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The cricetid rodents from Gratkorn (Austria, Styria): a benchmark locality for the continental Sarmatian *sensu stricto* (late Middle Miocene) in the Central Paratethys

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Abstract: The recent discovery of a terrestrial vertebrate assemblage in the clay pit St. Stefan at Gratkorn (Austria, Styrian Basin) is of major importance for our understanding of the evolution of late Middle Miocene mammal assemblages in the Paratethys realm. The cricetid rodent assemblage includes four species: *Megacricetodon minutus* Daxner, 1967, *Democricetodon* sp. nov. (*sensu* Kälin & Engesser 2001), *Eumyarion* sp., and "*Cricetodon*" *fandli* sp. nov. The latter species belongs to the "*Cricetodon*" *fandli-C. klariankae* Hír, 2007 lineage, which allows for a long-distance correlation with other late Middle Miocene/earliest Late Miocene European localities. The biostratigraphic conclusions drawn from the study of the fossils from Gratkorn concurs with the age estimates based on regional geology, paleomagnetic measurements, and the gastropod-based biostratigraphy at the base of the Late Sarmatian *s. str.* (late Serravallian, latest Volhynian), around 12–12.2 Ma (Chron C5An.1n) ago.

Key words: Middle Miocene, Paratethys, Gratkorn Basin, bioprovince, long-distance correlations, Mammalia, Rodentia.

Introduction

Sarmatian continental faunas have rarely been reported from Austria. Moreover, most of the known localities have only yielded fossils of large mammals (e.g. Thenius 1960; Mottl 1970). Discovery of a terrestrial fauna from the Sarmatian deposits near Gratkorn (clay pit St. Stefan, SE Austria, Styria; Gross et al. 2007a; Harzhauser et al. 2008; Prieto et al. in print a and b) is thus essential for our understanding of the evolution of the late Middle Miocene faunas in the circum-Alpine and Paratethyan realms: 1) Small and large mammals, as well as a large spectrum of vertebrate groups (fishes, amphibians, reptiles; Gross et al. 2009a,b) co-occur in this rich assemblage; 2) The deposits are fairly well dated as late Middle Miocene on the basis of the invertebrate fauna (Gross et al. 2007a; Harzhauser et al. 2008).

Cricetids are often the most useful rodent group regarding Middle Miocene high-resolution biostratigraphy. Their generally high evolutionary rate allows for the recognition of phylogenetic lineages, and thus permits long-distance correlation and high-resolution biochronological evaluation (e.g. Abdul Aziz et al. 2008 and in print). This paper describes the cricetid rodents from Gratkorn and discusses their biostratigraphic significance.

Geographic and geologic settings

The clay pit St. Stefan is situated in the small intramontane Gratkorn Basin (7 km long and 3 km wide), at the northwestern margin of the Styrian Basin (Fig. 1). Although outcrops and biostratigraphic tiepoints are rare, recent studies of the regional geology have produced a detailed correlation with the stratigraphic framework of the open Styrian Basin.

The poorly sorted silts located at the base of the clay pit are rich in mammal, amphibian, and reptile remains, as well as terrestrial molluscs (Harzhauser et al. 2008; Gross et al. 2009a,b). This vertebrate-bearing horizon rests upon the "Gratkorn Gravel", which is correlated with the "Mid-"Sarmatian so-called "Carinthian Phase" (see Harzhauser & Piller 2004) that corresponds to a widely recorded regressional event around the Early/Late Sarmatian boundary. Biostratigraphic data (molluscs, foraminifers, ostracods) obtained from the under- and overlying strata, together with the gastropod fauna of the vertebrate-bearing horizon, indicate an early Late Sarmatian age (Upper *Ervilia* Zone, *Porosononion granosum* Zone) for the Gratkorn fauna. The recorded normal polarity of the mined pelites in the hanging wall of this bone-bed appears to correlate with Chron C5An.1n (ca. 12.16–12.07 Ma according to Hüsing et al. 2007). This age estimate is in strong agreement with the astronomically-tuned age of the Early/Late Sarmatian boundary (ca. 12.2 Ma; Lirer et al. 2009).

Although the depositional environment is a paleosol, the vertebrate remains are exceptionally well preserved, sometimes even articulated. The occurrence of almost complete rodent skulls is especially noteworthy.

For detailed information on the regional geological context, and the section and taphonomy of the deposits exposed in the

St. Stephan clay pit, refer to Gross et al. (2007a,b), Gross (2008), and Harzhauser et al. (2008).

Material and methods

The fossils from Gratkorn are housed in the collections of the Universalmuseum Joanneum in Graz (Geologie & Paläontologie, abbreviated UMJG) and the Bayerische Staatssammlung für Paläontologie und Geologie in Munich (abbreviated BSPG). Measurements were taken with an occular micrometer and are indicated in mm. Length and width were measured at right angles. The baselines used are the lingual border in lower molars and labial border in the M1 and M2. The baseline for the M3 is the anterior border. The terminology used in the description of the molars follows Freudenthal et al. (1994), while the terminology for the molar planation follows Hershkovitz (1967: fig. 4). The length of the mesoloph(id)s is understood as follows: 'long', 'medium' and 'short' describe lengths either longer, similar or shorter, respectively, than half the length of the valley (mesosinusid and mesosinus). All teeth in the illustrations are shown in left orientation, reversing the right specimens.

Systematic paleontology

Order: **Rodentia** Bowdich, 1821
Family: **Muridae** Illiger, 1811
Subfamily: **Cricetodontinae** Schaub, 1925

Genus: *Cricetodon* Lartet, 1851

Diagnosis (emended): de Bruijn et al. (1993: 177).
Differential diagnosis: de Bruijn et al. (1993: 178).
Type species: *Cricetodon sansaniensis* Lartet, 1851.

Other species included in *Cricetodon*: *C. caucasicus* Argyropulo, 1938; *C. meini* Freudenthal, 1963; *C. aureus* Mein & Freudenthal, 1971; *C. jotae* Mein & Freudenthal, 1971; *C. albanensis* Mein & Freudental, 1971; *C. pasalarensis* (Tobien, 1978); *C. candirensis* (Tobien, 1978); *C. cariensis* (Sen & Ünay, 1979) (attributed to *Byzantinia* by Rummel 1998); *C. hungaricus* (Kordos, 1986); *C. aliverensis* Klein Hofmeijer & de Bruijn, 1988; *C. versteegi* de Bruijn et al., 1993; *C. tobieni* de Bruijn et al., 1993; *C. kasapligili* de Bruijn et al., 1993; *C. bolligeri* Rummel, 1995; *C. jumaensis* Rummel, 2001; *C. engesseri* Rummel & Kälin, 2003; *C. soriae* Hernandez Fernandez et al., 2006; *C. klariankae* Hír, 2007.

The generic assignment of the molars from Gratkorn to *Cricetodon* remains problematic. The arguments in favour of assigning the new species from Austria to "*Cricetodon*" are discussed in the following sections.

"*Cricetodon*" *fandli* sp. nov.
(Fig. 2.A–F, Fig. 3)

Etymology: In memory of the late mayor of Gratkorn, Elmar Fandl (†), for his financial support and interest in the excavation campaigns.

Holotype: A fragmentary skull with left and right lower jaws and postcranial bones of the same individual embedded in a sedimentary block (UMJG 204.240, Fig. 3).

Paratypes: See Table 1.

Measurements: See Table 1.

Type locality: Gratkorn, clay pit St. Stefan (Styria, Austria). Clay pit of the company Wietersdorfer & Peggauer Zementwerke AG, 10 km northwest of the city of Graz (E 15°20′55″, N 47°08′15″).

Type horizon: Basal paleosol at top of the "Gratkorn Gravel" (Gross et al. 2007a,b), late Middle Miocene, Late Sarmatian *s. str.* (Upper *Ervilia* Zone; *Porononion granosum* Zone).

Diagnosis: Medium-sized Cricetodontinae species with moderately high cusps(ids). A very narrow anteroconid and reduced antero- and protosinusid of the m1 are characteristic. Ectolophs are complete in the upper molars. The anterior metalophulid is interrupted or missing in m1. The mesoloph is missing in the upper molars, while the mesolophid is absent to reduced in m1 and m2.

Differential diagnosis: The *Cricetodon* species lacking complete ectolophs and/or having the mesoloph on the upper molars are easily distinguished from "*C.*" *fandli*. The earliest *Hispanomys* species (see discussion section for more information), with the exception of *H. bijugatus*, usually possess a less well developed posterior metalophulid in m1. *H. bijugatus* typically displays an anterior metalophulid in m1. The overall morphology of the molars from Gratkorn is reminiscent of what is observed in *C. klariankae* from Hungary. Besides the slightly larger size, the latter species differs from "*C.*" *fandli* in the presence of a double metalophid in m1, and the spur of the anterocone that is directed lingually and thus not closing the anterosinus.

Description of the holotype: The skull is free from sediment on the anterior left side. The anterior part is preserved and the left molar row observable. The left mandible is more or less in its original position, and covers the right mandible, the posterior part of which is still buried in the sediment. Below the horizontal ramus of the left mandible a fragmentary bulla tympanica is preserved. Limb materials (hand bones) are preserved above and below the skull.

A detailed description and comparison of the cranial and postcranial material of "*Cricetodon*" *fandli* will be provided in a forthcoming paper. Here we focus on the dental material, which usually displays the most reliable diagnostic characters.

The tip of the incisor ends more or less on the level of the margo alveolaris of the mandible. The lower incisors have double parallel ridges on their ventral side; the left m1 and m2 are observable, but the m3 is almost completely covered by sediment.

