THE GLIRIDAE (MAMMALIA) FROM THE OLIGOCENE (MP 24) OF GRÖBEN 3 IN THE FOLDED MOLASSE OF SOUTHERN GERMANY

by

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CONTENTS

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Key-words: Mammals, Gliridae, Oligocene, level MP 24, *Cyrena* Beds, Germany, folded molasse, Biostratigraphy, Palaeoecology.

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ABSTRACT

This study describes four taxa of Gliridae from the Oligocene mammal locality Gröben 3: *Gliravus tenuis* BAHLO, 1975, *Bransatoglis micio* (MISONNE, 1957), *B. planus* (BAHLO, 1975) and *B. heissigi* n. sp. *Gliravus tenuis* from Gröben 3 is somewhat more advanced than the type population found in Heimersheim. This confirms previous research suggesting that Gröben 3 should be dated earlier than Heimersheim (MP 24). The first documented occurrence of *B. micio* around level MP 24 was found in Gröben 3. An abundance of tooth material from *B. planus* in Gröben 3 makes it possible, for the first time, to observe evolutionary stages within this species from MP 21 until MP 28. *B. heissigi* n. sp. is restricted to level MP 24. This species is located between *B. misonnei* (MP 20 - 23) and *Microdyromys praemurinus* (MP 25 - 28). Within the lineage *Bransatoglis bahloi* – *B. misonnei* – *B. heissigi*, a decrease in size is noticeable.

KURZFASSUNG

Aus der oligozänen Säugerlokalität Gröben 3 werden in dieser Arbeit vier Glridentaxa beschrieben: *Gliravus tenuis* BAHLO, 1975, *Bransatoglis micio* (MISONNE, 1957), *B. planus* (BAHLO, 1975) und *B. heissigi* n. sp.. *Gliravus tenuis* von Gröben 3 ist etwas weiter entwickelt als von Heimersheim und bestätigt somit die bisherige Einstufung dieser Lokalität in ein Niveau etwas jünger als Heimersheim (MP 24). *B. micio* von Gröben 3 ist der Erstnachweis dieser Art nahe des Niveaus MP 24. Aufgrund der relativ umfangreichen Funde von *B. planus* von Gröben 3 können erstmals Entwicklungsstufen innerhalb dieser Art vom MP 21 bis MP 28 beobachtet werden. *B. heissigi* n. sp. ist auf das Säugerniveau MP 24 beschränkt. Diese Art vermittelt zwischen *B. misonnei* (MP 20 - MP 23) und *Microdyromys praemurinus* (MP 25 - 28). Innerhalb der Linie *Bransatoglis bahloi* – *B. misonnei* – *B. heissigi* ist eine Größenabnahme feststellbar.

INTRODUCTION

The following monographs represent the only published research on Gliridae from Paleogene deposits in Central Europe: Vollmayr (1966), Bahlo (1975), Kristkoiz (1992), Werner (1994), and Fejfar & Storch (1994). Among other dental specimens, Mörs (1995) described seventeen glirid teeth from Rott near Bonn. Heißig (1987) and Ziegler & Heizmann (1991) mentioned glirids from certain fissure fillings in southern Germany. Fahlbusch & Heißig (1987), Göhlich & Fahlbusch (2000), and Uhlig et. al. (2000) mentioned Gliridae from several localities in the folded molasse of southern Germany (table 1).

The Paleogene glirids of Western Europe are somewhat better known, among others: Hugueney (1968, 1969, 1980, 1997), Bosma & de Bruijn (1979), Vianey-Liaud (1989, 1994), Peláez-Campomanes (1993, 1995), Vianey-Liaud *et al.* (1995), Freudenthal (1996, 1997a). Nevertheless, the knowledge of the Gliridae especially from MP 24 trough MP 29 is full of gaps.

	MP 19	MP 19-23	MP 21?	MP 24	MP 24	MP 24/25	MP 25	MP 27	MP 27/28	Chattian	MP 30	MP 30	MP 30	MP 30
	Lautern near Ulm ZIEGLER & HEIZMANN 1991	Southern Germany/fissure fillings HEISSIG 1987	Waltsch/Czech Republic FEJFAR & STORCH 1994	Heimersheim BAHLO 1975	Gr`ben 3 this work	Habach 14 UHLIG et al. 2000	Habach 5 G÷HLICH & FAHLBUSCH 2000	Ehrenstein 7 ZIEGLER & HEIZMANN 1991	Gaimersheim KRISTKOIZ 1992	Allg‰u/folded molasse VOLLMAYR 1966	Rott near Bonn M÷RS 1995	Rottenbuch 1, 2, 6, 7 FAHLBUSCH & HEISSIG 1987	Ehrenstein 4 WERNER 1994	Eggingen near Ulm WERNER 1994
Suevoglis wannemacheri														● (77)
Heteromyoxus wetzleri														● (5)
Glirudinus eggingensis														● (63)
Glirudinus glirulus											● (14)	○ (135)	● (3)	● (131)
Peridyromys murinus											cf. ● (1)			
Microdyromys monspeliensis														cf. ● (102)
Microdyromys praemurinus						cf. ● (2)	○ (67)		● (60)					
Bransatoglis concavidens												aff. ○ (3)		● (353)
Bransatoglis fugax											cf. ● (2)	○ (41)		aff. ● (96)
Bransatoglis planus		○ cf.		● (14)	● (71)				● (27)	● (9)				
Bransatoglis heissigi				● (6)	● (90)									
Bransatoglis micio			cf. ● (4)		● (20)									
Bransatoglis bahloi		○												
Gliravus bruijni							aff. ○ (170)	aff. ○ (42)	aff. ● (9)			cf. ○ (38)	● (5)	
Gliravus tenuis				● (91)	● (27)									
Gliravus minor		○ cf.												
Gliravus majori		○ cf.					aff. ○ (200)							
Glamys fordi		○ cf.												
Glamys priscus	○ cf.	○ cf.												

● described ○ mentioned

Table 1.— Occurrence of Paleogene glirids in Central Europe. The number of cheek teeth found in the respective locality is bracketed.

For this monograph, the author conducted intensive field work at the locality Gröben 3 in 1993, 1998 and 1999 (Uhlig 1999 and 2000). 1700 kg of sedimentary material was quarried out, producing nearly 500 teeth of Rodentia and including approximately 200 glirid teeth. The material was screen-washed at the Institute for Palaeontology and Historical Geology in Munich (dried 24 hours at 80° C, treated with 5 per cent hydrogen peroxide and washed with 0,3 mm and 2,0 mm sieves).

The dental terminology used is from Daams & de Bruijn (1995). The measurements of the cheek teeth are maximum lengths in the direction of the tooth row and maximum widths at right angles to the length. All the measurements were taken using an ocular micrometer at 27x magnification (Wild stereo microscope M3Z, Heerbrugg, Switzerland). The drawings of the teeth were self-made with a drawing mirror at 27x magnification.

THE LOCALITY GRÖBEN 3

The locality Gröben 3 is located ca. 55 km south southwest of Munich and ca. 6,5 km east of Murnau, in the southeast part of the Murnau syncline in the folded molasse of Upper Bavaria (fig. 1). The locality is lithostratigraphically situated in the Lower Cyrena Beds ("Untere Cyrenen-Schichten"), ca. 22 m over the top of the marine Upper Baustein Beds ("Höhere Baustein-Schichten") (Uhlig 1999: Abb. 1-4). The locality is ranged in the lowest Chattian and in a mammal-level somewhat younger than Heimersheim (MP 24) (Uhlig 1999: 162 and Uhlig *et al.* 2000).

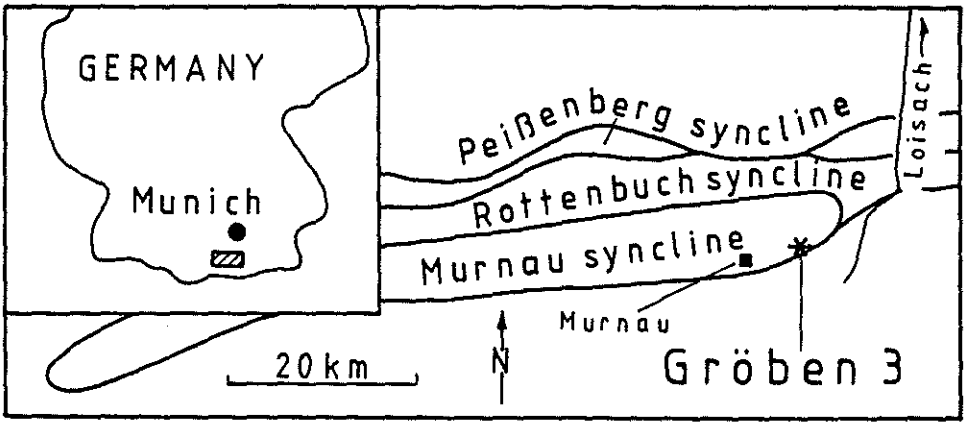

Fig. 1. — The mammal locality Gröben 3 in the folded molasse of southern Germany.

The deposit is a marl, approximately 50 cm thick and green-grey. Besides the four glirids, which are described in this work, the following mammals occur also in Gröben 3: Insectivora indet., *Sciurodon* sp., *Blainvillimys* aff. *heimersheimensis* BAHLO, 1975, *Eomys* sp., *Steneofiber* sp., *Paracricetodon* sp., *Eucricetodon* sp., *Pseudocricetodon* sp., and Cainotheriidae indet..

The associated flora contains *Rhabdochara praelangeri* CASTEL, 1967, *Sphaerochara ulmensis* (STRAUB, 1952) GRAMBAST, 1962, *Nitellopsis* (*Tectochara*) *meriani* (BRAUN *ex* UNGER, 1850) GRAMBAST & SOULIÉ-MÄRSCHE, 1972 (Bassler in Uhlig 1999: 158), and *Celtis lacunosa*. The associated fauna is composed of the following taxa: *Limax* sp., *Pomatias antiquum* (BRONGNIART), *Cepaea* sp., *Palaeumbra moguntina* WEILER, 1973, and "*Ophisaurus*" sp..

Due to the charophytes and the fish remain (otolith), Gröben 3 is interpreted as a lacustrine deposit (Uhlig 1999: 158, 159).

The fossils of Gröben 3 are housed with the numbers 1993 XVII and 2000 XIII in the Bavarian State Collection of Palaeontology and Geology (BSP) in Munich.

TAXONOMY

Family **GLIRIDAE** THOMAS, 1897

Genus *GLIRAVUS* STEHLIN & SCHAUB, 1951

Type-species: *Gliravus majori* STEHLIN & SCHAUB, 1951

Original diagnosis: Stehlin & Schaub 1951: 368

Emended diagnosis: Vianey-Liaud 1994: 128

Remarks: Among other features listed in the emended genus diagnosis of *Gliravus*, Vianey-Liaud (1994: 128) mentioned the following: " . . . protocône séparé . . . . des antérolophe et postérolophe, trigone généralement symétrique . . .". It should be noted, however, that the species *Gliravus tenuis*, does not generally exhibit these features. For example, in the M1 from Heimersheim (the type locality of *G. tenuis*), a narrow connection between the protocone and the posteroloph can be observed. Furthermore, an almost continuous endoloph can be seen in one M3 from Montalban. In the M1 of *G. tenuis*, it is possible for the trigone to have developed in a slightly asymmetrical manner (compare Bahlo 1975: fig. 32 c, Vianey-Liaud 1994: fig. 7 x). The present study, however, addresses only a few species from the Gliridae family. Given this framework, I will neither emend the genus diagnosis of *Gliravus* nor erect a new genus.

Gliravus tenuis BAHLO, 1975

(fig. 2-5)

v 1975 *Gliravus tenuis* n. sp.— Bahlo: 106-113, fig. 32, 33
1977 *Gliravus tenuis* BAHLO - Brunet, Hugueney & Jehenne: 749-752, fig. 12-13
1994 *Gliravus tenuis* BAHLO, 1975 - Vianey-Liaud: 128-129, fig. 7 k-ee

Stratigraphic and geographic range: upper part of the Lower Oligocene until the lowest Upper Oligocene (MP 22-24), Europe (Germany, France, Spain)

Original diagnosis: Bahlo 1975: 106-107

Emended diagnosis: Vianey-Liaud 1994: 128-129

Material: 27 isolated teeth (3 fragments included) from Gröben 3, housed in the BSP, Munich: 2 d4 (2000 XIII 1-2), 4 p4 (1 fragm. incl.) (2000 XIII 4-7), 4 m1/2 (2000 XIII 8-11), 5 m3 (2000 XIII 12-16), 3 P4 (2000 XIII 18-19, 1993 XVII 48), 5 M1/2 (2000 XIII 20-24), 4 M3 (1 fragm. incl.) (2000 XIII 25-27, 1993 XVII 7)

Measurements: table 2

		d4	p4	m1/2	m3	P4	M1/2	M3
L	n	2	3	3	2	3	4	1
	min./mm	0,77	0,90	1,07	1,05	0,75	1,00	0,9
	max./mm	0,78	0,92	1,15	1,15	0,80	1,10	-
	x/mm	0,77	0,91	1,11	1,10	0,77	1,04	-
W	n	2	4	4	5	3	5	3
	min./mm	0,65	0,80	1,02	1,02	0,97	1,10	1,07
	max./mm	0,67	0,87	1,22	1,10	1,05	1,23	1,17
	x/mm	0,66	0,85	1,14	1,06	1,02	1,18	1,10

Table 2.— Measurements of the teeth of *Gliravus tenuis* from Gröben 3

Description

Lower cheek teeth: The metaconid is the highest cusp.

d4: The two teeth are clearly smaller than the p4 and have fewer dental elements. (They will be interpreted here as d4.) The ento-, proto-, and hypoconid are approximately the same height. The mesolophid is the lowest crest. The remaining transverse crests, however, are comparable in size. The antero- and metalophid have a narrow contact with the base of the metaconid. There is no connection between the mesolophid and the low mesoconid. The posterolophid has a slight connection to the entoconid. In one specimen, a very small cuspulus (centrolophid?) appears in front of the mesolophid (2000 XIII 2). The roots of both teeth have been broken off.

p4: The labial border of the teeth is slightly concave. The ento- and hypoconid are

