

Cricetodon meini and other rodents from Mühlbach and Grund, Lower Austria (Middle Miocene, late MN5)

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(With 1 textfigure, 8 tables and 3 plates)

Abstract

The rodents *Cricetodon meini*, *Democricetodon mutilus*, *Democricetodon* cf. *gracilis*, *Megacricetodon minor*, *Eumyarion* sp., *Spermophilinus besanus* and *Prodryomys satus* were recovered from the localities Mühlbach and Grund in the Molasse Basin of Lower Austria, and *Eumyarion* cf. *weinfurteri* was found in Niederleis in the Northern Vienna Basin. The most abundant rodent, *C. meini*, is an immigrant from SW-Asia. In the Middle Miocene (MN5) it migrated from Southeast to Central Europe, ultimately reaching Western Europe and becoming extinct at the end of MN5. Its first and last occurrence in the Molasse Basin of Bavaria is below the "Brock" horizon (i.e. before the Ries event dated at 14.9 ma). In the Alpine Molasse Basin of Austria it was recovered from the upper Grund beds, which were identified based on the marine fauna to represent the late Lower Lagenidae Zone. *C. meini* and other burrowing cricetids and *Spermophilinus* hint at dry, woody environments with a low ground water table, and at more dry than humid climatic conditions locally.

Key words: Rodents, Grund beds, Mühlbach, Grund, Molasse Basin, Niederleis, Vienna Basin, Ries impact, biostratigraphy, late MN5, Early Badenian, late Lower Lagenidae Zone.

Zusammenfassung

Die Fundstellen Mühlbach und Grund im Molassebecken Niederösterreichs erbrachten folgende Nagetiere: *Cricetodon meini*, *Democricetodon mutilus*, *Democricetodon* cf. *gracilis*, *Megacricetodon minor*, *Eumyarion* sp., *Spermophilinus besanus* und *Prodryomys satus*. Aus Niederleis im nördlichen Wiener Becken wird *Eumyarion* cf. *weinfurteri* beschrieben. Das dominierende Faunenelement ist *C. meini*, ein Einwanderer aus SW-Asien. Im Mittel-Miozän (MN5) verbreitete er sich von Griechenland über Mitteleuropa nach Westeuropa und starb gegen Ende der Säugetierzone MN5 wieder aus. In der bayerischen Molasse wurde *C. meini* unmittelbar unter dem "Brock" Horizont, d.h. vor dem Ries Impact (14.9 Ma) nachgewiesen. Die Österreichischen Funde von *C. meini* stammen aus den oberen Grunder Schichten der Molassezone. Sie wurden auf Grund der marinen Fauna in die späte Untere Lageniden Zone eingestuft.

Das Vorherrschen grabender Nagetiere (des Erdhörnchens *Spermophilinus* und diverser Hamsterverwandter, vor allem von *C. meini*) und das fast völlige Fehlen einer Gliridae-Eomyidae-Petauristidae-Vergesellschaftung geben Hinweise auf Lebensräume mit niedrigem Grundwasserspiegel, auf trockene Waldlandschaften und lokal auf ein eher trockenes als feuchtes Klima.

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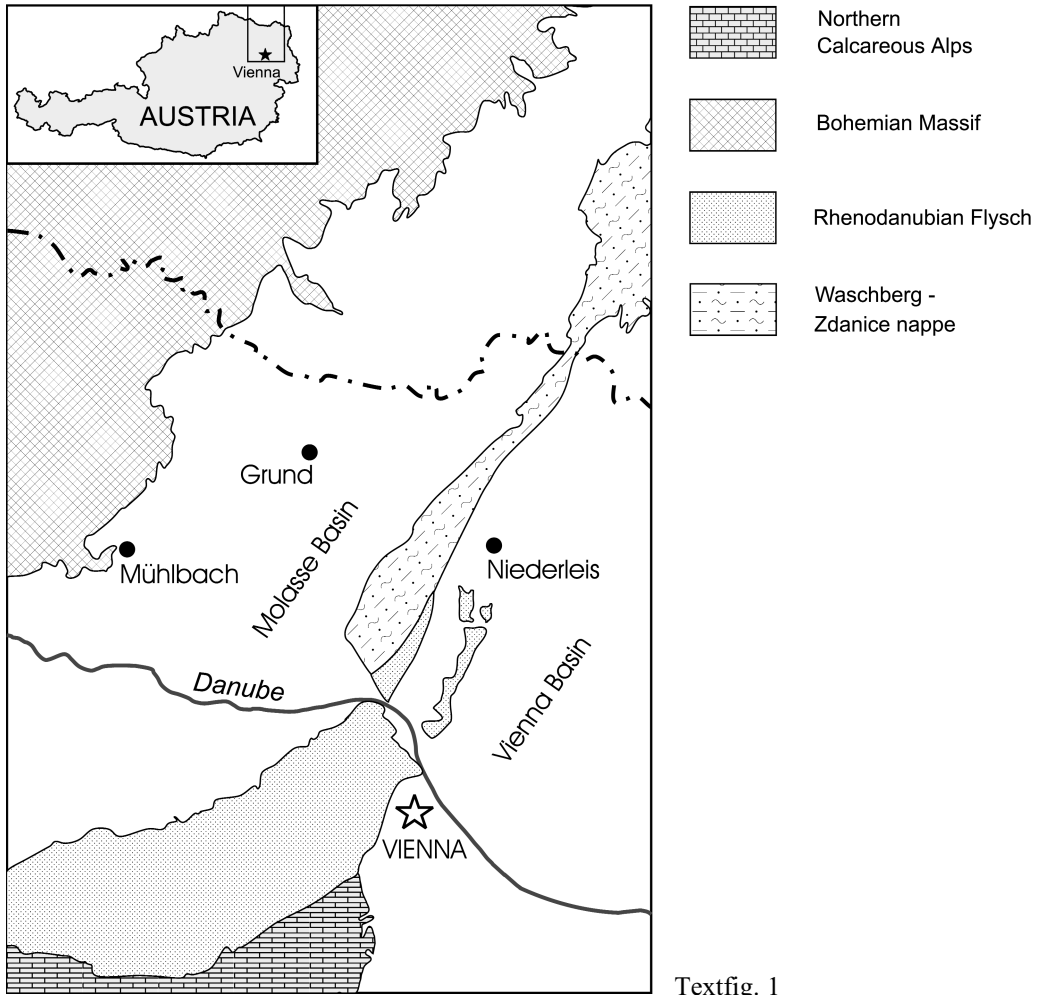
Introduction

The investigated rodents were recovered from three localities: Mühlbach, Grund and Niederleis. Mühlbach and Grund are located in the Molasse Basin in Lower Austria, Niederleis in the north of the Vienna Basin. For localization see textfigure 1. The fossil sites are artificial outcrops investigated by the Paleontological Institute of the University of Vienna, the Geological Survey and the Museum of Natural History, Vienna (1996, 1998, 1999, 2000). Sediments and fossils of these sections display marine conditions. Only few remains of terrestrial vertebrates such as mammals, reptiles, birds and amphibians are transported into these marine environments. The sections Grund and Niederleis yielded only a few rodent teeth and jaws. In Grund, fossils were recovered from the mollusc-shell-layers of two sections (GRU-F-11, GRU-B1-1) and from washed samples of the same layers (ROETZEL et al. 1999b: Abb. 19). Only one rodent tooth is available from Niederleis. Numerous rodent remains from Mühlbach were recovered by washing two large samples Mü1 and Mü2, in total about 700 kg sediment. For detailed localization see ROETZEL (this volume). The latter rodent fauna is not diverse, but highly relevant for stratigraphical and paleoecological interpretations, and for marine-continental correlations.

Tab. 1: List of rodents from Mühlbach, Grund and Niederleis.