The small anteroconid in the m1 is round, the broad labial anterolophid does not close the protosinusid, which is strongly reduced; the lingual anterolophid is absent; the anteroconid and protoconid are interconnected by a strong anterolophulid; a small crest is developed on the posterior wall of the anteroconid, but does not reach the metaconid; the protoconid hind arm and posterior metalophulid are connected with the ectolophid, forming a Y-shaped structure; the mesolophid is absent; the hypolophulid is directed forwards; the posterior part

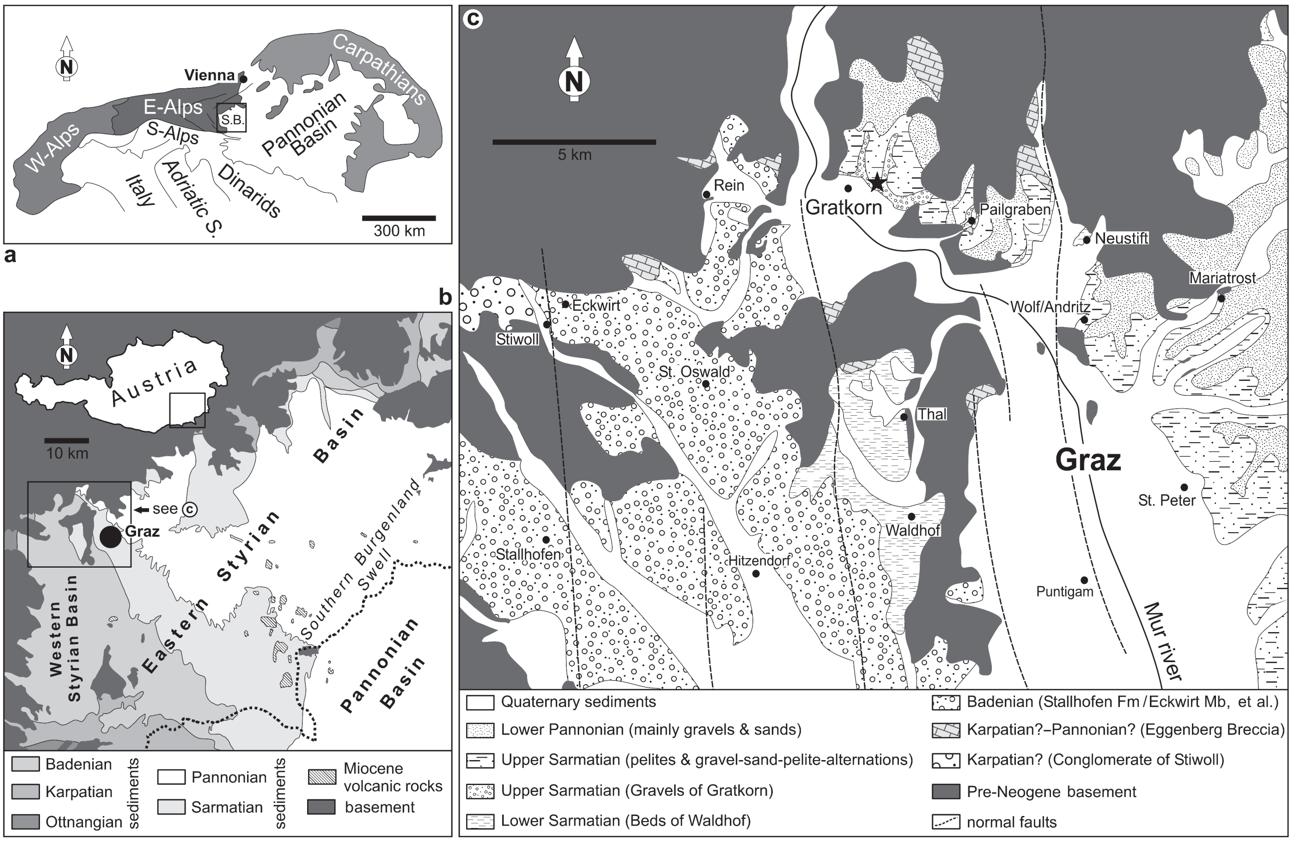

Fig. 1. Geographical setting and regional geology of the study area. **a** — Postion of the Styrian Basin (S.B.) within the Pannonian Basin System; **b** — Geological sketch of the Styrian Basin; **c** — Simplified geological map of the north-western margin of the Styrian Basin (from Gross et al. 2007a).

of the ectolophid is curved; the sinusid is directed backwards and is closed by a cingulid, which extends on to the labial wall of the hypoconid; the molar is bileveled.

In the m2 protoconid and metaconid are connected to the anteroconid; the labial anterolophid reaches the base of the protoconid, delimiting a deep and round protosinusid; the lingual anterolophid is missing; the mesolophid is very short; the mesosinusid is closed by a cingulid extending to the labial wall of the hypoconid; this cingulid is more pronounced than in the m1.

The upper incisors have a narrow longitudinal groove on their dorsal part.

M1: The anterocone is bifid; its anterior wall is fissured (reaching about half of the high of the cusp); the lingual anteroloph is absent and the massive protostyl closes the protocone platform; the posterior spur departing from the labial lobe of the anterocone merges with the anterior spur of the paracone, giving an irregular trace to the ectoloph; it has the same orientation as the paracone spur, which reaches the metacone; the two crests form complete ectolophs; the ento- and mesostyls are present; the mesoloph is reduced to a slight thickening of the entoloph (mesocone?); the metalophule is directed backwards and fused with the extremely short posteroloph.

M2: The ectolophs are complete and the lingual anteroloph is well developed; the overall morphology of the remaining teeth is similar to that of the M1; the lingual part of the tooth is hardly observable.

The M3 is covered by sediment on its posterior part; the transverse labial anteroloph does not close the anterosinus.

Description of the paratypes: m1: The teeth do not differ in basic structure from the holotype; the connection anteroconid-metaconid is interrupted (3 out of 5 m1) or absent; the mesolophid is very short or absent; the hypolophulid is directed forwards, joining the ectolophid near the mesolophid, if this structure is present; the broad posterolophid does not reach the base of the entoconid; a cingulid closes the space resulting from the constriction of the posterolophid near the hypoconid, and delimits a small posteriolabial valley; the mesosinusid is directed backwards and closed by a cingulid; the molars each possess two roots.

m2: The teeth are very similar to those seen in the type specimen; the mesolophid is either missing or very short, but in the latter case always directed towards the metaconid; on some molars, the sinusid is more transverse than in the m1; the curved posterolophid does not reach the base of the entoconid; the small posterior valley resulting from constriction of the posterolophid, as described for the m1, may be developed; the molars each possess three roots.

m3: The overall arrangement of the crests and cuspids is similar to that seen in m2; the main differences include a narrower talonid, a usually longer mesolophid, and a narrow and transverse sinusid; in one molar (Fig. 2E), the protosinusid is strongly reduced and incorporated into the base of the labial

Table 1: "*Cricetodon*" *fandli* nov. sp. Material and measurements.

Reference	Specimen	Orientation	Length (mm)	Width (mm)	Figure
BSPG 2008 IV 56	Maxillary with M1	left	3.20	1.97	
BSPG 2008 IV 57	M1	left	2.98	1.93	
BSPG 2008 IV 61	m1	left	*	1.72	
UMJG 204.225	m1	right	*	1.77	
UMJG 204.226	Mandible with m1	left	2.35	1.55	
UMJG 204.227	m1	left	2.55	1.68	2C
BSPG 2008 IV 59	M3	right	1.88	1.82	
UMJG 204.228	M3	right	*	*	
BSPG 2008 IV 58	Maxillary with M3	left	1.95	1.67	
BSPG 2008 IV 60	M3	right	1.93	1.63	
UMJG 204.229	Maxillary with M3	right	1.87	1.73	2B
UMJG 204.230	m2	right	*	*	
UMJG 204.231	m2	right	*	*	
BSPG 2008 IV 62	m2	left	2.48	1.87	
UMJG 204.232	m2	right	2.53	*	
UMJG 204.233	m2	right	*	1.87	
UMJG 204.234	m2	left	2.43	1.73	2D
BSPG 2008 IV 63	m3	right	2.2	*	
BSPG 2008 IV 64	m3	right	2.32	1.73	
UMJG 204.235	m3	right	2.27	1.78	
UMJG 204.236	m3	right	2.25	1.62	
BSPG 2008 IV 65	m3	right	*	1.68	
UMJG 204.237	m3	left	2.30	1.70	2E
UMJG 204.003	Mandible with m2	right	*	*	
UMJG 204. 016	Fragmentary skull with:				
	M1	right	3.05	*	
	M2	right	2.27	*	
	M3	right	1.73	*	
	M2	left	2.27	1.80	
	M3	left	*	1.57	
UMJG 204.020	Fragmentary skull with:				
	M1	left	3.03	*	
	M2	left	2.22	*	
	M3	left	*	*	
UMJG 204.025	Maxillary with				2A, F
	M1	right	3.08	1.90	
	M2	right	2.43	1.78	
	M3	right	1.88	1.70	
UMJG 204.049/2	m2	left	2.43	1.87	
UMJG 204.019	Mandible with				
	m2	left	2.43	2.03	
	m3	left	2.17	1.60	
UMJG 203.738	Mandible with:				
	m1	right	*	*	
	m2	right	*	*	
UMJG 204.018	Maxillary with:				
	M1	right	2.90	1.88	
	M2	right	*	*	
UMJG 204.029	Fragmentary skull with:				
	M1	left	*	*	
	M1	left	*	*	
	M2	left	*	*	
	M3	left	*	*	
UMJG 204.050	M3	left	*	*	
UMJG 204.238	Mandible with				
	m1	left	2.40	1.57	
	m2	left	2.27	1.85	
	m3	left	2.08	1.72	

wall of the protoconid, moreover, a well-developed crest divides this valley; the molars each possess three roots.

M1: The molars are very similar to those of the holotype; the mesostyl may be present or absent; the mesoloph is most often absent but a faint thickening of the entoloph (as in the holotype) may be present; the molars each possess 4 roots, and a fifth small root is developed on the posterior basis of the antero-labial root.

M2: The anterocone is triangular; the ectolophs are complete and the lingual anteroloph is well developed; the overall morphology of the remaining teeth is similar to that seen in M1; notable differences include a stronger cingulum closing the sinus and a narrower contact zone between the paracone spur and metacone.

M3: The transverse labial anteroloph does not close the anterosinus; the lingual anteroloph is short and incorporated into the anterior wall of the protocone; protocone, paracone and entoloph are interconnected in a Y-like structure; the spur of the paracone may be curved; the hypocone is highly reduced; a narrow posterosinus is usually present and completely closed, otherwise the posteroloph is missing and the metalophule very short; the cingulum closing the sinus may be as strong as in the M2; the metacone is indistinct; the molars each possess four roots.

Discussion: The molars from Gratkorn cannot be attributed to the following Cricetodontinae genera based on distinct differences in morphology and size: *Deperetomys* Mein & Freudenthal, 1971; *Ruscinomys* Depéret, 1890; *Plesiodipus* Young, 1927; *Tsaganocricetus* Topachevsky & Skorik, 1988; *Gobiocricetodon* Qiu, 1996; *Lartetomys* Mein & Freudenthal, 1971 (= (pars) *Mixocricetodon* Rummel, 1997 in Mein 2003: p. 411; Rummel pers. comm.).