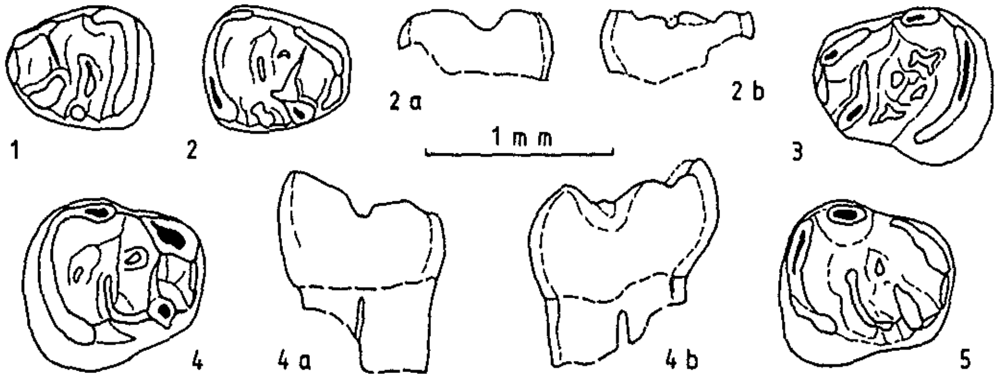

Fig. 2. — *Gliravus tenuis* Bahlo, 1975 from Gröben 3 (MP 24), d4 and p4; **1**: d4, sin., 2000 XIII 1, **2**: d4, dext., 2000 XIII 2, **3**: p4, sin., 2000 XIII 4, **4**: p4, dext., 2000 XIII 5, **5**: p4, dext., 2000 XIII 6; **a**: lingual, **b**: labial.

approximately the same height. The posterolophid is the highest crest; the antero- and mesolophid are the lowest. The antero- and metalophid only have contact with the base of the metaconid. There is never a connection between the mesolophid and the entoconid. In two specimens, however, the mesolophid is connected to the protoconid (2000 XIII 5, 7). The posterolophid is only connected to the base of the entoconid. The centrolophid is a small cuspulus in front of the mesolophid. An extra crest in the posterior valley is only visible in one specimen (2000 XIII 5). The p4 has two roots.

m1/2: While the M1 is trapezoidal, the M2 is approximately rectangular. The teeth are wider than they are long. The posterolophid is the highest crest; the antero- and mesolophid are the lowest. The antero- and metalophid only have contact with the base of the metaconid. The metalophid tapers off lingually. None of the four specimens show a connection between the mesolophid and the entoconid. Compared with the other transverse crests, the mesolophid reveals a slight indentation at the labial border. The posterolophid is only connected to the base of the entoconid. In the m1, the short and narrow centrolophid is connected to the mesolophid. This is not the case, however, in the m2. The extra crest in the anterior valley is always absent. The extra crest in the posterior valley exists only in one m1 (2000 XIII 9). The m1 has two small roots.

m3: The anterolophid is the lowest crest. The posterolophid is thickened. Neither the anterolophid nor the metalophid is connected to the metaconid. The metalophid tapers off lingually. The mesolophid is connected to the entoconid in three specimens. Compared with the other transverse crests, the mesolophid shows a slight indentation at the labial border. The posterolophid only has contact with the base of the entoconid.

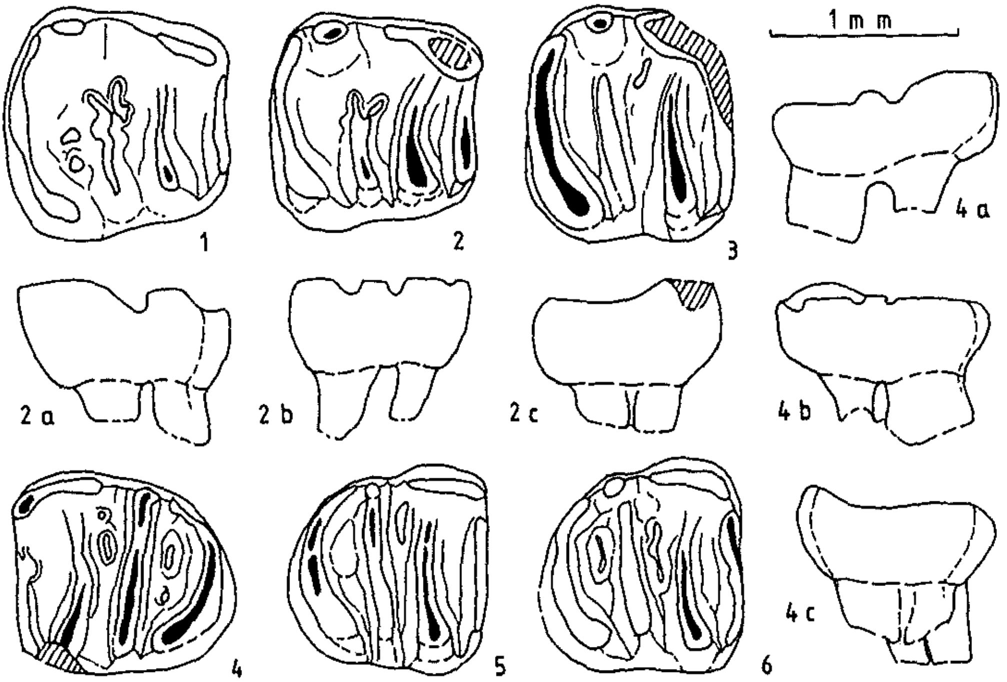

Fig. 3. — *Gliravus tenuis* BAHLO, 1975 from Gröben 3 (MP 24), lower molars; **1**: m1, dext., 2000 XIII 9, **2**: m1, dext., 2000 XIII 10, **3**: m2, dext., 2000 XIII 11, **4**: m3, sin., 2000 XIII 12, **5**: m3, dext., 2000 XIII 14, **6**: m3, dext., 2000 XIII 15; **a**: lingual, **b**: labial, **c**: anterior.

A low and short centrolophid always exists. In one specimen, it has contact with the mesostylid (2000 XIII 13). The extra crest in the anterior valley is always absent. In three specimens, a small, very low extra crest is found in the posterior valley. The m3 has two roots.

Upper cheek teeth:

P4: The occlusal surface is strongly concave. The paracone, which is the highest cusp, can be developed as a short sagittal crest (1993 XVII 48). The proto- and metaloph are the highest transverse crests. The short anteroloph is not connected to the paracone. It comes either into contact with about the middle of the protoloph or remains completely separate (2000 XIII 19). The trigone is V-shaped without being perfectly symmetrical. The posteroloph usually comes into contact with the metacone basally. It always connects to the protocone at the midpoint of the cone`s vertical axis. There is only a very narrow and low anterior centroloph inside the trigone, which is connected to the paracone. The P4 has three roots.

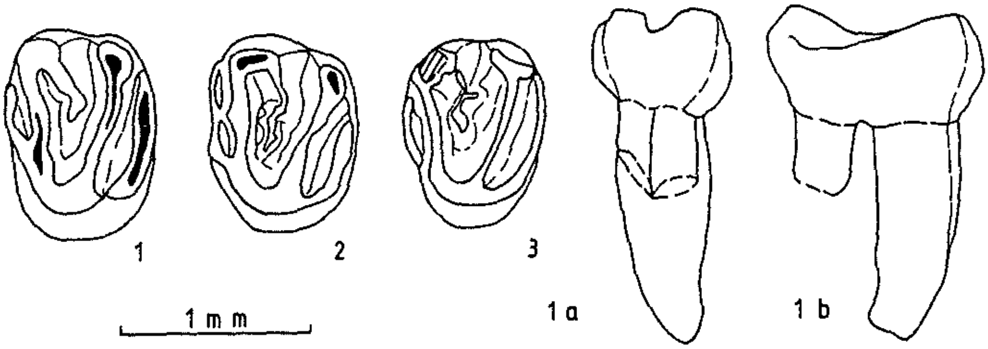

Fig. 4. — *Gliravus tenuis* BAHLO, 1975 from Gröben 3 (MP 24), P4; 1: P4, sin., 2000 XIII 18, 2: P4, sin., 1993 XVII 48, 3: P4, sin., 2000 XIII 19; a: labial, b: anterior.

M1/2: While the M1 is trapezoidal, the M2 is approximately rectangular. However, there are transitional shapes that can only be interpreted as M1/2. All five specimens are wider than they are long. Additionally, they are all very concave. The paracone, which is higher than the metacone, is developed as a short sagittal crest. In the M1 and M1/2, the anteroloph is the lowest transverse crest; in the moderately worn M2, the antero- and posteroloph are higher than the trigone crests. In the M1 and M1/2, the anteroloph is completely separated. In the M2, however, it is connected to the protocone basally. The trigone is V-shaped and has a blunt base. While the trigone is slightly asymmetrical in the M1, it is nearly symmetrical in the M2. The posteroloph is labially separated. In three specimens, the lingual end of the posteroloph is thickened (hypocone) (2000 XIII 20, 21, 24). In the M1, there is no connection between the posteroloph and the protocone. In the other specimens, there is either a basal contact (2000 XIII 22) or a very narrow connection at half the height of the protocone.

There are one or two very low centrolophs that can be divided. In three specimens, the anterior centroloph is connected to the paracone. There are three roots.

M3: The paracone is clearly the highest cusp. The remaining occlusal surface is slightly concave. The proto- and posteroloph are the highest crests. The anteroloph is separated labially. Lingually, it is either connected to the protocone or has only a contact basally (2000 XIII 27). The protoloph and the very short metaloph form a V-shaped trigone with a blunt base. The connection between the posteroloph and the low metacone is very narrow. The endoloph is continuously developed (except spec. 2000 XIII 27).

The extra crests inside the trigone are extremely low. The anterior centroloph is connected to the paracone in two specimens. The posterior centroloph, either branched or fragmented, is connected to the anterior centroloph in three specimens. The M3 has three roots.

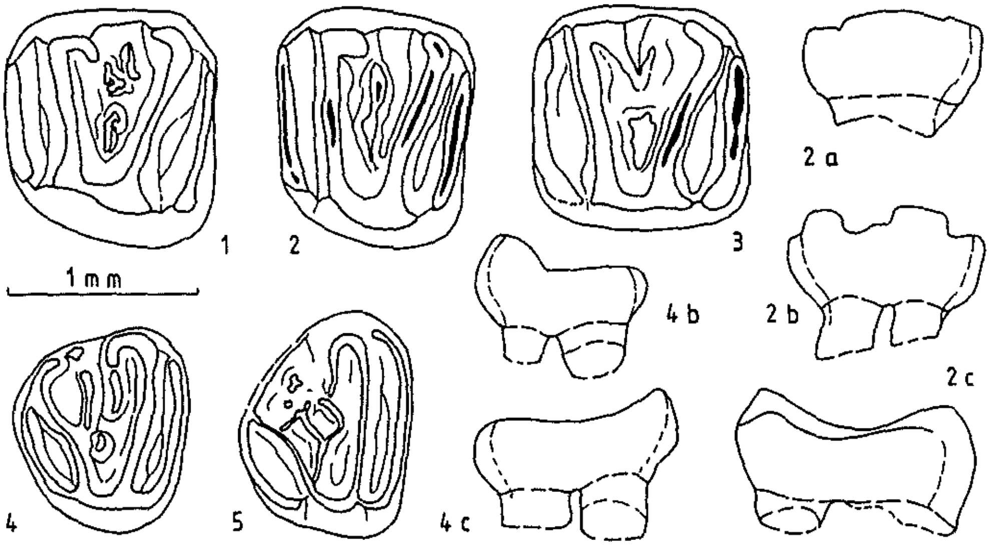

Fig. 5. — *Gliravus tenuis* BAHLO, 1975 from Gröben 3 (MP 24), upper molars; **1**: M1, sin., 2000 XIII 20, **2**: M1/2, sin., 2000 XIII 22, **3**: M2, sin., 2000 XIII 24, **4**: M3, dext., 2000 XIII 26, **5**: M3, dext., 2000 XIII 27; a: lingual, b: labial, c: anterior.

Comparison and discussion

For the most part, the teeth of *Gliravus tenuis* (BAHLO, 1975) found in the older localities Montalban and Heimersheim are smaller than those from Gröben 3 (fig. 6, 7). In the m1/2, the centrolophid is rarely developed. In the m3, it is always absent. In the upper molars from Montalban, the protocone is still isolated (except in one M3). In the M1/2 from Heimersheim and Gröben 3, narrow connections between the protocone and the antero- or posteroloph can already be observed. In the M3 from Gröben 3, the endoloph is almost continuous (compare Bahlo 1975: 106-113, fig. 31-33; Vianey-Liaud 1994: 128-129, fig. 7 k-ee; and fig. 5 in the present study).

(The connection between the protocone and the antero- or posteroloph in the upper molars does not correspond to the genus diagnosis of *Gliravus* given by Vianey-Liaud (1994). I should repeat, however, that the present study attempts neither to change the genus diagnosis of *Gliravus* nor to erect a new genus.)

Gliravus tenuis resembles *Glamys olallensis* FREUDENTHAL, 1996 from Olalla 4A and Fuenferrada 3B (MP 20-22). In the m1/2, the mesolophid is also weakly developed. In both species, the mesolophid is often connected to the protoconid in the p4. This is a primitive feature that is also observable in *Glamys robiacensis* (HARTENBERGER, 1965) (MP 16) (compare Hartenberger 1971: pl. 2/10 and 3/6). *Glamys olallensis*, however, is somewhat smaller than *Gliravus tenuis*. In the lower molars, extra crests are rarely developed, and in the upper molars, the base of the trigone is narrower (compare Freudenthal 1996: 25-28, pl. 6/1-8 and 1997a: 14-16, p. 1/8-16). Therefore, *Glamys olallensis* could be an ancestor of *Gliravus tenuis*. (If future research confirms this supposition, then these two species should either be placed in the same genus, or a new genus should be erected).

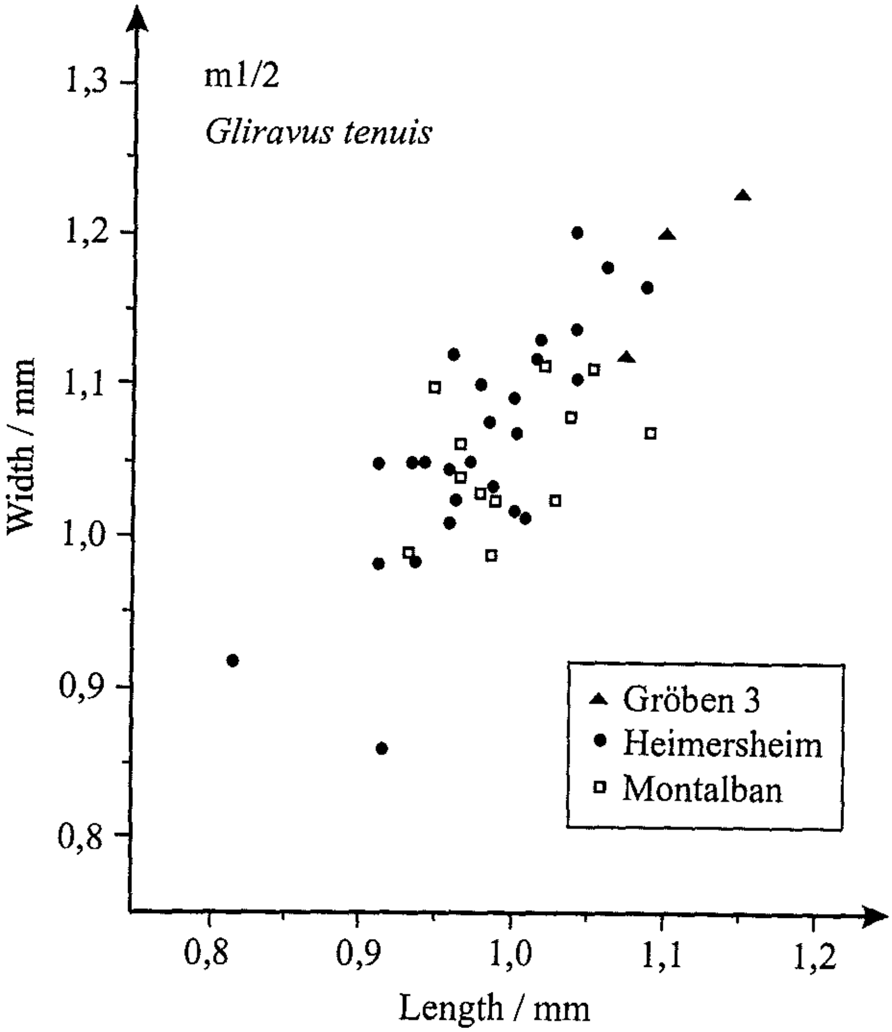

Fig. 6. — Scatter diagram representing length and width of m1/2 of *Gliravus tenuis* from Montalban, Heimersheim and Gröben 3.

