobosi (FT3/2)</i>	43	1.16	1.3	1.41	43	1.08	1.21	1.33
<i>C. dobosi (Hil)</i>	8	1.26	1.36	1.54	8	1.15	1.21	1.27
<i>C. primus</i>	0				0			
m1								
<i>C. transversus</i>	3	1.56	1.62	1.68	3	1.03	1.08	1.15
<i>C. aff. transversus</i>	8	1.72	1.78	1.85	9	1.1	1.14	1.18
<i>C. gudrunae</i>	5	1.7	1.85	1.96	5	1.15	1.2	1.25
<i>C. sp. 1 (Pet10)</i>	4	1.64	1.71	1.81	4	1.01	1.07	1.14
<i>C. hiri (Ham1)</i>	1		1.82				1.24	
<i>C. hiri (Ham3)</i>	12	1.66	1.72	1.84	12	1.05	1.1	1.14
<i>C. longidens</i>	7	1.7	1.86	2.06	8	1.08	1.15	1.2
<i>C. dobosi (FF2/3)</i>	2	1.83	1.84	1.85	2	1.11	1.12	1.12
<i>C. dobosi (FF2/7)</i>	2	1.85	1.87	1.89	2	1.15	1.17	1.19
<i>C. dobosi (FT3/2)</i>	76	1.71	1.86	2.09	76	1.06	1.19	1.3
<i>C. dobosi (Hil)</i>	15	1.83	1.96	2.13	15	1.15	1.22	1.33
<i>C. primus</i>	1		1.8		1		1.16	
m2								
<i>C. transversus</i>	2	1.35	1.4	1.45	2	1.12	1.14	1.15
<i>C. aff. transversus</i>	8	1.4	1.46	1.52	9	1.1	1.16	1.22
<i>C. gudrunae</i>	8	1.44	1.51	1.64	8	1.18	1.25	1.34
<i>C. sp. 1 (Pet10)</i>	3	1.41	1.46	1.52	3	1.16	1.19	1.23
<i>C. hiri (Ham1)</i>	1		1.48		1		1.22	
<i>C. hiri (Ham3)</i>	8	1.41	1.45	1.5	8	1.12	1.18	1.24
<i>C. longidens</i>	4	1.52	1.6	1.66	4	1.18	1.26	1.3
<i>C. dobosi (FF2/3)</i>	4	1.4	1.48	1.58	4	1.11	1.14	1.16
<i>C. dobosi (FF2/7)</i>	2	1.48	1.53	1.58	2	1.2	1.23	1.26
<i>C. dobosi (FT3/2)</i>	77	1.43	1.56	1.68	76	1.12	1.26	1.43
<i>C. dobosi (Hil)</i>	16	1.5	1.59	1.69	16	1.2	1.28	1.35
m3								
<i>C. transversus</i>	0				0			
<i>C. aff. transversus</i>	5	1.39	1.45	1.51	5	1	1.05	1.1
<i>C. gudrunae</i>	8	1.43	1.52	1.63	8	1.09	1.13	1.2
<i>C. sp. 1 (Pet10)</i>	2	1.3	1.32	1.33	2	1.06	1.07	1.08
<i>C. hiri (Ham1)</i>	1		1.52		1		1.1	
<i>C. hiri (Ham3)</i>	7	1.36	1.43	1.47	7	1.03	1.08	1.11
<i>C. longidens</i>	6	1.48	1.51	1.52	6	1.04	1.13	1.28
<i>C. dobosi (FF2/3)</i>	1		1.57		1		1.08	
<i>C. dobosi (FF2/7)</i>	0				0			
<i>C. dobosi (FT3/2)</i>	50	1.39	1.54	1.72	50	1.06	1.16	1.37
<i>C. dobosi (Hil)</i>	15	1.44	1.54	1.7	15	1.1	1.15	1.25
<i>C. primus</i>	1		1.32		0			