Furthermore, we propose that:

1) The following morphological characters seen in the Gratkorn material preclude assignment of the material to the genus *Byzantinia* de Bruijn, 1976:

— the cusp(id)s are less deeply incorporated into the loph(id)s (de Bruijn & Ünay 1996: p. 233);

— all check teeth possess terraced to bi-leveled wear surfaces (diagnostic character: de Bruijn 1976; Sen & Ünay 1979, surface relatively concave in *Byzantinia*);

— the molars are less distinctly hypsodont;

— the anterocone of the M1 is less deeply fissured;

— the posterior part of the M2 is not narrower than its anterior part (diagnostic character: Rummel 1998);

— a well developed anterior metalophulid is absent in the m1 (diagnostic character: Ünay & de Bruijn 1984; Rummel 1998);

— secondarily the molars do not show the longitudinally "stretched" appearance (*sensu* de Bruijn & Ünay 1996) of the evolved *Byzantinia* species.

2) The youngest species of *Hispanomys* (Late Miocene; including the type species *H. aragonensis*) clearly differ from the molars from Gratkorn because of:

— the absence of the posterior metalophulid in most m1 specimens. This character is variable and double metalo-

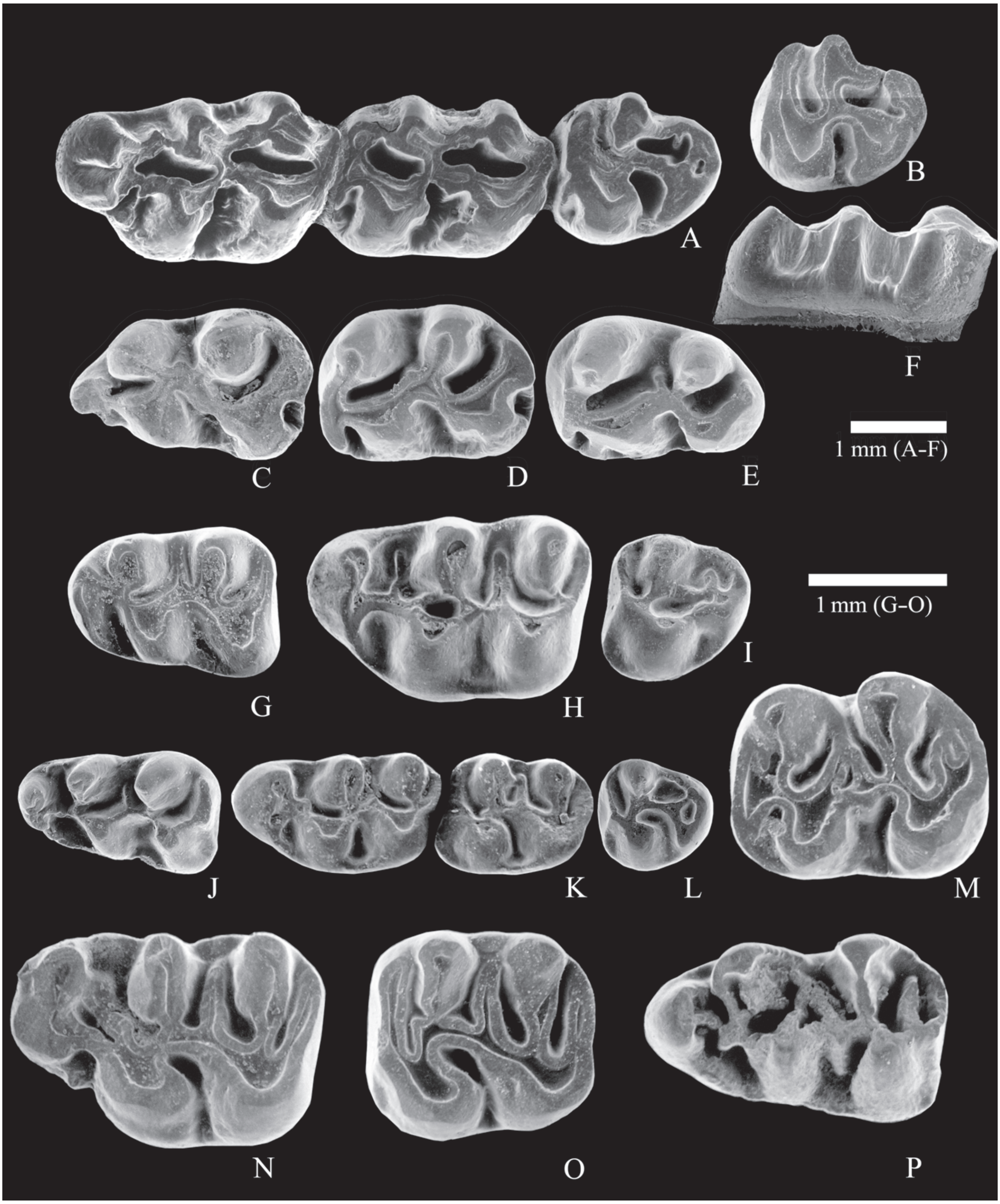

Fig. 2. Cricetid rodents from Gratkorn. All teeth shown in left orientation. **A–F — "*Cricetodon*" *fandli* nov. sp.:** A — right Maxillary with M1–M3 (UMJG 204.025); B — right M3 (reversed, UMJG 204.229); C — left m1 (UMJG 204.227); D — left m2 (UMJG 204.234); E — left m3 (UMJG 204.237); F — same specimen as in A, lingual view of M1. **G–I — *Democricetodon* sp. nov. (*sensu* Kälin & Engesser 2001):** G — left m1 (UMJG 204.191); H — left M1 (UMJG 204.192); I — left M3 (UMJG 204.193). **J–L — *Megacricetodon minutus* Daxner, 1967:** J — right m1 (reversed, UMJG 204.215); K — left maxillary with M1–M2 (UMJG 204.214); L — right M3 (reversed, UMJG 204.216). **M–P — *Eumyarion* sp.:** M — right m2 (reversed, UMJG 204.223); N — left M1 (UMJG 204.221); O — right M2 (reversed, UMJG 204.222); P — right m1 (reversed, UMJG 204.224).

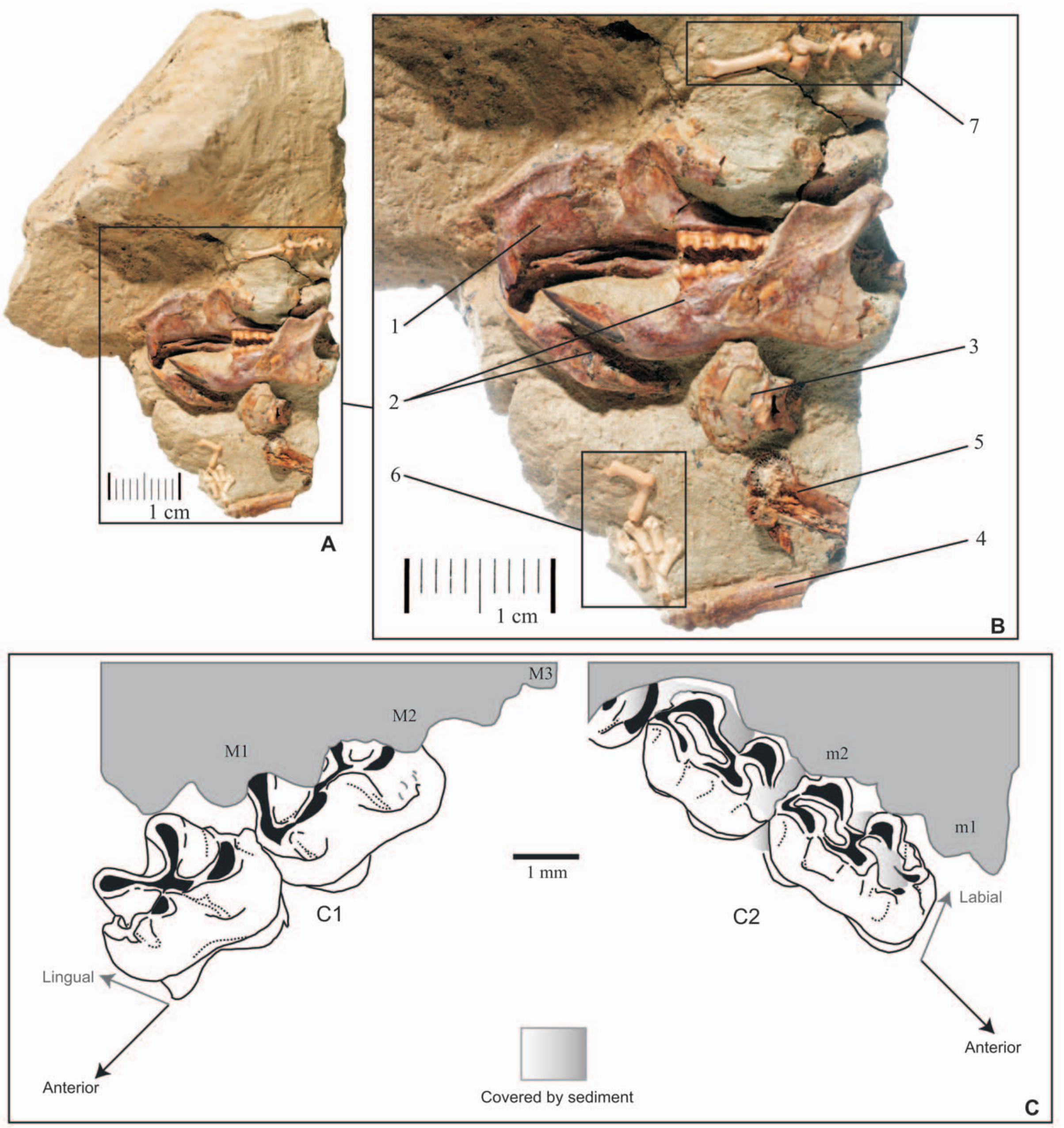

Fig. 3. “***Cricetodon***” ***fandli*** **nov. sp.** Holotype (UMJG 204.240): **A** — specimen overview; **B** — Details of the fossils. 1 — Skull; 2 — Left and right mandibles; 3 — Bulla tympanica; 4–7 — Forelimb, wrist and hand bones; **C** — Detailed view of dental elements. C1 — left lower tooth row (m1–m2); C2 — left upper tooth row (M1–M3).

phulids may be observed in some rare *Hispanomys* specimens (e.g. 1 out of 9 specimens in *H. mediterraneus* from Montredon; Aguilar 1981);

— the less bulbous cusp(id)s;

— the flat wear surface;

— the shorter posterolophid of the m2 and m3.

As a result, two genera are morphologically similar to the Gratkorn specimens: *Hispanomys* (the older, Middle to earliest Late Miocene species) and *Cricetodon*. *Cricetodon*, a genus with a long taxonomic history, initially accomodated most of the European fossil cricetid rodents. In the present sense, *Cricetodon* regroups a wide array of large cricetids. Differences between genera therefore may not be clear, which may lead to differences in taxonomic interpretation.