Mühlbach:	stratigraphical ranges	Grund:	stratigraphical ranges
<i>Cricetodon meini</i>	MN5 FAD+LOD	<i>Cricetodon meini</i>	MN5 FAD+LOD
<i>Democricetodon mutilus</i>	MN4-7	<i>Democricetodon mutilus</i>	MN4-7
<i>Democricetodon cf. gracilis</i>	MN4-6		
<i>Megacricetodon minor</i>	MN5-9		stratigraphical ranges
<i>Eumyarion</i> sp.		Niederleis:	
<i>Spermophilinus besanus</i>	MN4-5	<i>Eumyarion cf. weinfurteri</i>	MN4-6
<i>Prodryomys satus</i>	MN5 FAD+LOD		

For washing, sieves with mesh sizes of 0.5, 2.0 and 5.0 mm were used. SEM-photos of the fossils were taken with a Philips XL 20 scanning electron microscope at the Biozentrum/University of Vienna. The measurements were made with a Leica WILD M8 stereo microscope. For comparative studies, rodent collections from the localities listed below were available (Coll. NHMW and BSM):



Coll. NHMW: Vieux Collonges (F), Sansan (F), La Grive (F), Goldberg (D), Vermes 1 (CH), Rümikon (CH), Mettlen 4 (CH), Obergänsersdorf (A) and Teiritzberg (A). Coll. BSM: Unterneul 1a (D), Ziemetshausen 1a, 1c (D) and Vieux Collonges (F).

Abbreviations

FAD = first appearance datum
 LOD = last occurrence datum
 OSM = Upper Freshwater Molasse (=Obere Süßwassermolasse)
 NHMW = Naturhistorisches Museum Wien
 BSM = Bayerische Staatssammlung München
 F = France
 D = Germany

A = Austria
 CH = Switzerland
 CZ = Czech Republic
 * = type locality
 ma = million years
 MN = Neogene mammal units
 N = number of specimens

Taxonomic description

Order Rodentia BOWDICH, 1821

Family Sciuridae GRAY, 1821

Genus *Spermophilinus* de BRUIJN & MEIN, 1968

***Spermophilinus besanus* CUENCA, 1988** (Tab. 2; Plate 1, a-i)

Locality and stratigraphy: Mühlbach a. Manhartsberg (Mü1 and Mü2), Lower Austria; brownish silt of the Gaiendorf Formation, (see ROETZEL 2003, this volume), Lower Badenian, MN5.

Type locality: Vargas 1A (Spain); MN4

Stratigraphical range: MN4-MN5

Material (from samples Mü1 and Mü2): 24 teeth and 2 fragments

Mü1: 3 P4 r, 2 M1/2 r, 1 p4 l, 1 p4 r, 1 m1 r, 2 m2 r (NHMW2002z0138/0001-0004).

Mü2: 1 M3r, 1 p4 r, 1 m1 r, 1 m1 l, 3 m2 l, 3 m2 r, 1 m3 l, 3 m3 r (NHMW2002z0139/0001-0006).

Tab. 2: Measurements (in mm) of *Spermophilinus besanus* CUENCA, 1988 from Mühlbach.

	Length			N	Width		
	Range	mean	stdev		Range	Mean	stdev
P4	1.45-1.50	1.47	0.0288	3	—	1.50	0.0000
M1/2	1.60-1.65	—	0.0000	2	—	2.05	0.0000
M3	—	2.00	0.0000	1	—	1.90	0.0000
p4	1.40-1.50	1.45	0.0500	3	1.10-1.15	1.13	0.0288
m1	1.65-1.70	1.67	0.0289	3	1.55-1.75	1.65	0.1041
m2	1.50-1.80	1.70	0.1000	8	1.70-1.95	1.79	0.0863
m3	1.95-2.00	1.84	0.1031	4	1.55-2.00	1.75	0.1871

Remarks: *Spermophilinus* arrived as an immigrant in Europe in the Early Miocene (MN4), it dispersed rapidly all over Europe and became extinct in the Early Pliocene. The genus is known from considerably older faunas in Central Anatolia (de BRUIJN 1998: 102) and from the Early Miocene of Mongolia (described as Sciuridae indet. in HÖCK et al. 1999: Fig. 21/5) and is therefore considered to be of Asian origin. In Europe, four species are recognized: *S. besanus* CUENCA, 1988; *S. bredai* (VON MEYER, 1848); *S. turolensis* de BRUIJN & MEIN, 1968; and *S. giganteus* de BRUIJN, DAWSON & MEIN, 1970. These subsequent species do not differ significantly by morphological characters but have long been known to show size increase through time. De BRUIJN (1995: Fig.1) verified this trend to be gradual by plotting the mean length of the M1/2 from a number of *Spermophilinus* associations against time. *S. besanus* is oldest and smallest, with a mean M1/2 length around 1.5-1.6 mm. The subsequent *S. bredai* has mean measurements around 1.7-1.8 mm, *S. turolensis* around 2.0-2.1mm, and *S. giganteus* around 2.3 mm;

the latter is the youngest. Although ranging between *besanus* and *bredai*, the specimens from Mühlbach (Tab. 2) are attributed to *S. besanus*.

Following de BRUIJN's species concept, *S. besanus* is distributed all over Europe, ranging from MN4 to MN5 (DAXNER-HÖCK 1998b: 372)

Family Gliridae THOMAS, 1897

Genus *Prodryomys* MAYR, 1979

***Prodryomys satus* MAYR, 1979** (Tab. 3; Plate 1, j - l)

Locality and stratigraphy: Mühlbach a. Manhartsberg, Lower Austria; brownish silt of the Gaindorf Formation, sample Mü1 (see ROETZEL this volume), Lower Badenian, MN5.

Type locality: Sandelzhausen (Germany); MN5

Stratigraphical range: MN5

Material (from sample Mü1): 1 M2 r, 1 p4 r, 1 m2 r and 3 fragmentary molars (NHMW2002z0140/0001-0004).

Tab. 3: Measurements (in mm) of *Prodryomys satus* MAYR, 1979 from Mühlbach (Mü1).

	Length	N	Width
M2r	0.95	1	1.10
p4r	0.70	1	0.70
m2r	1.00	1	0.95

Remarks: *P. satus* has medium-sized, very low crowned teeth. The lophs are thin, the valleys are flat and wide. The four main lophs of upper molars are lingually connected by the endoloph. The anterior centroloph is longer than the posterior one. The lower m2 is wide; it has four main lophs and a relatively long centrolophid. There are two extra ridges, a small one in the anterior valley and a longer one in the posterior valley. *P. satus* from Mühlbach has slightly smaller tooth measurements than the specimens from Sandelzhausen and Puttenham (WU 1990) in Germany and from the Austrian localities Teiritzberg and Obergänserndorf (DAXNER-HÖCK 1998 b). As far as known to date, *P. satus* ranges from the early to the late MN5.

Family Cricetidae ROCHEBRUNE, 1883

Genus *Democricetodon* FAHLBUSCH, 1964

***Democricetodon mutilus* FAHLBUSCH, 1964** (Tab. 4; Plate 2, a-i)

Democricetodon mutilus - ROETZEL et al. : 331

Locality and stratigraphy: Mühlbach a. Manhartsberg (Mü1 and Mü2), Lower Austria, brownish silt of the Gaindorf Formation (see ROETZEL this vol-

ume), and Grund (GRU-F-11), Lower Austria; sand of the Grund Formation (ROETZEL et al.1999: 328: Abb. 19), Lower Badenian, MN5.

Type locality: Langenmoosen (Germany), MN5

Stratigraphical range: MN4-MN7.

Material from Grund (GRU-F-11): 1 M2 r (NHMW2002z0144/0001).

Measurements: Length = 1.40 mm, Width = 1.25 mm

Material from Mühlbach (Mü1, Mü2):

Mü1: 3 M2 l and 8 molar fragments (NHMW2002z0143/0001).