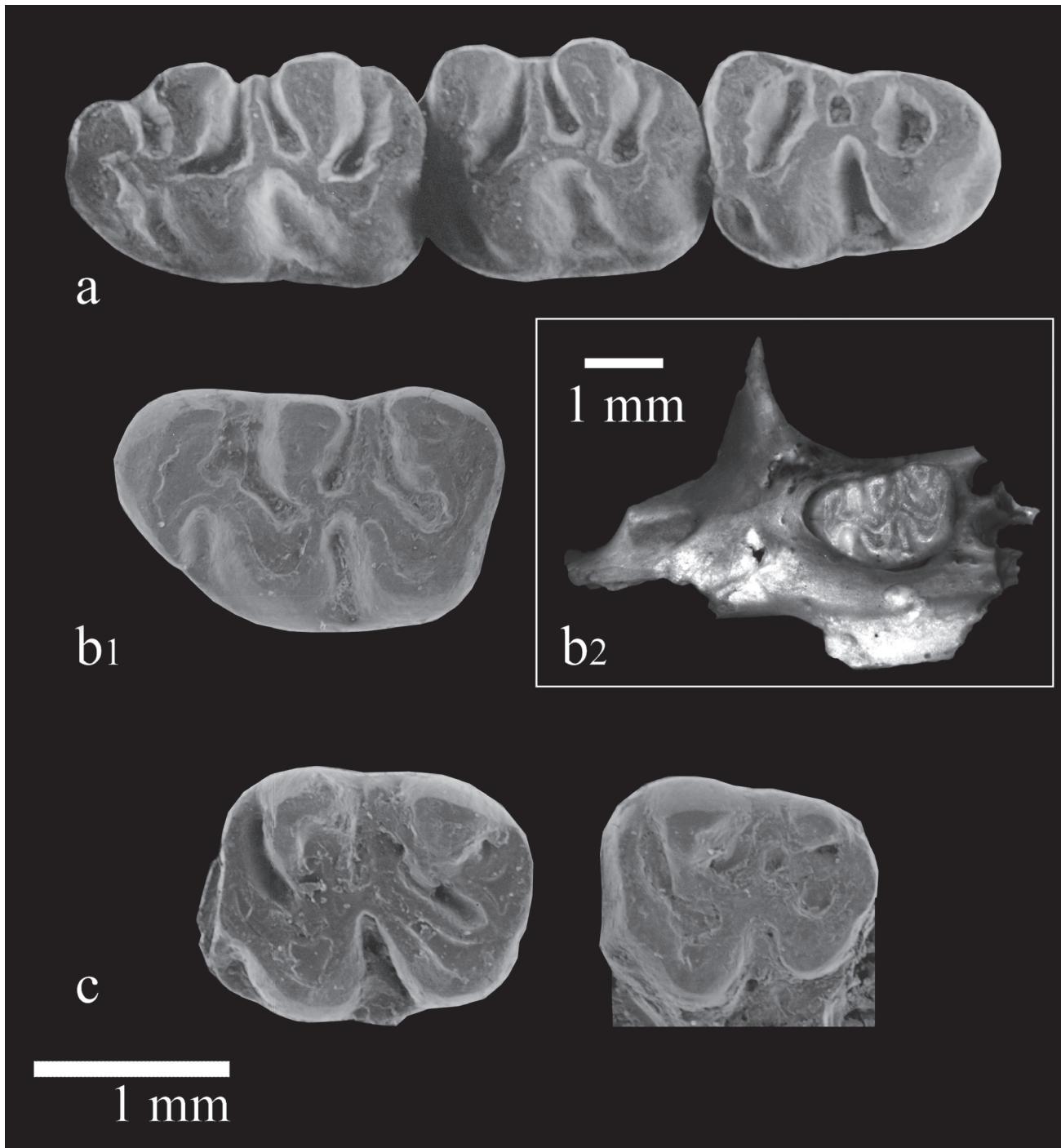


Figure 4: *Collimys gudrunae* sp. nov. from Petersbuch 31. All teeth are shown in occlusal and left view. **a.** Left lower jaw with m1-m3 (CRW P31-00001). **b1.** Holotype, right M1 (NMA 2007/1/2017). **b2.** Idem, view of the whole specimen. **c.** Left maxillary with M2-M3 (partially covered by sediment, CRW P31-00002).

Description of the holotype: The poorly preserved maxillary bone of the holotype is not sufficient for detailed analysis. For this reason, the description is limited to the first upper molar.

M1: Unsplit and broad anterocone and short lingual anteroloph; the labial anteroloph is missing; the labial spur of the anterolophule reaches the labial border of the molar close to the anterocone; the short anterolophule is directed forwards and connected to the broad anterior arm of the protocone; the posterior protolophule reaches the entoloph; the mesoloph re-

aches the border of the tooth; metalophule directed backwards; posterosinus highly reduced.

Description and measurements of the other specimens:

Material: 6 isolated teeth, 10 mandibles and 1 maxillary (CRW P31-00001 to 18).

Measurement: Table 1 and Figure 3.

Table 2: Main differences observed between the molars of the *Collimys* type species.

	<i>C. transversus</i>	<i>C. gudrunae</i>	<i>C. biri</i>	<i>C. longidens</i>	<i>C. dobosi</i>	<i>C. primus</i>
degree of hypsodonty	brachiodont	brachiodont				increase of the degree of hypsodonty →
m1	Mean lenght	1.62	1.85	1.71	1.86	1.8 (1 molar)
Upper molars	accessory enamel ridgeon metalophule	absent or very reduced	rare	rare	absent?	frequent
M1 M2	Lenght of mesoloph	medium sized to long	complete	medium sized to long	long to complete	most often complete
M3	"divided protolophule"	absent	absent	absent	absent	present

M1: Transversal and narrow sinus; mesoloph always reaches the labial border of the tooth; the backwards-directed metalophule reaches the reduced posteroloph; three roots.

M2: High and long labial anteroloph; lingual anteroloph reduced; transverse and narrow sinus; mesoloph complete, entomesoloph absent; metalophule directed backwards; three roots.

M3: The lingual anteroloph is highly reduced, the labial one is broad and transverse; the backwards directed protolophule forms a 90° angle to reach the neo-entoloph; the narrow mesoloph reaches the border of the molar; metacone present (small cusp); the metalophule splits into two and reaches the neo-entoloph and the posteroloph; three roots.

Mandible: see description and discussion of *Collimys* mandibles.

m1: Broad anteroconid with two directly adjacent cusps; the lingual anterolophid is missing; the labial anterolophid reaches the base of the protoconid; double anterolophulid; the labial branch of the anterolophulid is connected either to the labial part of the anteroconid (1 out of 5) or to the labial anterolophid near the anteroconid (3 out of 5); it may also be extremely reduced (1 out of 5; Fig. 4a); the lingual branch reaches the lingual part of the anteroconid; the mesolophid always reaches the lingual border of the m1; ectomesolophid complete (4 out of 5) or absent; two roots.

m2: Lingual anterolophid extremely reduced to absent; the labial anterolophid is connected to the base of the protoconid; mesolophid always complete; ectomesolophid absent; broad posterolophid; two roots.

m3: Lingual anterolophid absent; the labial anterolophid reaches the base of the protoconid; mesolophid always complete; the entoconid is developed as a crest; ectomesolophid-shaped ectostyli may close the sinusid; two roots.

Discussion: The overall morphology of the molars characterizes *C. gudrunae* as an evolved form of *C. transversus*.

Species: *Collimys* cf. *gudrunae*
Figure 5d

1994 *Collimys* sp. – BOLLIGER & RUMMEL: p. 246.

Occurrence: Petersbuch 10, Petersbuch 18

Material and measurements: Petersbuch 10 : 1 mandible with m1-m3 (CRW P10-00006; m1: 1.78 x 1.14; m2: 1.39 x 1.14; m3: 1.48 x 1.14); Petersbuch 18: 1 m1 (CRW P18-00001; 1.82 x 1.2)

Description and discussion: The single m1 of Petersbuch 18 is morphologically close to the lineage of *C. transversus*. The specimen is too large to correspond to *C. transversus* and agrees with *C. gudrunae*.

