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Jérôme Prieto, Chiara Angelone, Isaac Casanovas-Vilar, Martin Gross, Janós Hír, Lars W. van den Hoek Ostende, Lutz Christian Maul & Davit Vasilyan

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ORIGINAL PAPER

The small mammals from Gratkorn: an overview

Jérôme Prieto · Chiara Angelone · Isaac Casanovas-Vilar · Martin Gross · Janós Hír · Lars W. van den Hoek Ostende · Lutz Christian Maul · Davit Vasilyan

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Abstract The rich and diverse fossil mammalian assemblage from Gratkorn (Middle Miocene, Austria) is of primary importance for the understanding of the faunal evolution in Central Europe. Besides large mammals, the fauna comprises: *Schizogalerix voesendorfensis*, Galericinae gen. et sp. indet., *Desmanodon fluegeli, Dinosorex* sp., cf. *Myotis* sp., "*Cricetodon*" *fandli, Megacricetodon minutus, Eumyarion* sp., *Spermophilinus bredai, Blackia* sp., *Forsythia gaudryi, Albanensia albanensis, Muscardinus* aff. *sansaniensis, Miodyromys* sp., *Keramidomys* sp., *Euroxenomys minutus minutus, Prolagus oeningensis,* cf. *Eurolagus fontannesi* and Ochotonidae indet. Based on the degree of corrosion on the dental elements and the presence of pellets, most, but not all, of the material is tentatively interpreted as a result of accumulation by nocturnal raptors. In addition to the information provided by the lower vertebrates and the molluscs, which occur in abundance in the same thin fossil-enriched layer, the mammal fauna gives a mixed picture of the environment (basically forested vs. open landscape). This could indicate the presence of different microhabitats around the excavation place, but may also be a taphonomical artefact based on various different agents of accumulation contributing to the thanatocoenosis. Nevertheless, the extreme quick accumulation of the fossils provides an exceptional windows in the late Sarmatian s. str. ecosystems.

Keywords Miocene · Sarmatian s. str · Rodentia · Eulipotyphla · Chiroptera · Lagomorpha

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This article is a contribution to the special issue "The Sarmatian vertebrate locality Gratkorn, Styrian Basin."

J. Prieto (✉)
Department of Earth- and Environmental Science, Palaeontology,
Ludwig-Maximilians-University Munich, Richard-Wagner-Str. 10,
80333 Munich, Germany
e-mail: j.prieto@lrz.uni-muenchen.de

C. Angelone · I. Casanovas-Vilar
Institut Català de Paleontologia Miquel Crusafont, Universitat
Autònoma de Barcelona, Edifici ICP, Campus de la UAB s/n,
08193, Cerdanyola del Vallès Barcelona, Spain

C. Angelone
e-mail: chiara.angelone@icp.cat

I. Casanovas-Vilar
e-mail: isaac.casanovas@icp.cat

M. Gross
Department for Geology and Palaeontology, Universalmuseum
Joanneum, Weinzöttlstrasse16, 8045 Graz, Austria
e-mail: martin.gross@museum-joanneum.at

J. Hír
Municipal Museum, 3060 Pásztó, Pf. 15, Hungary
e-mail: hirjanos@gmail.com

L. W. van den Hoek Ostende
Naturalis Biodiversity Centre, Darwinweg 2,
2333 CR Leiden, The Netherlands
e-mail: lars.vandenhoekostende@Naturalis.nl

L. C. Maul
Senckenberg Research Station of Quaternary Palaeontology,
Am Jakobskirchhof 4, 99423 Weimar, Germany
e-mail: lmaul@senckenberg.de

D. Vasilyan
Department of Geosciences, Eberhard Karls Universität Tübingen,
Sigwartstraße 10, 72076 Tübingen, Germany
e-mail: davit.vasilyan@ifg.uni-tuebingen.de

Abbreviations

NAFB	North Alpine Foreland Basin
UMJGP	Universalmuseum Joanneum in Graz

Introduction

The late Middle Miocene is fascinating for the study of terrestrial palaeoecosystems. Following the long period of the mid-Miocene Climatic Optimum, drastic climatic changes induced important faunal re-arrangement and migration within Europe (e.g. Böhme 2003; Maridet et al. 2007). Rich and diverse fossil faunas are thus of primary importance for the understanding of these processes. The late Middle Miocene is well recorded in various Iberian basins, but complete faunas of this period are rare in Central Europe. Therefore, the recent discovery of an exceptional fossil assemblage of macro- and microvertebrates in Gratkorn (early late Sarmatian, Austria, Styria; Gross et al. 2007), allows a fresh look at the palaeocommunity at higher latitudes following the Mid-Miocene cooling (e.g. Gross et al. 2011). Continued work at the site has yielded new material, allowing us to refine previous conclusions on the taxonomy of the small mammals (rodents, insectivores, bats), which are presented in the first section of this contribution. In the second section, the biostratigraphic implications will be discussed. The third part of this article concentrates on the origin of the fossil accumulation processes, allowing a better view on the palaeoenvironment of Gratkorn (section "Biostratigraphical remarks").

Materials and methods

The fossils from Gratkorn are housed in the collections of the Universalmuseum Joanneum in Graz (Geology & Palaeontology), the Bayerische Staatssammlung für Paläontologie und Geologie in Munich, and in the collections of the Eberhard Karls University in Tübingen. SEM images were captured at the Biogeology and Applied Palaeontology Laboratory of the Eberhard Karls University at Tübingen, Germany.

Insectivores, rodents, lagomorphs and chiropters from Gratkorn: taxonomic notes

The insectivores, comprising two gymnures, one talpid and one soricid, and one single chiroptera have been described by Prieto et al. (2010a). The rest of the small mammal fauna comprises four species of cricetid rodents previously described by Prieto et al. (2010b), two glirids, four sciurids, one eomyid, all described by Daxner-Höck (2010), and one beaver (Prieto et al. 2014, this issue). The lagomorphs, all pikas, are diverse, with three species (Angelone et al. 2014, this issue). Gratkorn is the type locality of two species ("*Cricetodon*" *fandli* and *Desmanodon fluegeli*), plus a potential new species of a large-sized pika (Ochotonidae indet.) never recorded elsewhere.

Eulipotyphla

Erinaceidae

Schizogalerix voesendorfensis (Rabeder, 1973)

The species is the most abundant mammal in Gratkorn, and fossils are regularly found in the locality. Besides a large number of mandibles (Fig. 1), upper jaws and isolated teeth, a newly discovered fragmentary skull completes the inventory (UMJGP 204693; Fig. 2). The specimen has been prepared in its ventral part. It preserves only the palate region; the part posterior to the crista transversa has been lost. The left P3–M1, as well as the right canine and M1–M2, are conserved in situ. The skull has been crushed as shown by the different occlusal orientations of the tooth rows.

European Miocene gymnure skulls are a rarity. The giant insular form *Deinogalerix* is known from several skulls (Butler 1980; Villier 2010; Villier et al. 2013). Ziegler (1983) describes in detail an exceptionally complete specimen of *Galerix exilis* from Steinberg (Germany, Badenian), a species of which partial skulls were previously known from the French fissure fillings of La Grive (Butler 1948). In addition, several skulls in excellent state of preservation from the sites of Cerro de Batallones are under study (Spain, late Vallesian; L.W. van den Hoek Ostende, personal data) (See also section "Semi-articulated specimens and proposed evidences of fossil pellets of birds of prey" and related figures).

Originally, the deciduous dentition was only represented by a single d4 in Gratkorn, but now two upper milk premolars (D3) are also available (Fig. 5s, t).

Taxonomical note: *Schizogalerix voesendorfensis* is morphologically closer to *Parasorex socialis* and *S. pasalarensis* than to any other species. Traditionally, the Iberian late Middle–Late Miocene Galericini findings are identified as *Parasorex* (Van den Hoek Ostende 2001). However, these species closely resemble their Central European counterparts, which are placed within the genus *Schizogalerix,* for instance because of the shape of the mesostyle in the upper molars (Prieto et al. 2011). This implies that a revision of these forms is necessary to assess the geographical range of both genera, as well as of its constituting species, at the end of the Middle Miocene, and assure that the biogeographical patterns found are not a taxonomic artefact.

Galericinae gen. et sp. indet.

This species is only represented by a single M1 which is somewhat larger than *Schizogalerix voesendorfensis,* and has

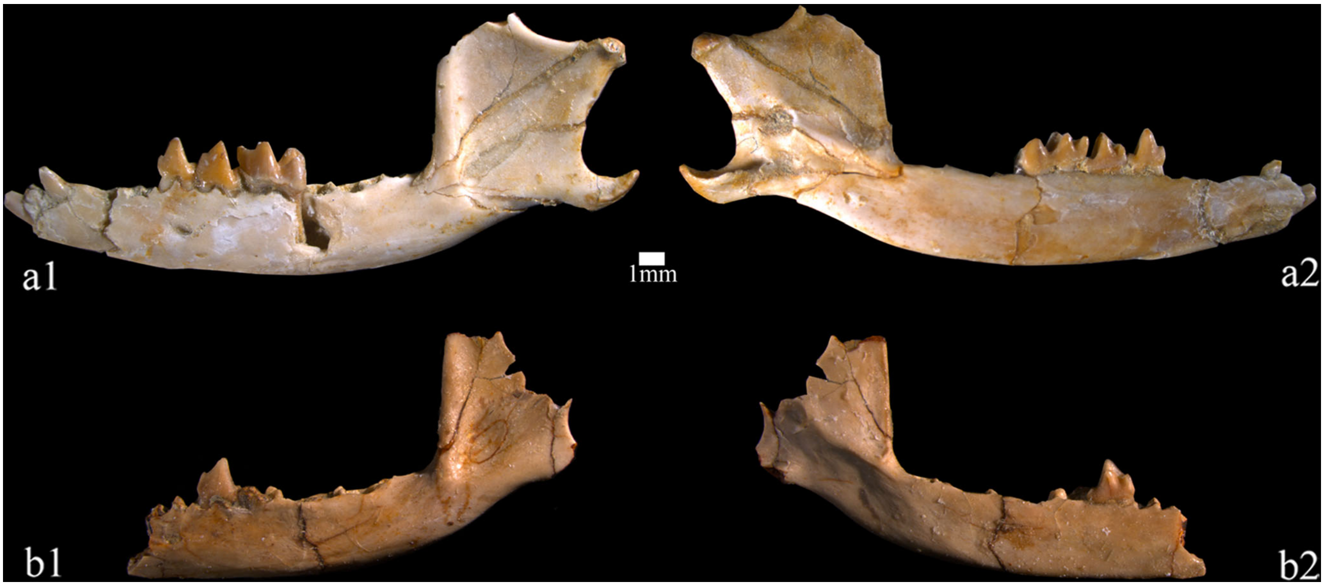


Fig. 1 Mandibles of *Schizogalerix voesendorfensis* (Rabeder, 1973) from Gratkorn. **a** Left mandible with i1–2 + p3–m3 (UMJGP 204691; **a1** from labial view, **a2** from lingual). **b** Left mandible with p4 (UMJGP 204735; **b1** from labial, **b2** from lingual).

a different configuration of the mesostyle. Prieto et al. (2012a: 230) noticed that this molar closely resembles the one classified as *Parasorex* sp. from the Middle Badenian of Sámsonháza 3 (Hungary, Nógrad County). However, as we only have one element and, given the taxonomic confusion in the Galericini mentioned above, we hesitate to assign the Gratkorn specimen to a genus. More material is needed to clarify its taxonomic position.

Talpidae
Desmanodon fluegeli Prieto, Gross, Böhmer and Böhme, 2010

Additional material: UMJGP 204705: right humerus; UMJGP 204738: Fragmentary mandible with m3 (1.47× 1.19-0.87).

Gratkorn is the type locality of the species. *Desmanodon fluegeli* shares characteristics found in the Anatolian lineage *D. minor–D. major* but is not directly linked to it. Nevertheless, it may represent an eastern immigrant, which is interesting, as *Schizogalerix* also has its origin in Anatolia (Engesser - 1980; de Bruijn et al. 2006). The most interesting new specimen is a complete humerus (Fig. 3).

Soricidae
Dinosorex sp.