Gliravus daamsi BOSMA & DE BRUIJN, 1982 (MP 17-19) is larger than *Gliravus tenuis*. In the m1/2, the mesolophid is longer and already connected to the entoconid (compare Bosma & de Bruijn 1982: 370-373, pl. 2). *Glamys priscus* (STEHLIN & SCHAUB, 1951) (MP 17-23) covers the lowest size range of *Gliravus tenuis*. However in the p4-m2, the mesolophid is already longer. Additionally in the p4, the connection of the mesolophid and the protoconid is already absent. *Glamys devoogdi* (BOSMA & DE BRUIJN, 1979) and *G. fordi* (BOSMA & DE BRUIJN, 1979) (MP 19-22) already have numerous extra crests (compare Stehlin & Schaub 1951: 368, fig. 513, Bosma & de Bruijn 1979). *Miniglis minor* (BOSMA & DE BRUIJN, 1982) (MP 17) is clearly smaller than *Gliravus tenuis*. However in the M1/2, the endoloph is already better developed (compare Bosma & de Bruijn 1982: 366-370, pl. 1). Although these species (*Gliravus daamsi*, *Glamys priscus*, *G. devoogdi*, *G. fordi*, and *Miniglis minor*) occur in stratigraphically older deposits than *Gliravus tenuis*, they already exhibit some more modern features. Therefore, it is unlikely that any of these species is an ancestor of *Gliravus tenuis*.

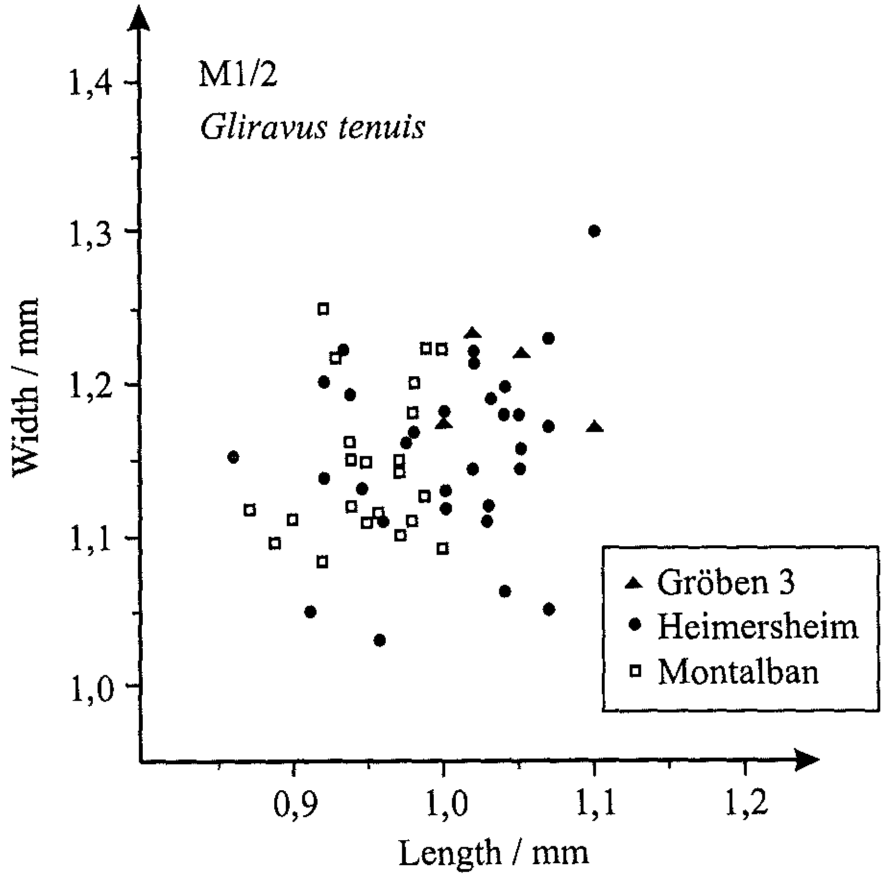

Fig. 7. — Scatter diagram representing length and width of M1/2 of *Gliravus tenuis* from Montalban, Heimersheim and Gröben 3.

In *Gliravus garouillensis* VIANEY-LIAUD, 1994 (MP 25) and *G. majori* STEHLIN & SCHAUB, 1951, the antero- and the posteroloph in the M1/2 show a greater lingual extension. Furthermore in the lower molars, the mesolophid is usually weaker and in the P4, the centroloph is still isolated (see Vianey-Liaud 1994: 129-132, fig. 6 and Vianey-Liaud *et al.* 1995: 261-264, fig. 3 a-m). The two final features mentioned above can be regarded as more primitive in comparison with *Gliravus tenuis*. Thus, it appears that neither *Gliravus garouillensis* nor *G. majori* is a descendent of *Gliravus tenuis*.

Gliravus bruijni HUGUENEY, 1967 (MP 25-30) is clearly larger than *G. tenuis*. In the lower molars, however, the mesolophid is weaker. In Garouillas and nearly contemporaneous fissure fillings of the Quercy (MP 25), the centroloph is still isolated in the P4. Moreover in the M1/2, only a single centroloph is developed (compare Hugueney 1969: 123-129, fig. 66-88, Vianey-Liaud *et al.* 1995: 260, fig. 2). These morphological features (a weaker mesolophid, only one isolated centrolophid) can be considered more primitive in comparison with *Gliravus tenuis* (compare Stehlin & Schaub 1951: 137, 299). Bahlo suggested (1975: 121) that *G. bruijni* is a descendant of *G. tenuis*. Given my own observations, however, I cannot support this hypothesis. Vianey-Liaud, I would argue, introduced a more tenable hypothesis: that *G. tenuis* became extinct without descendants, and *G. bruijni* is a potential successor of *G. daamsi* (1994: 153).

Genus ***BRANSATOGLIS*** HUGUENEY, 1967
(= ***OLIGODYROMYS*** BAHLO, 1975)

Type-species: *Bransatoglis concavidens* HUGUENEY, 1967

Original diagnosis: Hugueney 1967: 92

Emended diagnosis: Vianey-Liaud 1994: 138

Remarks: Vianey-Liaud (1994) and Freudenthal (1996) have varying opinions concerning the species belonging to the genus *Bransatoglis*. Vianey-Liaud (1994: 138) attributed the following species to the genus *Bransatoglis*: *B. micio* (MISONNE, 1957) (= *Gliravus itardiensis* VIANEY-LIAUD, 1989), *B. concavidens* HUGUENEY, 1967, *B. meridionalis* (HARTENBERGER, 1971), *B. fugax* (HUGUENEY, 1967), *B. cadeoti* BULOT, 1978, *B. bahloi* BOSMA & DE BRUIJN, 1982, *B. planus* (BAHLO, 1975), *B. sjeni* ÜNAY-BAYRAKTAR, 1989, and *B. misonnei* VIANEY-LIAUD, 1994. According to Vianey-Liaud (1994: 157), these species have a common origin in the area of *B. meridionalis*.

On the other hand, Freudenthal (1996: 33) argues that these species constitute a heterogeneous group, which accommodates a very wide range of size and morphologies. He notes that the phylogenetic relationships suggested by Vianey-Liaud are far from certain. To advance his argument, Freudenthal mentioned the remains of a medium-sized *Bransatoglis* from the Upper Eocene locality Aguatón 2I with a very advanced morphology, comparable to that of *B. concavidens*.

If *B. concavidens* - like forms occured already in the Upper Eocene, then I would suggest that the genus name *Bransatoglis* should be used for this lineage, given the fact that *B. concavidens* is the type species of this genus. Additionally, the genus name "*Oligodyromys* BAHLO, 1975" is available for species whose common origin can be traced back to the area of *B. meridionalis*. Far-reaching taxonomic changes, however, should be reserved for future research. Such changes are dependent upon the description of the Aguatón remains, and this information is still outstandig.

Freudenthal (1996: 33) also mentioned the remains of a very small glirid from Aguatón 2I, which is either identical or similar to *B. misonnei*. According to him, it forms a homogeneous group together with the Late Oligocene *Microdyromys*. This material, however, was not described until recently. Additionally, *B. misonnei* differs from *Microdyromys* in important ways: for example in the lower molars, the anterolophid is not connected to the protoconid, and the mesoconid is not hook-shaped; in the upper molars, the endoloph is not continuously developed, and the lingual border does not show an ornamentation. Moreover, if *B. misonnei* would be attributed to the genus *Microdyromys*, then it would be necessary to change the genus diagnosis of *Microdyromys* DE BRUIJN, 1966.

Bransatoglis micio (MISONNE, 1957)

(fig. 8-11)

1957 *Peridyromys micio*, sp. n. - Misonne: 6, 7, pl. II/1, 2
1987 *Bransatoglis* nov. sp. aff. *bahloi* - Anadon *et al.*: 128, fig. 6 f-i
1989 *Gliravus itardiensis* nov. sp. - Vianey-Liaud: 215-220, fig. 6, 7
1994 *Bransatoglis micio* (MISONNE 1957) - Vianey-Liaud: 138-143, fig. 13-16, 17
1994 *Bransatoglis* cf. *micio* (MISONNE, 1957) - Fejfar & Storch: 25, 26, fig. 1, 4

Stratigraphic and geographic range: (for the first time in the Upper Eocene from le Batut, MP 19, with *B.* aff. *micio*), Lower Oligocene until the lowest Upper Oligocene (MP 21 - 24), (with *B.* aff. *micio* still present in Pech Desse, MP 28), Europe (Belgium, France, Czech Republic, Germany)

Original diagnosis: Misonne 1957: 6, 7

Emended diagnosis: Vianey-Liaud 1994: 140, 141

Material: 20 isolated teeth from Gröben 3, housed in the BSP, Munich (2000 XIII): 2 d4 (28-29), 1 p4 (30), 5 m1/2 (31-35), 3 m3 (36-38), 1 D4 (39), 3 P4 (40-42), 2 M1/2 (43-44), 3 M3 (45-47)

Measurements: table 3

		d4	p4	m1/2	m3	D4	P4	M1/2	M3
L	n	2	1	3	3	1	3	2	3
	min. / mm	0,70	0,82	1,00	1,02	0,67	0,77	1,00	0,97
	max. / mm	0,72	-	1,05	1,10	-	0,87	1,07	1,00
	x / mm	0,71	-	1,02	1,06	-	0,80	1,03	0,99
W	n	1	1	5	2	1	3	1	3
	min. / mm	0,60	0,70	1,02	1,00	0,82	0,92	1,12	1,05
	max. / mm	-	-	1,12	1,02	-	0,97	-	1,07
	x / mm	-	-	1,07	1,01	-	0,95	-	1,06

Table 3: Measurements of the teeth of *Bransatoglis micio* from Gröben 3.

Description

d4: The meta- and the hypoconid are the highest cusps of the two teeth. The posterolophid is the highest crest, the antero- and the mesolophid are the lowest. The anterolophid is connected to the metaconid at mid-height while, the connection to the protoconid is complete. The metalophid has a very narrow connection to the metaconid. There is no connection between the mesolophid and the entoconid. The mesoconid is connected to the protoconid, and the posterolophid is connected to the entoconid. Extra crests are absent. The roots have been broken off.

p4: In the unique tooth, the labial border is nearly straight. The posterolophid is the highest transverse crest. The anterolophid is connected to the metaconid at mid-height; there is no connection to the protoconid. The metalophid is connected to the metaconid. The mesolophid is not connected to the entoconid, however labially, it has a connection to the anterolophid. The posterolophid is connected to the entoconid. The very small centrolophid meets the mesolophid. There is a narrow extra crest directed sagittally in the posterior valley.

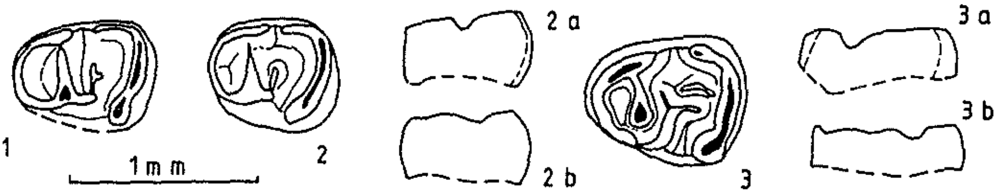

Fig. 8. — *Bransatoglis micio* (MISONNE, 1957) from Gröben 3 (MP 24), d4 and p4; 1: d4, sin., 2000 XIII 28, 2: d4, sin., 2000 XIII 29, 3: p4, sin., 2000 XIII 30; a: lingual, b: labial.

Lower molars: The metaconid is the highest cusp. The extra crests are lower than the main crests.

m1/2: The anterolophid is the lowest crest. It is only connected to the base of the metaconid. The connection to the protoconid exists only after a strong wear. The metalophid ends at the base of the metaconid abruptly. The mesolophid is not connected to the entoconid. (There is only a connection in a strongly worn specimen: 2000 XIII 32). The mesoconid is similarly robustly developed as the protoconid and lies on a line with the other labial cusps. The posterolophid is connected to the entoconid either at mid-height (2000 XIII 31, 33) or only basally (2000 XIII 34).

In one specimen, the centrolophid is connected to the mesolophid (2000 XIII 33) otherwise, it is isolated. A small extra crest exists in the anterior valley only in two of five specimens. Always, the posterior valley shows a narrow extra crest. There are two roots (seen only in the specimen 2000 XIII 32).

m3: Always, the posterolophid is somewhat higher than the other three transverse crests. The anterolophid is separated. The metalophid ends at the base of the metaconid abruptly. The mesolophid has a narrow connection to the entoconid. The mesoconid lies on a line with the other labial cusps. There is no connection between the posterolophid and the entoconid.