In the following analysis, and in order to simplify the comparisons, six groups of Middle to Late Miocene *Cricetodon*-*Hispanomys* species are considered (the Early Miocene Anatolian *Cricetodon* species, de Bruijn et al. 1993, and the Greek *C. aliverensis* Klein Hofmeijer & de Bruijn, 1988, are not taken into account because of their stratigraphic distance):

Group 1: The Middle Miocene Anatolian *Cricetodon* group. Originally, these *Cricetodon* species were described as *Turkomys* (Tobien 1978). Boon (1991) placed this taxon into the synonymy of *Cricetodon*, arguing that a short posterior ectoloph, a posterior or double metalophid, and the enlarged M3/m3 also occur in some western European *Cricetodon* species. The species considered by this author include *C. candirensis* and *C. pasalarenis*. Moreover, Rummel (1998) included the species *cariensis* in *Byzantinia*. Regarding the clear morphological resemblance with the two other species, the species *cariensis* is here included in *Cricetodon* and in this group.

Group 2: *C. hungaricus* group from Hasznos, Sámsonháza and Mátraszölös (Hungary, Kordos 1986; Hír & Mézáros 2002; Middle Miocene, Badenian). De Bruijn et al. (1993: p. 210) recognized a close resemblance between the Anatolian species (especially *C. candirensis*) and *C. hungaricus* (main difference: presence/absence of mesolophid in the m1). Based on the figured material of *C. candirensis* (Tobien 1978: figs. 7–9; Sen & Ünay 1979: figs. 7–11; de Bruijn et al. 1993: plate 5), *C. pasalarensis* (Tobien 1978: figs. 1–6; Ünay 1990: plates I–II) and *C. cariensis* (Sen & Ünay 1979: figs. 1–6) on the one side, and *C. hungaricus* on the other (Kordos 1986: plates I–III), additional differences can be seen: especially in the M1 of the Anatolian *Cricetodon* group the labial cusps typically are clearly standing out from the outline, whereas the labial border is almost straight in the Hungarian species; there is also a trend towards development of an anterior ectoloph in the M2 of the *C. hungaricus* group. Furthermore, the Anatolian *Cricetodon* species (group 1) either have a short labial anterolophid in the m1 (*C. pasalarensis*) or this structure is absent.

Group 3: *Cricetodon klariankae* from Felsötarkany-Felnémet (Hungary, Late Sarmatian; Hír 2007). This species differs from the other *Cricetodon* groups in having a very narrow anteroconid and a reduced antero- and protosinusid of the m1 (Hír 2007: plate I, fig. 16). In addition, this group differs from the *C. hungaricus* group by the relatively longer M2 and shorter M3.

Group 4: Early *Hispanomys* species (Middle Miocene to earliest Late Miocene) from Spain and France. This group refers to *H. aguirrei*, *H. dispectus*, *H. castelnovi*, *H. daamsi*, *H.* sp. from Can Vila (Casanovas-Vilar 2007; Casanovas-Vilar et al. 2008, now assigned to *H.* cf. *aguirrei*, Casanovas-Vilar pers. comm.), *H. bijugatus*, and *H. decedens*. The species *lavocati*, which has long remained uncertain with regard to its generic status, is today included in *Hispanomys* (Casanovas-Vilar 2007; López Guerrero et al. 2008: p. 260; López-Antoñanzas & Mein 2009). The members of group 4 differ from the late *Hispanomys* species by having less hypsodont and reduced longitudinally “stretched” molars.

Group 5: Brachiodont *Cricetodon*s characterized by ectolophs that are very short or absent (Middle Miocene). This group refers to the western European *C. meini*, *C. aureus*, *C. jotae*, *C. albanensis*, *C. sansaniensis*, and *C. soriae*, the central European *C. bolligeri*, *C. jumaensis*, and *C. engesseri* (except *Cricetodon* sp. from Nebelberg TGL in Rummel & Kälin 2003 (*Hispanomys* sp. in Kälin & Kempf 2009); Boon 1991; Bolliger 1992, 1994; Kälin 1993; Rummel 1995, 2000, 2001; Rummel & Kälin 2003; Prieto 2007), and *C. meini* from Austria (Daxner-Höck 2003) and Greece (de Bruijn et al. 1993). The rare findings of *Cricetodon* sp. from Anwil correspond taxonomically to a new *Cricetodon* from the German faunas Giggenhausen and Kleineisenbach, which also contain *Deperetomys hagni* (Prieto 2007).

Group 6: *Cricetodon caucasicus* from Belometchetskaya (Middle Miocene, Tshokrakian respectively/or more precisely Badenian, Langhian; Argyropulo 1938; Sen & Ünay 1978; Pickford et al. 2000). The species is characterized by M1 with undivided anterocone and no ectolophs.

Comparison of the molars from Gratkorn with these groups

The groups with very short or missing ectolophs are distinctly different from the species from Gratkorn (groups 5, 6, both attributed to *Cricetodon*). In the other groups, the ectolophs are well developed. The transition from *Cricetodon* to *Hispanomys* in Western Europe, and likewise from *Cricetodon* to *Byzantinia* in the eastern Mediterranean, is probably complicated by parallel evolution (de Bruijn 1976; Sen & Ünay 1979; Ünay 1980; Ünay & de Bruijn 1984: p. 125; Casanovas-Vilar 2007: p. 226). Moreover, the generic attribution of the species also depends on whether a morphological or phylogenetic approach to taxonomy is used (van de Weerd 1976: p. 104). Thus, the generic assignment of the early members of these three Cricetodontinae is not well-defined (de Bruijn et al. 1993: 177). De Bruijn et al. (1993) emended the diagnosis of *Cricetodon*, but did not consider *Hispanomys* in their differential diagnosis. Consequently, the differences between *Hispanomys* and *Cricetodon* rely exclusively on the differential diagnosis of *Hispanomys* in van de Weerd (1976).

One special feature of the m1 from Gratkorn is the very short or missing anterior metalophulid, while the posterior metalophuid is well developed. In the early *Hispanomys* (group 4), the posterior metalophulid is usually absent in the m1, while it is well developed in the members of group 1. This character does not allow for the unambiguous separation of the two genera due to the morphological variability of this structure. In fact, 13 % of the m1 from Paşalar (*C. pasalarenis*) possess a complete anterior metalophulid, and in 34 % of the molars this crest is incomplete, whereas in the rest of the sample only the posterior metalophulid is present (Ünay 1990). Similarly the posterior metalophulid is present in 25 % of the *H. aguirrei* teeth from Escobosa (Sese 1977), and double metalophulids occur in most of the molars of *H. bijugatus* (Mein & Freudenthal 1971; López-Antoñanzas & Mein 2009; Casanovas-Vilar pers. comm.).

The morphology of the m1 from Gratkorn is characterized by the extremely narrow anteroconid and reduced antero- and protosinusids. However, this character is also found in *C. klariankae* (see Hír 2007: plate 1). Hír (2007) excluded this species from *Hispanomys* based on the following characters: the presence of a well-developed anterolophulid in m1; the presence of a posterior metalophulid; the absence of reduction of the hypoconid and posterolophid in m3. A well-developed anterolophulid is actually present in the m1 of *H. daamsi*, *H. castelnovi*, *H. aguirrei*, *H. decedens* and *H. bijugatus*. Moreover, the hypoconid and posterolophid are only weakly reduced in the species of the group 4. Finally, the anterior and posterior metalophulids are equally well developed in all *C. klariankae* (group 3) m1, while this feature is rather rarely seen in most of the early *Hispanomys*. However, this difference is not sufficient to clearly exclude the Western European genera because it is also common in *H. bijugatus* (see above and etymology of the species).

C. candirensis and *C. cariensis* (group 1) both possess a very simple anteroconid and lack anterolophids.

Based on the formal diagnoses for *Cricetodon* and *Hispanomys* (Mein & Freudenthal 1971: p. 19; van de Weerd 1976: 106; de Bruijn et al. 1993), the Gratkorn material could be assigned to either of these genera, even though the teeth clearly differ from the type species of both genera. In the light of these problems, we prefer to include the new Austrian species in the genus "*Cricetodon*" in quotation marks because de Bruijn et al. (1993) pointed out that the majority of the *Cricetodon* m1 have a double metalophulid or posterior metatophulid, and the lower incisors have two ridges on their ventral part (see Flynn et al. 1985). However, the co-occurrence of a complete ectoloph in the upper molars and groove in the upper incisors argues against assignment to *Cricetodon* in the restricted sense (= *Cricetodon* (*Cricetodon*) of Mein & Freudenthal 1971: p. 17, as group 5 in this paper).

Phylogenic relationships

The record of Cricetodon *from the North Alpine Foreland Basin*

As mentioned above, the Western European and Swiss/German *Cricetodon* species are morphologically clearly different from "*C.*" *fandli* sp. nov. However, the unnamed high-crowned *Cricetodon* from Nebelberg TGL III, and probably also documented in Petersbuch 14 (Rummel 2000; Rummel & Kälin 2003 (assigned to *Hispanomys* by Kälin & Kempf 2009, without comments); material not seen), possesses lower molars that, with regard to size, range between the molars of "*C.*" *fandli* and *C. klariankae*, whereas the upper molars are as big as those of the Hungarian species. These molars probably do not belong to either "*C.*" *fandli* or *C. klariankae* based on the absence of complete ectolophs.

The Austrian record of Cricetodon

Cricetodon has rarely been reported from Austria; the records to date include Mühlbach, Grund (*C. meini*, 15.1 Ma Daxner-Höck 2003; Harzhauser et al. 2003) and Bullendorf (Pannonian "Zone B/C", Daxner-Höck 1996, 2004). Gudrun Daxner-Höck (Vienna) kindly provided images of the specimens from Bullendorf. A single M3 is similar to "*C.*" *fandli*, whereas the other molars cannot be attributed to the new species, and probably do not belong to *Cricetodon*. As a result, we cannot rule out that two large cricetid species occur in the Bullendorf site.