Additional material: 204743: Fragmentary mandible with m1–m2; m1: 2.24×1.54–1.59; m2: 1.87×1.58–1.45.
Unfortunately, the morphologic information supplied by this specimen does not allow a species determination. The molars

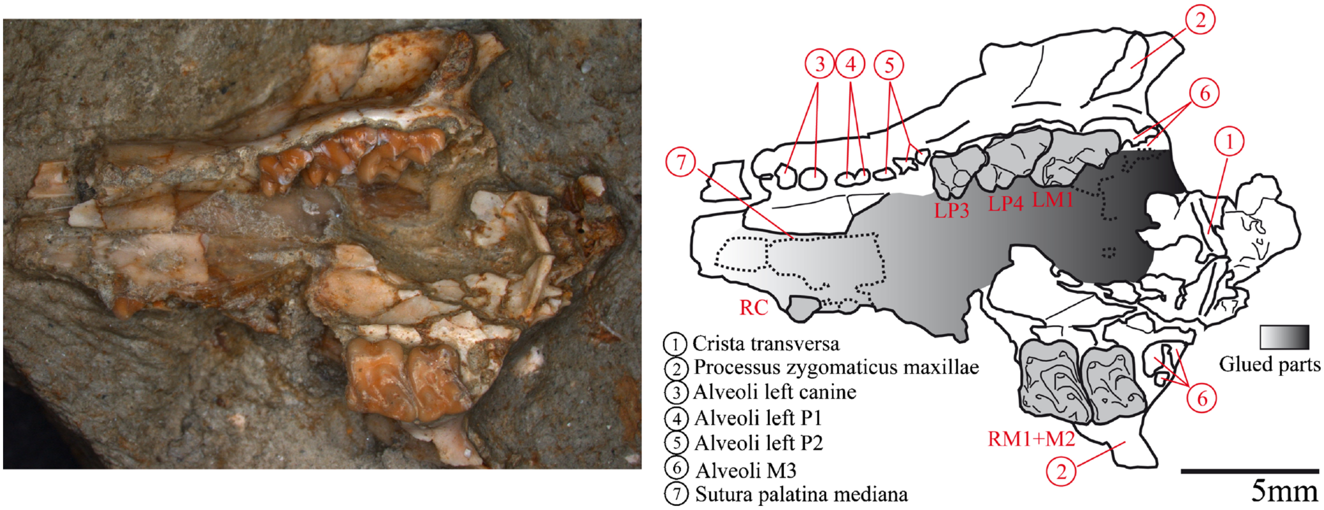


Fig. 2 Fragmentary skull of *Schizogalerix voesendorfensis* (Rabeder, 1973) from Gratkorn (UMJGP 204693)

are somewhat smaller than those in the only mandible found thus far (Prieto et al. 2010a).

Fig. 3 Humerus of *Desmanodon fluegeli* Prieto, Gross, Böhmer and Böhme, 2010: **a1** posterior view. **a2** anterior view

Fig. 4 "*Cricetodon*" *fandli* Prieto, Böhme and Gross, 2010. **a** Right mandible with m2 (UMJGP 204003). **b** Fragmentary skull with two upper incisors and left M1–M3 (UMJGP 204020)

Chiroptera

cf. *Myotis* sp.

Two bat molars have so far been discovered. Only one broken tooth (UMJGP 211015) is added to the known sample.

Rodentia

Cricetidae

"*Cricetodon*" *fandli* Prieto, Böhme and Gross, 2010

Gratkorn is the type locality of the species, and the holotype is a very well-preserved skull with the mandibles in anatomic connection. A second skull has been found (Fig. 4b; currently under study) and, although being more fragmentary, provides new morphological information because it presents parts which were covered by sediment in the holotype (see also section "Semi-articulated specimens and proposed evidences of fossil pellets of birds of prey" and related figures).

Taxonomical note: The generic status of the early species of *Byzantinia* and *Hispanomys*, as well as that of some species of *Cricetodon* is under discussion (e.g. Prieto et al. 2010b; López-Guerrero et al. 2013). As a consequence, related species may have been assigned to different genera, and thus have not been compared to one another. In the following, we discuss the relationships of the Cricetodontini listed in Table 1 (for the discussion of other taxa, see Prieto et al. 2010b).

Hispanomys cf. *bijugatus* is described from Gaweinstal based on one M1. Harzhauser et al. (2011) recognised some similarities with *C. klarankiae*, but refrained to link the molar to this species without a clear explanation. A similar observation was previously made by Prieto et al. (2010b: 427), who hypothesised a relationship between *C. klarankiae* and *H. bijugatus,* without entering into details. Unfortunately, López-Antoñansas and Mein (2009) did not take the Hungarian species into account in their detailed review of *H. bijugatus*. The two species are of comparable size, but *C. klarankiae* has longer m2/M2. A detailed morphological comparison is indeed needed. For this reason, the Hungarian species is classified as "*C.*" *klarankiae,* and the species from Gaiweinstal as ? "*C.*" *klarankiae* in Table 1. It is hypothesised here that these species belong to a single lineage, but the inclusion of ? "*C.*" *klarankiae* could be questioned.

In addition, the newly discovered and unpublished *Cricetodon* sp. sample from Vărciorog (Romania, Bihor District; Hír 2010) might be related to these species.

Table 1 Small mammal composition of selected fossil localities surrounding geographically and stratigraphically Gratkorn

				Deperetomys hagni	***"Cricetodon" fandli***	*"Cricetodon" klariankae*	*Hyspanomys* sp.	cf. *Byzantinia* sp/div. sp.	*Cricetodon* sp. nov.	cf. *Cricetodon* sp.	*Democricetodon brevis*	*Democricetodon zarandicus*	***Democricetodon* sp. nov.**^{A}	*Democricetodon* cf. *brevis* (large)	*Democricetodon freisingensis*	*Democricetodon* sp. nov.^{B}	*Democricetodon* sp.	*Collimys hiri*	*Collimys longidens*	*Collimys dobosis*	*Collimys* sp.	*Schizocricetodon huerzeleri*	*Microtocricetus mollassicus*	*Megacricetodon minor*	*Megacricetodon similis*	***Megacricetodon minutus***	*Megacricetodon germanicus*	*Megacricetodon robustus*	*Eumyarion bifidus*	*Eumyarion medius*	*Eumyarion latior*	***Eumyarion* sp.**	Cricetidae indet.
1	Austria	Götzendorf	Pannonian, F														sp.,11						11									11	
2	Austria	Vösendorf	Pannonian, E														11									11							
3	Slovakia	Borský Sv. Jur	Pannonian, E														49						49			49					49		
4	Austria	Atzelsdorf	Pannonian, C																														
5	Austria	Mariathal	Pannonian, C/D																														
6	Austria	Gaweinstal	Pannonian, C			?25^{2}							?25^{1}													25							
7	Austria	Bullendorf	Pannonian, B							11^{33}																11							
8	Austria	Jamm	Pannonian, B																														
9	Austria	Mataschen	Pannonian, B																							26							
10	Austria	Magersdorf	Lower Pannonian																														
11	Germany	Hillenloh	Middle to late Miocene transition																	37			x			x							
12	Hungary	Felsőtárkány 3/10	late Sarmatian																	15			15			15				15			
13	Hungary	Felsőtárkány 3/8	late Sarmatian																				15							15			
14	Germany	Hammerschmiede 1-3	Middle to late Miocene transition										x^{19}					37^{19}					1,39			39^{18}					cf.,x, 17^{43}		
15	Poland	Bełchatów A	Middle to late Miocene transition										?,50^{24}	50							50^{23}		2,50			?,50^{25}					cf.,50		
16	Hungary	Felsőtárkány 3/2 (Güdör-Kert)	late Sarmatian																	8,12						8				8			
17	Switzerland	Nebelbergweg	Middle to late Miocene transition										27						27			27				?27^{6}		27			cf.,27		
18	Switzerland	Nebelberg TGL III	Middle to late Miocene transition				34																			?34^{15}							
19	Poland	Opole 2	?Late Sarmatian										?54^{30}					?54^{29}														54^{31}	
20	Poland	Opole 1	?Late Sarmatian																														53^{27}
21	Hungary	Felsőtárkány 2	late Sarmatian										cf.,14^{34}							14						14							
22	Hungary	Felsőtárkány 1	late Sarmatian										cf.,14^{34}							14						14							
23	Hungary	Felsőtárkány 2/3	late Sarmatian			9							cf.,9^{33}							9				9						9			
24	Hungary	Felsőtárkány 2/7	late Sarmatian			9							cf.,9^{33}							9				9						9			
25	Romania	Tauţ	(upper Volhnyan-Bessarabian)									45																				45	
26	Romania	Comăneşti 1	(Late) Volhynian					45							cf.,45											cf.,45							
27	**Austria**	**Gratkorn**	**early late Sarmatian**		**18**								**18**													**18**						**18**	
28	Romania	Tăşad	Early Sarmatian							56			56^{33}													cf.,56^{36}				56			
29	Romania	Bogota	Volhynian																														
30	Romania	Subpiatră 2/2	MN7/8														?57^{38}													57			
31	Romania	Subpiatră 2/1R	MN6														?57^{38}							sp.,57									
32	Hungary	Mátraszőlős 1	late Badenian							10														cf.,10^{39}					10				
33	Hungary	Mátraszőlős 2	late Badenian							10	cf.,45				cf.,10									cf.,10^{39}					10				
34	Hungary	Mátraszőlős 3	late Badenian							45	cf.,45																					45	
35	Germany	Giggenhausen	Late Badenian	33,43					33		cf.,33,43				33,43	33,43^{44}								cf.,33,43^{45}	33,43						cf.,33,43^{31}		
36	Switzerland	Anwil	Late Badenian	32					33		29				29						34			aff.,29	29		31				cf.,29		

x pers. Data J. Prieto; temporar taxonomy
1 as *Democricetodon* sp.
2 as *Hispanomys* cf. *bijugatus*, see text
3 as *Dinosorex* aff. *pachygnathus*
4 originally described as belonging to two species
5 large form
6 as *Megacricetodon minor*
7 as *Steneofiber minutus*
8 as *Pseudodryomys hamadryas*
9 as Soricidae I gen. et sp. indet.
10 as Soricidae II gen. et sp .indet.
11 as Gliridae VIII
12 as Gliridae X
13 as *Myoglis larteti*
14 as *Sciuropterus* sp. in Engesser 1972
15 as *Megacricetodon minor* (hypothesys)
16 originally described as *Desmanella* in Mayr and Fahlbusch 1975
17 originally described as *Augustens* in Mayr and Fahlbusch 1975
18 as *Megacricetodon* aff. *debruijni*
19 pars originally as *Democricetodon gaillardi freisigensis* in Mayr and Fahlbusch 1975
20 as cf. *Hemisorex robustus*
21 not described
22 as *Heterosorex* sp.
23 as *Collimys transversus*
24 as *Democricetodon* sp. nov.
25 as *Megacricetodon* aff. *minor*
26 as *Sciuropterus gibberosus*
27 as *Cricetodon minus*
28 as *Pseudotheridomys carpathicus*
29 as *Democricetodon* (*D.*) *gaillardi*
30 as cf. *Democricetodon* (*M.*) *bavaricus*
31 as *Comitus bifidus*
32 as *Glis* sp.
33 as *Cricetodon* sp., see text
33 as *Democricetodon brevis* and *Megacricetodon germanicus*, see text
34 as *Democricetodon* sp., see text
35 Doubtfull data
36 as *Megacricetodon* cf. *minor*
37 as *Keramidomys carpathicus*
38 as *Democricetodon freisengensis* and *D. brevis*
39 as *Megacricetodon minor*
40 as *Dinosorex zapfei*
41 as *Eliomys truci*
42 as *Anomalomys kowalskii*
43 as *Eumyarion leemanni*
44 as *Democricetodon* (*D.*) *affinis* cf. *mutilus*
45 as *Democricetodon* (*M.*) aff. *schaubi*
46 as *Microdyromys miocaenicus*

A sensu Kälin and Engesser 2001
B sensu Prieto 2007
C sensu Prieto et al. 2012a
D see Angelone et al. (this issue) for detail on taxonomy

The *Cricetodon* sp. from Tăşad (Hír et al. 2001) and Mátraszőlős 1-3 (Hír and Kókay 2004, 2011) are also characterised by long ectolophs, but their relationship with "*C.*" *klarankiae* cannot be satisfactorily established (Prieto et al. 2010b). They also share some characteristics with *Cricetodon hungaricus* from Hasznos (Badenian, Kordos 1986). Whether these forms belong to another lineage, or are related to "*C*". *klariankae*, remains an open question. Depending on its outcome, the evolution of the lineage "*C.*" *fandli*–"*C.*"*klarankiae* as proposed by Prieto et al. (2010b) may have to be re-considered.

On the other hand, the following taxa cannot be related to the Gratkorn form:

- *Hispanomys* sp. from Nebelberg TGL III was originally assigned to *Cricetodon* by Rummel and Kälin (2003:140), who underline the similarity of the species with *C. jumaensis* from the German fissure fillings of Petersbuch. This form has been excluded from the "*Cricetodon*" lineage by Prieto et al. (2010b) based on the absence of complete ectolophs on the M1. In addition, the m1 lacks the posterior metalophulid.
- *Cricetodon* sp. from Bullendorf (Daxner-Höck 1996, here as cf. *Cricetodon* sp.) needs to be described.
- cf. *Byzantinia* sp./div. sp. from Comăneşti 1 (Hír et al. 2011) is/are too poorly documented.

In conclusion, it has to be stressed that the lack of sufficient Cricetodontini material in the Central/East European Sarmatian s.str. and early Pannonian does not allow to precisely decide on the relationship of most of the finds. For the moment, the taxonomic position of "*C.*" *fandli* from Gratkorn as stated by Prieto et al. (2010b) is considered the most viable working hypothesis.

Megacricetodon minutus Daxner, 1967

Small-sized *Megacricetodon* species have been reported from a wide range of localities at the end of the Middle Miocene and the beginning of the Upper Miocene. Their taxonomy is often controversial (see Hír et al. 2011). Here, the proposal of Joniak (2005) is followed, who confirms the validity of *M. minutus*, a species defined on a few specimens from Brunn-Vösendorf (Daxner 1967). However, detailed study is needed to clarify the phylogeny of these forms. The main characteristics of the species from Gratkorn (Fig. 5e–j), apart from its size, are the anterolophulid being frequently not directly connected to the anteroconid in m1, as shown in Fig. 5g, and the forked anterolophule which connects to both cusps of the divided anterocone in M1. Several mandibles are known from Gratkorn: two mandibles with m1–m3 (UMJGP 204742; Fig. 5e; UMJGP 204194; Fig. 5f) and one mandible with m2–m3 (UMJGP 210799).