In one specimen, the centrolophid is connected to the mesostylid. None of the three specimens show an extra crest in the anterior valley. However in the posterior valley, a low extra crest exists. There are two or three roots.

D4: In the unique tooth, the proto- and the posteroloph are the highest transverse crests. The anteroloph touches the para- and the protocone at mid-height. There is no connection between the metaloph and the protocone. The posteroloph comes into contact with the metacone only basally while, the connection to the protocone is complete. The anterior centroloph, which is somewhat lower and narrower than the protoloph, is connected to the paracone.

P4: Two specimens are slightly concave, one specimen with a high degree of wear is strongly concave (2000 XIII 40). The para-, meta- and protocone are approximately the same height. The paracone is developed as a short sagittal crest. The anteroloph is either completely separated or touches the protocone (2000 XIII 40). The metaloph has either a very narrow contact to the protocone or it is separated lingually (2000 XIII 42). The posteroloph is connected to the metacone usually at mid-height while, the connection to the protocone is complete.

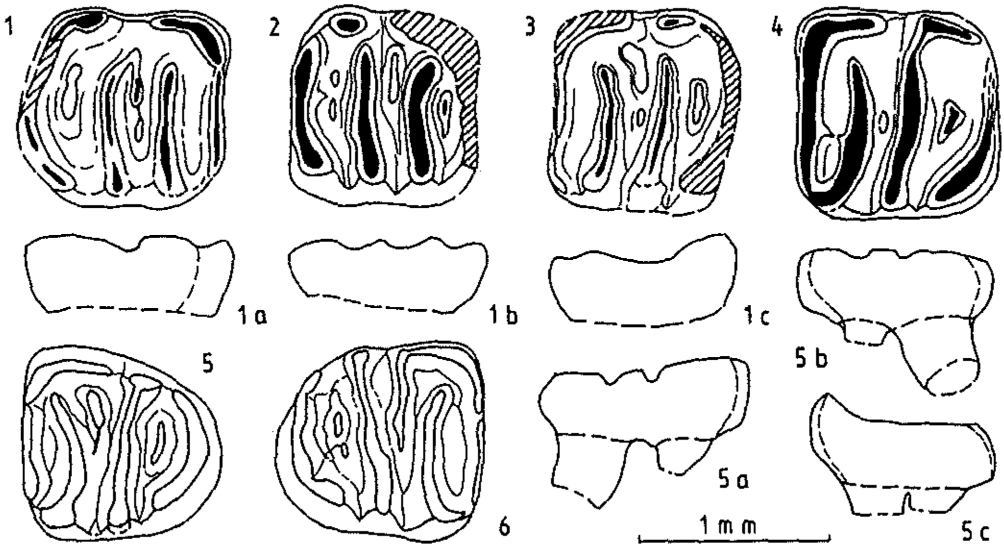

Fig. 9. — *Bransatoglis micio* (MISONNE, 1957) from Gröben 3 (MP 24), lower molars; **1**: m1?, dext., 2000 XIII 33, **2**: m1/2, dext., 2000 XIII 34, **3**: m2?, sin., 2000 XIII 31, **4**: m2?, sin., 2000 XIII 32, **5**: m3, sin., 2000 XIII 36, **6**: m3, dext., 2000 XIII 38; a: lingual, b: labial, c: anterior.

The anterior centroloph, which is always connected to the paracone, has almost the same height as the trigone crests. There is a small and low posterior centroloph only in one specimen. The P4 has three roots.

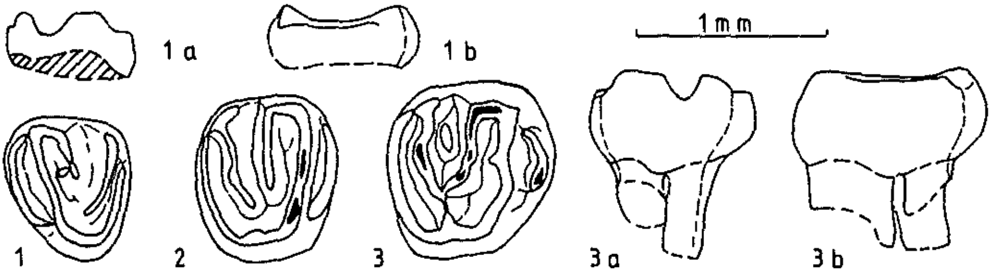

Fig. 10. — *Bransatoglis micio* (MISONNE, 1957) from Gröben 3 (MP 24), D4 and P4; **1**: D4, sin., 2000 XIII 39, **2**: P4, dext., 2000 XIII 42, **3**: P4, dext., 2000 XIII 41; a: labial, b: anterior.

Upper molars: The paracone is the highest cusp.

M1/2: Only one specimen can be interpreted as M1 (2000 XIII 43) while in the other specimen, the lingual border has been broken off. The teeth are moderately concave. Both labial cusps are developed as short sagittal crests. The four transverse crests are approximately the same height. The anteroloph is separated while, the posteroloph comes into contact to the metacone basally; to the protocone exists a narrow connection. The anterior centroloph, which is connected to the paracone, has almost the same height as the trigone crests. The posterior centroloph is shorter, and it touches the metacone at mid-height. In one specimen, there is a narrow, low extra crest in the anterior centrosinus. The roots of both teeth have been broken off.

M3: The occlusal surface is slightly concave. The four transverse crests have approximately the same height. The anteroloph touches the paracone at mid-height while, the connection to the protocone is almost complete. The protoloph and the short metaloph construct an U-shaped trigone with a broad base. The posteroloph is connected to the meta- and to the protocone. Both centrolophs have usually the same height and the same thickness as the protoloph. As a rule, they contact the respective labial cusp. The posterior centrosinus exhibits one or two extra crests. The M3 has three roots.

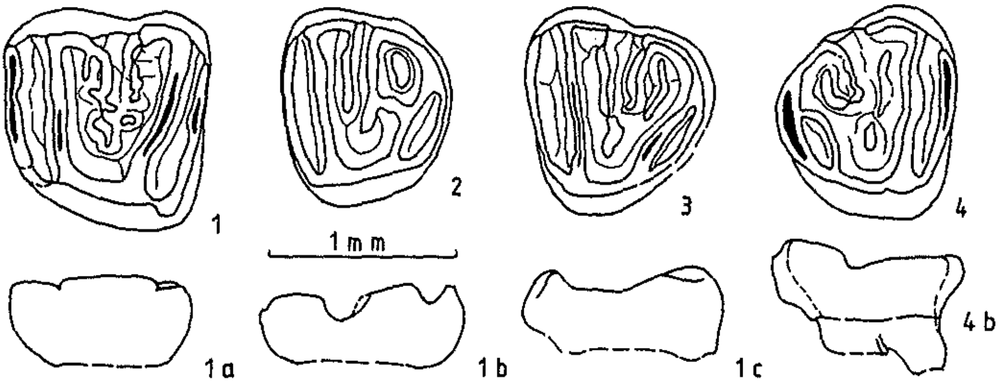

Fig. 11. — *Bransatoglis micio* (MISONNE, 1957) from Gröben 3 (MP 24), upper molars; 1: M1, sin., 2000 XIII 43, 2: M3, sin., 2000 XIII 45, 3: M3, sin., 2000 XIII 46, 4: M3, dext., 2000 XIII 47; a: lingual, b: labial, c: anterior.

Comparison and discussion

Bransatoglis micio (MISONNE, 1957) from the type locality Hoogbutsel is somewhat larger. In the d4 and p4, the connection between the entoconid and the posterolophid is narrower. In the m1/2, the mesolophid is more weakly developed. In the D4, P4, and M1, the connection between the posteroloph and the protocone is still usually absent. In the M3, the base of the trigone is narrower, and the connection between the anteroloph and the protocone is usually either quite narrow or completely absent (compare Vianey-Liaud 1994: 138-143, fig. 13-16).

B. micio from Itardies (syn. *Gliravus itardiensis* VIANEY-LIAUD, 1989) differs from the populations from Hoogbutsel and Gröben 3 in that there is never an extra crest in the anterior valley in the m1/2. Thus, it could possibly represent a morphotype of this species (see discussion in Vianey-Liaud 1994: 139-140).

Material from Olalla 4A, described by Freudenthal as *Gliravus itardiensis* (1996: 28-32, pl. 6/9-18), is similar to *Bransatoglis micio* from Itardies - the extra crest in the anterior valley is also always absent. In the M1, however, the anteroloph extends more lingually than the protocone, a feature that can be observed mainly in *Gliravus majori* STEHLIN & SCHAUB, 1951. It may be necessary to erect a new species for the material from Olalla 4A. This question, however, cannot be answered in the context of the present work.

Bransatoglis micio from Waltsch (MP 21?) is more similar to the population from Hoogbutsel than that from Gröben 3. This is because the connection between the entoconid and the posterolophid in the p4 is very narrow, and the mesolophid is quite weakly developed (compare Fejfar & Storch 1994: 20-22, fig. 1).

B. micio from Calaf 13 and 14 (MP 22) has an evolutionary level between Hoogbutsel and Gröben 3: in the M2, the connection between the posteroloph and the protocone is still absent, and in the M3, the base of the trigone is still narrow (as in Hoogbutsel); on the other hand, in the p4, the entoconid and the posterolophid are already connected, and in the M3, the anteroloph is already connected to the protocone (as in Gröben 3) (compare Anadon *et al.* 1987: 128, fig. 6 f-i).

B. aff. *micio* from le Batut (MP 19) is somewhat smaller, but otherwise similar to Hoogbutsel (compare Vianey-Liaud 1994: 143, fig. 17).

The four teeth from the Charbon syncline (MP 20), described by Herb *et al.* (1984: 227, fig. 4 a-d) as *B.* cf. *micio*, show a relatively large extra crest in the anterior valley in one of the two m1. In the m2, they have a long and straight metalophid, and in the m1/2, a long mesolophid almost reaches the entoconid. In this respect, this material rather resembles *B. bahloi* from Headon Hill 3 (compare Bosma & Bruijn 1982: pl. 3).

The four teeth from Pech Desse (MP 28), mentioned and drawn by Vianey-Liaud (1994: 140, fig. 9 n, o) as *B.* aff. *micio*, show, in contrast to the material from Gröben 3, the following differences: in the p4, the entoconid is still isolated; in the m1/2, the mesolophid is narrower than the metalophid, the extra crest in the anterior valley is always absent, and in one m1, the mesolophid reaches only the middle of the tooth. In the type locality Hoogbutsel, however, these features can be observed in a few specimens. It seems that despite its distinctively younger age, the population from Pech Desse has a closer phylogenetic relationship to Hoogbutsel than to Gröben 3.

B. meridionalis (HARTENBERGER, 1971) (MP 17) is somewhat smaller than *B. micio* from Hoogbutsel, but the morphology is very similar (compare Hartenberger 1971: 124-125, pl. 4/1-6). According to Vianey-Liaud (1994: 157), however, the mesolophid is more frequently connected to the entoconid than in Hoogbutsel. Despite this different feature, I would agree with Vianey-Liaud (1994: fig. 33) that there is a close phylogenetic relationship between *B. meridionalis* and *B. micio.*

B. bahloi BOSMA & DE BRUIJN, 1982 (MP 17 - 18) is smaller. In most cases, however, the lower molars show a connection between the mesolophid and the entoconid (cf. Bosma & de Bruijn 1982: 376, pl. 3).

Bransatoglis planus (BAHLO, 1975)

(fig. 12-15)

v 1966 *Peridyromys* ? nov. spec. B - Vollmayr: 90-94, pl. 7/16, pl. 8/1, 9-12
v 1966 *Peridyromys* ? spec. indet. - Vollmayr: 96-98, pl. 9/7,10
v 1966 Gliridae, spec. inc. subfam. - Vollmayr: 95, pl. 9/16
v 1975 *Oligodyromys planus* n. g., n. sp. - Bahlo: 124-128, fig. 36
1980 *Oligodyromys planus* BAHLO, 1975 - Hugueney: 61-62, fig. 10, 11
v 1992 *Bransatoglis* aff. *planus* (BAHLO, 1975) - Kristkoiz: 43-49, fig. 18-20
1994 *Bransatoglis planus* (BAHLO, 1975) - Vianey-Liaud: 144-147, fig. 7j, 18, 19, 20 a-d
1997 *Bransatoglis planus* (BAHLO, 1975) - Hugueney: 302, pl. 1/14-23

Stratigraphic and geographic range: Upper Eocene until Upper Oligocene (MP 20 - 28), Europe (Germany, France, Belgium, Spain)

Original diagnosis: Bahlo 1975: 122-124

Emended diagnosis: Vianey-Liaud 1994: 144

Material: 71 isolated teeth (10 fragments included) from Gröben 3, housed in the BSP, Munich (2000 XIII): 3 d4 (48-50), 7 p4 (52-58), 27 m1/2 (7 fragm. incl.) (60-85, 1993 XVII 6), 11 m3 (1 fragm. incl.) (86-96), 2 D4 (212, 213), 1 P3 (97), 7 P4 (98-104), 7 M1/2 (1 fragm. incl.) (105-111), 6 M3 (1 fragm. incl.) (112-117)

Measurements: table 4

		d4	p4	m1	m2	m3	D4	P3	P4	M2	M3
L	n	2	7	10	8	9	2	1	7	6	3
	min. / mm	0,81	0,87	0,95	1,00	1,00	-	0,62	0,75	0,97	0,87
	max. / mm	0,83	1,12	1,15	1,17	1,10	-	-	0,87	1,12	0,92
	x / mm	0,82	0,93	1,05	1,07	1,03	0,69	-	0,82	1,05	0,90
	s / mm	-	0,058	0,054	0,054	0,032	-	-	0,048	0,057	-
	V / %	-	6,30	5,47	5,03	3,11	-	-	5,93	5,43	-
W	n	3	7	10	8	9	2	1	7	6	4
	min. / mm	0,77	0,77	1,00	1,02	0,95	0,74	0,85	0,97	1,12	0,97
	max. / mm	0,80	0,92	1,20	1,25	1,07	0,80	-	1,10	1,33	1,11
	x / mm	0,79	0,84	1,09	1,15	1,00	0,77	-	1,01	1,24	1,06
	s / mm	-	0,055	0,063	0,089	0,041	-	-	0,041	0,071	-
	V / %	-	6,56	5,75	7,73	4,09	-	-	4,08	5,76	-

Table. 4: Measurements of the teeth of *Bransatoglis planus* from Gröben 3.