The Central and Eastern European and Anatolian record of Cricetodon

Pannonian Basin. The oldest representative of the genus is *C. hungaricus*, reported from the Badenian of Hasznos and Szentendre (Kordos 1986). A descendant of *C. hungaricus* occurs in the Middle Badenian of Sámsonháza (Hír et al. 1998; Hír & Meszáros 2002). From the Late Badenian of Mátrazölös, a small sample of *Cricetodon* sp. has been described (Hír & Kókay 2004). The upper molars of this fossil have a funnel structure and fit within the upper segment of the size range of *C. hungaricus*. A few teeth have been reported from the Early Sarmatian (*Mohrensternia* Zone, Early Volhynian) of Tăşad (Hír et al. 2001). The identification of *Cricetodon* sp. from this locality remains problematic. The molars are distinctly larger than those of "*C.*" *fandli*, in spite of the fact that the locality is slightly older than Gratkorn. The absence of m1 in the specimen from Tăşad does help in assigning *Cricetodon* sp. to either "*C.*" *fandli* sp. nov., *C. klariankae* or the *C. hungaricus* lineages. Cricetodontinae have not been recorded for the early Late Sarmatian (Late Volhynian) locality Tauţ (Feru et al. 1979), wheras the slightly older earliest Late Sarmatian locality Comăneşti 1 contains *Hispanomys* cf. *lavocati* and *H.* cf. *bijugatus*, which are briefly described but not illustrated (Feru et al. 1980; material not seen). These two taxa are distinguished from one another by the presence of a double metalophulid in the m1 of *H.* cf. *bijugatus*. However, this feature may be variable as demonstrated in the molar population of *Cricetodon pasalarensis* (Ünay 1990) and *H. bijugatus* from La Grive (Casanovas-Vilar pers. comm.), which suggests that all specimens from Comăneşti 1 belong to one species. The m1 from Comăneşti 1 are somewhat larger than the specimens from Gratkorn (L m1 *H.* cf. *lavocati*: 2.72 mm, n = 1; L m1 *H.* cf. *bijugatus*: 2.69 mm, n = 1; Feru et al. 1980), and thus are within the size range of *C. klariankae*. A final decision, however, cannot be reached at present. The Late Sarmatian record of *Cricetodon* (*C. klariankae*) is better from Felsötárkány-Felnémet (Hír 2006, 2007). The abundance of this genus decreases in the upward direction of the profile, and the taxon is absent from the younger strata (Hír 2004, 2006; Hír & Kókay 2010). As a consequence, *Cricetodon* has not yet been recorded for the Pannonian localities of this basin (e.g. Comăneşti 2 — Feru et al. 1980, and Rudabánya — Kretzoi & Fejfar 2005). "*C.*" *fandli* is morphologically close to *C. klariankae* from Felsötárkány-Felnémet. We suggest an ancestor/descendant relationship between the two species. If this hypothesis is accurate, then the "*C.*" *fandli*–*C. klariankae* lineage pricipally characterized by: 1) an increase in size of the molars, 2) development of the anterior metalophulid in m1, 3) loss of the complete anterior ectoloph.

Despotovac and Kolubara Basins (Serbia). *Cricetodon meini* has been reported from Mala Miliva (Despotovac Basin, Marković 2003), Lazarevac and Bele Vode (Kolubara Basin, Marković 2008). Moreover, *Cricetodon* sp. has been mentioned from the Sarmatian of Vracevici (Marković 2003), from the small Kolubara Basin SSW of Belgrade, a locality originally correlated with Anwil based on the presence of *Deperetomys hagni*. Marković in fact revised his determinations in his unpublished dissertation, and instead listed *Byzantinia bayraktepensis* from Vracevici.

Southern Bohemian Massif (České Budějovice Basin). Fejfar (1974) reported two *Cricetodon* cf. *meini* molars from the Early Badenian of Strakonice (Abdul Aziz et al. in print). However, the sample is too small to speculate the phylogenetic relationships of these fossils.

Table 2: Measurements of *Megacricetodon minutus* Daxner, 1967 from Gratkorn, and small *Megacricetodon* populations from the Paratethys late Middle Miocene/lower Upper Miocene (F — Felsötárkány, FF — Felsötárkány-Felnémet).

Upper molars		**M1**			**M2**			**M3**			**References**
		n	Length	Width	n	Length	Width	n	Length	Width	
M. minor	FF 2/3	19	1.44	0.9	7	1.14	0.93	5	0.73	0.75	Hír 2006
M. minor	FF 2/7	*1*	*1.43*	*0.94*	2	*1.05*	*0.84*				Hír 2006
M. minutus	F 3/2	10	1.38	0.86	5	1.08	0.97	*3*	*0.74*	*0.76*	Hír 2003
M. minor	Sámsonháza	19/18	1.55	0.98	9	1.16	0.95	2	*0.79*	*0.77*	Hír & Mészáros 2002
M. minor	Matraszölös 1+2	9	1.42	0.9	*3*	*1.09*	*0.87*	*3*	*0.79*	*0.76*	Hír & Kókay 2004
M. minor	Taşad	2	*1.52*	*0.96*							Hír, Kókay & Venczel 2001
M. minutus	Inzersdorf	*1*	*1.39*	*0.86*	*1*	*1.09*	*0.88*				Daxner 1967
M. minutus	Brunn-Vösendorf	*1*	*1.47*	*0.92*							Daxner 1967; Daxner-Höck 2004
M. minutus	Mataschen				*1*	*1.1*	*0.95*				Daxner-Höck 2004
M. minutus	Richardhof-Golfplatz				2	*1*	*0.85*	*1*	*0.65*	*0.65*	Daxner-Höck 2004
M. minutus	Bullendorf	*1*	*1.45*	*0.85*							Daxner-Höck 2004
M. minor	Nebelbergweg	29	1.44	0.89	32	1.09	0.92	20	0.78	0.78	Kälin & Engesser 2001
M. crisiensis	Comăneşti 1	*3*	*1.51*	*0.97*	5	1.16	0.99				Radulescu & Samson 1988
M. minutus	Gratkorn	*1*	*1.44*	*0.88*	6	1.08	0.94	2	*0.82*	*0.80*	this paper
Lower molars		**m1**			**m2**			**m3**			**References**
		n	Length	Width	n	Length	Width	n	Length	Width	
M. minor	FF 2/3	17	1.35	0.82	13	1.09	0.86	9	0.92	0.73	Hír 2006
M. minor	FF 2/7	*1*	*1.41*	*0.87*	*1*	*1.11*	*0.94*				Hír 2006
M. minutus	F 3/2	7	1.34	0.77	5	1.06	0.8	9	0.92	0.71	Hír 2003
M. minor	Sámsonháza	16	1.43	0.85	19	1.15	0.92	5	1.03	0.84	Hír & Mészáros 2002
M. minor	Matraszölös 1+2	10	1.37	0.83	*4*	*1.09*	*0.82*	*1*	*0.87*	*0.76*	Hír & Kókay 2004
M. minor	Taşad	2	*1.45*	*0.84*	*1*	*1.15*	*0.88*				Hír, Kókay & Venczel 2001
M. minutus	Inzersdorf										Daxner 1967
M. minutus	Brunn-Vösendorf	*1*	*1.5*	*0.9*							Daxner 1967; Daxner-Höck 2004
M. minutus	Mataschen	*1*	*1.45*	*0.8*	*1*	*1.1*	*0.9*	2	*0.95*	*0.78*	Daxner-Höck 2004
M. minutus	Richardhof-Golfplatz	2	*1.33*	*0.75*	*3*	*1.03*	*0.78*	*1*	*0.75*	*0.6*	Daxner-Höck 2004
M. minutus	Bullendorf										Daxner-Höck 2004
M. minor	Nebelbergweg	22	1.36	0.8	33	1.09	0.86	14	0.98	0.75	Kälin & Engesser 2001
M. crisiensis	Comăneşti 1	*1*	*1.46*	*0.93*	*1*	*1.27*	*1.05*	*2/1*	*1.14*	*0.8*	Radulescu & Samson 1988
M. minutus	Gratkorn	8	1.4	0.86	*4*	*1.15*	*0.90*	2	*0.91*	*0.74*	this paper

Turkey and Greece. The Miocene record of Cricetodontinae from Anatolia is well documented (e.g. de Bruijn & Ünay 1996). We thus restrict our discussion to the Middle Miocene forms. The *Cricetodon* fossils from Anatolia are morphologically close to "*C.*" *fandli*. Nevertheless, it is not possible to affiliate the Gratkorn species with the Anatolian lineage because dissimilarities exist with regard to size and morphology. Following Ünay & de Bruijn (1984: p. 125) the transition from *Cricetodon* to *Byzantinia* was completed when most of the m1 had developed an anterior or double metalophulid. A transitional form has been described from Kalamiş (Ünay 1990). The genus *Byzantinia* has been recorded for the latest Middle Miocene of Turkey and Greece (e.g. de Bruijn & Ünay 1996; Koufos 2006). If a similar evolutionary pattern is accepted for the lineage "*C.*" *fandli*–*C. klariankae*, then the double metalophulid-level is recognizable in Felsötárkány-Felnémet, while the specimens from Gratkorn are more primitive.

Spain and France. The overall resemblance between "*C.*" *fandli* and *Hispanomys* from the late Middle Miocene of Spain is impressive. The transition from *Cricetodon* to *Hispanomys* is characterized by the presence of an anterior metalophulid in the m1 of *Hispanomys*. In the Vallès-Penedès Basin, *H. decedens* occurs at the base of the "*Megacricetodon ibericus*+*Democricetodon larteti*" Zone, which correlates to the lower part of the Zone G3 of the Catalayud-Daroca Basin (Casanovas-Vilar 2007). *H. daamsi* probably appeared at some time during the top of this zone, and extended into the following *M. ibericus*+*D. crusafonti* Zone, which correlates with the upper part of the G3. *H. dispectus* and *H. lavocati* have been reported from this zone. *Hispanomys* appeared later in the Catalayud-Daroca Basin where the association *H. aguirrei*+*H. lavocati* has been recorded for Nombrevilla 2 (Top of the G3, Garcés et al. 2003; López Guerrero et al. 2008). All these species are characterized by a well-developed anterior metalophulid, and thus a direct relationship with "*C.*" *fandli* is unlikely. The double metalophulids are present in most of the m1, but do not reach 100 % as observed in Felsötárkány-Felnémet. One of the French species is perhaps related to *C. klariankae*: *H. bijugatus* from the fissures infillings of La Grive L3 and L5 (Mein & Ginsburg 2002).

Subfamily: **Megacricetodontinae** Mein & Freudenthal, 1971

Genus: *Megacricetodon* Fahlbusch, 1964

Diagnosis: Fahlbusch (1964).
Type species: *Cricetodon gregarius* Schaub, 1925.