Fig. 5 Some rodents and insectivores from Gratkorn. **a**–**d**, **k**▶ *Democricetodon* sp. nov. (sensu Kälin and Engesser 2001). **a** Left maxillary fragment with M1 (UMJGP 211014). **b** Right M1 (UMJGP 211015). **c** Left m1 (UMJGP 204728). **d** Left m2 (UMJGP 211016). **k** Left mandible with i+m3 (UMJGP 204181). **e**–**j** *Megacricetodon minutus* Daxner 1967. **e** Left mandible with m1-m3 (UMJGP 204742) **f** Right mandible with m1-m3 (UMJGP204194). **g** Left m1(UMJGP 211017). **h** Left m2 (UMJGP 211018). **i** Right m3 (UMJGP 211019). **j** Left maxillary with M2 (UMJGP 211020). **l** *Eumyarion* sp.. Left M2 (UMJGP 211013). **m** *Spermophilinus bredai* (von Meyer, 1848), left m1,2 (UMJGP 211006). **n** *Keramidomys* sp., left m1,2 (UMJGP 211011). **s**, **t** *Schizogalerix voesendorfensis* (Rabeder, 1973). **s** Right D3 (UMJGP 204155). **t** Left damaged D3 (UMJGP 211021). **o**–**r** *Miodyromys* sp. **o** Left m1 (UMJGP 211007). **p** Right m1 (UMJGP 211008). **q** Left p4 (UMJGP 211009). **r** Right p4 (UMJGP 211010)

Democricetodon sp. nov. (sensu Kälin and Engesser 2001)

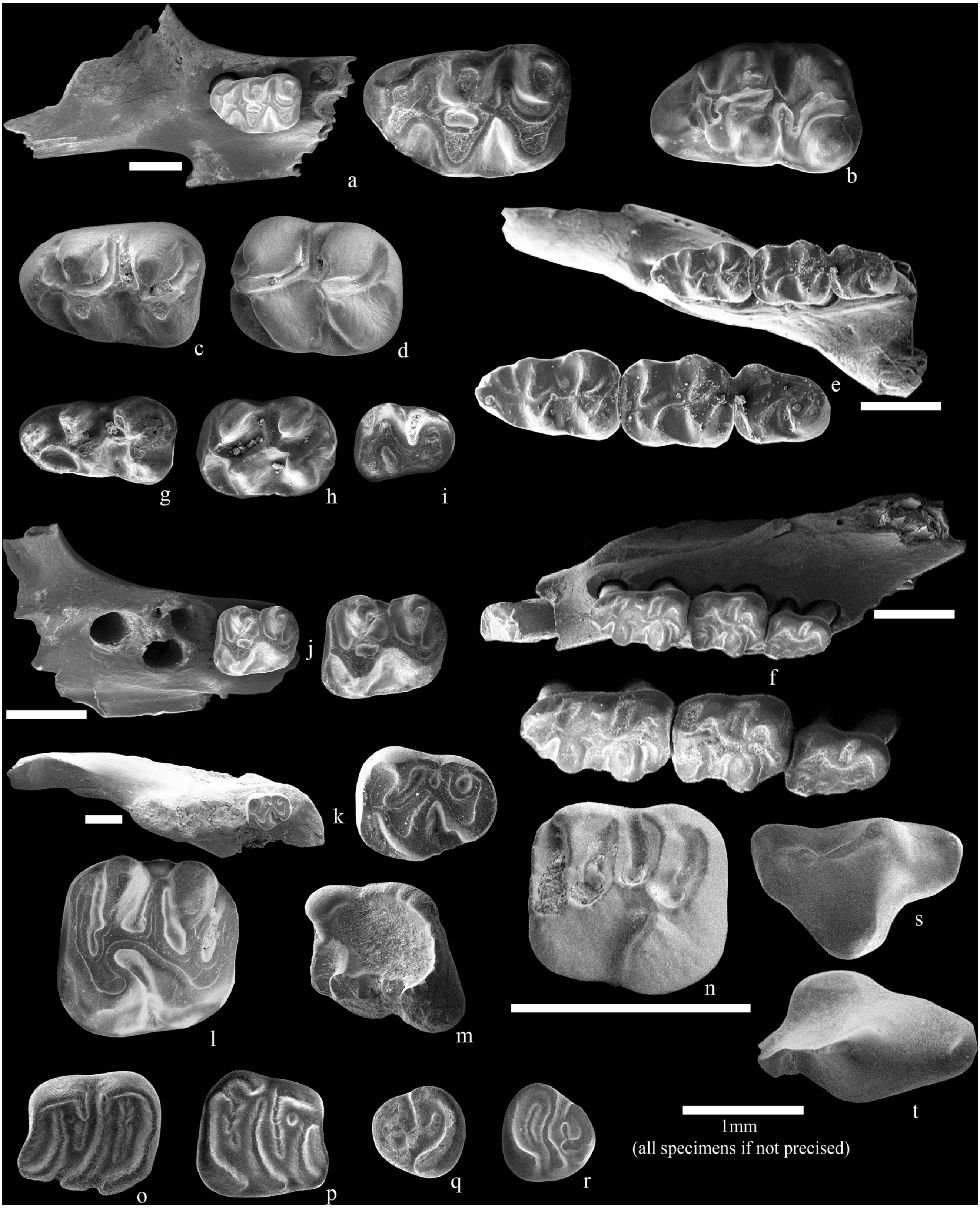
This species is related to the *Democricetodon* species found in Nebelbergweg (Switzerland, Middle/Late Miocene transition). Kälin and Engesser (2001) considered this to be a new form, but refrained from naming it, awaiting further investigation by G. Daxner-Höck.

The entire dentition has been previously described in Prieto et al. (2010b). The additional material, partially presented in Fig. 5a–d, confirms the taxonomic homogeneity of the *Democricetodon* sample (see also section "Semi-articulated specimens and proposed evidences of fossil pellets of birds of prey"). The main characteristics of the species are: its relatively small size, the M1 having an anterocone subdivided into two adjoining cusps by a superficial groove on its anterior wall and the presence of a low but long labial spur of the anterolophule on some specimens (present in the two figured M1); and a long mesolophid on the lower molars.

Eumyarion sp.

Additional material: UMJGP 204683: several associated remains of this species are preserved on a slab (Fig. 6c). These include a fragmentary maxillary with M1–M3 (M1: 1.98×1.36; M2: 1.45×1.41; M3: 1.11×1.22) which belongs to a relatively old specimen. It lies close to a tibia. The dental morphology is difficult to access, because the specimen has been covered by glue that obscures some details. Its study would require removing the glue without breaking the fragile specimen. An upper right incisor with part of the premaxilla (Fig. 6b) lies about 4.5 cm from this specimen. Some other pieces have been detached from the main block and prepared as such: UMJGP 204683/2: a fragmentary right mandible with i–m3 (m1: 1.97×1.22; m2: 1.56×1.31; m3: 1.43×1.16; Fig. 6a) and UMJGP 204683/3, a fragment of a left lower incisor.

Additionally, we have also recovered a left M2 (UMJGP 211013; Fig. 5l; 1.49×1.51)



Taxonomical note: Because of taxonomic ambiguities and the limited number of specimens, the species from Gratkorn could not be identified with confidence in previous works. The specimens added here, although

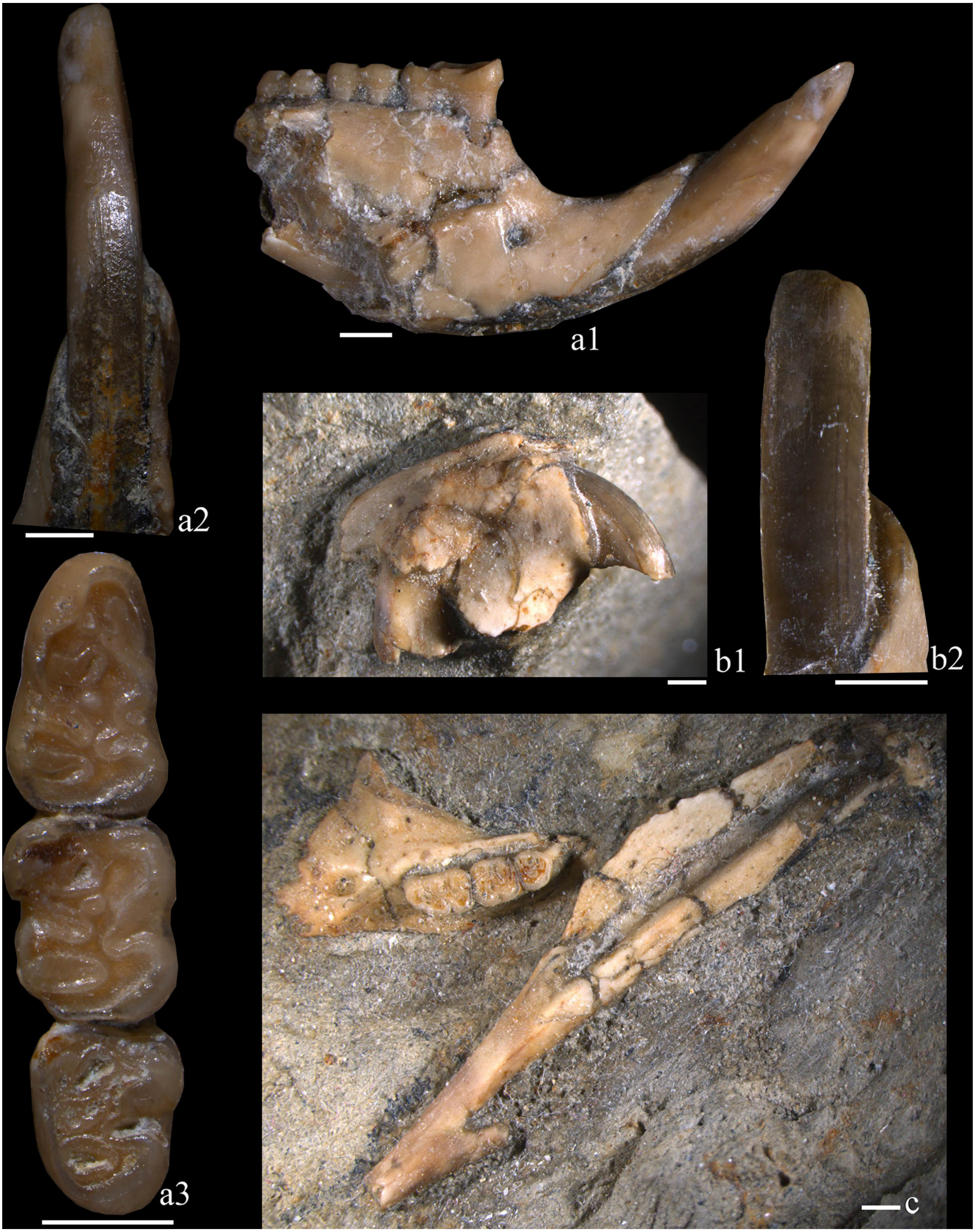


Fig. 6 *Eumyarion* sp. from Gratkorn (UMJGP 204.683). **a** Right fragmentary mandible with i–m3 **a1** labial view **a2** anterior view of the incisor **a3** occlusal view of the molar row. **b1** Upper right incisor with remains of corpus maxillae in sediment, **b2** Detail of the anterior part of the incisor. **c** Left fragmentary maxillary with M1–M3 and tibia

providing new morphological information, do not help any further. Interestingly, both lower and upper incisors are now assignable to *Eumyarion* sp.. The lower incisor is slightly damaged (Fig. 6a2), but two striae are observable on the anterior part of the enamel. Similarly, on the upper incisor (Fig. 6b2), two striae run along the enamel, but they are placed closer to the lateral margin of the incisor. Similar striae were also observed in *E. leemanni* from the Vallès-Penedès Basin (Casanovas-Vilar 2007).

Sciuridae

Spermophilinus bredai (von Meyer, 1848)

Note: Here, we follow De Bruijn and Bosma (2012) regarding the use of the genus *Spermophilinus*.

The previously described *Spermophilinus* tooth sample consisted of two d4 and one M3; its specific assignment was made on a dimensional basis. Only one m1,2 is added here (Fig. 5m; UMJGP 211006). The tooth belongs to a juvenile specimen (not completely erupted at the time of the death of the animal).

Blackia sp.

No additional material is reported herein.
The single tooth found from Gratkorn, a d4, shows the typical morphology of *Blackia*, but is very large in comparison to *B. miocaenica.*

Forsythia gaudryi (Gaillard, 1899)

No additional material is reported here.

The rare monospecific genus *Forsythia* is fortunately recorded by one mandible in Gratkorn. *Pliopetaurista* and *Forsythia* have very similar tooth patterns and differences are best shown in the upper dentition. However, the assignment of the Austrian specimen to this genus is based on characteristics of the lower tooth row provided by Daxner-Höck (2010: 515).