Description

Lower cheek teeth: The metaconid is higher than the entoconid.

d4: Three teeth are interpreted as d4. They are smaller than the p4 and have less dental elements. The four transverse crests are approximately the same height. The anterolophid is connected to the metaconid while, the connection to the protoconid is absent in two specimens. There is a connection between the metalophid and the metaconid. Both, the meso- and the posterolophid are connected to the entoconid. The extra crests are lower than the main crests. In all specimens, a centrolophid occurs, which touches the metalophid labially. Two specimens exhibit a small extra crest in the posterior valley. There is probably only a single root.

p4: The labial border is nearly straight. In one specimen, the mesostylid and the entoconid are connected by a very narrow crest (2000 XIII 53). The posterolophid is the highest transverse crest. In four specimens, the anterolophid is connected to the metaconid while, the connection to the protoconid occurs in six specimens. There is a connection between the metalophid and the metaconid as well as between the mesolophid and the entoconid. The posterolophid has a narrow contact to the base of the entoconid (2 spec.), a narrow connection to the entoconid (2 spec.), or it is connected to the entoconid completely (3 spec.).

The extra crests have nearly the same height as the main crests. The centrolophid, which meets the metalophid labially, is connected to the mesostylid in four specimens. Six of seven specimens show extra crests in the anterior and posterior valley. The p4 has a single root.

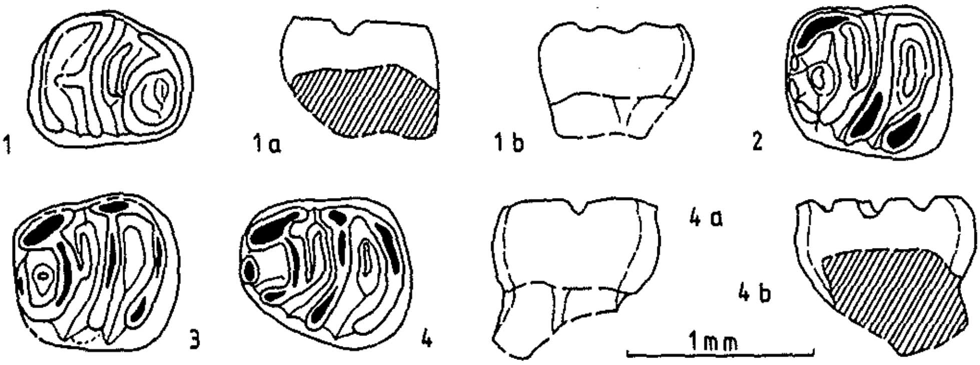

Fig. 12. — *Bransatoglis planus* (BAHLO, 1975) from Gröben 3 (MP 24), d4 and p4; **1**: d4, dext., 2000 XIII 48, **2**: p4, sin., 2000 XIII 55, **3**: p4, sin., 2000 XIII 53, **4**: p4, sin., 2000 XIII 54; **a**: lingual, **b**: labial.

m1/2: While the m1 is trapezoidal, the m2 is approximately rectangular. In the m1, the posterior border is nearly straight while in the m2, it is somewhat rounded. The m2 are always wider than they are long. Usually, the anterolophid is somewhat lower, and the posterolophid is somewhat higher than the other transverse crests in all m1/2. The anterolophid is connected to the metaconid. In three specimens, however, this connection is very narrow. In the m1, the connection between the anterolophid and the protoconid is always absent while in the m2, this connection exists in four of eight specimens. In the m1, the metalophid is connected to the metaconid in eight of twelve specimens while, only one of eight m2 shows this connection. In three m1, a short sagittal crest branches off at mid-length of the metalophid and meets the centrolophid in two specimens (for instance 2000 XIII 61). The mesolophid is connected to the entoconid in 19 of 22 m1/2. In four of ten m1 (for instance 2000 XIII 61), the mesoconid is hook-shaped. There is always a connection between the posterolophid and the entoconid. In eight specimens, however, this connection is very narrow (for instance 2000 XIII 73).

In the m1, the extra crests usually have the same height as the main crests while in the m2, they are often somewhat lower. The centrolophid is connected to the mesostylid in eleven of 20 m1/2. The extra crest in the anterior valley is absent only in one m2 (2000 XIII 71). All m1/2 have an extra crest in the posterior valley. It can contact the posterolophid (5 spec.), be divided (5 spec.), or be lingually split up (3 spec.). There are two roots.

m3: Usually, the anterolophid is the lowest crest while, the posterolophid is the highest one. The anterolophid is always connected to the metaconid while, the connection to the protoconid occurs only in eight of ten specimens. The metalophid is connected to the metaconid only in three of ten specimens. The meso- and the posterolophid are always connected to the entoconid. However, the connection between the posterolophid and the entoconid is very narrow in two specimens.

The extra crests are almost always a little lower than the main crests. In five of nine specimens, the centrolophid is connected to the mesostylid. The extra crest in the anterior valley is absent in one specimen (2000 XIII 91). In most cases, there is an extra crest in the posterior valley, which meets the posterolophid in three specimens (for instance 2000 XIII 86). The m3 has two roots.

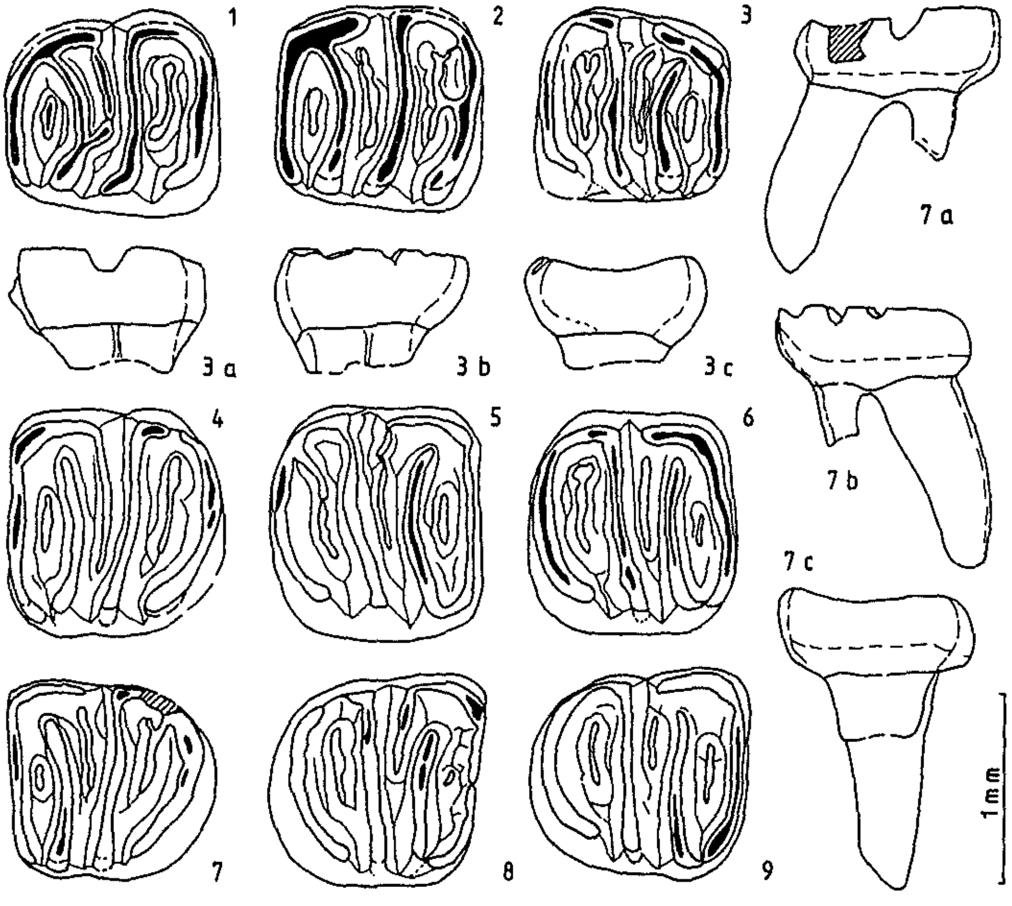

Fig. 13. — *Bransatoglis planus* (Bahlo, 1975) from Gröben 3 (MP 24), lower molars; **1**: m1, sin., 2000 XIII 61, **2**: m1, sin., 2000 XIII 62, **3**: m1, dext., 2000 XIII 68, **4**: m2, sin., 2000 XIII 73, **5**: m2, dext., 2000 XIII 75, **6**: m2, dext., 2000 XIII 76, **7**: m3, sin., 2000 XIII 86, **8**: m3, dext., 2000 XIII 92, **9**: m3, dext., 2000 XIII 94; **a**: lingual, **b**: labial, **c**: anterior.

Upper cheek teeth: The posteroloph ist always connected to the protocone. Always, there is a connection between the anterior centroloph and the paracone.

D4: The teeth are moderately concave marked by the both labial cusps and the protocone. The antero- and the posteroloph are lower than the trigone crests. The anteroloph touches the paracone basally while, a connection to the protocone does not exist. The posteroloph has a very narrow connection to the metacone. The anterior centroloph is somewhat lower than the trigone crests. Roots have been broken off.

P3: This tooth resembles the P4 of *Bransatoglis heissigi* n. sp. However, it is clearly larger. The trigone crests of the slightly concave tooth are approximately the same height as the posteroloph, which is connected to the metacone. Both centrolophs are lower than the trigone crests. The P3 has two roots.

P4: The moderately concave teeth are either O-shaped or approximately triangular. The paracone is either higher or has the same height as the metacone. In one specimen, a third labial cusp exists between the para- and the metacone (2000 XIII 101). The anteroloph, which is lower and narrower than the other transverse crests, is connected to the paracone only in a very strongly worn specimen (2000 XIII 100). There is a connection between the anteroloph and the protoloph in four specimens (2000 XIII 99-102). The posteroloph comes into contact with the metacone at mid-height.

The anterior centroloph has almost the same height as the trigone crests. The posterior centroloph is lower, shorter and narrower than the anterior one. Four specimens show a very small, low extra crest in the anterior centrosinus. The P4 has three roots.

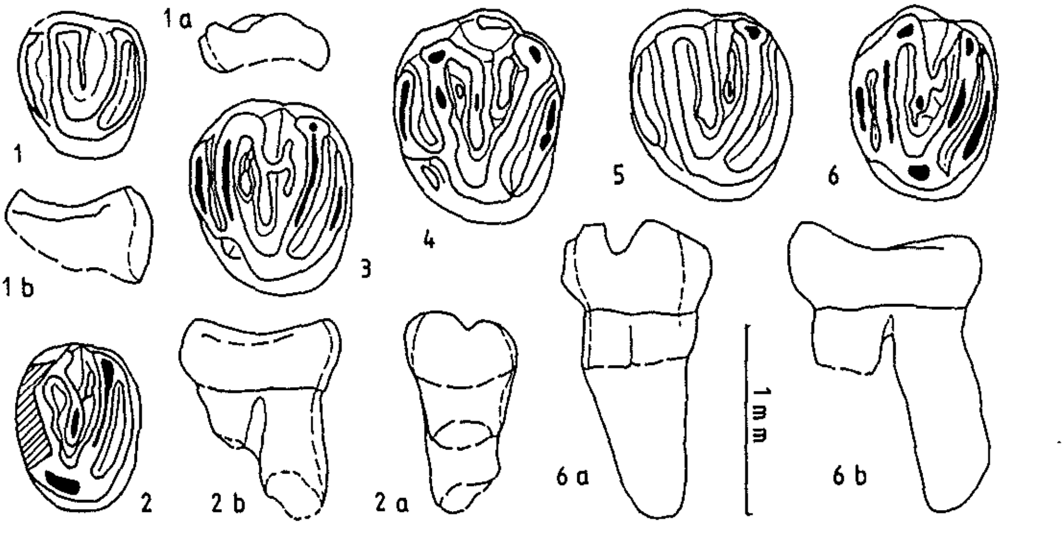

Fig. 14. — *Bransatoglis planus* (BAHLO, 1975) from Gröben 3 (MP 24), D4, P3 and P4; **1**: D4, sin., 2000 XIII 213, **2**: P3, sin., 2000 XIII 97, **3**: P4, sin., 2000 XIII 99, **4**: P4, sin., 2000 XIII 101, **5**: P4, sin., 2000 XIII 98, **6**: P4, sin., 2000 XIII 100; **a**: labial, **b**: anterior.

M2: There are six complete specimens lacking an oblique lingual border. Most probably, they are all M2. The teeth are slightly concave. The paracone is higher than the metacone. Both labial cusps are developed as short sagittal crests. The four, relative narrow transverse crests are approximately the same height. Only in a single specimen, the anteroloph has contact to the paracone. The anteroloph is either connected to the protocone (4 spec.) or only a very narrow contact exists (2 spec.). In four of six specimens, the posteroloph has a narrow connection to the metacone.

The posterior centroloph is connected to the metacone. Both centrolophs, either divided or branched, are almost the same height as the trigone crests. However, they are generally somewhat narrower. The V-shaped connection of both centrolophs lingually is a characteristic feature. Always, the anterior centrosinus shows an extra crest while, the posterior one exhibits such crest only in four specimens. One single specimen (2000 XIII 107) has a small extra crest in the anterosinus. In the posterosinus, there is an extra crest also only in one specimen (2000 XIII 106). There are three roots.

M3: The paracone is the highest cusp, the remaining occlusal surface is flat. As a rule, the four transverse crests are approximately the same height. The metaloph is usually somewhat narrower than the other main crests. The anteroloph touches the paracone at mid-height, the connection to the protocone is developed in all specimens.

The extra crests inside the trigone have the same height as the main crests. However, they are usually narrower and construct an irregular network. In one specimen (2000 XIII 117), there are extra crests in the antero- and posterosinus. The roots have been broken off.

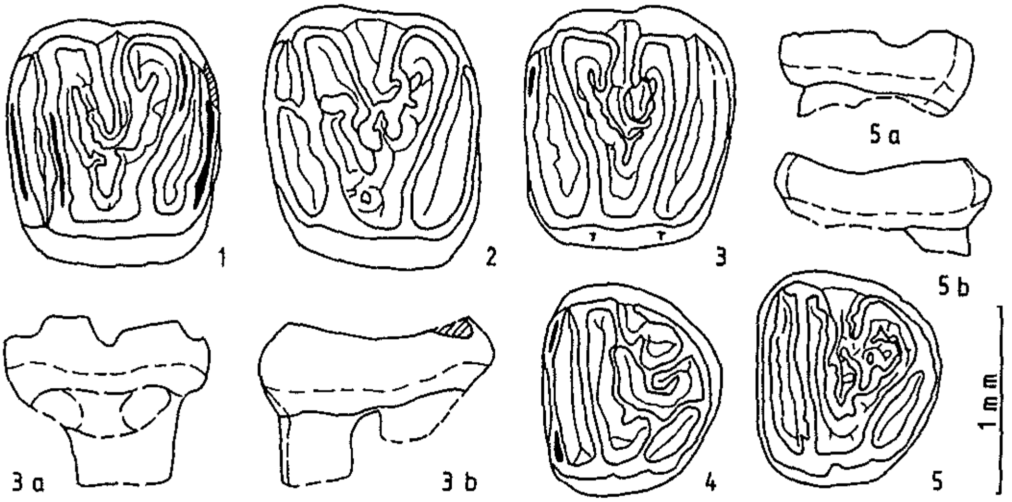

Fig. 15. — *Bransatoglis planus* (BAHLO, 1975) from Gröben 3 (MP 24), upper molars; **1**: M2, sin., 2000 XIII 105, **2**: M2, sin., 2000 XIII 107, **3**: M2, dext., 2000 XIII 110, **4**: M3, sin., 2000 XIII 112, **5**: M3, sin., 2000 XIII 113; **a**: labial, **b**: anterior.