Mü2: 2 M1 l, 5 M1 r, 4 M2 l, 2 M2 r, 1 M3 r, 1m1 l, 1 m1 r, 4 m2 l, 1 m3 r and 5 molar fragments (NHMW2002z0142/0001-0009).

Tab. 4: Measurements (in mm) of *D. mutilus* from Mühlbach (Mü1 and Mü2).

	Length		N	Width			
	Range	mean		stdev	Range	Mean	stdev
M1	1.75-1.90	1.84	0.069	7	1.20-1.25	1.24	0.020
M2	1.35-1.50	1.41	0.063	9	1.20-1.25	1.10	0.022
M3	—	1.10	0.000	1	—	1.05	0.000
m1	—	1.55	0.000	1	—	1.23	0.000
m2	1.40-1.45	1.44	0.025	4	1.40-1.45	1.79	0.029
m3	—	1.35	0.000	1	—	1.05	0.000

Remarks: The teeth from Mühlbach and Grund correspond with *D. mutilus* in size and molar morphology. The main characters are: Anterocone of M1 narrow and of asymmetrical shape, no labial spur of the anterolophule, length of mesoloph varying from short to long, metalophule of M1 posterior, metalophule of M2-3 transverse, protolophule of M1-3 double; short anteroconid of m1, mesolophid of m1-3 absent or short, lingual anterolophid of m2 weak.

The four species *D. franconicus*, *D. crassus*, *D. hispanicus* and *D. gracilis* differ from *D. mutilus* by smaller sizes and the longer mesolophid. *D. vindobonensis* and *D. gailardi* differ by the long mesoloph(id), the labial spur of the anterolophule of M1, and by the tendency of m1 to have an ectomesolophid.

D. mutilus was recovered and described from many European localities, i.e. in Germany, Switzerland, Austria and in France. Although the species ranges from MN4 to MN7, it is most abundant in MN5 (DAXNER-HÖCK 1998b: 377).

***Democricetodon cf. gracilis* FAHLBUSCH, 1964**

Locality and stratigraphy: Mühlbach a. Manhartsberg (Mü2), Lower Austria, brownish silt of the Gaindorf Formation, Lower Austria (see ROETZEL 2003, this volume), Lower Badenian, MN5.

Type locality: Sandelzhausen (Germany), MN5

Stratigraphical range: MN4-6.

Material (from Mü2): 1 M2 l (NHMW2002z0141/0001).

Measurements: Length = 1.20 mm, Width = 1.20 mm

Remarks: The small size, the double protolophule and double metalophule, and the relatively long mesoloph indicate the tooth to be *D. gracilis*. The species is very common in faunas from the Bavarian and Swiss Molasse. In Austria (DAXNER-HÖCK 1998a and 1998b) it was recovered from the localities Oberdorf (MN4), Obergänserndorf (MN5) and Teiritzberg (MN5).

Genus *Eumyarion* THALER, 1966

***Eumyarion cf. weinfurteri* (SCHAUB & ZAPFE, 1953) (Plate 2, n)**

Locality and stratigraphy: Niederleis, Lower Austria, Lower Badenian, MN5.

Type locality: Neudorf / fissure (Slovakia), MN6

Stratigraphical range: MN4-6.

Material: 1 M2 l (NHMW2002z0147/0001).

Measurements: Length = 1.50 mm, Width = 1.40 mm

Remarks: The molar morphology and measurements (length, width and height of the crown) are within the variation of *E. weinfurteri*. The species is very common in early to middle Miocene faunas. In Austria (DAXNER-HÖCK 1998a and 1998b) it was recovered from the localities Oberdorf (MN4), Obergänserndorf (MN5) and Teiritzberg (MN5).

***Eumyarion* sp.**

Locality and stratigraphy: Mühlbach a. Manhartsberg (Mü2), Lower Austria, brownish silt of the Gaiendorf Formation, Lower Austria (see ROETZEL 2003, this volume), Lower Badenian, MN5.

Type locality: Sansan (France), MN6

Stratigraphical range: MN5-7.

Material (from Mü2): 1 fragmentary m1 r (NHMW2002z0148/0001).

Measurements: Length = 2.00 mm, Width = 1.30 mm

Remarks: Size and morphology indicate some relationship with *E. weinfurteri* and *E. medius*, but for species determination the material is too poor.

Genus *Megacricetodon* FAHLBUSCH, 1964

***Megacricetodon minor* (LARTET, 1851) (Tab. 5; Plate 2, j-m, o)**

Locality and stratigraphy: Mühlbach a. Manhartsberg, Lower Austria; brownish silt of the Gaiendorf Formation, sample Mü1 and Mü2 (see ROETZEL 2003, this volume), Lower Badenian, MN5.

Type locality: Sansan (France), MN6

Stratigraphical range: MN5-9

Material (from samples Mü1 and Mü2): 11 molars, 2 molar fragments and a fragmentary left mandible.

Mü1: 1 M1 l, 1 M2 r 1 m1 r, 1 m2 l, 2 m2 r (NHMW2002z0146/0001-0002).

Mü2: 1 M1 l, 1 M2 l, 1 M2 r, 2 m1 r (NHMW2002z0145/0001-0003).

Tab. 5: Measurements (in mm) of *Megacricetodon minor* (LARTET, 1851) from Mühlbach (Mü1 and Mü2).

	Length Range	N	Width Range
M1	1.55-1.60	2	1.00-1.00
M2	1.15-1.20	3	0.95-1.00
m1	1.40-1.40	3	0.90-0.90
m2	1.10-1.15	3	0.90-1.00

Remarks: The morphology of the present molars is characterized as follows: m1 has a simple, high and rounded anteroconid; mesoloph(id) of medium length or long; anterocone of M1 well split; paracone spur of M1-2 present. For comparison, teeth of *M. minor* from the type locality Sansan and of *M. collongensis* from the type locality Vieux Collonges were studied. They turned out to be very similar in morphology and size. Some morphotypes of *M. minor* are almost identical with *M. collongensis*, and even the tooth measurements overlap. In my opinion the *M. minor-collongensis* - taxonomy requires new investigations. For the time being the Mühlbach specimens were determined as *M. minor*.

In Spain (DAAMS et al. 1999) *M. collongensis* ranges from the upper MN4 to the end of MN5 (Aragonian local zones C-E), and *M. minor* ranges from MN6 to the lower MN9 (local zones G1-H). In Central Europe (HEISSIG 1997) an evolutionary *Megacricetodon*-line goes along with size increase of the subsequent species: *M. aff. collongensis* (MN4) - *M. bavaricus* (early MN5) - *M. aff. bavaricus* (middle MN5) - *M. lappi* (late MN5). Towards the end of MN5 the large-sized *M. lappi* co-occurred with the small immigrant *M. minor*. Then *M. lappi* became extinct, but *M. minor* survived until the early Vallesian (KÄLIN & ENGESSER 2001).

Genus *Cricetodon* LARTET, 1851

Cricetodon meini FREUDENTHAL, 1963 (Tab. 6-7; Plate 3, a-h)

Cricetodon sp. - ROETZEL et al.: 331

Locality and stratigraphy: Mühlbach a. Manhartsberg (Mü1 and Mü2), Lower Austria, brownish silt of the Gaindorf Formation (ROETZEL 2003, this volume),

and Grund (GRU-B1-1 and GRU-F-11), Lower Austria; sand of the Grund Formation (ROETZEL 1999: 328, Abb.19), Lower Badenian, MN5.

Type locality: Vieux Collonges, MN5

Stratigraphical range: MN5

Material from Grund:

GRU-B1-1: 1 maxilla without teeth (NHMW2002z0152/0001).

GRU-F-11: 1 jaw without teeth, and 1 M1 l (NHMW2002z0151/0001-0002).