Albanensia albanensis (Major, 1893)

No additional dental material is reported here.
The fossils from Gratkorn, including mandibles, fragmentary skulls, and post-cranial material, are among the most complete published record available for the genus. Also*, A. sansaniensis* (Lartet, 1851) from the French locality Sansan is well documented, and a mandible, a maxillary and numerous isolated teeth have been described (Ginsburg and Mein 2012). *Albanensia* fossils are recognised in the literature as subspecies of *A. albanensis* (*A. a. quirensis*) are only known by scarce material from the Vallès-Penedès Basin (Catalonia, e.g. Mein 1970), and thus of questionable validity. *Albensia grimmi*, originally only known from its holotype (found at the Middle Miocene German locality Marktl), is now recorded by dozens of teeth from various Pannonian localities, also including sites from Austria (Daxner-Höck 2004a) and Hungary (Kretzoi and Fejfar 2004). The descriptions of the cranial and post-cranial material, together with comparisons to fossil and extant flying squirrels, will be published separately.

Gliridae

Muscardinus aff. *sansaniensis* (Lartet, 1851)

No additional material is reported here.
The small tooth sample from Gratkorn (three specimens) is considered to belong to a relative advanced (large) species in the lineage *Muscardinus sansaniensis*–*M. vallesiensis* (Daxner-Höck 2010)

Miodyromys sp.

Additional material: Left m1 (UMJGP 211007; 1.09×1.03), right m1 (UMJGP 211008; 1.08×1.05), left p4 (UMJGP 211009; 0.77×0.77), right p4 (UMJGP 211010; 0.78×0.83); see Fig. 5o–r.

The scare material did not allow Daxner-Höck (2010) to provide any assignment at the species level. Although new dental elements are now available (p4 and m1), a definite identification of the species is still hazardous. Compared to the previously published m2, the two lower molars presented here are a bit more complicated because they both have a very short extra ridge between metalophid and centrolophid. The connection mesolophid/entoconid is interrupted in one m1. In the same specimen, the posterotropid connects to the posterolophid. The two p4 have five transversal crests.

Eomyidae

Keramidomys sp.

Previously, a d4 and a m3 have been described from Gratkorn. The m1,2 (UMJGP 211011; Fig. 5n; 0.84× 0.81) presented here has five long transversal lophids and a continuous longitudinal crest. The crest-like entoconid is directed forwards, and the posterolophid ends shortly before it. Daxner-Höck (2010) places the species near to *K. mohleri* or *K. ermanorum.* Unfortunately, the new molar cannot lead to a more precise taxonomic assignment.

Castoridae

Euroxenomys minutus minutus (von Meyer, 1848)

This small-sized beaver is known from a few specimens, including a fragmentary skull with the two associated mandibles in almost anatomic connection that have recently been excavated. This exceptional find is described in Prieto et al. (2014, this issue). *Euroxenomys minutus* is a common element of the Badenian-Pannonian fauna in Austria.

Lagomorpha

Ochotonidae

The pika remains are described by Prieto et al. (2012b) and Angelone et al. (2014, this issue).

Prolagus oeningensis (König, 1825)

This species is the most abundant pika in Gratkorn, and upper and lower jaws have been excavated in the locality. It shows more primitive characters than western and central–western European populations of *P. oeningensis.*

cf. *Eurolagus fontannesi* (Depéret, 1887)

The remains consist of isolated teeth and an upper jaw. This rooted ochotonid is very similar but does not completely fit the morphometric characteristics of *E. fontannesi* (Angelone et al. 2014, this issue). Indeed, the taxonomical status and the phylogeny of the Middle and Late Miocene rooted ochotonids are in need of revision. Pending such a revision, our identification is somewhat tentative.

Ochotonidae indet.

Only two isolated upper molariforms are available from Gratkorn. This ochotonid is characterised by its large size, and ever-growing robust teeth. To our knowledge, nothing equivalent has ever been previously recorded in Europe.

Biostratigraphical remarks

Arrangement of the localities provided in Tables 1, 2, 3 and 4

The tables summarise the small mammal fossil record of various Central–Eastern European localities which are chronologically close to Gratkorn. The relative order of the localities, between and even within basins, is partly unresolved. Therefore, the ordering proposed here should be regarded as a working hypothesis; future work in those sites may change the relative age of the sites.

Pannonian localities of the Vienna and Styrian basins

The Pannonian localities of the Vienna and Styrian basins are ordered following the division of Papp (1951). The relative positions of, respectively, Vösendorf/Borský Sv. Jur, Atzelsdorf/Gaweinstal, and Bullendorf/Mataschen are arbitrary. The stratigraphic position of Magersdorf is uncertain.

North Alpine Foreland Basin (NAFB)

The mammal localities of the NAFB are not directly correlated to the Central/Eastern Parathethys subdivision. Hillenloh, Nebelbergweg, Nebelberg TGL III and Hammerschmiede 1–3 are traditionally correlated to MN 9, but this is not satisfactory for our purposes, because it cannot be clearly demonstrated at present if these localities are equivalent to Sarmatian s.str. or to Pannonian (see below). Moreover, in the MN system (e.g. Mein 1999), MN 9 is characterised by the entrance of the hipparionine horses, which provides a problem for localities of small mammals in which no large mammal remains have been found (Prieto et al. 2011). Therefore, we assigned these localities in our tables to the 'Middle to Late Miocene transition'.

Giggenhausen and Anwil belong to the *Deperetomys hagni* taxon range zone of the Swiss local biozonation (Kälin and Kempf 2009), which ranges from 13.8 to 13.2 My (equivalent Badenian).

Late Sarmatian s.str. localities

The ordering of the succession of the Felsőtárkány localities (Hungary) follows the proposal of Hír and Kókay (2010). Some mammal taxa are considered important stratigraphic markers.

First of all, *Microtocricetus molassicus* was often used as typical species of the MN 9. This would imply that the localities containing this species correlate with Pannonian deposits. This was, however, challenged by Prieto and Rummel (2009) and Prieto et al. (2011) based on a cricetid rodent lineage and the migration of a gymnure (see below). Arranging the localities from the NAFB and Hungary using *Microtocricetus* leads to placing Nebelbergweg and Nebelberg TGL III below the first occurrence of the species (in Hungary, Felsőtárkány 3/8), near to Felsőtárkány 3/2. This proposal is in apparent conflict with the occurrences of the eomyid rodents *Eomyops catalaunicus* (Late Miocene species; Daxner-Höck and Höck 2009) in Nebelbergweg and *E. oppligeri* (Middle Miocene species) in Felsőtárkány 3/8, for instance. Originally, both species of *Eomyops* were recognised in the Swiss locality (Kälin and

Table 2 Small mammal composition of selected fossil localities surrounding geographically and stratigraphically Gratkorn

	Anomalomys gaudryi	*Anomalomys gaillardi*	*Anomalomys rudabanyensis*	Anomalomys sp. 2	Anomalomys sp.	*Neocometes brunonis*	*Microdyromys complicatus*	*Microdyromys koenigswaldi*	*Microdyromys* sp.	***Miodyromys* sp.**	*Miodyromys hamadryas*	*Miodyromys aegercii*	*Miodyromys grycivensis*	***Muscardinus sansaniensis***	*Muscardinus hispanicus*	*Muscardinus vallesiensis*	*Muscardinus* sp.	*Glirudinus gracilis*
1		cf.,4,11													cf.,11	40		
2					4,11													
3															49			
4																		
5															40			
6			cf.,25															
7	11																	
8																		
9																		
10																		
11			cf.,4,55		x													
12	15																15	
13	15																	
14	4, 39						39								40			
15	3,50								50						50			
16	8													8,aff.			8	
17		aff.,27							27			27^{5}					27	
18									34									
19	4^{42},55																	
20																		
21																		
22				14			14											
23	9										9						9	
24	9						9										9	
25															45			
26													aff.,45					
27										**20**				**aff.,20**				
28																		
29																		
30														aff.,57				
31														57				
32	10																	
33														aff., 10				
34	45																	
35	33						33,41^{46}	cf.,33				41		aff.,33,41				
36	29					29	29	cf.,29			29^{8}	29^{11}		aff.,29			29	cf.,29

	Glirulus lissiensis	*Glirulus conjunctus*	*Glirulus* sp.	*Paraglirulus werenfelsi*	cf*Paraglirulus werenfelsi*	*Bransatoglis astarensis*	Gliridae gen. et sp. indet.	*Bransatoglis* sp. ?	*Eliomys truci*	*Eliomys reductus*	*Eliomys assimils*	*Myoglis meini*	*Myoglis ucrainicus*	*Glis vallesiensis*	*Glis* sp.	Glirinae gen. et sp. indet.	Gliridae indet.
1				11									40		11	40	
2																	
3	cf.,49						49										
4																	
5																	
6																	
7																	
8																	
9																	
10																	
11							x										
12				15								15		15			
13	cf., 15			15													
14		4								41	41	39^{13}					
15	50			50		50								50			
16			8	8, aff.								8					
17				27	27	cf.,27											
18																	
19																	54^{32}
20																	
21	14																
22				14								14					
23												9					
24												9					
25	45		45										45				
26																	
27																	
28									?sp.,56								
29																	
30	57			57								57					
31												57					
32																	
33				sp., 10^{41}				10									
34																	
35		41		33,41								33,41					
36	cf.,29			29		29^{12}						29^{13}					

Table 3 Small mammal composition of selected fossil localities surrounding geographically and stratigraphically Gratkorn

	Spermophilinus bredai	*Palaeosciurus ultimus*	*Blackia miocaenica*	*Hylopetes* sp.	*Neopetes hoeckarum*	*Neopetes* sp.	*Pliopetes* sp.	***Blackia* sp.**	***Forsythia gaudryi***	*Albanensia grimmi*	***Albanensia albanensis***	cf. *Albanensia albanensis*	*Albanensia a. quirensis*	*Miopetaurista gaillardi*	*Albanensia* sp.	Pteromyinae indet.	Sciuridae indet.	*Eomyops oppligeri*	*Eomyops catalaunicus*	*Eomyop* sp. nov.s	*Keramidomys mohleri*	*Keramidomys anwilensis*	*Keramidomys pertesunatoi*	*Keramidomys* sp. nov.	***Keramidomys* sp.**	*Eozapus* sp.	Castoridae	***Euroxenomys minutus***	*Chalicomys jaegerci*	*Steneofiber eseri*	*Steneofiber* sp.	*Castor* sp.	*Lagopsis verus*	***Prolagus oeningensis***	***Eurolagus fontannesi*** [D] **and rooted ochotonids**	**Ochotonidae indet. (large)**	*Parasorex socialis*	**Galericinae gen. et sp. indet.**	***Schizogalerix voesendorfensis***	***Schizogalerix pasalarensis***	*Schizogalerix* sp. nov.	*Schizogalerix* sp.	*Galerix exilis*
1	11		24	?sp.,11						11				sp.,11					11							11		11				11											
2																												11											13				
3	49																		49						49			49			49			sp.,49								49	
4																												46			46				47								
5																																											
6																												25						25	25								
7																																						38					
8																																										36	
9																												26															
10										24																																	
11																			28															x	x								
12						15												15			15							15							15				x				
13																		15																	15				x				
14	39									20									28						x			42	42					x	39								cf.,36
15																		50		50				50											52								
16	8,16		8	8						8								8			8							8											x				
17	27		27							24									28[4]									sp.,27						27	27				27		27		
18																	34		aff.,34						?34[37]									34									
19																							?,54[28]					42	42	42													
20											53[26]																		?,42						53								
21																14					cf., 14														14				x				
22	14																	14			cf., 14																		x				
23	9		9												9			9							9			9						9					x				
24	9		9																						9			9						9					x				
25	45		45		45									sp.,45	?45			45																									
26																																					58[35]						
27	**20**							**20**	**20**		**20**														**20**			**21**						**22,23**	**cf., 23**	**23**		**19**	**19**				
28	56																																							cf.,56			
29																																											
30	57		57													57																											
31																																			57								
32	10																																		10				cf.,x				
33																		10			10														10				cf.,x				
34	45		45												45																								cf.,x				
35	33		33						33		33	33						33			33														33		33						
36	29		29				34[14]		29		29			29				30			29	29						29[7]					29	29	29		29						

Table 4 Small mammal composition of selected fossil localities surrounding geographically and stratigraphically Gratkorn

	Lanthanotherium sansaniense	*Lanthanotherium sanmigueli*	*Mioechinus oeningensis*	*Amphechinus* sp.	*Atelerix depereti*	Erinaceidae indet.	*Metacordylodon schlosseri*	*Chainodus* sp.	*Plesiodimylus chantrei*	*Plesiodimylus johanni*	*Plesiodimylus* sp.	cf. *Crusafontina* sp.	*Crusafontina exalta*	*Crusafontina endemica*	cf. *Paenelimnoecus* sp.[c]	*Paenelimnoecus repenningi*	*Paenelimnoecus* sp.	*Paenesorex* sp.	*Dinosorex pachygnathus*	*Dinosorex* sp. nov.	*Dinosorex zapfei*	*Dinosorex engesseri*	***Dinosorex* sp.**	Soricidae gen. et sp. indet.	*Desmanodon crocheti*	***Desmanodon fluegeli***	*Archaeodesmana vinea*	*Archaeodesmana* sp.	Desmaninae indet.	*Desmanella stehlini*	*Desmanella rietscheli*	*Desmanella* sp.
1		38			cf.?,38				aff.,38					aff.,38								38		38			cf.,38				38	
2																							13[21]									
3																							49[22]									
4																																
5																																
6									cf.,25				25			25												cf.,25				
7												38																				
8																																
9																																
10																																
11							cf.,x			x			35																			
12													cf.,x											x								x
13																																
14							sp.,x			x			35[17]					?x		x												
15								cf.,,51	51			51											51							cf.,51		
16													cf.,x										x	x								x
17										27										27[3]									27			27
18																																
19																																
20							53																									
21																								x								
22											x												x									
23											x												x	x								x
24													cf.,x				x						x									x
25	sp.,58			58																				58								
26																																
27																							**19**			**19**						
28																																
29																							48[40]									
30																																
31																																
32						x	cf.,x				?,x													x								
33											?,x							?,x														
34																		?,x														
35												33			33[20]			33	33					33	44					33		
36	29		34				29		29			6,7,35[10]						?33[9]	29											29		