Other species included in *Megacricetodon*: *M. minor* (Lartet, 1851); *M. bourgeoisi* (Schaub, 1925); *M. gregarius* (Schaub, 1925); *M. ibericus* (Schaub, 1944); *M. collongensis* (Mein, 1958); *M. lappi* (Mein, 1958); *M. crusafonti* (Freudenthal, 1963); *M. primitivus* (Freudenthal, 1963); *M. bavaricus* Fahlbusch, 1964; *M. similis* Fahlbusch, 1964; *M. minutus* Daxner, 1967; *M. bezianensis* Bulot, 1980; *M. ger-*

manicus Aguilar, 1980; *M. gersii* Aguilar, 1980; *M. sinensis* Qiu et al., 1981; *M. lopezae* Garcia Moreno, 1986; *M. roussilonensis* Aguilar et al., 1986; *M. crisiensis* Radulescu & Samson, 1988; *M. rafaeli* Daams & Freudenthal, 1988; *M. fournasi* Aguilar, 1995; *M. lemartinelli* Aguilar, 1995; *M. pusillus* Qiu, 1996; *M. fahlbuschi* Aguilar et al., 1999; *M. wuae* Aguilar et al., 1999; *M. lalai* Aguilar et al., 1999; *M. andrewsi* Pelaez-Campomanez & Daams, 2002; *M. tautavelensis* Lazzari & Aguilar, 2007; *M. aunayi* Lazzari & Aguilar, 2007; *M. yei* Bi et al., 2008.

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

M. debruijni Freudenthal, 1968 is considered as junior synonym of *M. minutus* by Joniak (2005).

Megacricetodon minutus Daxner, 1967
(Fig. 2J–L)

Diagnosis: Daxner (1967).

Type locality: Inzersdorf (Austria).

Age: Late Miocene, Pannonian “Zone E” (*sensu* Papp 1951).

Material: 1 mandible with m1–m3, 1 maxillary bone with M1/–M2/ and 21 isolated molars (UMJG 204.194–216).

Measurements: See Table 2.

Description: m1: The anteroconid is most often round, with a long labial anterolophid extending to the protoconid as a cingulum; one molar shows a broad anteroconid; the labial anterolophid *sensu stricto* is then missing, but a strong cingulid closes the protosinusid; the anterolophulid runs in more or less longitudinal direction, but always connects to the anteroconid on its postero-labial wall; meta- and hypolophulid are directed forwardly; the mesolophid more frequently is of medium length, but may also be shorter or reach the lingual border of the molar; the molars each possess two roots.

m2: Two crests connect the protoconid and the metaconid to the anteroconid; the labial anterolophid reaches the base of the protoconid; the mesolophid is short to medium-sized; the molars each possess two roots.

m3: The two m3 are heavily worn, so the morphology is difficult to assess; the molars each possess two roots.

M1: The anterocone is subdivided; the lingual anteroloph extends to the base of the protocone; the anterolophule is double, with each of the branches connecting the protocone to the two cusps of the anterocone; the anterior protolophule is short and does not reach the paracone; the short posterior protolophule and the metalophule are directed backwardly; the mesoloph is short; the sinus is closed by a cingulum; the posterosinus is strongly reduced.

M2: The two anterolophs are either well developed or the lingual one is reduced; protolophule and metalophule are transverse in some molars but the protolophule may also be directed forwards and the metalophule backwards; a double protolophule is observed in one specimen; the broad sinus is directed backwardly; the mesoloph is long and may reach the labial border of the M2, or it is connected to the posterior spur of the paracone; the molars each possess three roots.

M3: Only the proto- and paracone can be recognized as cusps; the labial anteroloph extends to the base of the paracone, while the lingual anteroloph is reduced; the protolophule is directed forwardly; the posterosinus is present; the mesoloph reaches the labial border of the M3 in one tooth, but is missing on the other molar; the molars each possess three roots.

Discussion: The molars from Gratkorn are characterized by their small size, the anterolophulid of the m1 connects to the anteroconid on the labial side, and the double anterolophule in most of the M1.

These traits are characteristic of *M. minutus*, a species instituted on the basis of a small molar sample from Inzersdorf and Brunn-Vösendorf (Daxner 1967). Based on the rich sample from Borský Svätý Jur (Slovakia), Joniak (2005) confirmed the validity of the species. *M. minutus* has also been reported from Austria in Mataschen, Bullendorf, Richardhof-Golfplatz (Daxner-Höck 2004) and St. Margarethen/Zollhaus (G. Daxner-Höck pers. comm.).

In Germany the small *Megacricetodon* from Hammerschmiede 1 (initially described as *M.* aff. *debruijni* (Mayr & Fahlbusch, 1975) and Hillenloh corresponds well in size and morphology to the teeth from Gratkorn; the same species is present in Nebelbergweg, although Kälin & Engesser (2001) ascribe those fossils to *M. minor*. Comparison of the teeth from Gratkorn with these molar populations allows for the following preliminary observations:

— In the M1, the anterocone is broader in Gratkorn and the metacone stands out from the outline of the labial border in the Hammerschmiede molars.

— In the M2, the posterosinus is better developed due to a more rounded posteroloph in Hammerschmiede. These molar samples are tentatively interpreted as belonging to *M.* cf. *minutus*.

The molars from Gratkorn, although sharing some morphological features (i.e. the double anterolophule) with *M. crisiensis* from Comăneşti 1 (Radulescu & Samson 1988), cannot be attributed to this species because of the somewhat larger molars and the presence of a lingual spur of the anterolophulid in the m1 of *M. crisiensis*. In any case, the limited number of specimens from Comăneşti 1 render comparisons with other *Megacricetodon* molars difficult. Hír (2004, 2006) assigns the small-sized *Megacricetodon* from Hungary and Romania either to the species *M. minor* or *M. minutus* based on size (Table 2). We hold the opinion that a detailed comparison of the morphology of these forms is required in order to attribute the samples to any species.

Small-sized *Megacricetodon* species also occur in the Middle Miocene of Anatolia, for example in Çandir (de Bruijn et al. 2003). These teeth are identified as *M. collongensis* and correspond well in size with the Gratkorn molars. Several morphological characters can be used to distinguish these two populations (e.g. length of the mesoloph in the M1).

The few specimens from Gratkorn are here assigned to *M. minutus*.

Subfamily: **Copemyinae** Jacobs & Lindsay, 1984

Genus: *Democricetodon* Fahlbusch, 1964

Diagnosis: Fahlbusch (1964).

Type species: *Democricetodon crassus* Freudenthal, 1969 (= *D. minor* (Lartet, 1851) *sensu* Fahlbusch 1964).

Other species included in *Democricetodon* (we limit the list to Freudenthal (2006)'s concept): *Democricetodon affinis* (Schaub, 1925); *D. brevis* (Schaub, 1925); *D. gaillardi* (Schaub, 1925); *D. vindobonensis* (Schaub & Zapfe, 1953); *D. romieviensis* (Freudenthal, 1963); *D. freisingensis* Fahlbusch, 1964 (considered by de Bruijn as junior synonym of *D. gaillardi* in de Bruijn et al. 2003); *D. gracilis* Fahlbusch, 1964; *D. mutilus* Fahlbusch, 1964; *D. hispanicus* Freudenthal, 1964; *D. sulcatus* Freudenthal, 1964; *D. franconicus* Fahlbusch, 1966; *D. cretensis* de Bruijn & Meulenkamp, 1972; *D. nemoralis* Agustí, 1981; *D. kohatensis* Wessels et al., 1982; *D. hasznosensis* Kordos, 1986; *D. iazygum* Radulescu & Samson, 1988; *D. zarandicus* Radulescu & Samson, 1988; *D. walkeri* Tong & Jaeger, 1993; *D. lindsayi* Qiu, 1996; *D. tongi* Qiu, 1996; *D. hanniae* Aguilar et al., 1999; *D. sudrei* Aguilar et al., 1999; *D. fourensis* Maridet et al., 2000; *D. doukasi* Theocharopoulos, 2000; *D. anatolicus* Theocharopoulos, 2000; *D. moralesi* van der Meulen et al., 2004.

Democricetodon sp. nov. (*sensu* Kälin & Engesser, 2001)
(Fig. 2.G–I)

Material and measurements: 1 fragmentary lower jaw with m3, 1 fragmentary upper jaw with M2, 10 isolated molars (UMJG 204.181 to 193). M1: 1.85×1.26, 1.84×1.28, 1.88×1.28; M2: 1.40×1.30, 1.44×1.30; M3: 1.06×1.13; m1: 1.65×1.13, 1.68×1.21, 1.59×1.11; m3: 1.28×1.03.

Description: m1: The anteroconid is round in young individuals but becomes ovaloid in worn molars by integration of the long convex labial anterolophid; the lingual anterolophid is absent or very short; the anterolophulid is very short; the metalophulid connects to the anterolophulid; the mesolophid is long and reaches the border of the molars or the cingulid closing the mesosinusid; the hypolophulid is proverse; the molars each possess two roots.

m2: The single tooth is broken on the labial side; the low mesolophid reaches the border of the molar.

m3: The entoconid is indistinct; the labial anterolophid extends to the labial wall of the protoconid; mesolophid and hypolophulid are of about the same length.

M1: The anterocone has two adjoining cusps with a superficial groove on its anterior wall; the two anterolophs are present, forming a bow-shaped structure with the anterocone; the anterolophule is broad and transverse; the labial spur of the anterolophule is most often absent, but may also be present and low and long; the protolophule is directed forewardly or double, the mesoloph is of medium length or somewhat longer; the sinus and the mesosinus are closed; the metalophule is directed backwardly; the posterosinus is reduced to a narrow valley; the molars each possess three roots.

M2: The two M2 are either damaged or partially covered by hard sediment; the two anterolophs are present; the protolophule is double; the metalophule is directed backwardly in one molar, directed forwardly in the second; the molars each possess three roots.

M3: The hypocone is highly reduced, the metacone absent; the two anterolophs are well developed; double protolophule, the posterior protolophule extends into the axioloph; the mesoloph is of medium length; sinus and mesosinus are closed by a cingulum; three roots.

Discussion: The molars from Gratkorn are clearly related to the *Democricetodon* species found in Nebelbergweg. Although that material shows a number of resemblances with *Democricetodon brevis*, Kälin & Engesser (2001) assigned the fossils to a new species, but refrained from naming it. The same species occurs in the German locality Hammerschmiede (Mayr & Fahlbusch 1975). The mesoloph of the three M1 from Gratkorn are somewhat smaller than those from the two other localities.

Democricetodon from Felsötárkány-Felnémet (Hír 2006: plate 2, figs. 5 and 10) is similar in size and morphology to the Gratkorn specimens.

Casanovas-Vilar (2007) reports *Democricetodon* sp. (= *D.* cf. *sulcatus* in Casanovas-Vilar et al. 2006) from Creu Conill (Spain, Vallès-Penedès Basin). The single M1 has a slightly subdivided anterocone, but the labial spur of the anterolophule is missing and the corresponding m2 has no mesolophid. *D. brevis brevis* from the Barranc de Can Vila 1 is characterized by long mesoloph(id)s and M1 with a slightly divided anterocone and long labial spur of the anterolophule (Casanovas-Vilar 2007). This subspecies differs from *D. brevis nemoralis* by the presence of a double protophule in the M1 and the undivided anteroconid of the m1. The fact that the teeth from Gratkorn and Barranc de Can Vila 1 may belong to the same (sub)species cannot be ruled out.