Measurements of M1l: Length = 2.75 mm, Width = 1.85 mm

Material from Mühlbach:

Mü1: 1 M2 l, 2 M2 r, 1 M3 l, 3 M3 r, 1 m1 l, 1 m1 r, 3 m2 l, 3 m2 r, 1 m3 r and some molar fragments (NHMW2002z0149/0001-0006).

Mü2: 2 M1 r, 1 M1-2 l, 4 M1 l, 1 M2 l, 4 M2 r, 5 M3 l, 2 M3 r, 3 m1 l, 3 m1 r, 4m2 r, 4 m3 l, 1m3 r and numerous molar fragments (NHMW2002z0150/0001-0003).

Tab. 6: Measurements (in mm) of *C. meini* from Mühlbach (Mü1 and Mü2).

	Length			N	Width		
	Range	mean	stdev		Range	Mean	stdev
M1	2.35-2.80	2.59	0.141	7	1.70-1.95	1.81	0.093
M2	1.95-2.30	2.13	0.125	9	1.55-1.90	1.78	0.130
M3	1.60-2.10	1.84	0.152	11	1.50-1.80	1.62	0.103
m1	2.25-2.65	2.35	0.139	8	1.45-1.60	1.52	0.053
m2	2.15-2.30	2.21	0.055	10	1.60-1.75	1.67	0.071
m3	2.15-2.30	2.20	0.055	6	1.65-1.75	1.69	0.038

Description (Plate 3; a-h):

The anterocone of the four-rooted M1 consists of two cusps of about equal size. The anterolophule connects the protocone with the lingual part of the anterocone. A cingulum between the labial part of the anterocone and the paracone closes the anter sinus. There is a weak cingulum between the paracone and the metacone. A posterior paracone spur is present in all specimens. The mesoloph is short. The protolophule and the metalophule are posterior. There is no posteroloph and no poster sinus.

The four-rooted M2 has a well-developed anteroloph. It has a labial and a lingual arm and is connected with the protoloph. The paracone has a pronounced paracone spur. The mesoloph is short or of medium length. The protolophule and the metalophule are posterior. The lingual sinus is directed forwards. There is no posteroloph.

The three-rooted M3 is variable in length. The larger specimens are similar to the M2. They have a long mesoloph but a reduced metacone and hypocone. The shorter specimens lack the mesoloph.

The anteroconid of the m1 has a central position. In all specimens it is connected with the protoconid. The posterior metalophulid is always present, the anterior one is present in six out of eight specimens. The mesolophid is absent or short. Sometimes there is a very short ecomesolophid. The hypolophulid is anterior. The posterolophid is strong. The m2 has a strong labial and no lingual anterolophid. The metalophulid is anterior. The mesolophid is short and sometimes directed forwards. One m2 has a weak ectomesolophid. The posterolophid is strong.

The m3 is almost as long as the m2. The mesolophid is short or of medium length and directed transversally or posteriorly. The posterior part of m3 is reduced.

D i s c u s s i o n : *C. meini* is one of the small-sized species of *Cricetodon*. The original diagnosis was given by FREUDENTHAL (1963: 71). MEIN & FREUDENTHAL (1971: 6) renewed the diagnosis and separated the smaller species *C. meini* from the larger *C. aureus*, both species known from the type locality Vieux Collonges. Besides morphological differences, *C. meini* is smaller than all European species assigned to the genus (i.e. *C. sansaniensis* LARTET 1851, *C. lavocati* FREUDENTHAL 1966, *C. aureus* MEIN & FREUDENTHAL 1971, *C. jotae* MEIN & FREUDENTHAL 1971, *C. albanensis* MEIN & FREUDENTHAL 1971, *C. aguirrei* SESE 1977, *C. hungaricus* KORDOS 1986, *C. bolligeri* RUMMEL 1995, *C. jumaensis* RUMMEL 2001) ranging from MN5 to MN9. There is only one exception, *C. aliveriensis* from Aliveri in Greece. It is the smallest and has a more primitive molar morphology; it is also the eldest (MN4) European species (HOFMEIJER & de BRUIJN 1988).

According to DE BRUIJN et al. (1993) at least six more *Cricetodon* species are known from Asia Minor ranging from MN1 to MN7/8: i.e. *C. pasalarensis* (TOBIEN 1978), *C. candirensis* (TOBIEN 1978), *C. cariensis* (SEN & UNAY 1979), *C. versteegi* de BRUIJN et al. 1993, *C. kasapligili* de BRUIJN et al. 1993, *C. tobieni* de BRUIJN et al. 1993, and *C. n. sp.1-3*. The oldest occurrences (MN1-3) of *Cricetodon* from Anatolia comprise a limited number of species that have never been found in Europe. Diversification started in MN4 and was accompanied by migration westwards.

Cricetodon first migrated from Anatolia to SE-Europe (*C. aliveriensis* / Aliveri / MN4 and *C. meini* / Komotini / MN5 - both occurrences in Greece); then it reached Central and Western Europe (*C. meini* / MN5). During MN6-8, *Cricetodon* reached its maximum geographic range and species diversification, and finally the last species, *C. lavocati* from Spain, became extinct in MN9. Following de BRUIJN et al. (1993: 206), the *C. versteegi* from Kilcak 3a in Anatolia (MN1), *C. aliveriensis* (MN4) and *C. meini* (MN5) may represent one evolutionary line. The Asian ancestry and the occurrences of *C. meini* in Greece, Central Europe and France point to a migration from East to West. *C. meini* was recorded from Middle Miocene (MN5) localities of SE-Europe (Komotini/Greek Thrace) and Central and Western Europe almost simultaneously. Some *Cricetodon* occurrences (Strakonice and Wannentobel 2) from the late MN5 and/or the MN5/6 transition are rather poor in tooth numbers. These *C. aff. meini* determinations are not reliable, and the stratigraphical relevance is limited. (Tab. 7).

In the type locality Vieux Collonges, *C. meini* is associated with *C. aureus*, which differs from the former by significantly larger molar measurements. The differences in molar morphology are minor and cannot be verified based on small tooth numbers. Recently some *Cricetodon*-occurrences from the fissure fillings of the Franconian Alb

in Germany (Petersbuch 32, 33, 38, 39) were identified to be intermediate between *C. meini* and *C. aureus* in molar morphology and size, and they were described as *C. aff. aureus*. All these determinations are based on rich materials and are well comparable with the occurrences from Goldberg and Steinberg deposits from the crater lake in the "Nördlinger Ries" (RUMMEL 2000).

Tab. 7: Occurrences of *Cricetodon meini*, *C. aff. meini*, *C. aureus* and *C. aff. aureus* in Europe

<i>C. meini</i>	Vieux Collonges (F)*	MN5	MEIN & FREUDENTHAL (1971: 7 ff.)
<i>C. meini</i>	Komotini (G)	MN5	BRUIJN & MEULEN (1979: 205)
<i>C. meini</i>	Mühlbach (A)	MN5	present paper
<i>C. meini</i>	Grund (A)	MN5	present paper
<i>C. meini</i>	Petersbuch 41 (D)	MN5	RUMMEL (2000: 150)
<i>C. meini</i> = <i>C. aff. meini</i>	Ziemetshausen 1a, 1c (D)	MN5	BOLLIGER (1994: Tab.2), RUMMEL (2000: 163) BOON (1991: 95 f.)
<i>C. meini</i> = <i>C. aff. meini</i>	Ebershausen (D)	MN5	BOLLIGER (1994: Tab.2), RUMMEL (2000: 163) BOON (1991: 95 f.)
<i>C. aff. meini</i>	Edelbeuren-Maurerkopf (D)	MN5	SACH (1999: 63 ff., 90)
<i>C. aff. meini</i>	Strakonice (CZ)	MN5	FEJFAR (1974: 141)
<i>C. aff. meini</i>	Wannentobel 2 (D)	MN5/6	SACH (1999: 63 ff., 94)
<i>C. aureus</i>	Vieux Collonges (F)*	MN5	MEIN & FREUDENTHAL (1971: 26)
<i>C. aureus</i>	Pont Levoy-Theney (F)	MN5	BRUIJN et al. (1992: 111)
<i>C. aff. aureus</i>	Petersbuch 38 (D)	MN6	RUMMEL (2000: 151)
<i>C. aff. aureus</i>	Petersbuch 39 (D)	MN6	RUMMEL (2000: 151)
<i>C. aff. aureus</i>	Petersbuch 32 (D)	MN6	RUMMEL (2000: 154)
<i>C. aff. aureus</i>	Petersbuch 33 (D)	MN6	RUMMEL (2000: 154)
<i>C. aff. aureus</i>	Goldberg (D)	MN6	RUMMEL (2000: 163)
<i>C. aff. aureus</i>	Steinberg (D)	MN6	RUMMEL (2000: 163)
<i>C. aff. aureus</i>	Laimering 2/3 (D)	MN6	BOLLIGER (1994: Tab.2)