	Gehardstorchia quinquecuspid	*Gehardstorchia biradicata*	*Scaptonyx edwardsi*	*Proscapanus sansaniensis*	*Proscapanus* sp.	*Talpa minuta*	*Talpa gilothi*	*Urotrichus giganteus*	Talpidae indet.	*Plesiosorex schaffneri*	*Plesiosorex evolutus*	**cf. *Myotis* sp.**	Chiroptera div. sp.
1		38					cf.,38	38			38		
2													
3									49				
4													
5													
6													
7													
8													
9													
10													
11									x				
12					x	sp.,x							
13					x	?,x			x				
14	38[16]									38			x
15						cf.,51			51				
16					x	sp.,x			x				
17				27		27							27
18													
19													
20						53							
21									x				
22					x								
23					x				x				
24					?,x	sp.,x							
25													
26									58				
27												**19**	
28													
29													
30													
31													
32									x				x
33						cf.,x			x				x
34									x				x
35			33						33				
36			29	29		29				29			29

1 Fejfar 1999
2 Kowalski 1993
3 Kowalski 1994
4 Bolliger 1996
5 Hír and Meszaros 2002
6 Van Dam 2004
7 Van Dam 2010
8 Hír 2004
9 Hír 2006
10 Hír & Kókay 2004
11 Daxner-Höck 1996
12 Hír 2005
13 Kordos 2005
14 Hír & Kókay 2009
15 Hír & Kókay 2010
16 Hír & Pászti 2012
17 Jung and Mayr 1980
18 Prieto et al. 2010 b
19 Prieto et al. 2010 a
20 Daxner-Höck 2010
21 Prieto et al. 2014, this issue
22 Prieto et al. 2012b
23 Angelone et al. 2014, this issue
24 Daxner-Höck 2004a
25 Harzhauser et al. 2011
26 Daxner-Höck 2004b
27 Kälin and Engesser 2001
28 Prieto 2012
29 Engesser 1972
30 Engesser 1990
31 Aguilar 1980
32 de Bruijn et al. 1993
33 Prieto 2007
34 Kälin and Kempf 2009
35 Prieto and van Dam 2012
36 Prieto et al. 2011
37 Prieto and Rummel 2009
38 Ziegler 2006b
39 Mayr and Fahlbusch 1975
40 Daxner-Höck and Höck 2009
41 Mayr 1979
42 Hugueney 1999
43 Fahlbusch 1964
44 Prieto 2010
45 Hír and Kókay 2011
45 Hír et al. 2011
46 Daxner-Höck and Bernor 2009
47 Angelone 2009
48 Codrea and Ţibuleac 1999
49 Joniak 2005
50 Garapich 2002
51 Rzebik-Kowalska 2005b
52 Fostowicz-Frelik et al. 2012
53 Wegner 1913
54 Kowalski 1967
55 Bolliger 1999
56 Hír et al. 2001
57 Hír and Venczel 2005
58 Rzebik-Kowalska 2005a

Table 5 Synopsis of the small-mammals from Gratkorn

	Screen-washing	Surface sampling	Abundance (based on screen washing)	Type of fossils	Ecology	Corrosion	Presence in pellets	accumulation agent
Schizogalerix voesendorfensis	x	x	most commun taxon	Isolated teeth, skull fragment, mandibles Probably post-cranial to be determinate	not clear	not or slightly corroded: 89%	yes	Mostly nocturnal raptor
Galericinae gen. et sp. indet.	x		1 tooth	Isolated tooth	not clear	strong (1 tooth)	no	Predator indet.
Desmanodon fluegeli	x	x	rare	Isolated teeth, mandibles, post-cranial (humeri)	not clear, not fossorial specialist	not or slightly corroded: 83%	no	Mostly nocturnal raptor
Dinosorex sp.	x	x	very rare	Isolated teeth, mandibles	not clear	none to rarely moderate	no	Noctural raptor?
cf. *Myotis* sp.	x		very rare	Isolated teeth	not clear	none	no	Not clear
"Cricetodon" *fandli*	x	x	commun	Isolated teeth, skulls, mandibles and post-cranial	open habitat, abrasive food	not or slightly corroded: 74%	yes	Mostly nocturnal raptor
Megacricetodon minutus	x	x	commun	Isolated teeth, mandibles Probably post-cranial to be determinate	ubiquist?	not or slightly corroded: 74%	yes	Mostly nocturnal raptor
Democricetodon sp. nov.	x	x	commun	Isolated teeth, mandibles Probably post-cranial to be determinate	forest-dweller?	not or slightly corroded: 90%	yes	Mostly nocturnal raptor
Eumyarion sp.	x	x	rare	Isolated teeth, mandibles Probably post-cranial to be determinate	humid and forested environments?	Data strongly biassed because of the presence of palate and mandible and few isolated teeth	yes	Mostly nocturnal raptor
Spermophilinus bredai	x		very rare	Isolated teeth	open habitat	none	no	Not clear
Blackia sp.	x		1 tooth	Isolated tooth	forest-dweller?	none	no	Not clear
Forsythia gaudryi		x	-	Mandible	forest-dweller?	none	no	Not clear
Albanensia albanensis		x	-	skull fragment, mandibles, post-cranial	forest-dweller	none	no	Other taphonomy?
Muscardinus aff. *sansaniensis*	x		very rare	Isolated tooth	forest-dweller?	none	no	Not clear
Miodyromys sp.	x		rare	Isolated teeth, upper jaw	open habitat?	none	no	Not clear
Keramidomys sp.	x		very rare	Isolated teeth	not clear	none	no	Not clear
Euroxenomys minutus minutus		x	-	skull fragment, upper jaws, mandibles (as isolated teeth)	agile when moving on the ground	to be studied	no	Other taphonomy
Prolagus oeningensis	x	x	commun	Isolated teeth, upper jaws and mandibles Probably post-cranial to be determinate	not clear	none	no	Not clear
cf. *Eurolagus fontannesi*	x	x	rare	Isolated teeth, upper jaws and mandibles	forest-dweller, browser	none	no	Not clear
Ochotonidae indet.	x		2 teeth	isolated teeth	not clear	none	no	Not clear

Engesser 2001). However, Prieto (2012) considered the sample as monospecific, with a relatively large intra-specific variability. Actually, it cannot be ascertained that the material from Nebelbergweg and Felsőtárkány 3/2 would represent different species. Because the intraspecific variability of *Eomyops* is accessible only in few localities, and with the lack of general recognition of the taxonomic homogeneity of the genus in Nebelbergweg, it is better not to use the genus here for fine biostratigraphic purposes.

Finally, Prieto and Rummel (2009) proposed a biostratigraphical sequence based on the size increase of the cricetid rodent *Collimys*. These authors recognise a lineage *C. hiri* (Hammerschmiede)–*C. longidens* (Nebelbergweg)–*C. dobosi* (e.g. Felsőtárkány 3/2). While clear differences are observed between *C. hiri* and *C. dobosi* from Hillenloh, *C. longidens* and *C. dobosi* (Hungary) show a larger intraspecific variability, and both species differ only slightly in size and morphology. Arranging Hammerschmiede at the basis of this lineage implies that this locality is older than Felsőtárkány 1, 2, 2/3 and 2/7, which do not contain *Microtocricetus*. This arrangement could evidently be discussed but the following points restrain us: (1) the value of the lineage *C. hiri*–*C. dobosi* is in need of confirmation, because regional variation cannot be ruled out, and (2) the appearance of *Microtocricetus* in a restricted area is documented in the Felsőtárkány Basin.

In short, based on small mammals only, different approaches result in different arrangements of the late Sarmatian localities, and in our current state of knowledge, the stratigraphical sequence is unresolved. Moreover, it cannot be excluded that a part of the localities from the NAFB belong to the base of the Pannonian. Also, Felsőtárkány 3/8 and 3/10 could belong to the base of the Pannonian (Pannon A or B) (Hír and Kókay 2010). It has been chosen here: (1) to correlate these localities to the Sarmatian s.str., mainly because of the presence of Sarmatian molluscs in Felsőtárkány 3/8 and 3/10; and (2) to arrange the localities with *Microtocricetus* together. In order to provide a better arrangement in the tables, Bełchatów A is included in this group (association *Microtocricetus* + *Collimys*), as well as Opole 1 and 2, based on the presence of *Collimys* as proposed by Prieto and Rummel (2009).

The late Volhynian/Bessarabian localities Tauț and Comăneşti 1 correlate with the central Parathethys stages to the late Sarmatian s.str. (Harzhauser and Piller 2007), and are thus slightly younger than Gratkorn.

Early Sarmatian s.str.

Tăşad belongs to the *Mohrensternia* Zone of the early Sarmatian s.str. The exact correlation of the faunas from Subpiatră is not clear in this scheme, and they are here placed at the Badenian/Sarmatian s.str. transition

Biostratigraphic position of Gratkorn based on small mammals

For the integrative studies dealing with the dating of the locality, we refer to Harzhauser et al. (2008) and Gross et al. (2011).

Considering the small mammals, the following taxa, either because of their long stratigraphic range or taxonomic incertitude, provide little information for our purpose:

Galericinae gen. et sp. indet., *Dinosorex* sp., cf. *Myotis* sp., *Eumyarion* sp. *Miodyromys* sp., *Keramidomys* sp., *Spermophilinus bredai, Blackia* sp., *Forsythia gaudryi, Euroxenomys minutus minutus,Prolagus oeningensis*, Ochotonidae indet.

The genus *Eurolagus* was thought to be a marker of MN7+8, but recent studies bring the temporal range of *Eurolagus* into question, and thus its value as a marker (Angelone et al. 2014, this issue and references therein). For the moment, we prefer not to use cf. *Eurolagus fontannesi* for fine biostratigraphical purposes.

Similarly, *Desmanodon fluegeli* cannot be integrated in the Anatolian lineage *D. minor*–*D. major* without reservations, and the use of the taxon for correlation purposes is limited. According to Prieto et al. (2010a), Gratkorn represents the first occurrence of *Schizogalerix voesendorfensis*. New investigations (Table 3) indicate that a related form might be present in the late Badenian of Hungary. Recent advances in the study of the late Middle Miocene fissure fillings from Petersbuch (J. Prieto, personal data) suggest the presence of the genus in Germany. These new discoveries show that the galericine record is even more complicated than indicated by Prieto et al. (2011) in their discussion of this record in the NAFB.

Democricetodon sp. nov. (sensu Kälin and Engesser 2001): *Democricetodon brevis* and *Megacricetodon germanicus* from Felsőtárkány 2/3 and 2/7 (Hír 2006: plate II, figs. 5, ?6, 10 and 21) are most probably related to this form and are listed as *Democricetodon* cf. sp. nov. in Table 1. The same observation can be made for Tăşad. In Subpiatră, the specimens assigned to *Democricetodon freisingensis* and *D. brevis* by Hír and Venczel (2005) share some characteristics with this form, but any conclusion is hazardous at the present state of knowledge. *Democricetodon zarandicus* resembles the Nebelbergweg *Democricetodon* in many points (Hír et al. 2011), and might possibly be closely related to this form, as well as *Democricetodon* sp. from Felsőtárkány 1 and 2. Even though we cannot name the species, it is clear that the morphospecies from Gratkorn is a common faunal element of the Sarmatian s.str.

Among the Gliridae and the Sciuridae, Daxner-Höck (2010) considers *Muscardinus* aff. *sansaniensis*, *Albanensia albanensis* and *Forsythia gaudryi* to be good biostratigraphic markers. Based on the evolutionary stage of *Muscardinus*, she concludes that Gratkorn is somewhat younger than La Grive and Anwil, and about the same age as Giggenhausen and Kleineisenbach (NAFB, Germany). Here, part of this proposal cannot be followed because, as stated above, the Swiss and German localities are close in age (e.g. Prieto 2007), and most probably even Badenian. A revision of the *Muscardinus* material listed in Table 2 is of interest to better understand the evolution of the taxon. Gratkorn most probably shows one of the last records of *Albanensia albanensis* and *Forsythia gaudryi* in the studied area.

On the other hand, Gratkorn records one of the earlier *Megacricetodon minutus* for Central/Central–East Europe, although we must acknowledge that the taxonomic identity is quite ambiguous. As underlined by Prieto et al. (2010b: 428), interesting forms of *Megacricetodon* that probably share morphologic characteristics with *M. minutus* are documented earlier in Anatolia. For instance, De Bruijn et al. (2012) figure fossil material from Zambal and Bağili which deserves comparison with the Austrian specimens (figures are printed erroneously in chapter 25 of Wang et al. 2012).

Considering these localities, the figured Cricetodontini, especially *Cricetodon* cf. *pasalarensis*, are of interest for our purpose. As stated above, the lineage “*C.*” *fandli*–“*C.*” *klarankiae* as proposed by Prieto et al. (2010b) is a working hypothesis which permits to relatively date Gratkorn, but has to be confirmed by further finds, and by the study of its relationship with, for instance, Anatolian forms.