D. zarandicus from Tauţ (early Late Sarmatian, Romania) is characterized by M1 with fissured anterocone and complete labial spur of the anterolophule (Radulescu & Samson 1988). The mesolophid of the m1 is long and reaches the labial border. The specimens from Gratkorn differ from this species in their shorter transversale crests of the M1 and the somewhat larger size. A phylogenetic relationship between these species is possible.

The limited sample of molars of *D. iazygum* from Comăneşti 1 (earliest Late Sarmatian, Romania) also contains M1 with fissured anterocone but with mesolophs and labial spur of the anterolophule shorter than in *D. zarandicus*. With regard to these characters, the form from Gratkorn does not differ substantially. However, the sample from Comăneşti is too small to depict the intraspecific variability of *D. iazygum*. For this reason, the Gratkorn material should not be attributed to this species.

The *Democricetodon* molars from Çandir and Gratkorn are of almost equal size and similar in basic morphology. De Bruijn et al. (2006) attributed the Turkish specimens to *D.* aff. *gaillardi* (where *D. freisingensis* is a junior synonym of *D. gaillardi*). Moreover, they noted the resemblance of this form to the poorly documented *D. kohatensis* from Pakistan.

Democricetodon lindsayi from Moergen (Nei Mongol, China; Qiu 1996) has a well-fissured anterocone in the M1. However, it differs from the species from Gratkorn in the presence of a lingual anterolophid and shorter mesolophid in the m1.

We conclude that the teeth from Gratkorn are related to a suite of European and Asiatic species characterized by a fissured anterocone in the M1. The earliest representatives come from Çandir (Anatolia, middle part of Middle Miocene), which allows for the hypothesis to be advanced that the evolutionary origin of this type of *Democricetodon* was located somewhere in the East. The molars from Gratkorn are provisionally assigned to the species from Nebelbergweg.

Subfamily: **Eumyarioninae** Ünay, 1989

Genus: *Eumyarion* Thaler, 1966

Diagnosis (emended)**:** Mein & Freudenthal (1971).
Differential diagnosis: Ünay (1989).
Type species: *Cricetodon medium* Lartet, 1851 (= *Cricetodon helveticum* Schaub, 1925).

Other species included in *Eumyarion*: *E. latior* (Schaub & Zapfe, 1953); *E. weinfurteri* (Schaub & Zapfe, 1953); *E. bifidus* (Fahlbusch, 1964); *E. leemanni* (Hartenberger, 1965); *E. valencianum* Daams & Freudenthal, 1974 (nomen dubium in de Bruijn & Saraç 1991: 14 and de Bruijn 2009: 78); *Eumyarion montanus* de Bruijn & Saraç, 1991; *E. intercentralis* de Bruijn & Saraç, 1991; *E. microps* de Bruijn & Saraç, 1991; *E. carbonicus* de Bruijn & Saraç, 1991; *E. orhani* de Bruijn et al., 2006.

Eumyarion sp.
(Fig. 2.M–P, Fig. 4)

Material and measurements: Fragmentary skull with two complete molar rows (UMJG 204.017), 2 fragmentary upper jaws (one with M1, the other with M3), 6 isolated teeth (UMJG 2004.217-224). M1: 2.16×1.50, 2.15×1.63, 2.06×1.41; M2: 1.56×1.54, 1.54×1.48; M3: 1.15×1.33, 1.26×1.29; m1: 2.11×1.38; m2: 1.75×1.39.

Description: Skull: The fragmentary skull (Fig. 4) is prepared so that it can be viewed from the ventral side; the maximal length of the specimen is 15 mm; it includes the two molar rows; the left row shows slight corrosion marks, whereas the left row is clearly more corroded, especially on the labial side; the palatine is anteriorely broken; the posterior foramen palatinum is located lingual to the M2, and is about 1.2 mm long; with the exception of the basisphenoid, which is isolated, the posterior part of the skull is missing.

m1: The single m1 is hardly worn; the ovaloid anteroconid is positioned in the centre of the width of the molar and isolated from the metaconid, although a small longitudinal crest is present on the postero-lingual part of the anteroconid; the strong labial anterolophid begins at about half of the high of the anteroconid and ends at the base of the protoconid; the anterolophulid is oblique, reaching the posterior wall of the anteroconid centrally (the anterolophulid appears to be interrupted in the specimen illustrated in figure 4P, but this is not the case); a short labial anterolophulid spur extends to the metalophulid; this crest is double close to the metaconid, whereas a single crest reaches the anterolophulid; protoconid hind arm, mesolophid and ectolophid together form a triangular structure that lingually merges with the posterior wall of the metaconid; the strong metaconid ridge closes the mesosinusid; a small ectomesolophid is present along the labial wall of the ectolophid; the broad posterosinusid contains a well-developed posterior hypolophulid; two roots.

m2: The metaconid and entoconid are high, worn on their labial wall, whereas the other cuspids and crests are worn on the occlusal plan of the molar, forming a somewhat horizontal surface; the anteroconid is triangular with the labial anterolophid extending to the base of the protoconid; the small lingual anterolophid connects to the base of the metaconid; the metalophulid is directed forwardly and extends to the anteroconid; the protoconid hind arm connects to the medium-sized mesolophid; the two fused crests reach the metaconid; small ectomesolophid present; hypolophulid transverse; the posterolophid connects to the posterior wall of the entoconid and well-developed posterior hypolophulid; two roots.

m3: The m3 is heavily worn and broken; two roots.

M1: The anterocone is subdivided; anterolophs are missing but the anterior valleys are closed by massive cinguli; a double anterolophule connects to both cusps of the anterocone; the protolophule is transverse; the long mesoloph does not reach the mesostyl closing the mesosinus; metalophule and posteroloph are parallel; three roots.

M2: The para- and metacone are high, worn on their labial walls, whereas the other cusps and crests are worn in the occlusal plan of the molar, forming a somewhat horizontal surface; the anterocone is indistinct; the lingual anteroloph is very short; all transversal crests are parallel; the long mesoloph does not reach the mesostyl closing the mesosinus; entomesoloph absent or very short; a very short “anterior” mesoloph can be distinguished on the entoloph of one molar; three roots.

M3: Anterocone and protocone abut; the lingual anteroloph missing; anterolophule and protolophule joining the axioloph; a posterior crest occurs on the protolophule; in one specimen it is very short, while it is developed as a “second axioloph” in the second molar; the neo-entoloph is absent as the two lingual cusps are abut; the sinus is delimited by a cingulum or absent; metalophule, posteroloph and mesoloph are of equal length.

Discussion: Due to the high intraspecific variability of the *Eumyarion* species (e.g. de Bruijn 2009), and the fact that more than one species may be present at one locality (e.g. Wu 1982; de Bruijn et al. 2006), the attribution of small molar samples is mostly difficult. The molars are morphologically and metrically similar to *E. latior*, a species defined in the Middle Miocene of Neudorf (Slovakia; Schaub & Zapfe 1953; Fejfar 1974). The stratigraphically younger *E. leemanni*, reported from latest Middle Miocene and Late Miocene deposits of the Vallès-Penedès Basin, is characterized by cusps integrated into the ridges that join them. A different taxonomic approach has been proposed by Kretzoi & Fejfar (2005: p. 127), who recognized a *latior* lineage in Central Europe. Based on taxonomic ambiguities (early *E. leemani* vs. *E. latior*) and the limited number of specimens at hand, the molars from Gratkorn cannot be identified with confidence at species level.

Biostratigraphic discussion

Stratigraphic range of the cricetid species from Gratkorn

Four cricetid rodents have been recorded in the fauna from Gratkorn:

— *Megacricetodon minutus* was discovered in St. Margarethen/Zollhaus, within the Late Sarmatian *s. str.* part of the

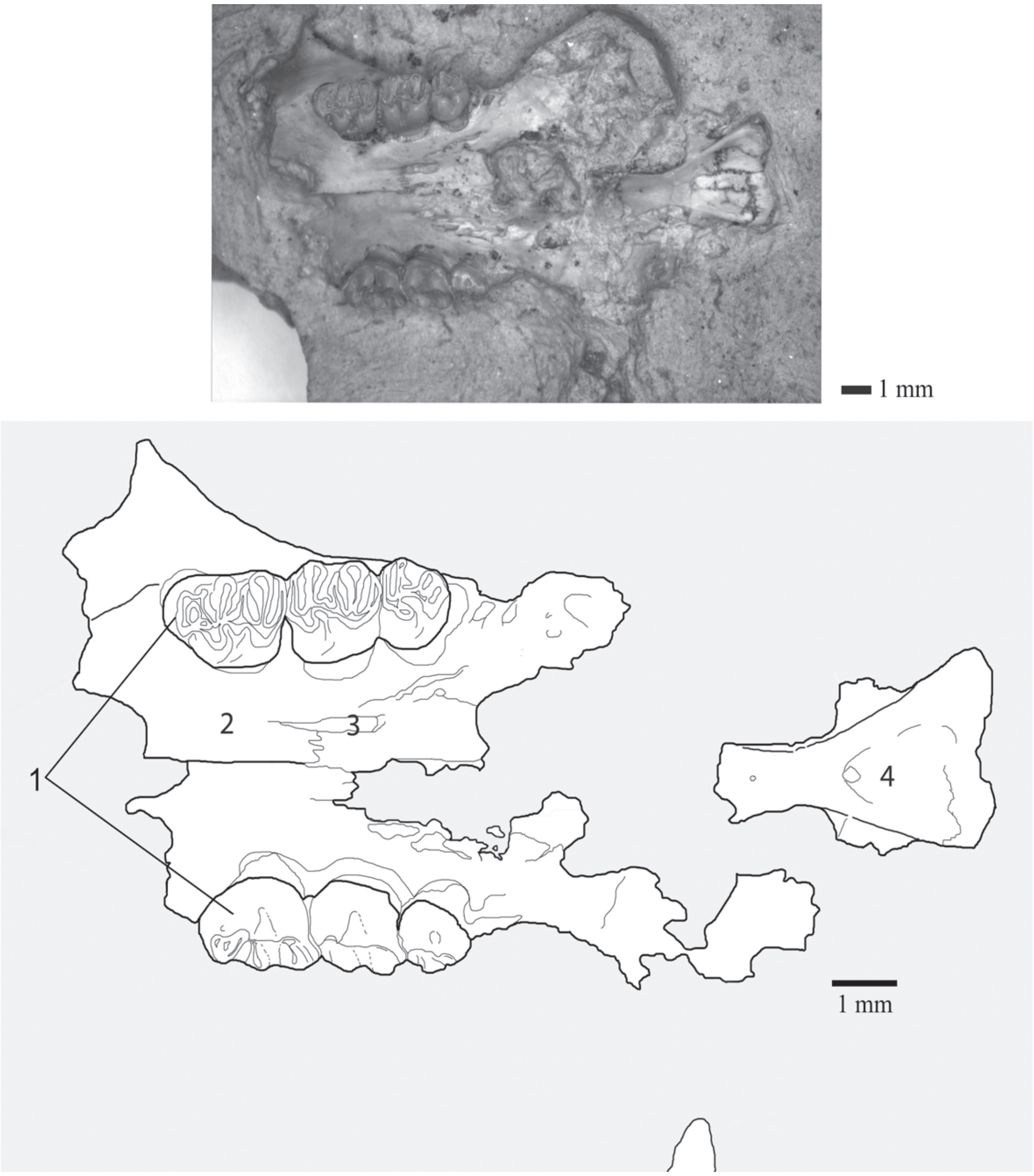

Fig. 4. ***Eumyarion* sp**. Fragmentary skull in ventral view (UMJG 204.017). **1** — Molar rows; **2** — Os palatinum; **3** — Foramen palatinum posterior; **4** — Basisphenoidale.