Stratigraphy (Tab. 8)

The vertebrate faunas from Mühlbach and Grund were recovered from the higher part of the Grund beds ("Obere Grunder Schichten") in the Alpine Molasse Basin in Lower Austria and from Niederleis in the NW of the Northern Vienna Basin. The upper part of the Grund Formation consists of marine yellowish fine sands and silts. There are channels filled with mollusc debris and occasional terrestrial fossils. The rodents were recovered from artificial outcrops in the type area of Grund north of Hollabrunn (ROETZEL et al. 1999b: 331). To the west, the Grund Formation is replaced by coarser marine sediments of the Gaindorf Formation (ROETZEL et al. 1999a: 44), which yielded the terrestrial vertebrate fauna from Mühlbach. The marine microfauna of the upper Grund beds is attributed to the Lower Lagenidae Zone. According to RÖGL et al. (2002), *Praeorbulina glomerosa circularis* (LOD 14.8 ma) and *Orbulina suturalis* (FAD 15.1 ma) co-occur in the upper Grund Formation (locality: Grund), in the Gaindorf Formation (locality:

Mühlbach see RÖGL & SPEZZAFERRI this volume), and in the Northern Vienna Basin (locality: Niederleis). These co-occurrences are limited to 14.8 - 15.1 ma, which shifts the age of the Grund fauna much later than previously thought. The first stratigraphical correlation (DAXNER-HÖCK 2001: 29, Fig. 2) with the middle part of the mammal zone MN5 / early Lower Lagenidae Zone / Chron C5Cn1 is no longer defensible since an extended lower Badenian hiatus was recognized in the Molasse Basin, and the upper Grund beds were identified to represent the late Lower Lagenidae Zone (RÖGL et al. 2002).

The vertebrate faunas from Mühlbach and Grund are not diverse, but detailed investigations proved the assemblages to be highly relevant for stratigraphical and paleoecological interpretations. The rodent assemblage from Mühlbach is dominated by cricetids, first of all by *C. meini*, and secondly by *D. mutilus*. In Grund, only these two species are present. The mammal zone MN5 is indicated by the stratigraphical ranges of the following taxa: *C. meini* and *P. satus* only occurred in MN5. *M. minor* first appeared, *S. besanus* last occurred, and *D. mutilus* was most abundant in MN5. *C. meini* not only indicates the MN5, but even the highest part of MN5: the numerical age is ~15 million years as demonstrated below. This stratigraphical position corresponds with the marine data from the upper part of the Grund beds (RÖGL et al. 2002 and RÖGL & SPEZZAFERRI this volume).

The occurrence of *C. meini* in Central Europe (Tab. 7) and its co-occurrence with *M. minor* and/or *M. lappi* marks a short time interval in the upper part of MN5. This is evidenced by several rodent faunas from the Upper Freshwater Molasse of Germany and from fissure fillings of the Franconian Alb, where *C. meini* is present only in one well-defined horizon (BOLLIGER 1994, HEISSIG 1997, SACH 1999, RUMMEL 2000).

In the Upper Freshwater Molasse of Bavaria (OMS) this horizon is marked by biostratigraphical and lithostratigraphical characters and by radiometric age datings:

1. *C. meini* + *M. lappi* appear first and occur last below a horizon of debris of the Ries impact crater. According to HEISSIG (1997) the extinction of *M. lappi* marks the end of an evolutionary line which goes along with size increase of the subsequent species: *M. aff. collongensis* (MN4) - *M. bavaricus* (early MN5) - *M. aff. bavaricus* (middle MN5) - *M. lappi* (late MN5).
2. This lithostratigraphically characteristic debris-horizon is widely distributed within the Molasse Basin and is termed the "Brock" horizon in the Bavarian Molasse and "Block" horizon in the Swiss Molasse. The Ries impact was dated at 14.9 ma (REICHENBACHER et al. 1998: 139). So far, the Ries is the last occurrence date of *M. lappi* + *C. meini* because the OSM faunas (Unterneul 1a, Ebershausen, Ziemetshausen 1a, 1c, Edelbeuren- Maurerkopf) which yielded these two characteristic cricetids are situated below the "Brock" horizon.
3. Above the "Brock" horizon *C. meini* was replaced by *C. aff. aureus* (Tab. 7). The large-sized *M. lappi* disappeared without having any descendant. The OMS faunas Unterneul 1c, Ziemetshausen 1b, and Wannentobel 2 are situated above this horizon (SACH 1999) and are biostratigraphically transitional between MN5 and MN6. The following faunas indicate MN6: Goldberg and Steinberg recovered from post-Ries sediments of the crater lake; Petersbuch 32, 33, 38, 39 from fissure fillings of the Franconian Alb; among OMS faunas Laimering 2,3,4, Göttschlag 1b, Unterzolling 1a are most representative (HEISSIG 1997).

In the Swiss Molasse Basin the equivalent markers are:

1. *M. lappi* characterizes the OSM faunas of Frohberg and Aspitobel 520 m (KÄLIN 1997, KÄLIN & ENGESSER 2001). Lithologically, Frohberg is positioned below the bentonite from Küsnacht dated at 14.9 ma (GUBLER et al. 1992).
2. A few meters above the "Block" horizon (= Swiss equivalent of the Bavarian "Brock" horizon) the faunas Chatzenstrelbel and Uzwil-Nutzenbuech show new rodent associations: *C. aff. aureus*, *M. minor*, *Lartetomys cf. zapfei*, *Eomyops hebeiseni*. There are no more large-sized *M. lappi*. The faunas have been identified as transitional between MN5 and MN6 (REICHENBACHER et al. 1998), but the similar faunal composition compared with the Slovakian fauna Devinska Nova Ves (Neudorf/Spalte) clearly indicates early MN6 age. The Rümikon assemblage (KÄLIN et al. 2001) is somewhat more advanced (MN6) and positioned above the Leimbach bentonite (14.15 - 14.22 ma). The subsequent faunas Wiesholz (BOLLIGER 2000), Oeschgaben (KÄLIN & ENGESSER 2001) and Mettlen 4 (KÄLIN pers. comm.) follow in MN6.