In short, the small mammal fauna does not contradict the conclusions provided by the integrative studies available for Gratkorn. While a correlation to the early late Sarmatian s.str. can be justified, it has to be stressed that the lack of sufficient knowledge regarding the evolution of the fauna in Sarmatian s. str. in Central Europe makes it difficult to definitively demonstrate this correlation based on rodents and insectivores.

Origins of the small mammal accumulation and indirect evidence of the rodent activity

Prieto et al. (2010b) and Gross et al. (2011) discussed the origin of a few dozen of small mammals and ectothermic vertebrate remains (skulls, jaws, extremities) discovered in the upper part of the palaeosol from Gratkorn, and concluded that it represents an accumulation of fossil owl pellets, at least in part. This type of accumulation is well known for fissure and cave infillings, where thousands of remains can be accumulated in a very short period (e.g. Mellet 1974; Andrews 1990; Kowalski 1990). For instance, the potential of bone accumulation by raptors is illustrated by Guérin (1928) who showed that *Tyto alba* can accumulate around 1,200 small vertebrates in 6 weeks. In the case of flood plain sediments, the picture might be more complicated because of time averaging and the multiple sources of the fossil remains that may ultimately define the accumulation.

Fig. 7 Examples of moderate to strongly corroded “*Cricetodon*” *fandli* ▶ Prieto, Böhme and Gross, 2010. **a** Moderate corroded right m1 (UMJGP 211022) showing marks preferentially on its labial side. **b** Moderate corroded left M1 (UMJGP 211023) with lingual part free of marks. **c** Moderate and occlusaly corroded right m2 (UMJGP 211024). **d** Strongly damaged right M1 (UMJGP 211025)

A detailed taphonomic study of Gratkorn would require a separate paper, but as an understanding of the origin of the thanatocoenosis is vital for any palaeoenvironmental reconstruction, some indicative data follow.

Corrosion on small mammals teeth

The presence/absence and amount of corrosion are used, among other evidence, as proxies to determine potential predators (e.g. Andrews 1990; Fernández-Jalvo and Andrew 1992; Fernández-Jalvo et al. 1998; Laudet 2000). The intensity of the corrosion on bone and especially teeth, the frequency of the damage and the relative abundance of skeletal elements allow the recognition of damage categories, ranging from predators that induce little damage (e.g. *Tyto alba*) to predators in which the digestion violently disturbs the remains (e.g. Carnivora).

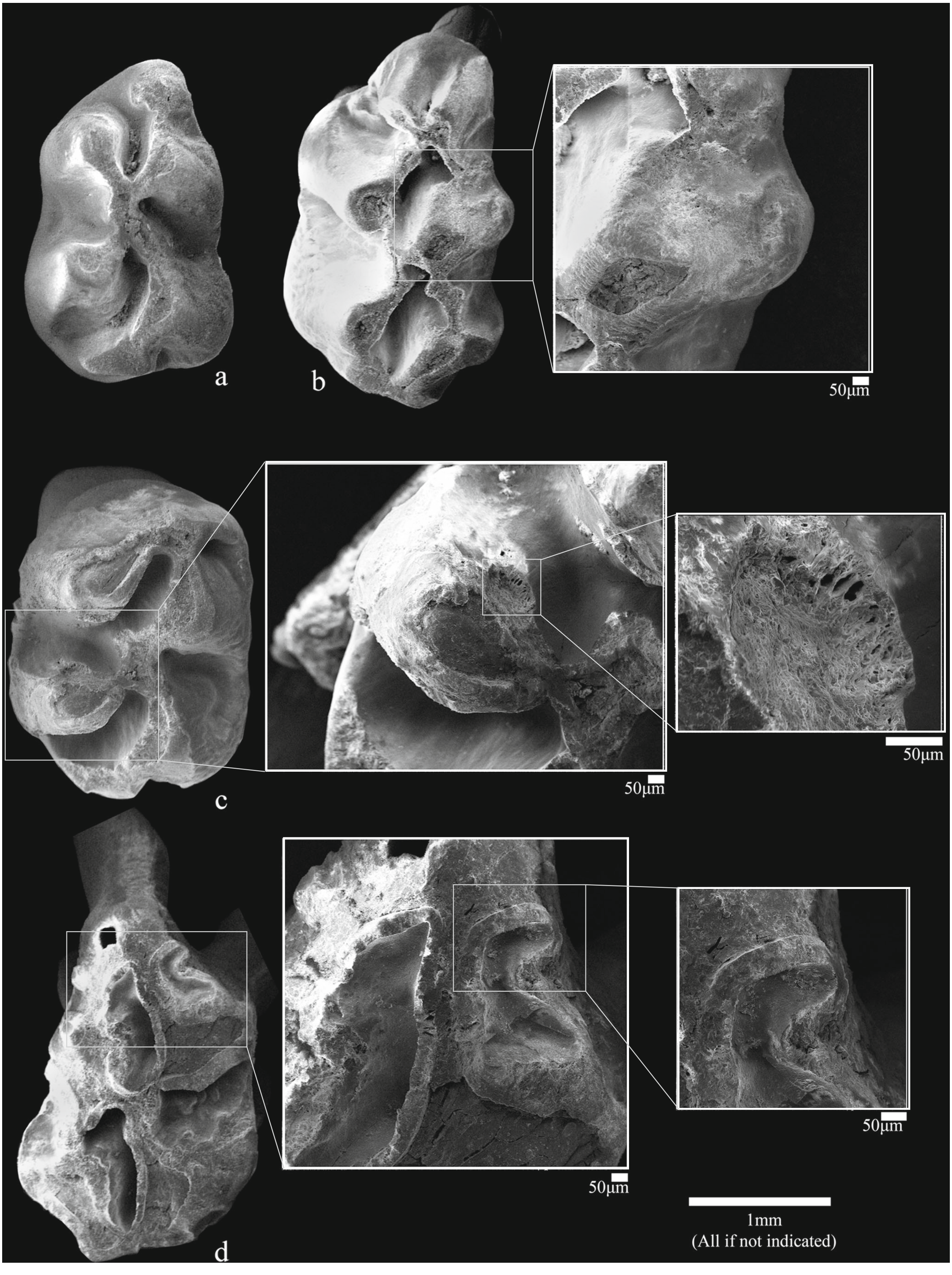
Corrosion on molars and premolars has been scored here in four categories (absent, light, moderate and strong) in order to get a general idea of the trend of corrosion in the sample. The moderate and strong grades are presented in Figs. 7a–c, and d, respectively. Light grade indicates that marks are observed that only superficially attack the enamel.

Chiropteran teeth do not show any corrosion traces, and the same goes for the teeth of the Gliridae, Sciuridae and Eomyidae. The single M1 of the Galericinae gen. et sp. indet. shows relatively strong spurs (Prieto et al. 2010a: fig. 2k). Among the *Dinosorex* sp. teeth, only the isolated P4 is damaged, but clearly less than the former erinaceid molar (Prieto et al. 2010a: fig. 2l). The skull of the small-sized beaver *Euroxenomys minutus minutus* does not show corrosion that can be assigned to the effect of predation. In the second individual recorded in Gratkorn (Prieto et al. 2014, this issue), the damage deserves a more in-depth analysis.

The molars conserved in situ in the partial skull of *Eumyarion* sp. are slightly corroded (Prieto et al. 2010b: fig. 4). Minor damage is also observed on the enamel of the incisor of the mandible in Fig. 6a1, a2.

Much more material is available for the each of the other taxa. The corrosion grade can be different in each teeth of a single jaw, and therefore we consider each teeth independently.

Most specimens are not or only slightly corroded: 83 % in *Desmanodon fluegeli* (22 teeth observed), 74 % in *Megacricetodon minutus* (34 teeth), 90 % in


a
b
50µm
c
50µm
50µm
d
50µm
50µm
1mm
(All if not indicated)

Democricetodon sp. nov. (21 teeth), 74 % in "*Cricetodon*" *fandli* (42 teeth), and 89 % in *Schizogalerix voesendorfensis* (91 teeth). We did not see any digestion marks on pikas.

The rare species cannot provide a clear idea on the potential predator(s).

Most commonly, the fossils are either not or little corroded. It would indicate that the accumulation is mostly due to the action of night-active birds of prey (which have less aggressive gastral fluids than their diurnal counterparts; e.g. Andrews 1990), or/and natural death.

In addition, it is interesting to notice that the gastric juice damages the specimens in different ways. While most of the teeth are corroded on their occlusal surface (e.g. Figs. 7c, d), a representative part of the sample shows marks preferentially on the labial part (e.g. Figs. 7a, b) indicating that the lingual side was protected from the juice. This effect would result from the ingurgitation of complete skull with mandibles by the predators, and thus a reinforced protection of the lingual area (Andrews 1990; Casanovas-Vilar et al. 2008a).

In conclusion, a large part of the sample seems to have been accumulated by nocturnal raptors which produce little corrosion on the cheek teeth, as is the case for *Tyto alba* or *Asio otus* in the recent fauna. The most corroded specimens might have been provided by predators which induce moderate to strong dissolution of the dental parts, as occurs with *Bubo bubo* or *Athene noctua*, for instance. The rare extreme strong corrosion may also be the result of digestion by mammal predators, diurnal raptors or others.

This proposal excludes, because of their size, the beaver specimens. The remains of the large-sized *Albanensia albanensis*—skulls, mandibles, and post-cranial of several individuals—taxa were excavated from a very restricted area, and no additional finds have been recovered elsewhere in the fossil-enriched layer(s) since then. This might indicate a different cause for the fossil accumulation. Flying squirrels might be victims of raptors (e.g. Airapetyants and Fokin 2003), but *Albanensia* is a large species, which would require a different agent of accumulation than the small rodents and insectivores. Potential predators of large size have been reported in recent fauna, as for instance by Fan and Jiang (2009), who report black-crested gibbons attacking large *Petaurista* in China or in Taiwan, where the most common prey of the mountain hawk-eagle might be the giant flying squirrel *Petaurista philipensis* (Sun et al. 2009).

Semi-articulated specimens and proposed evidences of fossil pellets of birds of prey

Evidence of intact fossil pellets is, because of their fragility, extremely rare to our knowledge. For instance, Meng and Wyss (1997) tentatively recognise such fossils from the Late Paleogene beds from Inner Mongolia.

Transport, even across small distances disintegrates the fragile rejecta and leads to the dispersal of the bony remains (e.g. Terry 2004). However, bone concentrations of only a few individuals have been recovered and interpreted as such (e.g. Czaplewski 2011). Semi-articulated and exceptionally well-preserved specimens are also supposed to derive from such regurgitates (e.g. Tobien 1977; Kälin 1993).

In the following, we list bone accumulations from a very restricted area (few cm^2), which are prepared in such a way that at least part of the original bone arrangement is conserved.

UMJGP 204700/1 (Fig. 8)

"*Cricetodon*" *fandli*: In sediment: left maxillary fragment with M1–M2. Left upper incisor in bone fragment. Right incisor in bone fragment. Isolated: left fragmentary M3.

Schizogalerix voesendorfensis: In sediment: left maxillary fragment with P4–M2. Left mandible fragment with m1—m3, ascendens ramus is missing and the anterior part of the mandible, interiorly to the missing p4. Right mandible fragment (with part of the ascendens ramus). Left P3. Fragmentary bulbae. On the backside of a sediment piece (outlined by dotted lines in Fig. 8), right mandible with p4 (strongly damaged)–m3 Isolated: left M3. Left fragmentary mandible with m1 (damaged, only talonid)–m3. Left mandible fragment with p4–m2, and alveoli of p2, p3, m3.

The remains belong to one "*Cricetodon*" and at least three "*Schizogalerix*" individuals. Only one long bone is present but not identifiable. In the sediment plate, the labial part of the M2 of *Schizogalerix*, as well as the P3, show light corrosion spurs. In contrast, the trigonid of the m1 in the mandible is well corroded. Lingual parts of the molars are corroded, while the labial sides are intact. The isolated specimens show all light to more rarely moderate damages, most often on the occlusal part.

Almost only cranial parts are found in this specimen. This reflects, at least in two cases, the situation in recent pellets: (1) during the nidifications, adults might consume only the skulls, while the rest of the animal is destined to the young (Vein and Thévenot 1978); and (2) when prey is in abundance, the skull might be preferentially eaten (Raczynski and Ruprecht 1974).