A lower jaw of Petersbuch 10 can also be assigned to this lineage. The ectomesolophids are complete on both m1 and m2. The attribution of this specimen to *C. gudrunae* remains uncertain, as the molars agree also in their size with *C. aff. transversus* from Petersbuch 26.

Species: *Collimys* sp. 1
Figures 5a and 6

- 1994 *Collimys* sp. – BOLLIGER & RUMMEL: p. 243 and 246.
1994 *Collimys* sp. – HEISSIG: p. 28, fig. 2.
1995 *Collimys* sp. – RUMMEL: p. 120.
2000 *Collimys* cf. *transversus*. – RUMMEL: p. 166.

Occurrence: Petersbuch 6, Petersbuch 10

Material and measurements: Petersbuch 6: 1 mandible with m1-m3 (BSPG 1993 IV 1688; m1: 1.66 x 1.12; m2: 1.48 x 1.21; m3: 1.5 x 1.16); Petersbuch 10: 14 isolated molars and 2 upper jaws (CRW P10-00001 to P10-00017); measurements see Table 1.

Description (Petersbuch 10): M1: unsplit anterocone with lingual anteroloph well developed and labial anteroloph absent; short anterolophule; the anterocone may also have two directly adjacent cusps without clear fissuration (1 out of 2 molars); the anterolophule is extremely reduced on one tooth (Fig. 6d), whereas this crest is developed (longitudinal) on the second one; the labial spur of the anterolophule ends on the labial border of the molar, near the anterocone, in a style-like structure; the broad posterior protolophule is connected to the entoloph; the long mesoloph ends on the labial border of the M1; the labial part of the mesoloph is distinctly lower than the rest of the structure; the anterior arms of both protocone and posterior part of the entoloph are broad crests, in which the protocone and hypocone respectively are integrated, causing the sinus to be broader and more backwards-directed than in *C. transversus*; metalophule directed backwards; three roots.

M2: Well developed and curved lingual anteroloph; the strong and transverse labial anteroloph reaches the base of the paracone; well developed anterocone; strong posterior protolophule; the long mesoloph ends in the mesostyl or reaches the border of the molar; the broad paracone spur may be connected to the mesostyl or mesoloph; the metalophule is

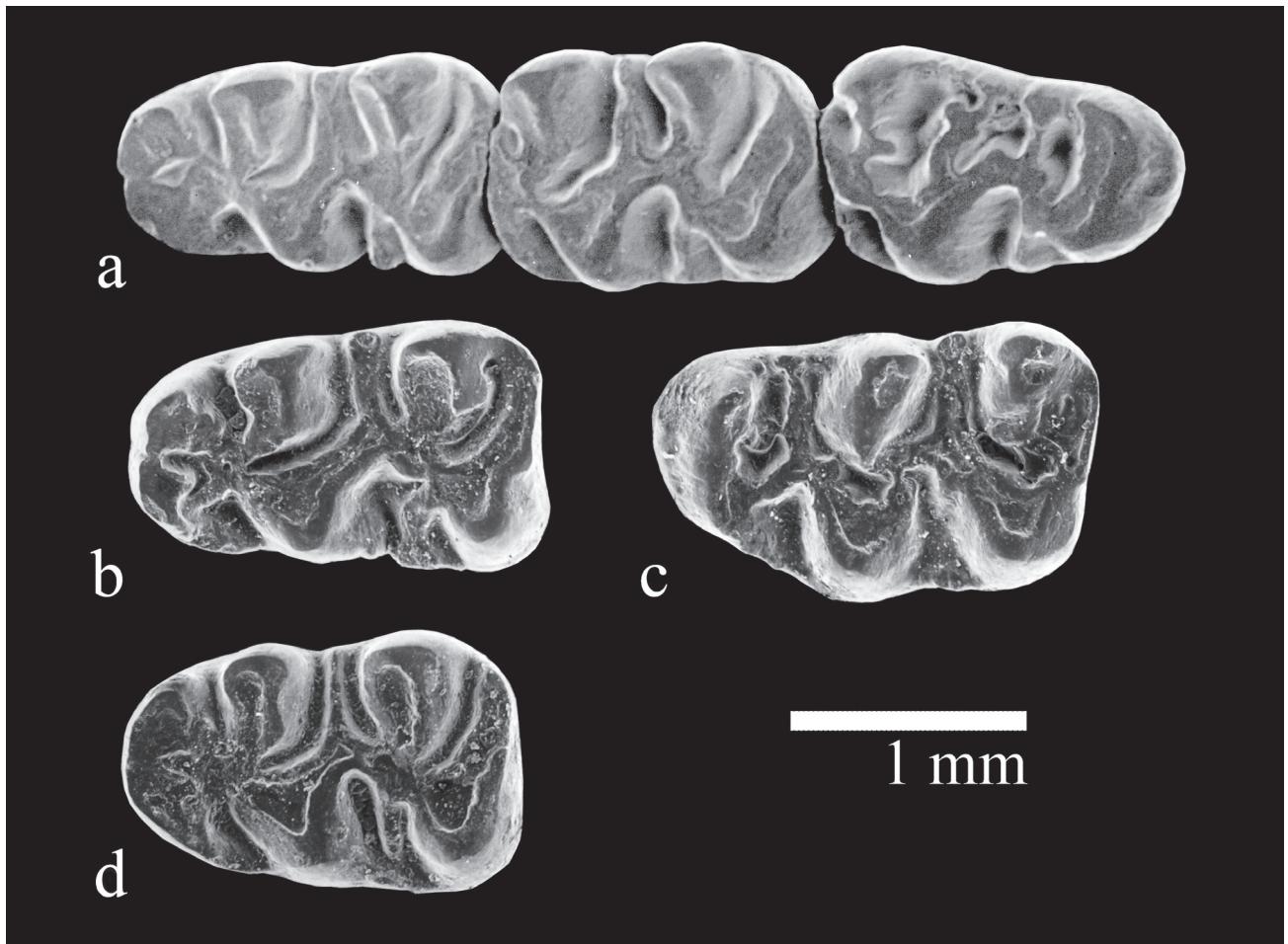


Figure 5: *Collimys* cf. *gudrunae*, *Collimys* sp.1 and 2 from Petersbuch. All teeth are shown in occlusal and left view. **a.** Right lower jaw with m1-m3, *Collimys* sp. 1, Peterbuch 6 (BSPG 1993 IV 1688). **b.** Left m1, *Collimys* sp. 2, Petersbuch 48 (BSPG 1998 XVI 1197). **c.** Left M1, *Collimys* sp. 2, Petersbuch 48 (BSPG 1998 XVI 1198). **d.** Left m1, *Collimys* cf. *gudrunae*, Petersbuch 18 (CRW P18-00001).

directed backwards; a remainder of the anterior metalophule is present on four molars (out of 6); three roots.