succession (G. Daxner-Höck pers. comm.), stratigraphically close to Gratkorn. This species is the only cricetid found in Mataschen (Styrian Basin, Daxner-Höck 2004), and it has also been reported from Bullendorf (Vienna Basin, Daxner-Höck 1996). Both localities correspond to the Pannonian "Zone B", respectively "B/C" (*sensu* Papp 1951). The species also occurs in localities dated as Pannonian "Zone E" (e.g. Vösendorf, Inzersdorf and Richardhof-Golfplatz; Daxner-Höck 1996 and pers. comm.). Moreover, *M. minutus* has been reported from the lacustrine deposits of Borský Svätý Jur (Slovakia, Pannonian "Zone E"; Joniak 2005) and the Hungarian locality Felsötárkány 3/2 (Hír 2004). The genus *Megacricetodon* disappears from the record in Austria some time during the Late Pannonian ("Zone F"; Daxner-Höck 1996).

— *Democricetodon* sp. nov. (*sensu* Kälin & Engesser 2001) is documented in Gratkorn by a small sample of teeth, but the intraspecific variability remains incompletely documented. Nevertheless, its close relationships to the medium-sized *Democricetodon* populations characterized by a fissured anterocone in the M1 are obvious. These forms have been recorded from Spain in the West to China in the East, and are abundant in the late Middle Miocene and earliest Late Miocene. The genus does not persist to the end of the MN10 in Central Europe (Daxner-Höck 1996).

— *Eumyarion* has been reported in Austria from the Early Miocene of Oberdorf (*E.* cf. *weinfurteri*, Daxner-Höck 1998a). The species *E. weinfurteri* is also known from Obergänserndorf and Teiritzberg (Early Miocene, Late Karpatian; Daxner-Höck 1998b) and the Middle Miocene (Early Badenian) of Mühlbach and Grund (Daxner-Höck 2003). However, these samples are taxonomically not directly related to *Eumyarion* sp. from Gratkorn. *Eumyarion* sp. from Götzendorf (Pannonian "Zone F"; Daxner-Höck 1996) is stratigraphically younger. As a result, the molars from Gratkorn increase our knowledge of the fossil history of this genus in Austria. The youngest *Eumyarion* representatives have been recorded from the base of the MN10 (Suchomasty; Daxner-Höck 1996).

— The fourth cricetid, "*Cricetodon*" *fandli*, represents a new species. *Cricetodon meini* from Mühlbach and Grund (Daxner-Höck 2003) is not directly related to the form from Gratkorn. The small Cricetodontini sample from Bullendorf (Daxner-Höck 1996) has not yet been precisely determined.

Biostratigraphical implications and correlation of the small mammal fauna

A comparison of the Gratkorn fauna with faunas from localities of the North Alpine Foreland Basin (NAFB) suggests that the small mammals from Gratkorn generally are more closely related to faunas from NAFB-localities, which are traditionally regarded as corresponding to the base of the Late Miocene (MN9, occurrence of *Microtocricetus molassicus*), than to faunas from Middle Miocene sites (e.g. Anwil, Kleineisenbach, Giggenhausen; Prieto 2007).

For example, until recently the gymnure *Schizogalerix voesendorfensis* was believed to have appeared not before the Late Miocene (Kälin & Engesser 2001; Ziegler 2006). Its discovery in Gratkorn now shows that the species was already established in the Late Sarmatian (Prieto et al. in print a). Following the biostratigraphic concept proposed in Prieto & Rummel (2009), the NAFB-localities traditionally correlated with MN9 (Hammerschmiede, Hillenloh, Nebelbergweg) are older than, or at least of about the same age as, Felsötárkány 3/2, a locality correlated with the Sarmatian (Hír 2004). This implies that most of the MN9 cricetid rodents of the NAFB are Middle Miocene in age, or close to the Middle/Late Miocene boundary. This has fundamental biostratigraphic consequences, as Hammerschmiede is the type locality of *Microtocricetus molassicus*. The first occurrence of the genus *Microtocricetus* defines the beginning of MN9 (de Bruijn et al. 1992; Fejfar 1999; Mein 1999). *Microtocricetus* was unknown from Austria before the Late Pannonian "Zone F" of Götzendorf (Daxner-Höck 1996), and its absence in Gratkorn may argue for a first occurrence of the genus during the Late Miocene. However, taphonomic and ecological bias may alter the assemblage, because *Microtocricetus* is usually regarded as an inhabitant of moist, riparian environments (Fejfar 1999) that are different from the paleoenvironment represented by the Gratkorn fossiliferous beds (Harzhauser et al. 2008; Gross et al. 2009a,b and subm.). Humidity data from *Microcricetus*-bearing localities (e.g. Hammerschmiede 1–3, Rudabánya, Götzendorf) provide mean annual precipitation estimates (Böhme et al. 2006, 2008) ranging from 974 mm (Hammerschmiede 1) to 1303 mm (Götzendorf), which is significantly more humid than the estimate for Gratkorn (486 mm; Gross et al. subm.).

In Hungary, *Microtocricetus* is first recorded at the top of the Felsötárkány sequence (Felsötárkány 3/8 and 3/10). The co-occurring mollusc fauna is suggestive of a Sarmatian age (Hír 2006 and Hír & Kókay 2010). *Microtocricetus* has also been reported from the Ukrainian locality Grytsiv (Topachevsky & Skorik 1988; Kowalski 1993). The fissure fillings containing the fossil vertebrates share *Sarmatimactra vitaliana* (Topachevsky & Scorik 1992; Topachevsky et al. 1996; Rzebik-Kowalska & Topachevsky 1997; Vangengeim et al. 2006), a characteristic bivalve of the Late Sarmatian *s. str.* in the Central Paratethys (Papp 1954; Piller et al. 2007).

The value of *Microtocricetus* as an index fossil for the onset of the Late Miocene remains questionable and its first occurrence traces back into the Sarmatian *s. str.*

We interprete the new Gratkorn species "*C.*" *fandli* as an ancestor of *C. klariankae* from Felsötárkány-Felnémet (Sarmatian; Hír 2006), a form that may represent the youngest *Cricetodon* species from Central Europe. The proposed lineage *fandli–klariankae* cannot be directly related to other cricetodontine rodents. Nevertheless, parallel evolutionary patterns have been noted between the faunas in Europe and Anatolia. This allows the comparison of geographically distant fossil localities. For instance, Casanovas-Vilar et al. (2008) date Barranc de Can Vila 1 at between 12.0 and 12.5 Ma, more probably 12 Ma (Moyà-Solà et al. 2009). The faunal composition at this locality (Casanovas-Vilar 2007) is, with the exception of *Democricetodon larteti* (=*Fahlbuschia larteti*), very similar to that from Gratkorn (12.0–12.2 Ma): both localities have yielded a large cricetid rodent with moderate hypsodonty and of comparable size (*Hispanomys* sp./"*Cricetodon*" *fandli*), a medium-sized *Democricetodon* with fissured anterocone in the M1 (*D. brevis brevis*/*D.* sp. nov.), a small *Megacricetodon* (*M. minor minor*/*M. minutus*), and a form attributable to *Eumyarion* (*E. leemani*/*E.* sp.).

These parallel evolutionary patterns may pose an argument for the existence of different paleobioprovinces around the Middle to Late Miocene transition. The bioprovinciality is documented by the heterochrone last occurrences of taxa at the subfamily level, including the Cricetodontinae. While the Cricetodontini disappeared from the fossil record of Central Europe close to the Middle/Late Miocene boundary, *Hispanomys*/*Ruscinomys* persisted into the Pliocene in Western Europe, and *Byzantinia* survived until the end of the Miocene in Anatolia and Southeastern Europe. The insectivore fauna from Gratkorn in fact seems to be related to faunas from Eastern Europe/Anatolia (Prieto et al. in press a). The mole *Desmanodon fluegeli* shares several features with *D. minor*/*D. major* from Turkey. Similarly, *Schizogalerix voesendorfensis* has been assigned to an Austrian lineage that shares similarities with *Schizogalerix* from Turkey (Engesser 1980). The cricetid rodents from Gratkorn are generally more closely related to assemblages from the Pannonian Basin (Hungary in particular), and to a lesser degree also Anatolian assemblages, than to late Middle Miocene faunas from the NAFB (e.g. Anwil, Kleineisenbach, Giggenhausen). On the other hand, the lack of sufficient material and studies of Middle to Late Miocene fossil localities in Austria and especially Germany currently precludes a more decisive assessment of the suggested presence of two independent bioprovinces at least at the time of the accumulation of the Gratkorn fauna.

Conclusions

In spite of the low species diversity (four species), the cricetid rodent assemblage from Gratkorn increases our knowledge about the Austrian rodent succession. Well-dated as Late Sarmatian *s. str.*, the lineage "*Cricetodon*" *fandli–Cricetodon klariankae* may become a key to the correlation of fossil localities from Central Europe. In a broader context, the fauna Gratkorn is of major importance for the understanding of the continental biostratigraphy of the late Middle Miocene of Austria and in a general view of the Paratethyan realm. Moreover, the geographical position of the locality, relatively central in Europe, makes it important for the understanding the faunal interchanges and bioprovincialism at the end of the Middle Miocene.

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