UMJGP 204728

Böhme and Vasilyan (2014, this issue: fig. 3i, j) report a partial skeleton of a small Anguidae *Ophisaurus spinari*. Since this taxon is fossorial, they tentatively propose that the specimen is preserved in its own burrow. Actually, a right upper jaw with P3–M2 of *Schizogalerix voesendorfensis* comes from the three sediment plates holding the specimen and has been isolated. The teeth show consequent corrosion spurs on their

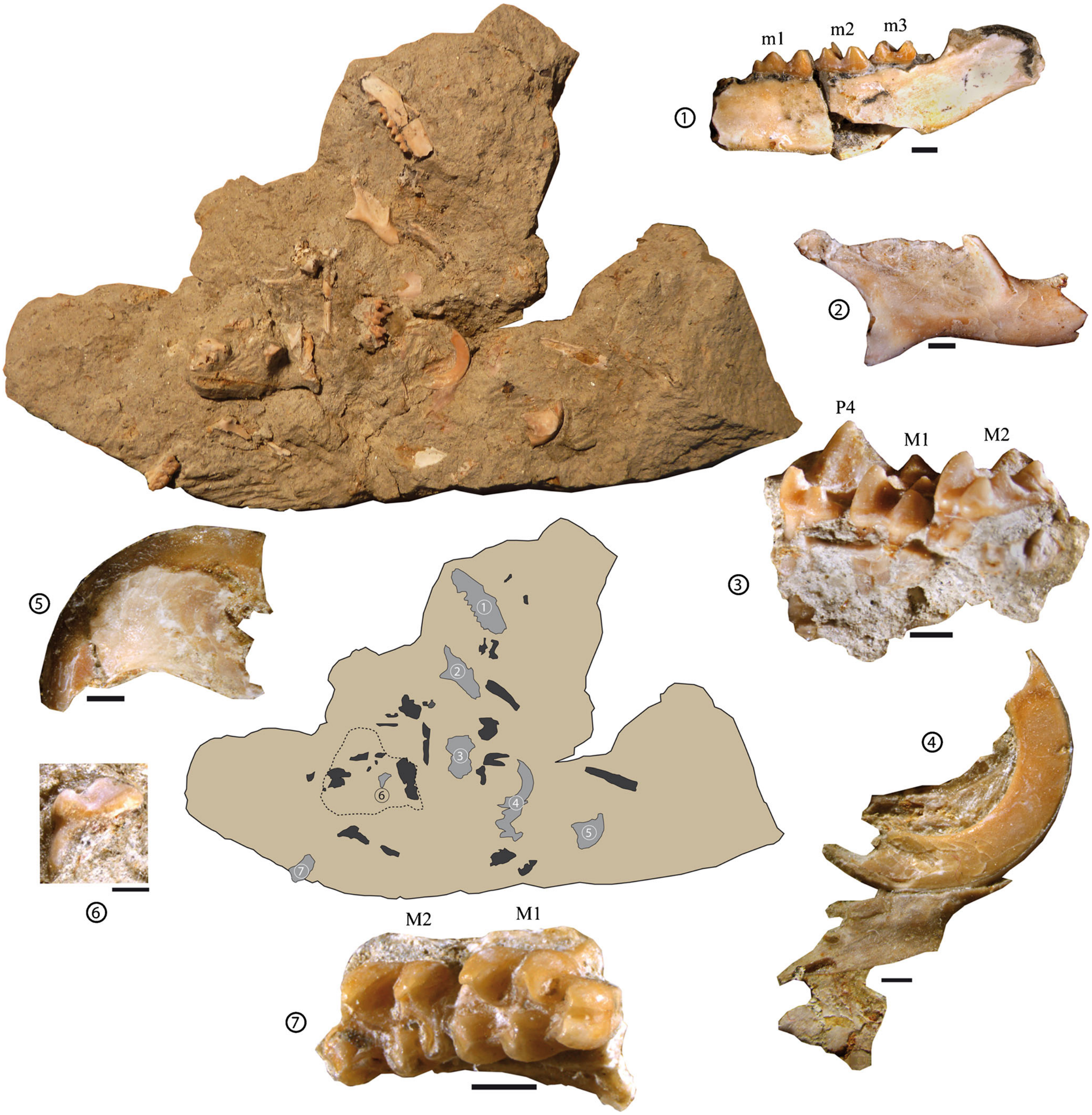


Fig. 8 Example of fossil pellet from Gratkorn (UMJGP 204700/1). Sediment piece with: *1 Schizogalerix voesendorfensis* (Rabeder, 1973) right mandible fragment with m1–m3; *2 S. voesendorfensis* right mandible fragment; *3 S. voesendorfensis* left maxillary fragment with P4–M2; *4* "*Cricetodon*" *fandli* Prieto et al., 2010, right upper incisor; *5* "*C.*" *fandli* upper left incisor; *6 S. voesendorfensis* left isolated P3; *7* "*C.*" *fandli* upper right maxillary fragment with M1–M2

whole surface, and thus indicate that at least this fossil derives from remains of a prey.

UMJGP 204730 and 204692

The amphibians are also documented by semi-articulated pieces. Partial skeletons of a crocodile newt *Chelotriton* aff. *paradoxus* (UMJGP204730) (frontal, trunk vertebra, ribs) and *Pelobates sanchizi* (UMJGP204692) (maxilla, premaxilla, sphenethmoid, squamosal, scapula, trunk and sacral vertebrae), is presented by Böhme and Vasilyan (2014, this issue). This specimen underlines the fact that part of the small vertebrate accumulation might derive from "natural" death. The spatefoot toads are fossorial amphibians, and the presence of an articulated skeleton of *Pelobates sanchizi* indicates an apparently dead animal in its own burrow. Such burrows are documented in the fossil record (e.g. Martin and Bennett 1977; Prieto et al. 2009), but no direct evidence has so far been found in at Gratkornt.

UMJGP 204240

The holotype of "*Cricetodon*" *fandli*, a skull with the two mandibles in anatomical position and forelimb, wrist and hand bones, is figured in Prieto et al. (2010b). In addition, post-cranial material was found in the vicinity of the specimen and most probably belongs to it. These are in need of detailed description. The skull does not show damage produced by gastric juices, but some original breakages are observed on the post-cranial. Whether the animal was a victim of predation or died naturally needs a more in-depth analysis.

UMJGP 204683

The remains belonging to *Eumyarion* sp. have been described in the "Insectivores, rodents, lagomorphs and chiropters from Gratkorn: taxonomic notes" of this paper (Fig. 6). The corrosion evidence demonstrates that the specimen was a prey.

UMJGP 211012

Several bone-enriched blocks originating from one accumulation place have been reserved for micro-CT analysis, and are not yet prepared. The most important material, as far as can be observed are the blocks rich in molluscs and the *Celtis* endocarps that are present. "*Cricetodon*" *fandli* is present in several plates with at least a fragmentary right mandible with m1–m2, a fragmentary left mandible with i + m1 and an in situ broken m2 (light corrosion spurs), a left fragmentary maxillary with M3, a left fragmentary maxillary with M1-M2, and a right upper jaw with M1-M3 (light corrosion spurs).

Democricetodon is also recorded by a right mandible with i–m1.

Much bony material is present, often fragmentary. In addition, osteoderms of *Ophisaurus* sp. have been recognised.

Synopsis concerning the small vertebrate fossil accumulation

1) Following the observations made on the corrosion traces on teeth and the evidence of pellets, it can be concluded that most of the small mammal remains derive from regurgitations of nocturnal raptors, but the influence of other types of predators is noticed. A similar origin is also proposed for part of the lower vertebrates.
2) This proposal cannot be demonstrated for the following taxa because of the lack of sufficient material and spurs: *Muscardinus*, *Miodyromys*, *Spermophilinus*, *Forsythia*, *Keramidomys*, *Dinosorex*, cf. *Myotis*.
3) While the pika might represent a representative part of the diet of the birds of prey, as shown, for instance, in the German fissure fillings from Petersbuch (Prieto 2007), the origin of the accumulation of *Prolagus*, cf. *Eurolagus* and Ochotonidae indet. cannot be confidentially enlightened here.
4) The "natural" death of some articulated specimens cannot be excluded, especially for lower vertebrates (amphibians and reptiles, indicated by their fossorial aptitude).
5) The accumulation of the beaver *Euroxenomys*—skull remains only—follows another pathway, probably closer to the accumulation factor linked to larger vertebrates.
6) Similarly, other factors may have been responsible for the presence of the large-sized squirrel *Albanensia albanensis*.

Indirect evidence of rodent activity

Gross et al. (2011) reported gnawing marks on many tortoise plates and mammalian bones. This kind of bone altering allows diverse conclusions. Due to the usually facet-like surface of gnawing marks produced by rodents, these traces are readily distinguished from bite marks of other animals. Based on the shape and the dimensions of the grooves and facets, the originators can sometimes be identified even to the specific level (e.g. Maul 2001). In addition, conclusions can be drawn on the behaviour of the gnawing rodents, because among extant rodents, not all gnaw bones or at least not with the same intensity. Nowadays, there are some 'specialists' (porcupines, squirrels, rats) who gnaw bones more frequently than others (e.g. Klippel et al. 2007; Kibii 2009). In addition, the ways and aims of gnawing might be taxa-related. Klippel and Synstelien (2007) demonstrated that the brown rat gnawed on fat-laden cancellous bone, while the grey squirrel took more advantage in attacking the thicker bone cortices. Consequently, gnawing marks might contribute to taphonomic inferences, since the gnawed bones must have been accessible during the gnawing process, so they were neither covered by water nor by sediment, and in most cases were in a very advanced grade of putrefaction (see section "Time averaging"). A detailed study of these marks is ongoing, but, at present, it has not been possible to clearly observe brown rat-type modifications.

Time averaging

Most small vertebrate finds, as well as invertebrates and *Celtis* endocarps, derive from the uppermost part of the fossil-enriched palaeosoil (Layer 11b in Gross et al. 2011), a layer which indicates a rising of the water table, switching from alluvial to lacustrine conditions. The thickness of this layer—around 15 cm—indicates a relatively short time of accumulation on the geologic scale.

The presence of pellet remains and semi-articulated vertebrates, because of their susceptibility to diagenetic processes, also indicates rapid burial of the fossils. The switch from alluvial to lacustrine conditions provided an ideal mixture for the accumulation and fossilisation of the specimens, the latter requiring a low energy environment with little disturbance (as in a lake), and providing a protecting layer above the fossil-enriched sediments.

Estimating the time of accumulation of the uppermost part of the palaeosol is much more problematic. Brand et al. (2003), in an actualistic experiment, come to the conclusion that the burial of small vertebrate remains is achieved from a maximum three months in aquatic conditions to over one year in soils. This gives an indication of burial times for single specimens, but not for the whole sample.

The gnawing marks observed on part of the larger bones occurring in the lower 40 cm of the fossil-enriched layer (Layer 11a in Gross et al. 2011) indicate that the remains were putrefied while the rodents damaged them. Klippel and Synstelien (2007) estimate that the post mortem interval for initial gnawing on human remains by the grey squirrel is over 30 months.

These observations underline the fact that a detailed taphonomic study of the small vertebrates from Gratkorn is needed, in order to better approach the accumulation process(es), and thus the deposit time of this exceptional locality. Anyway, the preliminary observations on small mammals certainly do not contradict the proposal of Gross et al. (2011), who suggest only a few decades for the accumulation of the layer 11, of which only a minor fraction would thus involve the small vertebrate-enriched part.

Impact of the sampling technics and accumulation agents on the relative abundance of the species

Two techniques were used for sampling the micro-vertebrate remains from Gratkorn. First, surface sampling allowed the discovery of the pellets, semi-articulated specimens and larger fossils, as, for instance, skull fragments and mandibles. In contrast, screen-washing techniques resulted in the winning of most of the isolated teeth. This induces an under-representation of the small-sized fossils, and restrains us from giving an important weight to the relative abundance of the species.

In addition, while this abundance might be useful for palaeoecological reconstructions (e.g. Daams et al. 1988; López-Martínez 2001), the impact of the accumulation agent (s), the diversity and ecology of the predator(s) (nocturnal vs. diurnal, for instance), as well as, consequently, the size of the prey plays a role in the repartition of the taxa in the fossil assemblage, and the abundance does not reflect the original abundance of the species in the fauna (e.g. Andrews 1990).

As a guide, the representativeness of the taxa in the screen-washing is indicated in Table 5. Only *Schizogalerix* dominates the samples from both surface and wet collecting methods.

Palaeoecological remarks

Insectivores

The assemblage consists of only *Schizogalerix voesendorfensis*, *Desmanodon fluegeli*, *Dinosorex* sp. and Galericinae gen. et sp. indet. The latter two are represented by just one individual. Indeed, the diversity is considerably lower than, for instance, at Anwil (13, Engesser 1972), Kleineisenbach (13, Prieto 2007), La Grive M (17, Mein and Ginsburg 2002), or Steinheim (9, Ziegler et al. 2005). Even in the late Sarmatian s. str., preliminary results show that the diversity is clearly higher in the rich Hungarian faunas (Tables 3, 4, 5). Prieto et al. (2010a) has already commented on the low α-diversity of the Gratkorn eulipothyphlans, concluding that there are taphonomical biasses. Although sample size will certainly play a role, the Gratkorn insectivore assemblage is by no means small, and *Schizogalerix* is even the most common micro-mammal of the fauna. Gymnures do not have spikes, and have played in some places an important role in the diet of birds of prey, as indicated by their over-representation in some fissure fillings from Germany (e.g. Ziegler 2005). Prieto (2007) observed that *Parasorex socialis* remains from Petersbuch 48 belong in large majority to young adults, and hypothesises that the animals were caught during their dispersion phase. Preliminary observations show that this picture cannot be applied at Gratkorn, where the proportion of adult *Schizogalerix* specimens is clearly higher, and might be closer to the results obtained in the floodplain locality of Kleineisensenbach.

The composition of the assemblage differs considerably from the late Middle Miocene insectivore assemblages of southern Germany (Ziegler 2006a). This fact probably results partially from the lack of sufficient Sarmatian s.str. fossil localities in the NAFB (see Table 1) and surrounding areas. *Schizogalerix* only enters that area near to the Middle–Late Miocene transition (Nebelbergweg, ?Aumeister; Prieto et al. 2011), the dominant Galericini in the late Middle Miocene still being *Parasorex socialis.* As stated in "Biostratigraphical remarks", this viewpoint might be nuanced in the future because new fissure fillings from Petersbuch probably contain *Schizogalerix*, but a detailed study is needed to confirm this observation, and a relative dating of the fauna cannot be provided at present. Galericini form the most common element in almost all insectivore assemblages of the Miocene

(Furió et al. 2011), but the late Middle Miocene is a notable period of change, with the entrance of *Schizogalerix* in Europe. In this respect, the re-occurrence of *Galerix* in the NAFB (Prieto et al. 2011) is also notable, showing that environmental changes led to the flux of this tribe of gymnures.