M3: The molar differs from the M2 in its reduced posterior part; indistinct metacone, integrated in a postero-labial crest which is connected to the hypocone to the base of the paracone; the broad mesoloph is shifted backwards (compared to M2) and connected to the metacone.

Mandible: see description and discussion of *Collimys* mandibles.

m1: Three molars have an anteroconid composed of two linked cusps, with a slight fissuration on the juvenile specimen that extends on the anterior wall of the anteroconid; one tooth has a triple anteroconid but the separation of the cusps is not clear; the strong labial anterolophid reaches the base of the protoconid and the lingual anterolophid is missing; the oblique lingual branch of the anterolophid reaches the lingual part of the anteroconid and the labial branch is connected to the labial anterolophid; the connection between protoconid and anterolophid is interrupted on 2 out of 4 molars; complete ectomesolophid present in all specimens; the mesolophid always reaches the lingual border of the m1; two roots.

m2: anteroconid present; highly reduced lingual anterolophid; ectomesolophid most often complete; two roots.

m3: the lingual anterolophid is missing; metaconid pre-

sent; the mesolophid terminates on the lingual border of the molar; the metalophid extends parallel to mesolophid, but on one molar these two structures can hardly be distinguished; a posterior fissuration is well developed between the hypoconid and the posterolophid in one molar (Fig. 6c); this structure is not recognizable in the other molars, although they all show a small indentation on the posterior wall of the posterolophid; two roots.

Discussion: The most noticeable differences between *Collimys* sp. 1 and the *Collimys transversus-gudrunae* group occurs in the broad and backwards-directed sinus of the M1 and especially M2 (Fig. 7). The m1 seems to be more elongated, but some rare extreme morphotypes from Petersbuch 26 and 31 show a somewhat similar outline. The cusps of the lower molars are also less voluminous, especially the hypoconid of the m3. In size, the molars are comparable to *C. aff. transversus*.

The form of the sinus of the M1 and M2 does not concur with the emended diagnosis of the genus as proposed by HEISSIG (1995). In fact, this author specifies that the valleys of the *Collimys* molars are fissure-like and narrow. Furthermore, he indicates in the diagnosis the sturdiness of the cusp(id)s, a characteristic that is not as clear in *Collimys* sp.1 as in the other species of the genus.