Comparison and discussion

Bransatoglis planus (BAHLO, 1975) from Gröben 3 is identical in size and morphology to the type population from Heimersheim (fig. 16) (compare Bahlo 1975: 124-136). The three P4 from Heimersheim have only a single centroloph. However, in other localities with more material (for instance Hoogbutsel), there are some specimens with two centrolophs.

The populations from Monac (MP 20), Hoogbutsel (MP 21), and Paguera (MP 23-24) have either only a very narrow connection between entoconid and posterolophid in the m3 or this connection is completely absent. In Hoogbutsel and Paguera, the posteroloph mostly has only a narrow contact to the protocone in the M2 and in the M3, the anteroloph often has only a narrow contact to the protocone (compare Vianey-Liaud 1994: 144-147 and Hugueney 1997: 302). These features can be regarded as more primitive compared with Gröben 3. However, the teeth from Hoogbutsel and Paguera are somewhat longer than from Gröben 3 (fig. 16).

B. planus from Saint-Menoux (MP 26) and Gaimersheim (MP 27-28) is somewhat larger than from Gröben 3 (fig. 16). In the m1/2, the centrolophid is always connected to the mesostylid. A second centrolophid can be developed (compare Hugueney 1980: 61, 62 and Kristkoiz 1992: 43-49). In comparison with Gröben 3, these features are more advanced.

Having compared Gröben 3 with Monac, Hoogbutsel, Paguera, Heimersheim, Saint-Menoux and Gaimersheim, it is possible to reconstruct a phylogenetic lineage of *Bransatoglis planus*. The oldest locality is Monac (MP 20), and the youngest is Gaimersheim (MP 27/28).

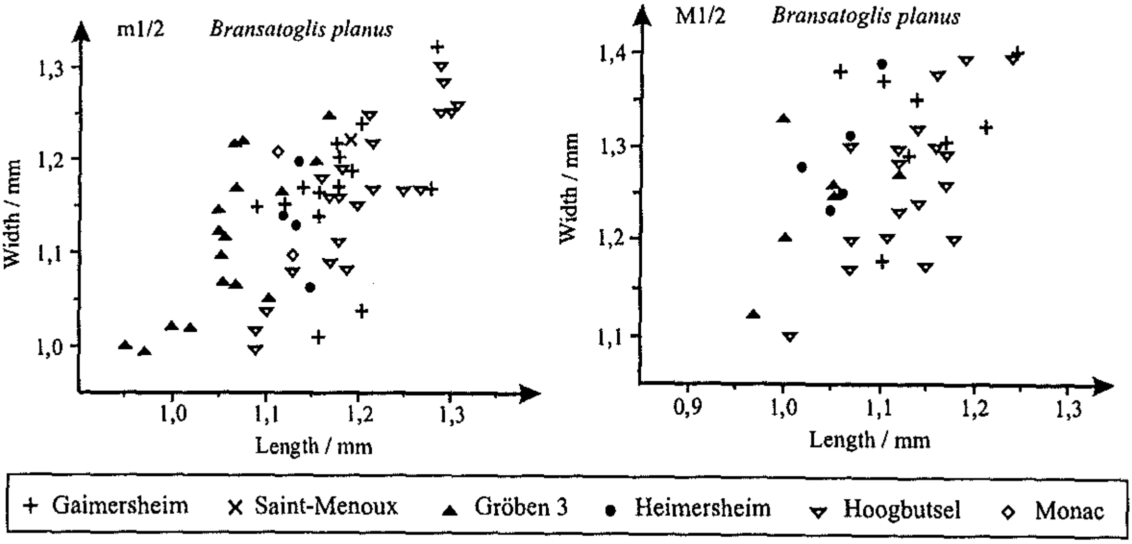

Fig. 16. — Scatter diagrams representing length and width of m1/2 and M1/2 of *Bransatoglis planus* from the most important Upper Eocene and Oligocene localities.

B. planus (advanced) from Aubenas-les-Alpes (MP 25) clearly has more extra crests in the upper molars than *B. planus* from Heimersheim, Gröben 3, and Gaimersheim (compare Vianey-Liaud 1994: 147). This could possibly represent either a short side-branch of the *B. planus*-lineage in the level MP 25 or a distinct population in Western Europe.

Bransatoglis fugax (HUGUENEY, 1967) from the type locality Coderet (MP 30), described by Hugueney (1967, 1969: 137f.) ist somewhat larger than *B. planus*. In the M2 of *B. fugax*, the endoloph is not continuously developed. In *B. planus* from the older localities Heimersheim, Gröben 3, and Gaimersheim, the M2 has a continuous endoloph usually. Vianey-Liaud (1994: 157, fig. 30) suggested that *B. fugax* is a successor of *B. planus*. Due to the somewhat more primitive feature mentioned above in *B. fugax*, it can be supposed that *B. fugax* branched off from the *B. planus* - lineage before the level MP 24.

I agree with Vianey-Liaud (1994: 157), that *B. sjeni* ÜNAY-BAYRAKTAR, 1989 from the middle Oligocene of Anatolia, probably derives from *B. planus*. In Heimersheim and Gröben 3, the posteroloph in the M2 and the anteroloph in the M3 are better connected to the protocone than in *B. sjeni*. Thus, the split probably occured before the level MP 24.

B. parvus FREUDENTHAL, 1996 from Fuenferrada 3B and Olalla 4A (MP 20-22) is similar in size to *B. planus* from Heimersheim and Gröben 3 (compare Freudenthal 1996, 1997a). However, the morphology is rather similar to the material from Hoogbutsel. Some features are even more primitive than from Hoogbutsel: In the p4 from Fuenferrada 3B, the extra crest in the anterior valley is absent and in the m2 and m3, it is often absent. The M1/2 usually have only two centrolophs. On the other hand, in the p4 and in the lower molars, there is a better connection between the metalophid and the metaconid and also between the centrolophid and the mesostylid than in the material from Hoogbutsel and Gröben 3. Therefore, *B. parvus* can be regarded as a separate phylogenetic lineage from the uppermost Eocene until the Lower Oligocene. Until now, this lineage is known only from Spain. Both species, *B. parvus* and *B. planus* have perhaps derived from *B. meridionalis* (MP 17). *B. bahloi* (MP 17-18) is most probably an older relative of *B. misonnei* (compare also Vianey-Liaud 1994: 157).

Bransatoglis heissigi n. sp.

(fig. 17-20)

v 1975 *Glirudinus* cf. *praemurinus* (FREUDENBERG, 1941) - Bahlo: 139-142, fig. 39

Derivatio nominis: Named in honour of Prof. Dr. Kurt Heißig, Centre of Palaeontology and Historical Geology, Munich
Locus typicus: Gröben 3 near Murnau in Upper Bavaria (southern Germany), map sheet 8333 Murnau am Staffelsee, R 44 46 500 H 52 83 265
Stratum typicum: Lower Cyrena Beds ("Untere Cyrenen-Schichten"), lowest Upper Oligocene (Chattian), somewhat younger than Heimersheim (MP 24)
Holotype: M1, sin., housed in the BSP, Munich (2000 XIII 175), fig. 20/2
Measurements of the holotype: 0,77 mm x 0,86 mm
Stratigraphic and geographic range: level MP 24, Germany
Diagnosis: Smallest species of the genus *Bransatoglis* HUGUENEY, 1967 (M1/2: 0,72-0,81 mm x 0,82-0,94 mm). The evolutionary level is higher than in *B. misonnei* VIANEY-LIAUD, 1994. The P3 is existing. The p4 frequently has an extra crest in the anterior valley. In the d4, p4, and in the lower molars, the entoconid is always connected to the meso- and posterolophid. The lower molars almost always have three extra crests, which are lower than the main crests; the connection between the anterolophid and the protoconid is only very rarely developed; and the mesoconid is very rarely hook-shaped. In the D4, in the upper praemolars and molars, the posteroloph is always connected to the protocone. The upper molars usually have two or three centrolophs (very rarely only one), which are somewhat lower than the main crests mostly, and extra crests in the antero- and posterosinus can be developed. In the M2 and

M3, the anteroloph is connected to the protocone. The lingual border of the M1/2 rarely shows an ornamentation.

Differential diagnosis:

B. heissigi n. sp. differs from *B. misonnei* VIANEY-LIAUD, 1994 by:

- the smaller size
- the frequent development of an extra crest in the anterior valley in the p4
- the connection between mesolophid and entoconid in the p4 and m1-3 (always present)
- the connection between entoconid and posterolophid in the m3 (always present)
- the connection between posteroloph and protocone in the D4, P4, M1, and M2 (always present)
- the complete endoloph in the M2
- the connection between anteroloph and protocone in the M3 (always present)

B. heissigi n. sp. differs from the other species of the genus *Bransatoglis* HUGUENEY, 1967 by its considerably smaller size.

B. heissigi n. sp. differs from *Microdyromys praemurinus* (FREUDENBERG, 1941) by:

- the possession of the P3
- the predominant lack of the connection between anterolophid and protoconid in the m1-3
- the usually not hook-shaped mesoconid in the m1-3
- the mostly lower and shorter extra crests in the m1-3
- the rarely ornamentation at the lingual border in the M1 and M2
- the incomplete endoloph and the narrow base of the trigone in the M1
- the very small or completely absent extra crest in the anterior centrosinus in the M2

B. heissigi n. sp. differs from the other species of the genus *Microdyromys* DE BRUIJN, 1966 by:

- the possession of the P3
- the incomplete endoloph in the M1
- the rarely ornamentation at the lingual border in the M1 and M2

Material: 90 isolated teeth (15 fragments included) from Gröben 3, housed in the BSP, Munich (2000 XIII): 5 d4 (118-122), 6 p4 (123-128), 19 m1/2 (3 fragm. incl.) (129-147), 14 m3 (3 fragm. incl.) (148-160, 1999 XVII 49), 2 D4 (163-164), 2 P3 (161-162), 9 P4 (1 fragm. incl.) (165-173), 24 M1/2 (8 fragm. incl.) (174-197), 9 M3 (203-211)

Measurements: table 5

		d4	p4	m1	m2	m3	D4	P3	P4	M1	M2	M1/2	M3
L	n	5	6	8	5	10	2	2	8	8	5	2	8
	min./mm	0,50	0,62	0,75	0,78	0,70	0,55	0,50	0,52	0,72	0,73	0,72	0,55
	max./mm	0,60	0,67	0,85	0,85	0,81	0,57	0,50	0,60	0,81	0,80	0,78	0,67
	x/mm	0,54	0,65	0,79	0,80	0,74	0,56	0,50	0,56	0,76	0,76	0,75	0,61
	s/mm	0,038	0,022	0,032	0,027	0,038	-	-	0,030	0,029	0,028	-	0,045
	V/%	7,05	3,37	4,06	3,42	5,13	-	-	5,40	3,88	3,78	-	7,51
W	n	5	5	7	6	10	2	2	7	7	5	2	9
	min./mm	0,47	0,54	0,71	0,79	0,68	0,60	0,63	0,66	0,82	0,85	0,85	0,67
	max./mm	0,59	0,60	0,80	0,89	0,78	0,62	0,65	0,72	0,93	0,94	0,85	0,82
	x/mm	0,52	0,57	0,76	0,83	0,73	0,61	0,64	0,69	0,86	0,88	0,85	0,75
	s/mm	0,043	0,026	0,027	0,034	0,032	-	-	0,024	0,033	0,035	-	0,043
	V/%	8,27	4,56	3,56	4,10	4,45	-	-	3,50	3,91	4,01	-	5,81

Table 5.— Measurements of the teeth of *Bransatoglis heissigi* n. sp. from Gröben 3.

Description

Lower cheek teeth: The anterolophid is connected to the metaconid (except in one m3). The meso- and the posterolophid are always connected to the entoconid. However, the connection between the posterolophid and the entoconid can be narrow. The four main crests are approximately the same height. The extra crests are lower than the main crests.

d4: Five teeth are smaller than the p4. Additionally, they have less dental elements. In contrast to the p4, they are either as long as broad or only somewhat longer than broad. (They are interpreted here as d4.) In two specimens, the mesostylid and the entoconid are connected by a very narrow crest (2000 XIII 121, 122). There are always a connection between the metalophid and the metaconid. In four specimens, the anterolophid is connected to the protoconid. The hypoconid is almost isolated in two specimens (2000 XIII 121, 122). The d4 has a single root.

p4: The metaconid is mostly higher than the entoconid. Between the mesostylid and the entoconid, there is either an incision (4 spec.) or a narrow crest (3 spec.). The anterolophid is always connected to the protoconid. The metalophid has usually a connection to the metaconid. There is a hook-shaped mesoconid in one specimen (2000 XIII 124).

The centrolophid is very short and isolated (2 spec.), sagittally directed and connected to the metalophid (2 spec.), or it reaches the middle of the tooth and is connected to the mesostylid (2 spec.). In four of the six specimens, extra crests exist in

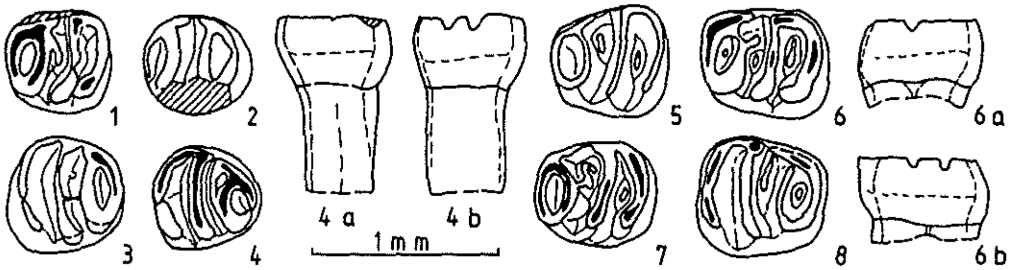

Fig. 17. — *Bransatoglis heissigi* n. sp. from Gröben 3 (MP 24), d4 and p4; 1: d4, sin., 2000 XIII 119, 2: d4, sin., 2000 XIII 120, 3: d4, dext., 2000 XIII 121, 4: d4, dext., 2000 XIII 122, 5: p4, sin., 2000 XIII 123, 6: p4, sin., 2000 XIII 124, 7: p4, sin., 2000 XIII 125, 8: p4, dext., 2000 XIII 127; a: lingual, b: labial.

the anterior and posterior valley. The p4 has two roots.

m1/2: Nine specimens are interpreted as m1, seven as m2. The m1 is wider posteriorly than anteriorly while, the m2 is wider anteriorly than posteriorly. In the m1, the posterior border is nearly straight while in the m2, it is somewhat rounded. As a rule, the m1 is longer than broad while, the m2 is broader than long.