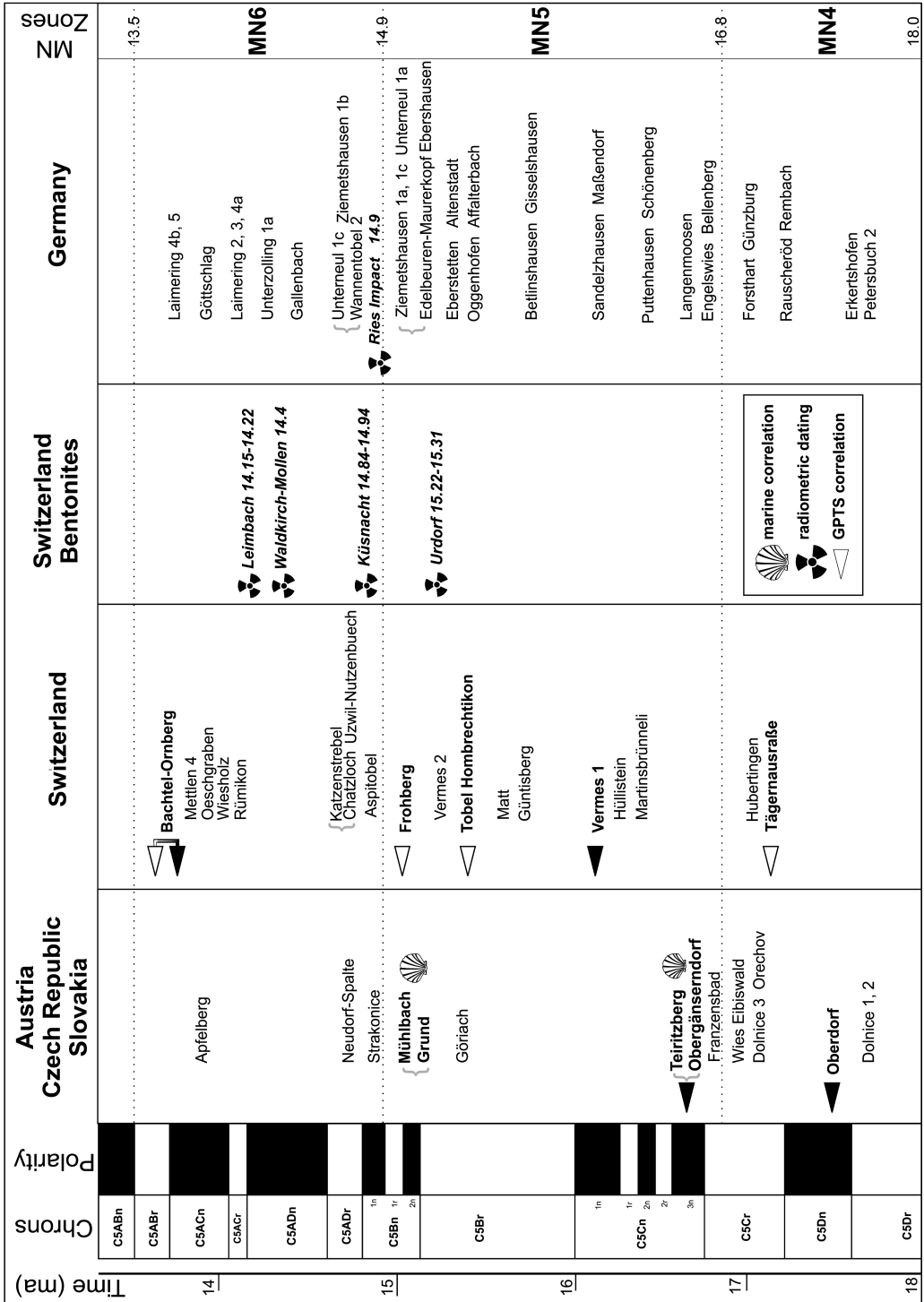
The mammal fauna from Devinska Nova Ves (Neudorf/Spalte) in Slovakia is indicated to be early MN6 by the presence of *L. zapfei*, *Keramidomys carpathicus*, *Anomalomys gaudryi*, *Democricetodon vindobonensis* and *Muscardinus sansaniensis* and by the absence of *M. lappi* and *C. meini*. Strakonice in the Czech Republic - so far considered (FEJFAR 1974) to be as old as Franzensbad (early MN5) - yielded a few teeth of a small *Cricetodon*, which would indicate late MN5 or early MN6.

In Austria, *C. meini*, *M. minor*, *P. satus*, *D. mutilus* and *S. besanus* confirm the faunas from Mühlbach and Grund to be late MN5 and to be correlative with OSM faunas below the "Brock"/"Block"-horizon, and with Pont Levoy-Thenay (MN5-reference fauna). Terrestrial and marine data from Mühlbach and Grund allow correlation of the late MN5 with the late Lower Lagenidae Zone (late Early Badenian). The estimated age of Mühlbach, Grund and Niederleis faunas is ~15 ma. So far, no middle MN5 rodent fauna has been recovered from Austria, but the early MN5 is well represented by the mammal faunas from Obergänserndorf and Teiritzberg in the Korneuburg Basin, Lower Austria (DAXNER-HÖCK 1998b, 2001). There the early MN5 is indicated by the presence of *Keramidomys thaleri* (being the most abundant fossil), *Microdyromys koenigswaldi*, *Glirulus diremptus*, *Bransatoglis aff. cadeoti*, *Miopetaurista aff. dehmi*, and by the absence of *C. meini* and *M. minor*. According to DAXNER-HÖCK (1998b) the faunas are correlative with the late Karpatian and the normal polarity interval Chron C5Cn3n. The estimated age of Teiritzberg and Obergänserndorf is 16.5-16.7 ma.

The latter faunas are comparable with Franzensbad in the Czech Republic, and Langenmoosen and Engelswies in the OSM of Germany (early MN5). In the OSM the middle MN5 faunas Puttenhausen, Sandelzhausen, Betlinshausen and Oggenhof follow (HEISSIG 1997, BOLLIGER 1994). In Switzerland the lower and middle part of MN5 is represented by the subsequent faunas Martinsbrünneli, Hüllistein, Vermes1, Tobel Hombrechtikon, Vermes 2 (BOLLIGER 1994, KÄLIN 1997) and Rämigraben (KÄLIN, personal comm.).

In accordance with KÄLIN (pers. comm.) the boundary of MN5 and MN6 is biostratigraphically best drawn between the LOD of *M. lappi* and/or *C. meini* and the FAD of *C. aff. aureus* and *Anomalomys gaudryi*. Lithostratigraphically this boundary is marked by the "Brock"/"Block"- horizon (resulting from the Ries impact), and the Küsnacht bentonite. The radiometric datings enable the boundary to be drawn at ~ 14.9 ma.

Tab. 8



Paleoecology

The significant differences in species richness and composition of Austrian faunas of the early MN5 (Obergängserndorf and Teiritzberg) and the late MN5 (Mühlbach and Grund) may express evolution and migration, but may also hint at major changes in climate and environments during the 1.5 ma years time interval from the late Karpatian to the late Early Badenian.

Rodents from Obergängserndorf and Teiritzberg (early MN5 / late Karpatian) DAXNER-HÖCK (1998b):

O b e r g ä n s e r n d o r f :	T e i r i t z b e r g 1 and Teiritzberg 2:
<i>Spermophilinus besanus</i>	<i>Spermophilinus besanus</i>
<i>Palaeosciurus sutteri</i>	<i>Palaeosciurus sutteri</i>
<i>Miopetaurista</i> aff. <i>dehmi</i>	<i>Miopetaurista</i> aff. <i>dehmi</i>
<i>Keramidomys thaleri</i>	<i>Keramidomys thaleri</i>
<i>Democricetodon mutilus</i>	<i>Democricetodon mutilus</i>
<i>Democricetodon gracilis</i>	<i>Democricetodon gracilis</i>
<i>Eumyarion</i> aff. <i>weinfurteri</i>	<i>Eumyarion</i> aff. <i>weinfurteri</i>
<i>Microdyromys koenigswaldi</i>	<i>Microdyromys koenigswaldi</i>
<i>Prodryomys satus</i>	<i>Prodryomys satus</i>
<i>Bransatoglis</i> aff. <i>cadeoti</i>	<i>Bransatoglis</i> aff. <i>cadeoti</i>
<i>Paraglrirulus werenfelsi</i>	<i>Bransatoglis</i> sp.
<i>Glirulus diremptus</i>	<i>Pseudodryomys</i> aff. <i>ibericus</i>
<i>Miodryomys</i> aff. <i>biradiculus</i>	Castoridae indet.