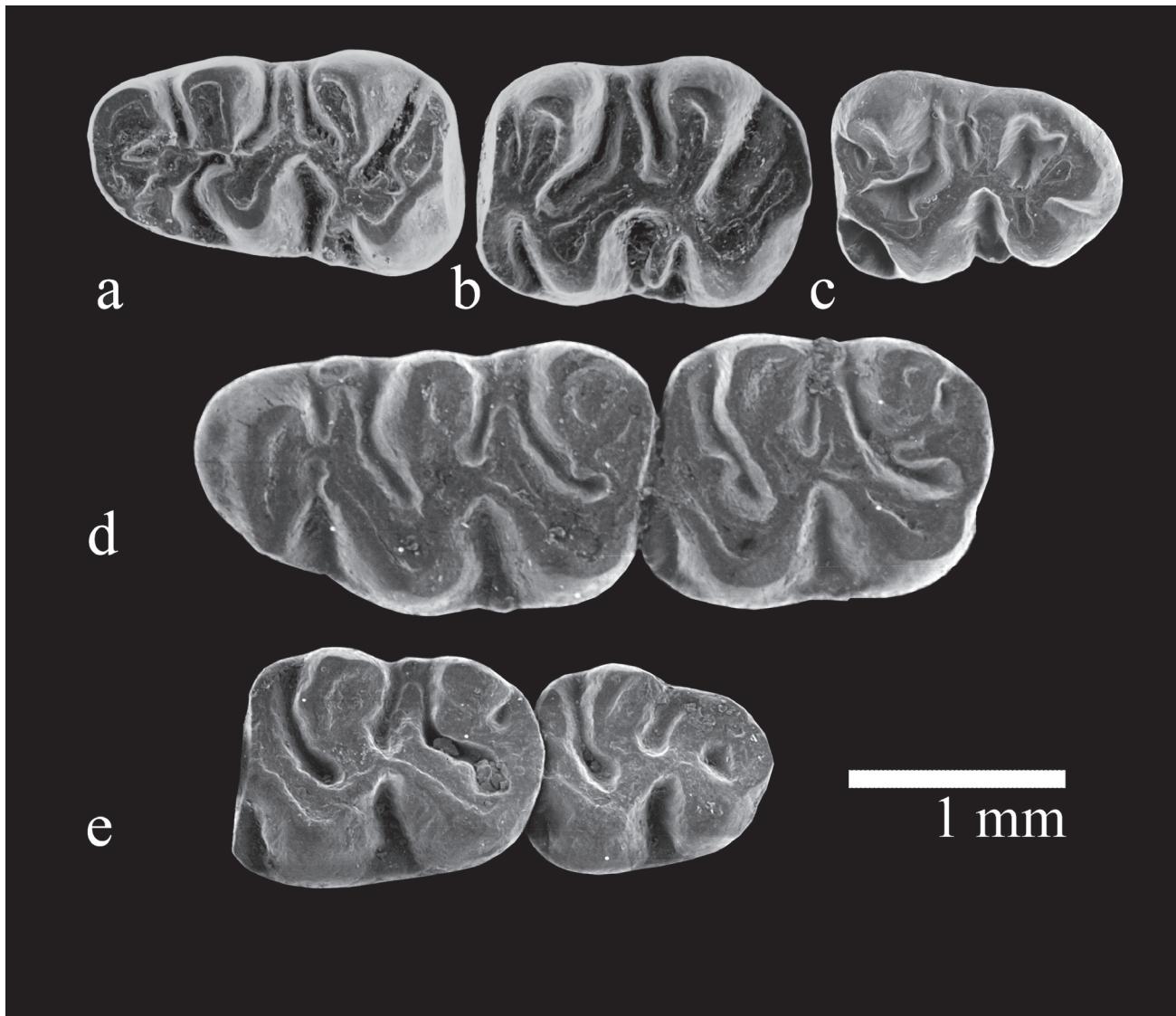


Figure 6: *Collimys* sp. 1. from Petersbuch 10. All teeth are shown in occlusal and left view. **a.** Left m1 (CRW P10-00001). **b.** Right m2 (CRW P10-00002). **c.** Right m3 (CRW P10-00003). **d.** Left maxillary with M1-M2 (NMA 2007/2/2017). **e.** Left maxillary with M2-M3 (CRW P10-00004).

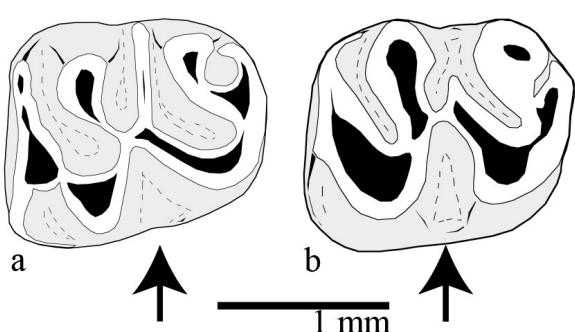


Figure 7: Differences in the morphology of the sinus between *Collimys* sp. 1. M2 from Petersbuch 10 (**a**, right M2, CRW P10-00016) and M2 of the *Collimys transversus/gudrunae* lineage (**b**, Petersbuch 26, CRW P26-00020). All teeth are shown in occlusal and left view.

On the other hand, the other morphologic characteristics of the molars – especially the absence of the anterior protolophule on the upper teeth – are also seen in the other *Collimys* species. Furthermore, the mandible from Petersbuch 6 shows clear affinities with *Collimys*. This specimen is attributed to *Collimys* sp. 1 based on the general outline of the m1 and the narrow hypoconid of the m3.

The morphologic differences observed in the molars from Petersbuch 10 justify the creation of a new species. However, the small number of teeth prohibits a more in-depth analysis of the morphologic variability of the species. As a result, taxonomic confusions may occur when comparing with other *Collimys* species. Furthermore, due to the presence of *C. cf. gudrunae*, along with the doubts concerning the relative age of the fissure filling Petersbuch 10, a new species is not described at this time.

Description and discussion of *Collimys* mandibles: Petersbuch 26 and 31: In labial view, the anterior end

Table 3: Width/length ratio of the *Collimys* DAXNER-HÖCK, 1972 molars. Ne: Nebelbergweg, Pet: Petersbuch, Ste: Steinheim, Ham: Hammerschmiede, Hil: Hillenloh, FF 3/2: Felsötárkány 3/2. *Italics*: samples with less than 5 molars.

	Ste	Pet26	Pet31	Ham3	Ne	FT 3/2	Hil
M1	0.63	0.65	0.64	0.59	0.59	0.64	0.63
M2	0.89	0.86	0.87	0.86	0.87	0.84	0.88
M3	1	0.89	0.9	0.93	1	0.93	0.89
m1	0.67	0.64	0.65	0.64	0.62	0.64	0.62
m2	0.81	0.79	0.83	0.81	0.79	0.81	0.81
m3		0.72	0.74	0.76	0.75	0.76	0.75

of the masseteric fossa is located ventral to the sinusid up to ventral to the anterior root of the m1. The mental foramen is positioned below the anteroconid of the m1, around the height of the end of the slightly concave masseteric fossa. The coronoid process conceals the posterior part of the m2. The slightly convex ventral edge of the horizontal ramus ends

ventral to the posterolophid of the m3 in lateral view. The top of the incisor ends above the occlusal plane of the molar row.

Petersbuch 6: The mandible from Petersbuch 6 differs from those from Petersbuch 26 and Petersbuch 31 mainly in the morphology of the ventral edge of the horizontal ramus, which is less convex.