In all m1/2, the metaconid is mostly somewhat higher than the entoconid. The anterolophid is connected to the protoconid only in teeth with a very strong wear. The metalophid is connected to the metaconid in seven of eight m1. However, this connection exists only in one of seven m2. Two specimens (both m1) show a hook-shaped mesoconid.

In five specimens (all m1), the centrolophid is connected to the mesostylid. The extra crest in the anterior valley is absent in two m2 while, in the posterior valley this crest is absent in two specimens. The m1/2 have two roots.

m3: The metaconid is higher than the entoconid. The anterolophid is connected to the protoconid in five of twelve specimens. The metalophid is connected to the lingual border in four specimens: either to the metaconid (2 spec.) or to the mesostylid (2 spec.). There is a hook-shaped mesoconid in four specimens. In two specimens, the hypoconid is connected to the mesoconid.

The centrolophid, absent only in one specimen (2000 XIII 149), is connected to the mesostylid in four of nine specimens. In two specimens, the extra crest in the anterior valley is absent while in the posterior valley, an extra crest exists always. The m3 has two roots.

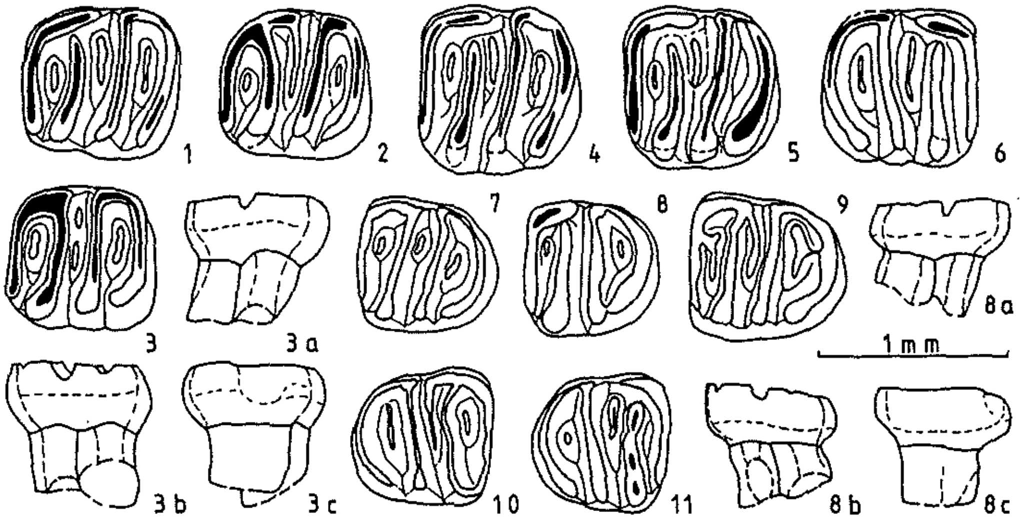

Fig. 18. — *Bransatoglis heissigi* n. sp. from Gröben 3 (MP 24), lower molars; **1**: m1, sin., 2000 XIII 129, **2**: m1, sin., 2000 XIII 131, **3**: m1, sin., 2000 XIII 132, **4**: m2, sin., 2000 XIII 139, **5**: m2, sin., 2000 XIII 141, **6**: m2, dext., 2000 XIII 142, **7**: m3, sin., 2000 XIII 148, **8**: m3, sin., 2000 XIII 149, **9**: m3, sin., 2000 XIII 150, **10**: m3, dext., 2000 XIII 153, **11**: m3, dext., 2000 XIII 154; **a**: lingual, **b**: labial, **c**: anterior.

Upper cheek teeth: In the D4, P3 and P4, the both labial cusps are approximately the same height while in the upper molars, the paracone is higher than the metacone. In all upper cheek teeth, the posteroloph is connected to the protocone.

D4: Two specimens differ from the P3 and the P4 by their almost triangular shape. The occlusal surface is moderately concave. In one specimen, the both labial cusps are connected by a very narrow crest. The antero- and the posteroloph are somewhat lower and narrower than the trigone crests. The anteroloph has a narrow connection to the paracone while, the connection to the protocone is developed only in one specimen. The trigone is either O-shaped and almost symmetrical or U-shaped and asymmetrical. The posteroloph is connected to the metacone. There is a single centroloph, which is clearly lower than the trigone crests. Roots have been broken off.

P3: Two specimens, which are clearly smaller than the P4, are interpreted as P3. The occlusal surface is moderately concave. The anteroloph, which is somewhat lower than the other three transverse crests, has no connection to the paracone. However, a narrow connection between the anteroloph and the protocone exists. The trigone is U- or O-shaped and almost symmetrical. The connection between the posteroloph and the metacone is very narrow. There is a low centroloph in the middle of the trigone. The P3 has two roots.

P4: The teeth are more or less O-shaped. The occlusal surface is slightly, moderately or strongly concave. In a single specimen, the anteroloph is lower than the other transverse crests (2000 XIII 173). Otherwise, the transverse crests have the same height. Only in two specimens, the anteroloph is clearly shorter than the protoloph. It is connected to the paracone in two of seven specimens, and a narrow connection to the protocone is developed in seven of nine specimens. The trigone is V- or U-shaped and often almost symmetrical. In three of eight specimens, the posteroloph is connected to the metacone. The extra crests are lower than the trigone crests. In five specimens, a single centroloph exists in the middle of the trigone. In one specimen, it is connected to the paracone, and in two specimens, there are two centrolophs. The P4 has two roots.

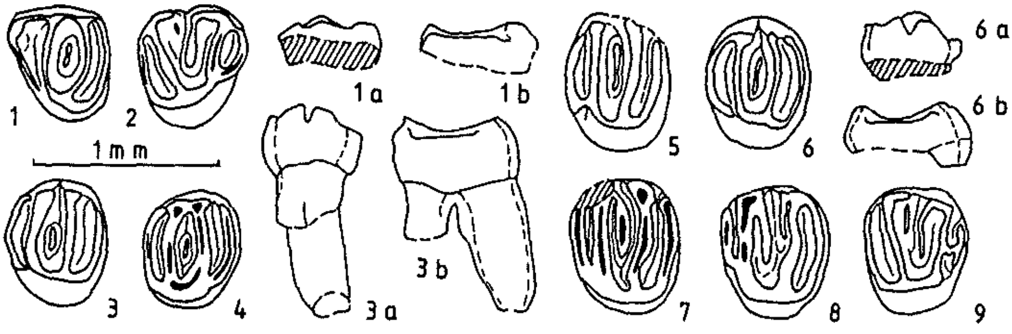

Fig. 19. — *Bransatoglis heissigi* n. sp. from Gröben 3 (MP 24), D4, P3 and P4; **1**: D4, sin., 2000 XIII 163, **2**: D4, dext., 2000 XIII 164, **3**: P3, sin., 2000 XIII 161, **4**: P3, dext., 2000 XIII 162, **5**: P4, sin., 2000 XIII 165, **6**: P4, sin., 2000 XIII 167, **7**: P4, sin., 2000 XIII 169, **8**: P4, sin., 2000 XIII 170, **9**: P4, dext., 2000 XIII 173; **a**: labial, **b**: anterior.

M1/2: The M1 has an oblique lingual border and an asymmetrical trigone (12 spec.) while, the M2 is approximately rectangular and its trigone is symmetrical (7 spec.). However, there are also transitional shapes (5 spec.). Both, the M1 and the M2, are wider than they are long. The occlusal surface is moderately concave.

The antero- and the posteroloph have almost the same height as the trigone crests. The anteroloph is connected to the paracone in five of 16 specimens. The connection to the protocone is not developed in the M1 while in the M2, the connection between anteroloph and protocone exists always. However, it is only very narrow in three specimens. In the M1, the trigone is usually U-shaped with a narrow base while in the M2, it is always U-shaped with a broad base. The posteroloph is connected to the metacone in six of 16 specimens.

The anterior centroloph, which has almost the same height as the trigone crests, is connected to the paracone (except in one specimen: 2000 XIII 178). The posterior centroloph is absent only in two of 19 specimens. It is always shorter and mostly lower than the anterior one and connected to the metacone in six of 14 specimens. In 14 of 20 specimens, the anterior centrosinus shows a very small extra crest. In the anterosinus, an extra crest exists in five specimens while in the posterosinus, such crest occurs in two specimens. In four specimens, the lingual border exhibits an ornamentation (two or three small holes). The M1/2 have three roots.

M3: The occlusal surface is almost flat. The four transverse crests have approximately the same height. The connection between the anteroloph and the paracone is developed in seven of nine specimens. Always, the anteroloph is connected to the protocone. The proto- and the metaloph construct an U-shaped, asymmetrical trigone. In four specimens, the metaloph is interrupted. Its lingual part touches often an almost sagittally directed extra crest in the posterosinus (for instance 2000 XIII 203). There is a connection between the posteroloph and the metacone in seven specimens.

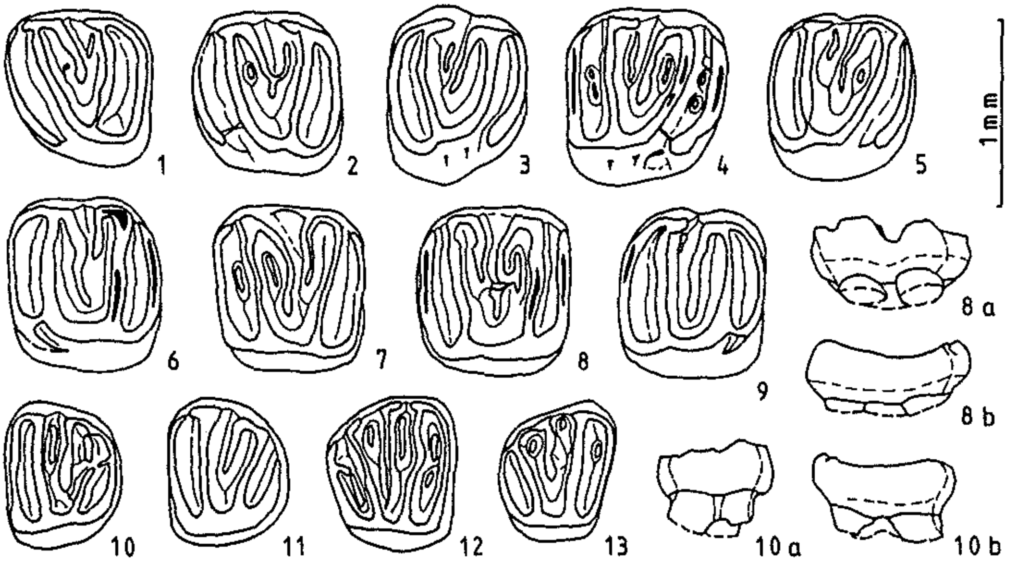

Fig. 20. — *Bransatoglis heissigi* n. sp. from Gröben 3 (MP 24), upper molars; **1**: M1, sin., 2000 XIII 174, **2**: M1, sin., 2000 XIII 175, **holotype**, **3**: M1, dext., 2000 XIII 179, **4**: M1, dext., 2000 XIII 180, **5**: M1, dext., 2000 XIII 181, **6**: M2, sin., 2000 XIII 186, **7**: M2, sin., 2000 XIII 187, **8**: M2, dext., 2000 XIII 189, **9**: M2, dext., 2000 XIII 190, **10**: M3, sin., 2000 XIII 203, **11**: M3, sin., 2000 XIII 205, **12**: M3, dext., 2000 XIII 208, **13**: M3, dext., 2000 XIII 210; **a**: labial, **b**: anterior.

The posterior centroloph, which has the same height as the trigone crests, is always connected to the metacone. In four specimens, a lower and shorter anterior centroloph is developed. It is connected to the paracone only in one specimen (2000 XIII 209). In two specimens (for instance 2000 XIII 208), there is a small extra crest in the posterior centrosinus. Extra crests in the anterosinus exist only in two specimens. In four specimens, there is an extra crest in the posterosinus, which is always connected to the posteroloph. The M3 has three roots.

Comparison and discussion

Bransatoglis heissigi n. sp. is also known from Heimersheim. The six teeth, described by Bahlo (1975: 139-142) as *Glirudinus* cf. *praemurinus*, cover the uppermost size range of *B. heissigi* from Gröben 3 (fig. 21). In the p4 from Heimersheim, the mesolophid is interrupted near the middle. The lingual half has a narrow connection to the centrolophid, and the labial half is connected to the extra crest in the posterior valley (compare Bahlo 1975: fig. 39a). Although the mesolophid is somewhat abnormally developed, the remaining dental morphology closely resembles the p4 from Gröben 3. In the m1, the anterolophid is connected to the protoconid (compare Bahlo 1975: fig. 39a). This m1, however, has a very strong wear already. Otherwise, the m1/2 from Heimersheim are very similar to *B. heissigi* from Gröben 3. Both M2 from Heimersheim closely resemble the material from Gröben 3 (compare Bahlo 1975: fig. 39b as well as one M2 in the Darmstadt museum, which was not drawn by Bahlo, with the number HLM 403).

Bransatoglis misonnei VIANEY-LIAUD, 1994 occurs in Hoogbutsel and Montalban (MP 21, MP 23) (Vianey-Liaud 1994: 147-149) as well as in the Charbon syncline (MP 20) (Herb *et al.* 1984: 227, fig. 5 a-g). The teeth from all three localities are usually larger than those of *B. heissigi* (fig. 21). The material from the Charbon syncline was described by Herb *et al.* under the name "cf. *Microdyromys praemurinus*". However, the characteristic features in *M. praemurinus* are missing (connection between anterolophid and protoconid and a hook-shaped mesoconid in the lower molars; the connection between posteroloph and protocone in the M1 as well as a broad base of the trigone in the M1/2). On the other hand, the material from the Charbon syncline corresponds in size and morphology with *B. misonnei* from the type locality Hoogbutsel. Additionally, there are the following differences from the new species *B. heissigi*: in one m1, there is no connection between the posterolophid and the entoconid, and in the M1, the connection between the posteroloph and the protocone is absent.

The different features of *B. heissigi* compared with *B. misonnei* (see differential diagnosis) can be interpreted as more advanced. Despite the smaller size, *B. heissigi* could possibly be a younger relative of *B. misonnei*. There is a decrease in size in this phylogenetic lineage, which can already be observed in the evolutionary step from *B. bahloi* until *B. misonnei* (compare Vianey-Liaud 1994: 157).

Microdyromys praemurinus from the type locality Gaimersheim (MP 27-28) and from Saint-Menoux (MP 26), described by Kristkoiz (1992: 49-55) and by Hugueney (1980: 62), is similar in size to *B. heissigi*. The different features of *B. heissigi* compared with *Microdyromys praemurinus* (see differential diagnosis) can be interpreted as more primitive.

Vianey-Liaud *et al.* (1995: 264) described three teeth from Garouillas and Rigal-Jouet 1 (MP 25) as *Microdyromys praemurinus*. This material shows two features still remnant of *B. heissigi* (absence of a connection between anterolophid and protoconid in the m1, incomplete endoloph in the M1).