Interestingly, Gratkorn is dominated by elements of Anatolian origin, viz. *Schizogalerix* and *Desmanodon*, which is also true for part of the rodents. This indicates environmental conditions favourable for Anatolian-related forms to extend their distribution further eastwards during the latest part of the Middle Miocene. *Desmanodon* has some incursions into the NAFB in the Latest Badenian/earliest Sarmatian s.str. (Prieto 2010; and see Table 4) but the species found in Kleineisenbach and Giggenhausen most probably had its origin in Hungary (J. Prieto, L.v.d. Hoek Ostende and J. Hír, personal data) and is most probably not related to *D. fluegeli*. Whereas Talpidae are usually considered good indicators of humidity, *Desmanodon* seems to take an exceptional position in the family. Van den Hoek Ostende (1997, 2003) noted that the genus was the only talpid to survive after the Early Miocene in the relatively open environment of the Daroca-Calatayud area of the Teruel Basin, and only went extinct when conditions became too dry. In the case of Gratkorn, the presence of *Desmanodon* as the only talpid is even more remarkable, as moles were quite common and diverse at the end of the Middle Miocene in the nearby NAFB (Ziegler 2006a) and surrounding areas (Ziegler 2003; Tables 4, 5).

Dinosorex has a wide geographical and stratigraphical range, and seems of limited palaeoecological use.

Although it is hazardous to draw conclusions on the basis of the absentees, the key to understanding the eulipotyphlan assemblage lies primarily in the species that were not found, either because of true absence or rarity. No true litter feeders (Uropsiline and Urotrichine moles and Soricidae) have been found. This would tie in nicely with the results from the sedimentology, suggesting moist soils in a rather open landscape. Also, burrowing talpids (*Talpa*, *Proscapanus*) have not been found. Although moist soils would allow these animals to make burrows, in the absence of sufficient litter production, the food supply in these burrows would be limited. Overall, the eulipotyphlans of Gratkorn suggest a relatively open and dry landscape.

Chiroptera

Regarding the few specimens recorded at Gratkorn, as well as their poor taxonomy, any conclusion is hazardous. In general, bats are much more abundant in fossil assemblages from cave environments (e.g. Rosina and Rummel 2012), and large taxonomic differences are observed when dealing with other types of localities (Sigé and Legendre 1983). Bats are usually rare in fluvio-lacustrine sediments, and in this respect Gratkorn is no exception. Only exceptional events lead to the conservation of representative samples (e.g. Messel: Storch et al. 2002; Anwil: Engesser 1972; Green River Formation: Simmons et al. 2008).

Rodents

Albanensia, *Forsythia* and *Blackia* are usually regarded as flying squirrels, although no postcranial material of any of these genera has been described to date. Thorington et al. (2005) have correctly pointed out that the dental features used to recognise fossil flying squirrels (such as the rugose enamel of their cheek teeth) also occur in tree squirrels, which, on the other hand, are very rare in the Miocene fossil record. It cannot be discarded that many purported Miocene ‘flying squirrels’ are in fact tree squirrels. Nevertheless, this would still indicate the presence of relatively dense forest environments when those taxa are found. Interestingly, the three species present at Gratkorn range in size from large (*Albanensia albanensis*) to very small (*Blackia*, which is the size of the smallest extant species of the genus *Petinomys*). Such a broad range of sizes is also observed in the extant diverse squirrel faunas of the tropical forests of SE Asia and Africa, where various species that differ in their diet and behaviour (being either nocturnal or diurnal) exploit the abundant plant resources of those environments (see MacKinnon 1978; Emmons 1980).

Spermophilinus bredai, on the other hand, is a ground squirrel the size of a chipmunk. The skull of *Spermophilinus* shows two small depressions posterior to the upper incisors for the attachment of the cheek pouch musculature (De Bruijn and Mein 1968). The presence of cheek pouches is a synapomorphy of the Marmotini, and these structures are not found in other ground squirrels such as the Xerini. Cheek pouches allow for the rapid collecting of food and serve as a temporary storage for food (mainly seeds and grains) until the squirrels bring it to their lairs or burrows. In the light of this evidence, a similar lifestyle to that of extant holartic ground squirrels can be inferred for *S. bredai*.

Eomyids, which only comprise *Keramidomys* sp., are supposed to have favoured humid forest environments. Such an interpretation is based on their co-occurrence with certain ‘flying’ squirrels and dormice (Daams and Van der Meulen 1984; Casanovas-Vilar and Agustí 2007). Most eomyids are known only from isolated cheek teeth, although several skull and mandible fragments as well as an exceptionally preserved skeleton are known (Storch et al. 1996). The latest belongs to *Eomys quercyi* from the Late Oligocene of Enspel (Germany) with preserved soft tissues, clearly showing the existence of a patagium similar to that of flying squirrels (Storch et al. 1996). Nothing is known of other European eomyid taxa, but it is unlikely that all the members of this diverse group were gliders (Engesser 1999).

Regarding the Gliridae, the extant representatives of this group are mostly associated to forest environments, although some of them, such as *Myomimus,* inhabit drier open landscapes. Van der Meulen and De Bruijn (1982) grouped living and fossil Gliridae species on the basis of characteristic features of their M1 and M2 and extrapolated the ecology of the living representatives to fossil species. Virtually all glirids have been interpreted as scansorial to arboreal frugivores/omnivores with the exception of most of the Myomiminae. *Miodyromys*, which shows a dental pattern similar to that of *Myomimus*, could have preferred somewhat open landscapes. The genus *Muscardinus* is still extant, and it inhabits the temperate forests of Europe and is arboreal and mainly frugivorous. It hibernates in winter and is capable of going into torpor at other times of the year when the weather is unfavourable and food is scarce. It is unknown whether the Miocene species of this genus were capable of hibernating or entering torpor, but this ability seems to be a synapomorphy of all extant species, so it is likely that it was also present in their fossil relatives.

The cricetids include four species that differ widely in size and morphology. Several authors (Van de Weerd and Daams 1978; Casanovas-Vilar and Agustí 2007) have suggested that *Eumyarion* would have preferred humid and forested environments, which would explain why it is only recorded when this kind of environment is sampled. Such an interpretation is based on its molar morphology (Casanovas-Vilar and Agustí 2007) as well as on the co-occurrence of this genus with other taxa that are assumed to have favoured forested environments (Van de Weerd and Daams 1978). Regarding *Democricetodon*, while the medium-sized species (former *Fahlbuschia*) are considered to have inhabited arid environments, the small-sized ones would have preferred moister biotopes. Such interpretations are based on the distribution of the different species in the Calatayud-Teruel Basin, where the small-sized *Democricetodon* are more abundant in sites that include a greater number of inferred forest dwellers (Van de Weerd and Daams 1978). The same pattern is observed in the Vallès-Penedès, with *D. brevis* (a species that could be closely related to *Democricetodon* n. sp. from Gratkorn) and *D. nemoralis* being more common in sites that include arboreal dormice, flying squirrels and/or beavers, such as Castell de Barberà and Barranc de Can Vila 1 (Aguilar et al. 1979; Casanovas-Vilar et al. 2010). Similarly, the small-sized *Megacricetodon* species, such as *M. minutus,* are believed to have inhabited more humid and forested environments than their larger-sized congeners (Daams et al. 1988), but, given the broad geographic range of these species, they may better be considered as ubiquists. Finally, '*Cricetodon*' *fandli* is a large-sized cricetid that shows relatively higher crowned molars and complete ectolophs in the upper molar series. The presence of complete ectolophs provides evidence for an important propalinal component in the mastication besides the usual lateral one. Therefore, this cricetid appears to have been able of coping with tougher or more abrasive plant material than the other cricetids present at Gratkorn.

The single beaver taxon, *Euroxenomys minutus minutus*, is interpreted based on the study of postcranial material as having been more agile when moving on the ground than other beavers (Daxner-Höck 2004b; Casanovas-Vilar et al. 2008; see Prieto et al. 2014, this issue for details).

Overall, the rodent fauna indicates the presence of forest environments, although some of its components such as "*Cricetodon*" *fandli* and *Spermophilinus bredai* may have inhabited more open landscapes.

Lagomorpha

The co-occurrence of three ochotonids (a primitive, rooted one plus two forms with ever-growing teeth, usually *Amphilagus*/*Eurolagus* + *Prolagus* + *Lagopsis*) has been documented in central and western Europe from the early to the late Middle Miocene (e.g. Wallenried, Sandelzhausen, Anwil; Engesser 1972; Angelone 2009; C. Angelone, personal data). This evidence probably reflects ecological/environmental conditions in which the food resources were abundant and diverse for the ochotonids.

The Gratkorn lagomorph assemblage differs from more western ones as it is composed of a rooted primitive lagomorph, *Prolagus*, and a large-sized pika, undetermined and probably recorded for the first time. The absence of *Lagopsis* is notable in Austria, but this may result from a lack of a sufficient amount of pre-Pannonian small mammal-bearing localities in the country. The genus is also missing at present from the rich Sarmatian s.str. record from Hungary (see Table 3).

Apart from the rooted ochotonid from Bełchatów A, assigned to *Eurolagus fontannesi*, detailed studies about the palaeodiet of European ochotonids are not available. Fostowicz-Frelik et al. (2012) analysed the dental microwear of these Polish remains and indicated that the species was a typical browser (fruit-leaf/fruit seed groups) or a seasonal—regional mixed−feeder in the sense of Solounias and Semprebon (2002), preferring most probably soft grass-like plants and fruits, and fine seeds. They deduce from this feeding pattern and from the study of the Bełchatów A fossil assemblage that the species was a forest dweller.

As for *Prolagus oeningensis*, considering the wide geographic and stratigraphic range, a certain degree of plasticity regarding the environmental condition can be suspected. At the genus level, and based on the variations *Prolagus* versus *Lagopsis* ratios in the Iberian fossil record, López-Martínez (2001 and references therein) and Hordijk (2010) propose that *Prolagus* preferred relative wet environments.

Summary

The small mammals provide a mixed picture for the palaeoevironment of Gratkorn: while part of the fauna tends to indicate the presence of forested covering, more open landscapes would have been favoured by some members of the assemblage. This can be partially explained by taphonomic bias, most of the fossil remains deriving from the regurgitation of nocturnal raptors. This implies restrictions in the faunal spectrum, although the predators are considered as generalists. These restrictions are influenced by the size of the taxa, their ecology (under-representation of diurnal and forager species, for instance), and their abundance. Importantly, the hunting preferences of the predator influence the prey spectrum, and could explain in some part the mixed picture obtained for Gratkorn. Indeed, Petty (1999) observes that *Strix aluco*, although nesting preferentially in forest, where the pellets can thus accumulate, hunts in open landscapes. Similarly, Michelat and Giraudot (1991) show that *Tyto alba* in a 21 %-forested surface, only consume 2 % of its active time in this habitat.

Interestingly, the reptiles and amphibians, which partly have a similar origin of accumulation, also speak for a mosaic of habitats (Böhme and Vasilyan 2014, this issue), but record, in addition to open dry landscapes, short-lived ponds, streams or rivulets in the close vicinity. The presence of such water-points is only indicated by the few beaver specimens. The savannah-like open landscapes environment under a semi-arid climate which these authors propose for the environment of Gratkorn seems in contradiction with the information provided by the small mammals, although a minority of the mammal species certainly preferred open habitats.

The environmental information provided by the molluscs occurring in abundance in the same layer corroborates the mixed vision of the palaeo-situation at Gratkorn, but emphasise woodland with moist soil (Harzhauser et al. 2008). This forested influence is underlined in the fauna studied here by the large-sized sciurid *Albanensia*.

A possible, but not restrictive, explanation is that the fossil accumulation was achieved in the margins of a forest area, providing nesting and roosting places for the birds (pellet accumulation), as well as a diverse mosaic of micro-habitats for their prey.

General conclusions

With regards to the previous works dealing with the small mammals from Gratkorn, the beaver taxon has been emended into *Euroxenomys minutus minutus*, while one large-sized—but indeterminated—pika is newly reported.

Some rare species (*Spermophilinus*, *Miodyromys*, *Keramidomys*, cf. *Myotis*) have yielded new material, but this did not allow the improvement of their taxonomy.

Based on the common occurrence of digestion traces on some of the teeth and the presence of pellets, most of the material is interpreted as being accumulated by nocturnal raptors. This could explain the low α-diversity of the fauna. But a plurality of accumulation factors, at least for part of the fauna, is certainly indicated.

Similarly, and based on the information provided by the lower vertebrates and the molluscs, which occur in abundance in the same thin fossil-enriched layer, the mixed picture of the environment (basically forested vs. open landscape) deriving from the study of the small mammal fauna might find its explanation in the plurality of accumulation factors and/or of microhabitats around the excavation site.

The extremely rapid accumulation of the fossils allows us to open an exceptional window onto the late Sarmatian s.str. life. The quality and the quantity of material promises that, in future ,Gratkorn will continue to provide further insight into the palaeontology of Miocene rodents and insectivores.

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