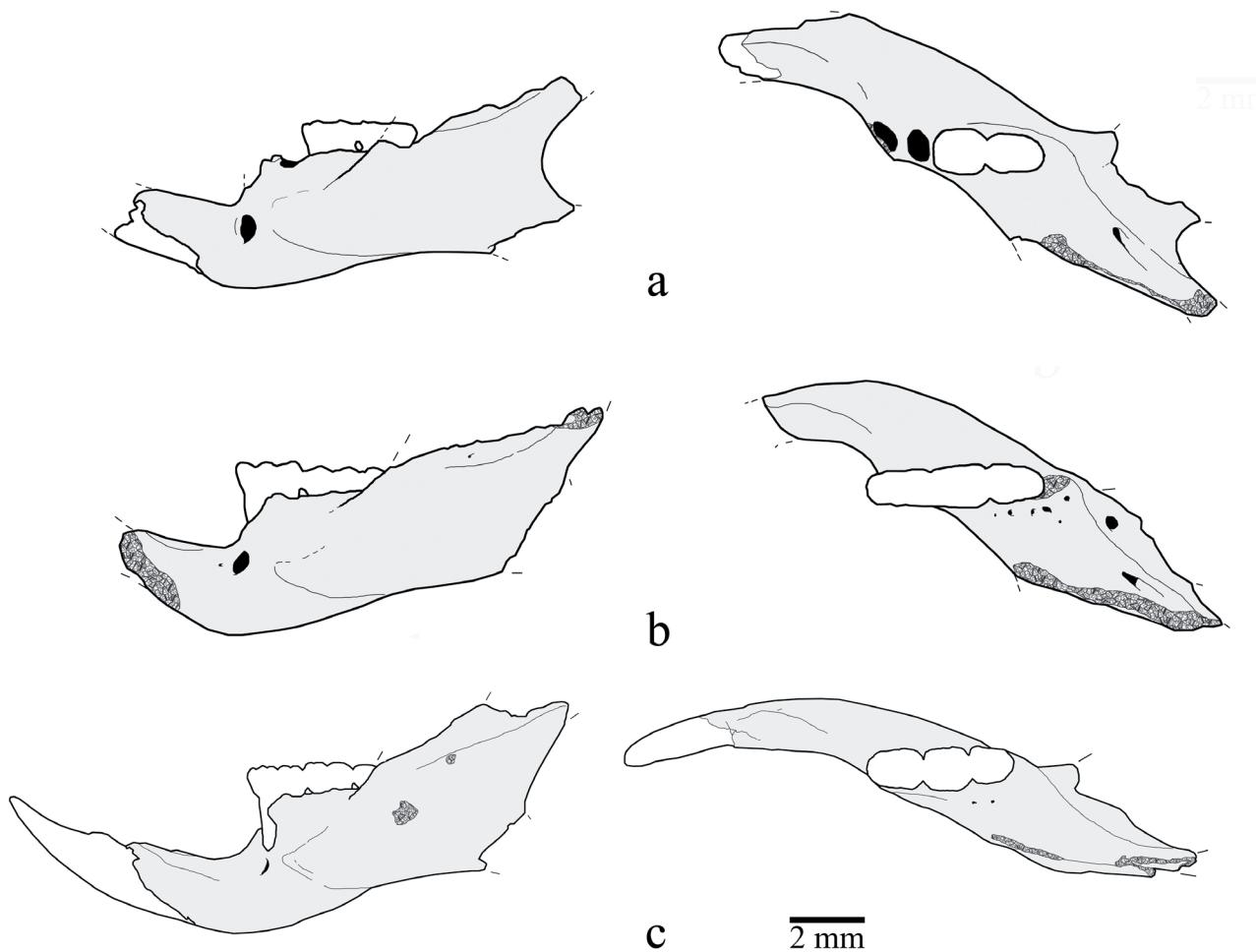


Figure 8: Mandibles of *Collimys* DAXNER-HÖCK, 1972 and *Democricetodon* FAHLBUSCH, 1964. **a.** *Collimys* aff. *transversus* HEISSIG, 1995 from Petersbuch 26: left mandible with m2-m3 (CRW P26-00030). **b.** *Collimys* sp. 1 from Petersbuch 6: right mandible with m1-m3 (BSPG 1993 IV 9). **c.** *Democricetodon* cf. *brevis* from Petersbuch 6: right mandible with m1-m3 (BSPG 1993 IV 912). All mandibles are presented in labial and occlusal views (left).

The differences observed in the mandibles from Petersbuch 26/31 and Petersbuch 6 confirm the separate status of the lineage *C. transversus / gudrunae*, as observed from the molars. The differences in both molar and jaw morphology might be used as an argument to separate *C. transversus / gudrunae* sp. nov. and *C. sp. 1* at generic level, although we refrain from describing this as a new genus because of: I) the restricted jaw material from Petersbuch 6 and Petersbuch 10, II) the absence of preserved mandibles in most of the *Collimys* species, III) the dental morphology, which does not clearly support this assumption (see above), IV) the fact that the micromammalian fossil record is mostly based on isolated teeth or highly damaged mandibles and such a generic definition, based on mandibular characters, could lead to unhelpful complications.

Species: *Collimys* sp. 2
Figure 5b,c

Occurrence: Petersbuch 48

Material and measurements: P48: M1 (BSPG 1998 XVI 1198; 2.03 x 1.25), m1 (BSPG 1998 XVI 1197; 1.84 x 1.10).

Description and discussion: The m1 from Petersbuch 48 corresponds morphologically with the molars of *Collimys* sp. 1, but is somewhat larger. The massive lingual branch of the double anterolophid reaches the anteroconid, whereas its labial branch ends in the labial anterolophid; the ectomesolophid is complete. In the M1, the slanted anterolophule reaches the lingual part of the broad anterocone; the labial spur of the anterolophule and mesoloph end on the border of the tooth; the sinus is directed backwards; a bulge on the anterior arm of the protocone may represent a highly reduced anterior protolophule.

The two molars are tentatively attributed to the genus *Collimys*. Based on the differences to *Collimys* sp. 1 from Petersbuch 10, these teeth are determined as *Collimys* sp. 2.

5. Evolutionary lineages

The German *Collimys* material suggests that at least two independent evolutionary lineages existed (Fig. 9):

I)- Lineage *transversus / gudrunae*: In Germany, this lineage is currently confined to Steinheim, the fissures fillings Petersbuch 26 and Peterbuch 31. The evolutionary trend within this lineage is primarily characterized by an increase in size, increase of the length of the mesolophs in M1 and M2 and development of the cusps of the anteroconid of the m1. The rare *C. cf. gudrunae* specimens from Petersbuch 10 and 18 represent the last occurrence of this species in the fossil record.

II)- Lineage *hiri / dobosi*: This lineage is only documented by molars from stratified localities (PRIETO & RUMMEL 2009). Main characteristics include: size increase, augmentation of the degree of hypsodonty and length of mesoloph in M1.

Assignment of *Collimys* sp.1 and 2 from the fissures fillings Petersbuch 6, 10 and 48 to the first lineage is rejected and is not evident in the *hiri / dobosi* lineage.