These Karpatian fossil sites are located within the southern estuarine part of the Korneuburg Basin. The lithological and the paleobotanical record, along with the diversity of terrestrial, aquatic and semi-aquatic animals, indicate swampy environments along rivers and brackish marshes of the Korneuburg Basin (HARZHAUSER et al. 2002). The diversity of glirids, the predominance of the eomyid *Keramidomys thaleri* and the large flying squirrel *Miopetaurista* require woodlands and dense thicket. The cricetid *Eumyarion* - known to be adapted to semi-aquatic environments - was most numerous in Obergängserndorf. However, not a single xerophyle rodent was recovered from these two localities. HARZHAUSER et al. (2002: 454) assume a subtropical climate with a mean annual temperature (MAT) of 14-17°C, frost-free winters, a minimal cold month temperature (CMT) of 3-8°C, and an annual precipitation of approximately 2000 mm.

The late Early Badenian (early Middle Miocene) fossil sites from Mühlbach and Grund are situated within the Alpine Molasse Basin, and Niederleis is in the north-western part of the Vienna Basin. The terrestrial molluscs and vertebrates were recovered from lenses and layers of terrestrial input into marine sediments.

Tab. 8: Correlation of Middle Miocene mammal faunas from Central Europe. Chronostratigraphy and mammal zonation according to (MEIN 1975) plotted versus magnetostratigraphically calibrated faunas (KEMPF et al. 1997, MAURITSCH & SCHOLGER 1998, SCHOLGER 1998), and radiometrical data of the Ries event and of bentonites in Switzerland (REICHENBACHER et al. 1998, GUBLER et al. 1992).

Rodents from Mühlbach, Grund and Niederleis (late MN5 / late Early Badenian):

M ü h l b a c h :

Cricetodon meini

Democricetodon mutilus

Democricetodon cf. *gracilis*

Megacricetodon minor

Eumyarion sp.

Spermophilinus besanus

Prodryomys satus

G r u n d :

Cricetodon meini

Democricetodon mutilus

N i e d e r l e i s :

Eumyarion aff. *weinfurteri*

These Badenian fossil sites yielded vertebrate fossils from terrestrial environments. The rodent faunas are poor in species, and some species are represented by a few molars only. The rodent fauna from Mühlbach is dominated by burrowing cricetids (5 species) and the ground-squirrel *Spermophilinus*. The predominating *C. meini* – known to be a xerophilic and burrowing rodent – requires dry soil above the groundwater level. This environment could have been represented by elevated regions of a peninsula, of islands, or small mountains in the hinterland, covered with woods, bushes and shrubs. Except for one glirid, i.e. *Prodryomys*, there is no evidence for a glirid-eomyid-petauristid association, which would have required more humid conditions, extended riverine forests, and would tolerate wet ground. There is a very reason to believe that temperature did not change much from the Karpatian to the Badenian, but changes from a humid to a more dry climate and environment could have enabled the immigration of *C. meini* and *M. minor*. According to BÖHME (2001:13), unchanged temperatures were accompanied by an increased seasonality (up to six dry months yearly) and by two phases of major aridity during the Badenian. The terrestrial faunas from Mühlbach and Grund, however, show a tendency to more dry than humid conditions.

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Plate 1***Spermophilinus besanus* CUENCA, 1988**

from Mühlbach (Mü1, Mü2), Lower Austria. Middle Miocene, Badenian, MN5. Collection of the Natural History Museum, Department of Geology and Paleontology, Vienna (NHMW). All right side molars are figured as if they were from the left side. Magnification 20 x (scale bar = 1 mm).

- a: Right D4; Mü1; NHMW2002z0138/0001
- b: Right M1-2; Mü1; NHMW2002z0138/0002
- c: Left M1-2; Mü1; NHMW2002z0138/0003
- d: Right M3; Mü2; NHMW2002z0139/0001
- e: Right P4; Mü1; NHMW2002z0138/0004
- f: Right m1; Mü2; NHMW2002z0139/0002
- g: Left m2; Mü2; NHMW2002z0139/0003
- h: Right m2; Mü2; NHMW2002z0139/0004
- i: Left m3; Mü2; NHMW2002z0139/0005

***Prodryomys satus* MAYR, 1979**

from Mühlbach (Mü1), Lower Austria. Middle Miocene, Badenian, MN5. Collection of the Natural History Museum, Department of Geology and Paleontology, Vienna (NHMW). All right side molars are figured as if they were from the left side. Magnification 20 x (scale bar = 1 mm).

- j: Right M2; Mü1; NHMW2002z0140/0001
- k: Right p4; Mü1; NHMW2002z0140/0002
- l: Right m2; Mü1; NHMW2002z0140/0003