Some more material of *Microdyromys praemurinus* from the level MP 25 exists from Bumbach 1 (Uhlig, 2002). Three of the four m1/2 have a connection between the anterolophid and the protoconid, and three specimens have a hook-shaped mesoconid. These remains represent an evolutionary stage between *B. heissigi* (MP 24) and *Microdyromys praemurinus* from Saint-Menoux and Gaimersheim (MP 26, 27/28).

Glis guerbuezi from the Oligocene of Anatolia, described by Ünay-Bayraktar (1989: 76-78), has higher and narrower main crests and longer extra crests in the lower molars. In the M1/2, the centrolophs and the protoloph are directed oblique and parallel to each other. In the M2, the endoloph is incomplete. Most likely, that there is no close phylogenetic relationship between *Glis guerbuezi* and *Bransatoglis heissigi*.

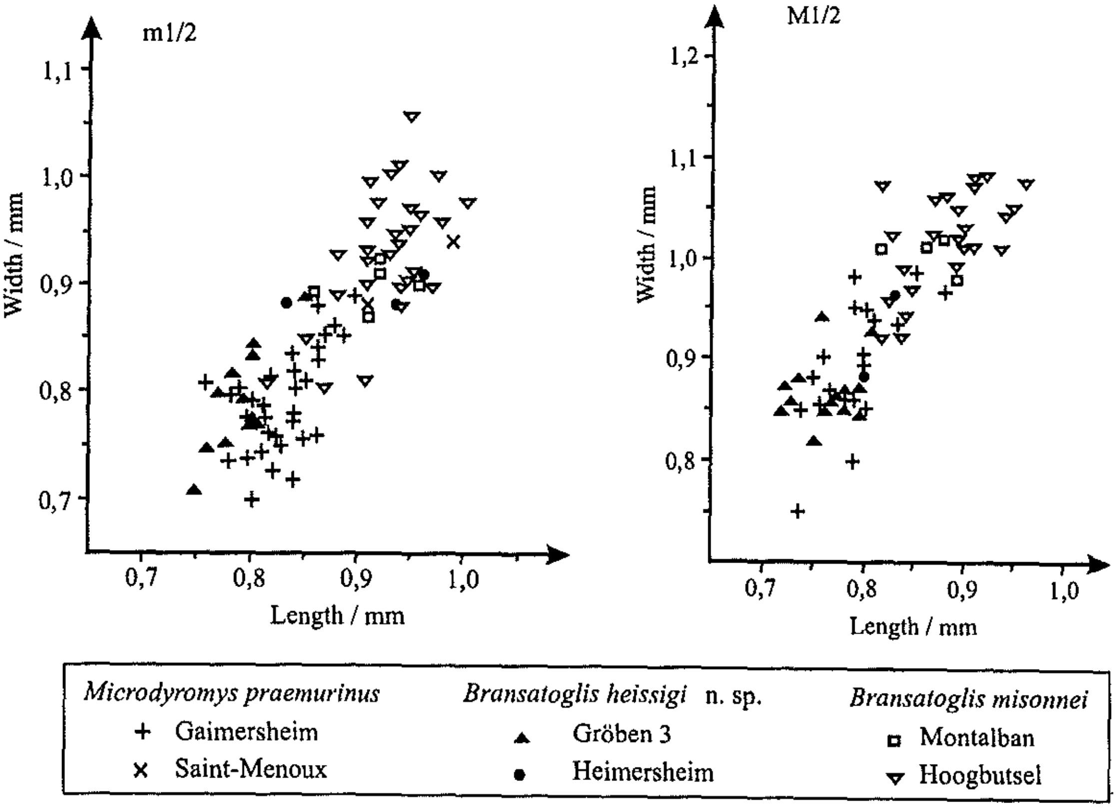

Fig. 21. — Scatter diagrams representing length and width of m1/2 and M1/2 of *Bransatoglis misonnei*, *B. heissigi* n. sp. und *Microdyromys praemurinus* from the most important Oligocene localities.

PHYLOGENY, BIOSTRATIGRAPHY AND PALAEOECOLOGY

Gliravus tenuis BAHLO, 1975 appears in the levels MP 22 (La Plante 2), MP 23 (Montalban) and MP 24 (Heimersheim, Vialence, Gröben 3). Within this phylogenetic lineage, a slight increase in size and a development of the centrolophid in the lower molars can be observed. In a level somewhat younger than Heimersheim (Gröben 3), the centrolophid in the lower molars is always developed. These evolutionary steps could be a useful biostratigraphic tool.

Bransatoglis micio (MISONNE, 1957) occurs in the levels MP 21 (Hoogbutsel, Waltsch), MP 22 (Calaf 13, 14), MP 23 (Itardies), and MP 24 (Gröben 3). The material from Gröben 3 shows compared with that from Hoogbutsel some advanced features: in the d4 and p4, the entoconid is somewhat better connected to the posterolophid, in the m1/2, the mesolophid is developed somewhat stronger, in the D4, P4 and M1, the connection between posteroloph and protocone is somewhat better, and in the M3, the base of the trigone is broader, the connection between the anteroloph and the protocone is usually somewhat better. The material from Waltsch and Calaf represents evolutionary levels between Hoogbutsel und Gröben 3.

However, the material from Itardies remains a problem, because in the m1/2, the extra crest in the anterior valley is always absent. It is either a short side branch or a distinct population occuring only in the region around Itardies.

Bransatoglis planus (BAHLO, 1975) is known from the levels MP 20 (Monac), MP 21 (Hoogbutsel), MP 23 (Montalban), MP 23/24 (Paguera), MP 24 (Heimersheim, Gröben 3), MP 26 (Saint-Menoux) and MP 27/28 (Gaimersheim). Within this lineage, three evolutionary stages can be observed:

- from MP 20 until MP 23/24: in the m3, the connection between entoconid and posterolophid is absent or only very narrow; in the M2, the connection between posteroloph and protocone is almost always very narrow; and in the M3, the connection between anteroloph and protocone is often very narrow.

- in MP 24 (and MP 25?): in the m3, the posterolophid is always connected to the entoconid; in the M2, the posteroloph is always connected to the protocone and in the M3, the anteroloph is always connected to the protocone.

- from MP 26 until MP 28: all features already occur in MP 24 (and 25?). Additionally, the centrolophid is always connected to the mesostylid, and a second centrolophid can be developed in the m1/2.

These three evolutionary stages could be a useful biostratigraphic tool.

Bransatoglis heissigi n. sp. is restricted to the level MP 24 (Heimersheim and Gröben 3). The species is located between *B. misonnei* (MP 20 - 23) and *Microdyromys praemurinus* (MP 25 - 28) (see chapter 3, comparison and discussion to *Bransatoglis heissigi* n. sp.). Within the phylogenetic lineage of *B. bahloi* - *B. misonnei* - *B. heissigi*, a decrease in size is observed (see fig. 21).

Microdyromys praemurinus is the oldest and most primitive representative of the subfamily Dryomyinae DE BRUIJN, 1967 (Daams & de Bruijn 1995: 16). As *Microdyromys praemurinus* most likely derives from *Bransatoglis heissigi*, it can be supposed that the origin of the subfamily Dryomyinae can be found in *B. heissigi*.

I agree with Vianey-Liaud (1994: 157) that the species *B. micio, B. planus, B. sjeni, B. fugax, B. bahloi*, and *B. misonnei* have a common origin in the area of *B. meridionalis* (see chapter 3, comparison and discussion to the species of *Bransatoglis*). Furthermore, the species *B. parvus* FREUDENTHAL, 1996 can be traced back to *B. meridionalis*. *B. parvus* is somewhat larger than *B. meridionalis*. In the lower molars, the extra crest in the anterior valley is often already developed (in *B. meridionalis*, it is always absent); in the upper molars, two centrolophs always exist (in *B. meridionalis*, there is sometimes only a single centroloph) (compare Hartenberger 1971 and Freudenthal 1996, 1997a). Moreover, the origin of the species *B. heissigi* n. sp. can also be traced back to the area of *B. meridionalis* by way of the species *B. misonnei* and *B. bahloi*.

B. concavidens is either a successor of *B. sjeni*, as Vianey-Liaud (1994: 157) proposed, or it has a separate origin in the Upper Eocene, as Freudenthal (1996: 33) presumed. This problem, however, cannot be clariefied in the context of the present work, because the description of the *B. concavidens*-like remains from the Upper Eocene of Aguatón is still missing.

The locality Gröben 3 is situated in the Lower Cyrena Beds, which are deposited in a deltaic palaeoenvironment. A typical feature is a fast and repeated change of brackish, lacustrine and fluviatile sediments (Barthelt 1989, Uhlig *et al.* 2000).

After Meulen & de Bruijn (1982: 520-522), *Bransatoglis* was mainly living in forests and open woodland, *Gliravus* prefered open countries and forests with rocky substrate. Therefore, the *Bransatoglis*-species from Gröben 3 were probably living in the forests of the deltaic plain, *Gliravus tenuis* in the hinterland near the Alps.

SUMMARY AND CONCLUSIONS

This study describes four taxa of Gliridae (208 isolated teeth, 28 fragments included) from the Oligocene mammal locality Gröben 3: *Gliravus tenuis* BAHLO, 1975, *Bransatoglis micio* (MISONNE, 1957), *B. planus* (BAHLO, 1975) and *B. heissigi* n. sp. Consequently, this work is the first monograph of a larger Gliridae-assemblage from a single deposit in the folded molasse of southern Germany (fig. 22).

Gliravus tenuis from Gröben 3 is somewhat more advanced than the type population found in Heimersheim. Thus, it confirms the correlation of Gröben 3 with a level somewhat younger than Heimersheim (MP 24), which was already supposed by the theridomyid *Blainvillimys* aff. *heimersheimensis* (compare Uhlig 1999).

B. micio from Gröben 3 is the first proof of this species near the level MP 24. From Hoogbutsel (MP 21) until Gröben 3, only very small evolutionary steps can be observed.

B. planus is known from MP 20 until MP 28. Due to the relatively abundant tooth material from Gröben 3, it is possible to observe three evolutionary stages within this lineage for the first time. These stages could be a useful biostratigraphic tool.

B. heissigi n. sp. is restricted to the level MP 24. The species is located between *B. misonnei* (MP 20 - 23) and *Microdyromys praemurinus* (MP 25 - 28). It can be interpreted as the origin of the subfamily Dryomyinae DE BRUIJN, 1967.

Within the phylogenetic lineage of *B. bahloi* - *B. misonnei* - *B. heissigi*, a decrease in size can be observed. This lineage and also the lineages of *B. planus, B. parvus, B. sjeni, B. fugax* and *B. micio* have their origin most probably in the area of *B. meridionalis* (MP 17).

The *Bransatoglis*-species from Gröben 3 were probably living in the forests of a deltaic plain (palaeoenvironment of the Lower Cyrena Beds), *Gliravus tenuis* in the hinterland near the Alps.

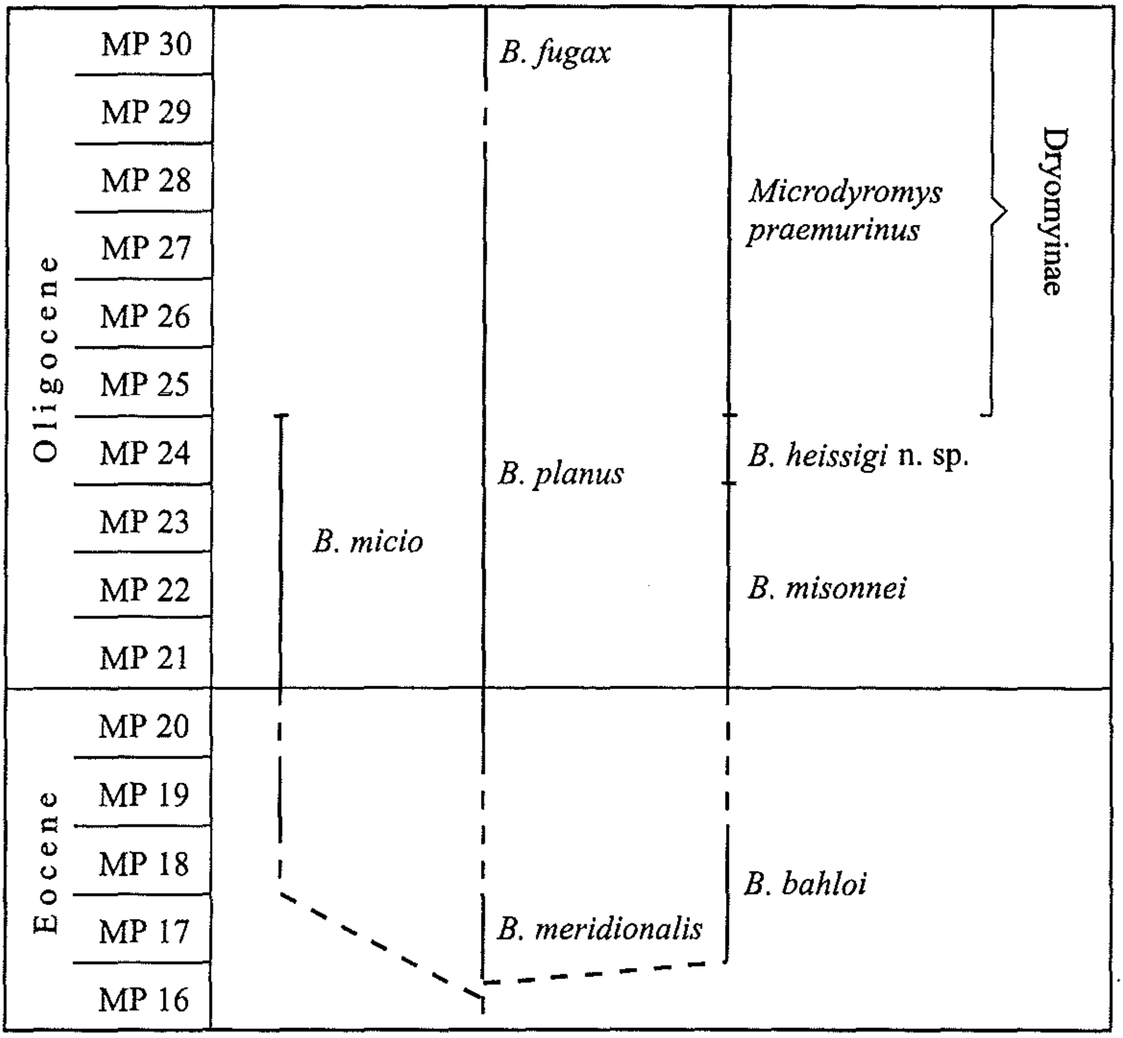

Fig. 22 Some phylogenetic lineages of *Bransatoglis* from the Upper Eocene and Oligocene in Europe.

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