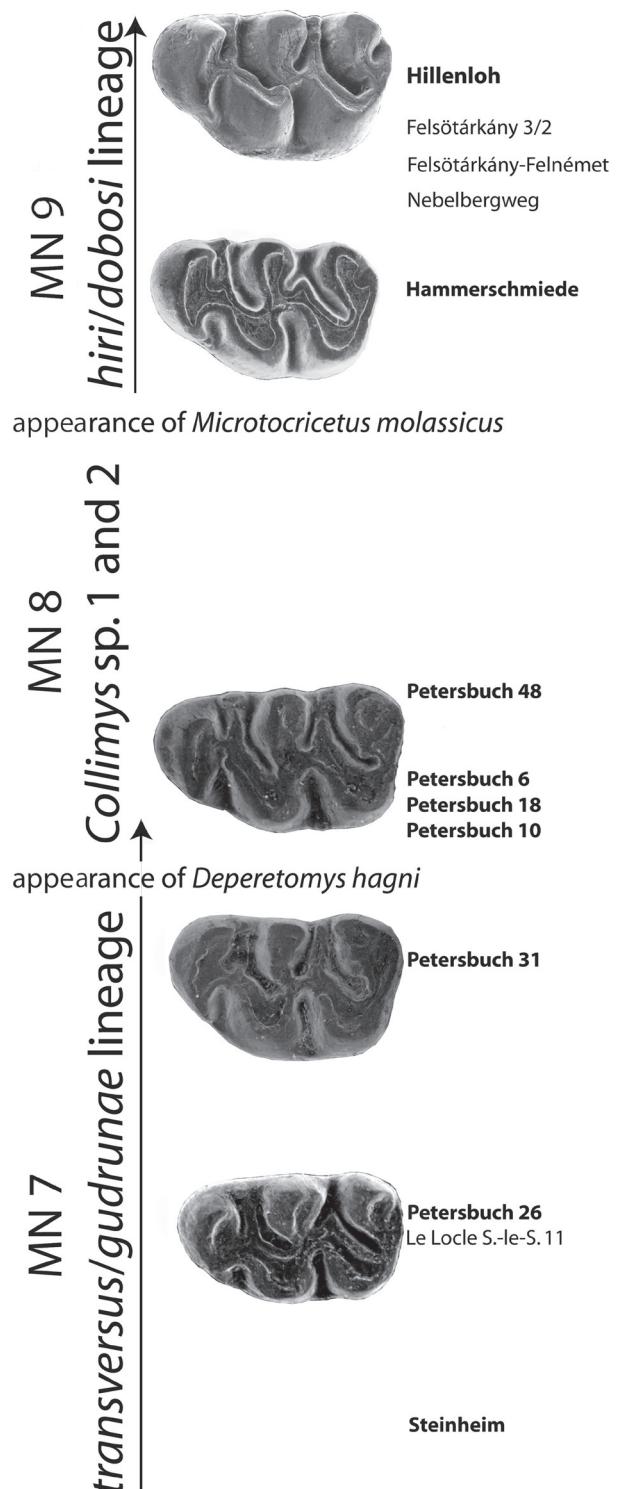


Figure 9: Evolution of *Collimys* DAXNER-HÖCK, 1972. The height of the MN-“zones”-rectangles is not proportional to their duration.

6. Discussion

6.1 Relationships and systematic position of *Collimys*

Note: The separation of the mammal “zones” 7 and 8 follows the concept presented by KÄLIN et al. (2001). This is used as a local zonation, and does not imply a general separation of MN 7/8 in the MN zonation.

Two main *Collimys* groups evolved independently in MN 7 (*transversus* / *gudrunae* lineage) and MN 9 (*hiri* / *dobosi* lineage) (Fig. 9). In MN 8, the *Collimys* populations cannot be correlated to these lineages (with the exception of the rare *C. cf. gudrunae* from Petersbuch 10 and 18) or the genus is not reported (Anwil, Giggenhausen, Kleineisenbach, see FAHLBUSH 1964; ENGESSER 1972; PRIETO 2007). It is then justified to hypothesize that the two lineages belong to different genera, and the morphologic similarities occur due to parallelism. On the other hand, the main morphologic character distinguishing the two lineages is the degree of hypsodonty of the molars. At present this character is insufficient to justify the establishment of a new genus for the species of the *transversus* / *gudrunae* lineage.

HEISSIG (1995: p. 104/105) proposed that *Collimys* evolved from a species morphologically close to *Democricetodon* aff. *freisingensis* (=*D. gaillardi* in BAUDELOT 1972) of Sansan. The resemblance of *Collimys* to *Democricetodon* species having highly developed transversal crests and slightly fissured anteroconid in m1 was also recognized by KÄLIN & ENGESSER (2001: p. 43). The consequences of these analyses are that some difficulties may occur in distinguishing the two genera (and *Neocricetodon* (=*Kowalskia*) and *Cricetulodon*) when dealing with m1 and m2, whereas the difference is clearer in the other tooth positions. The morphology of the mandible of *Democricetodon* differs from *Collimys*, especially in the more convex ventral edge of the horizontal ramus (Fig. 8), discriminating the two genera. The absence of the anterior protolophule of the upper molars – although this crest may be present in a few specimens of *C. dobosi* – is a sound taxonomic character of *Collimys*, but not restrictive. In fact, VAN DER MEULEN et al. (2003) synonymized *Fahlbuschia*, *Pseudofahlbuschia* and *Renzimys* with *Democricetodon*. The absence of the anterior protolophule in most of the M2 is present in some *Democricetodon* species (*lacombai* for example). FREUDENTHAL (2006) rejected these synonymies. Although the *Collimys* material does not provide new information with regard to this question, it is observed that *Fahlbuschia*, *Renzimys* and *Pseudofahlbuschia* molars, with narrow anterocone in the M1, are not recorded for central and eastern Europe (FREUDENTHAL 2006: p. 48, and personal observation). On the contrary, *Collimys* has not been reported from Western Europe to date. FREUDENTHAL’s interpretation of *Democricetodon* is applied in this work.

Because of the close resemblance of dental morphology, *Collimys*, at least the *transversus* / *gudrunae* lineage, should be integrated in the same subfamily as *Democricetodon*. Due to the lack of some important diagnostic features and the possibility of morphologic parallelism between the different *Collimys* lineages, we refrain from assigning the genus to a subfamily.