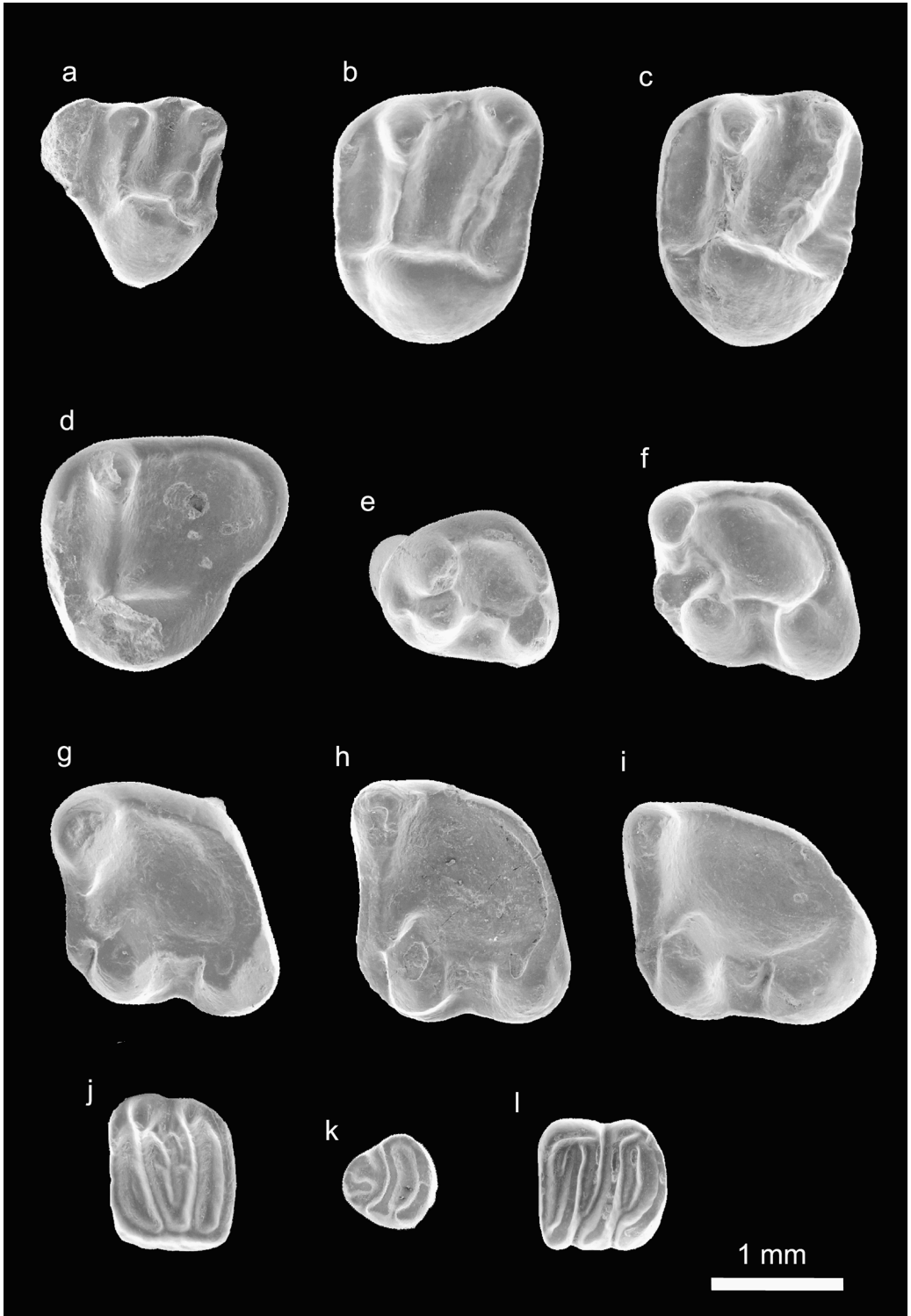


Plate 2

***Democricetodon mutilus* FAHLBUSCH, 1964**

from Mühlbach (Mü1, Mü2) and Grund (GRU-F-11), Lower Austria. Middle Miocene, Badenian, MN5. Collection of the Natural History Museum, Department of Geology and Paleontology, Vienna (NHMW). All right side molars are figured as if they were from the left side. Magnification 20 x (scale bar = 1 mm).

- a: Right M1; Mü2; NHMW2002z0142/0001
- b: Left M2; Mü2; NHMW2002z0142/0002
- c: Right M3; Mü2; NHMW2002z0142/0003
- d: Right M1; Mü2; NHMW2002z0142/0004
- e: Right M2; GRU-F-11; NHMW2002z0144/0001
- f: Left m2; Mü2; NHMW2002z0142/0005
- g: Left m1; Mü2; NHMW2002z0142/0006
- h: Left m2; Mü2; NHMW2002z0142/0007
- i: Right m3; Mü2; NHMW2002z0142/0008

***Megacricetodon minor* (LARTET, 1851)**

from Mühlbach (Mü1, Mü2), Lower Austria. Middle Miocene, Badenian, MN5. Collection of the Natural History Museum, Department of Geology and Paleontology, Vienna (NHMW). All right side molars are figured as if they were from the left side. Magnification 20 x (scale bar = 1 mm).

- j: Left M1; Mü2; NHMW2002z0145/0001
- k: Left M1; Mü1; NHMW2002z0146/0001
- l: Left M2; Mü2; NHMW2002z0145/0002
- m: Right m1; Mü2; NHMW2002z00145/0003
- o: Left m2; Mü1; NHMW2002z0146/0002

***Eumyarion cf. weinfurteri* (SCHAUB & ZAPFE, 1953)**

from Niederleis, Lower Austria. Middle Miocene, Badenian, MN5. Collection of the Natural History Museum, Department of Geology and Paleontology, Vienna (NHMW). Magnification 20 x (scale bar = 1 mm).

- n: Left M2; NHMW2002z0147/0001

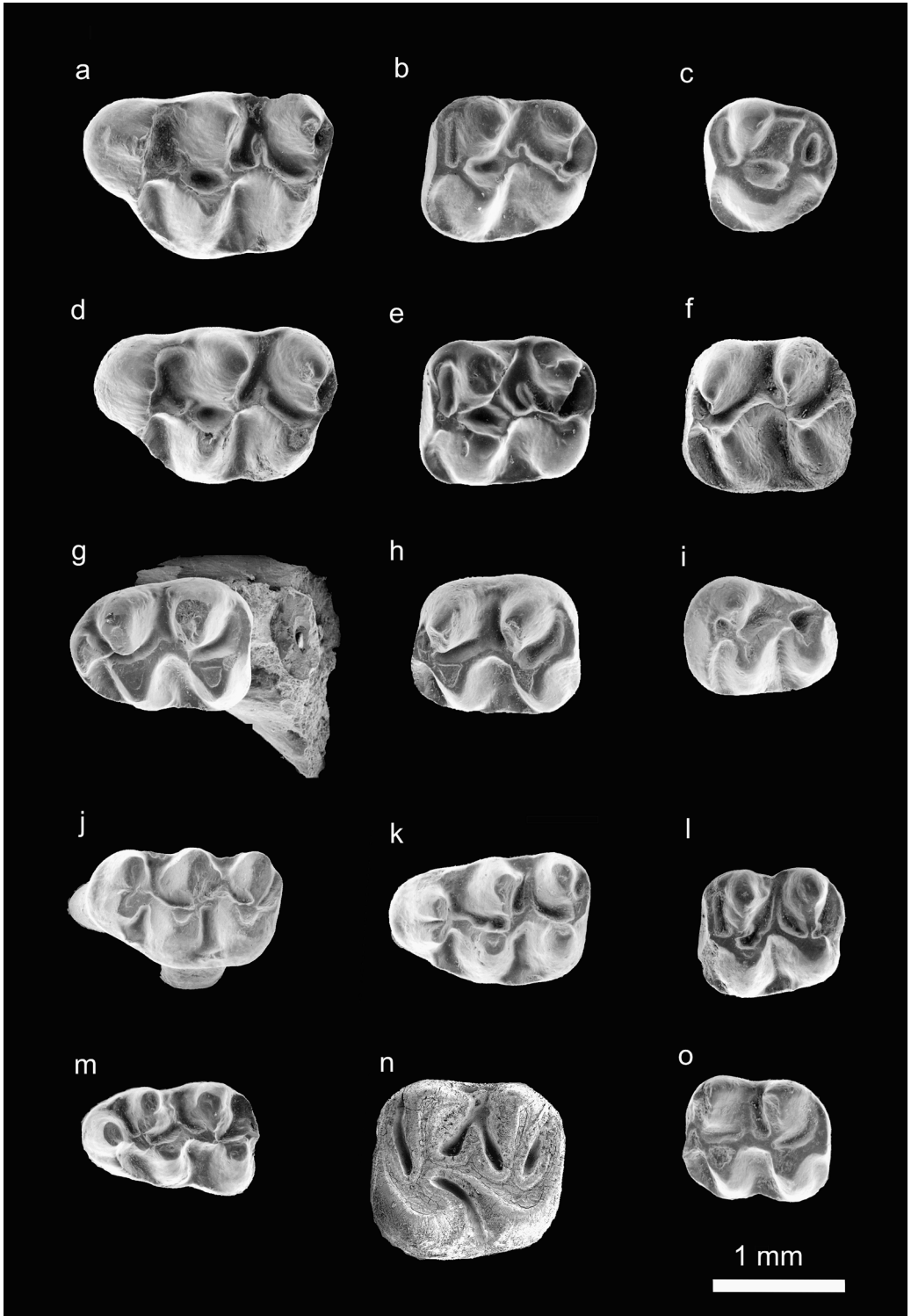


Plate 3***Cricetodon meini* FREUDENTHAL, 1963**

from Mühlbach (Mü1, Mü2) and Grund (GRU-F-11), Lower Austria. Middle Miocene, Badenian, MN5. Collection of the Natural History Museum, Department of Geology and Paleontology, Vienna (NHMW). All right side molars are figured as if they were from the left side. Magnification 20 x (scale bar = 1 mm).

a: Left M1; Mü1; NHMW2002z0149/0001

b: Right M2; Mü1; NHMW2002z0149/0002

c: Left M1; GRU-F-11; NHMW2002z0151/0001

d: Left M3; Mü1; NHMW2002z0149/0003

e: Right m1; Mü1; NHMW2002z0149/0004

f: Left m2; Mü1; NHMW2002z0149/0005

g: Left m2; Mü2; NHMW2002z0150/0001

h: Left m3; Mü2; NHMW2002z0150/0002