6.2 Biostratigraphic implications

The small mammalian fauna from locality Steinheim (MN 7) is characterized by a *gregarius*-like species of *Megacricetodon*, which differs from the species of La Grive specifically by a lesser split anterocone in the upper first molar. This species, also present in Petersbuch 31, is provisionally named *M. aff. gregarius*. A second species, *M. minor*, is found in the same localities. A different evolutionary stage of *Collimys* is found in each of these localities, with *C. gudrunae* evolving from *C. transversus*. MN 7 can easily be deduced from the evolutionary stage of *C. aff. transversus* at Petersbuch 26, which is intermediate between the populations from Steinheim and Petersbuch 31.

The localities Petersbuch 6, 10, 18 and 48 all contain *Deperetomys hagni*, so that MN 8 has to be proposed for these fissure fillings. In Petersbuch 6, 10 and 18 *M. aff. gregarius* is replaced by *M. aff. germanicus*, a species with high intraspecific variability (anteroconid simple to clearly divided). As the stratigraphic value of the single *Collimys* molar from Petersbuch 18 is questionable (*C. cf. gudrunae*), we follow RUMMEL (2000) who proposed that Petersbuch 18 is older than Petersbuch 6 based on the evolutionary stage of *Cricetodon*. The presence of *M. aff. germanicus* (morphotype with divided anteroconid) in Petersbuch 10 links this fissure filling with Petersbuch 6 and 18 rather than Petersbuch 31. *Cricetodon bolligeri*, a species that is only known from Petersbuch 10 (RUMMEL 1995), might indicate an older age for this fissure filling. The occurrence of two *Collimys* species (*C. cf. gudrunae* and *C. sp. 1*) in this fissure is singular for the studied samples. In Petersbuch 48 *Deperetomys hagni* is abundant, whereas *Cricetodon* is a rare component. The similar fauna found in Petersbuch 35 was dated by RUMMEL (2000) as younger than Petersbuch 6 and Petersbuch 18. A similar relative age is proposed for Petersbuch 48.

The renunciation of the choice of Steinheim and Anwil as reference localities for MN 7 and MN 8 respectively leads to the fusion of the two ”zones” (DE BRUIJN et al. 1992) with the fissure filling La Grive M as reference locality for MN 7+8. On the other hand, MEIN & GINSBURG (2002) proposed La Grive M and La Grive L3 as reference localities respectively for MN 7 and MN 8 where the MN 8 faunas are characterized by a few immigrations and new evolutionary stages in some lineages. If the ancestor/descendant relationship between the populations is accepted – an assumption rejected by AGUILAR et al. (1999: 23) – *M. aff. gregarius* from Steinheim and Petersbuch 31 might be more primitive than *M. gregarius* from La Grive M. Unfortunately, the latter locality does not contain *Collimys* (MEIN & GINSBURG 2002) and this hypothesis cannot be tested in the context of this study. The same problem appears for the MN 8 faunas, which are still rare in the NAFB, and *Collimys* is absent in the richest localities such as Anwil, which is younger than the faunas presented here based on the evolutionary level of *Megacricetodon* populations. La Grive L3 lacks *Collimys* as well.

Although deposits contemporaneous with Sansan are not recorded for the Bavarian molasse basin, either older or younger MN 6 localities are documented in the NAFB (HEISSIG 2006; KÄLIN et al. 2001). In Switzerland, deposits of the end of MN 6 and beginning MN 7 are marked by the immigration of *M. aff. gregarius*. This species is recorded in Helsighausen (BOLLIGER

1994) and is probably similar to the species of Petersbuch. Furthermore, KÄLIN et al. (2001) describe a *Collimys* M1 from Le Locle-Sous-le-Stand W&B 11 that shows clear similarities with *Collimys transversus*. The size of this specimen does not differ from the population from Petersbuch 26 and is classified here as *C. aff. transversus*. Nevertheless, Le Locle is older than Petersbuch 31, which contains the more evolved *C. gudrunae*. Based on the absolute dating of the bentonite from Leimbach, KÄLIN et al. (2001) estimated that the deposition of the sediments of the UFM from Le Locle occurred between 13,5 and 14 My bp, corresponding in the MN-zonation to a time ranging from the uppermost MN 6 to probably the base of MN 8. In this sequence the MN 7 deposits were accumulated during 100 to 200 ky. If the top of sequence of the Le Locle region is MN 8, the evolution from *C. aff. transversus* to *C. gudrunae* also happened within 100 to 200 ky. BOLLIGER (1998: 326) reports the presence of this genus from Chräzerentobel 650m, a site provisionally placed in the upper part of MN 8 (RUMMEL & KÄLIN 2003). The second Swiss locality containing the genus is Ottenberg 3 (BOLLIGER 1996; KÄLIN et al. 2001). *Deperetomys hagni* is found in this locality and the proposed age is placed at the base of the MN 8. However, the relative dating between these MN 8 localities and Petersbuch at present cannot be determinate based on *Collimys*.

7. Conclusions

The new fossils of *Collimys* from Germany contribute to an evaluation of the evolutionary trends within the interval MN 7–MN 9 (Middle to Late Miocene), and significantly improve our knowledge about mammalian biostratigraphy:

I) *Collimys gudrunae* rapidly evolves from *Collimys transversus*. This lineage characterizes MN 7 faunas although *C. gudrunae* may survive after the first occurrence of *Deperetomys hagni*. II) Parallel to the immigration of *Deperetomys hagni*, *Collimys* sp. appears as a possible immigrant near the MN 7/MN 8 transition. The phylogenetic relationships of these species remain elusive. III) In MN 9 the lineage *hiri* / *dobosi* is characterized by a size increase, in addition to an increase of the degree of hypodonty (PRIETO & RUMMEL 2009). Following DAXNER-HÖCK (2004: p. 6), this lineage perhaps terminates in *C. primus* from the Late Miocene (MN 11) of Eichkogel, as *Pseudocollimys steiningeri* from Schernham (MN 10) represents an evolutionarily independent branch.

The lineage *transversus* / *gudrunae* may be very useful in biostratigraphy due to its proposed rapid evolution in MN 7. However, additional material from stratified localities is required to support this suggestion. It is not directly related with the *C. hiri* / *dobosi* lineage which is the first useful small mammal lineage for around the base of the MN 9.

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8. References

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