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Insectivores and bat (Mammalia) from the late Middle Miocene of Gratkorn (Austria): biostratigraphic and ecologic implications

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With 5 figures and 1 table

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Abstract: The discovery of a late Sarmatian (latest Middle Miocene) small mammal fauna at the base of the clay pit St. Stefan near Gratkorn is of primary importance for the biostratigraphic and ecologic comprehension of the faunal evolution during the late Middle Miocene of Central Europe. In this paper five species of insectivores and one bat are described. The gymnure *Schizogalerix voesendorfensis* is the most abundant species of the small mammal fauna. The Gratkorn sample represents the earliest occurrence of the species in the fossil record. A single molar of a second, large-sized Galericinae cannot be attributed to any known species. The new talpid *Desmanodon fluegeli* n. sp. shares similarities with the Anatolian lineage *D. minor / D. major*. An exceptionally well preserved mandible of the large shrew *Dinosorex* cannot be determinate at the species level. In addition, some rare remains of the bat cf. *Myotis* sp. are also reported. From biogeographical point of view the insectivore fauna can be related to eastern Central European / Anatolian assemblages. Although taphonomic biases are suspected, the environmental conditions proposed on the basis of sedimentary analyzes (open forest with moist soil) can contribute to the low alpha diversity of insectivores in this locality.

Key words: Sarmatian, faunal relationships, Mammal, palaeoecology, insectivores, bats.

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1. Introduction

The fossil insectivore and chiropteran assemblages from Austria were recently intensively studied and revised (Ziegler & Daxner-Höck 2005; Ziegler 2006 a, b). As a result, the evolution of these mammalian groups is detailed for the Lower and early Middle Miocene and especially for the Late Miocene. The period in between, however, yielded few data. In this context the find of a late Middle Miocene (late Sarmatian, Harzhauser et al. 2008) small mammal fauna at the base of the clay pit St. Stefan by Gratkorn (Gross et al. 2007; Gross 2008, Prieto submitted) is of primary importance for the biostratigraphic and ecologic comprehension of the faunal evolution during this period, especially as it is critical in terms of climatic changes (Böhme 2003; Böhme et al. 2008). The insectivores are particularly interesting, as Ziegler (2006 b) found surprising differences between German and Austrian assemblages, in spite of the geographic vicinity. Furthermore, Sarmatian small mammal samples are still extremely rare in Central and Eastern Europe, making the finds from Gratkorn an important piece in the puzzle of the faunal interchanges at the end of the Middle Miocene.

2. Material and methods

The measurement method of the erinaceids is presented in Fig. 1, and the nomenclature follows Engesser (1980). The measurements and nomenclature of the talpids follow Ziegler (2003 a) based on Hutchison (1968, 1974); the

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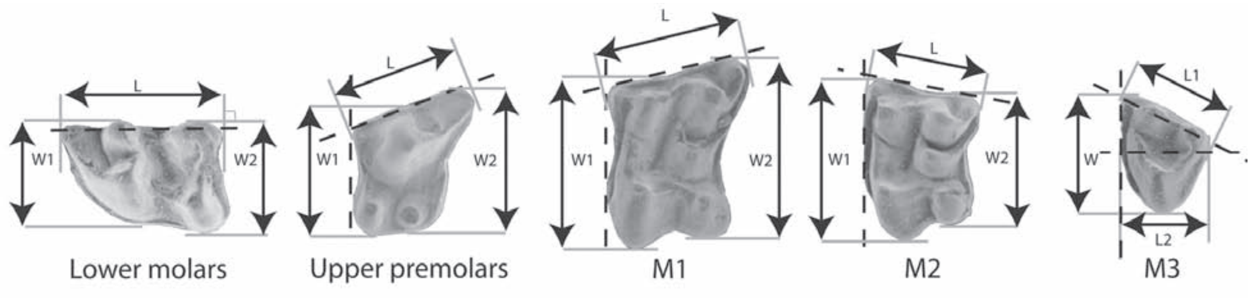


Fig. 1. Measurement method of the erinaceids (after Prieto & Rummel 2009a). Dotted lines: baselines. In case of T-shaped teeth (f. e. part of the P3, D3) the width will be measured perpendicular to the length. In case of reduced talonid (f. e. lower premolars) then just W1 is measured. L: length; L1: labial length; L2: shortest antero-posterior length; W: width; W1: anterior width; W2: posterior width.

soricids follow Reumer (1984). All measurements are given in mm and the specimens in the figures are presented in left orientation. Hence, right specimens are reversed. The fossils from Gratkorn are stored in the Landesmuseum Joanneum of Graz (Geologie & Paläontologie, abbreviated LMJG) and in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich (abbreviated BSPG).

3. Systematic paleontology

Order Erinaceomorpha Gregory, 1910
Family Erinaceidae Fischer, 1814
Subfamily Galericinae Pomel, 1848
Genus *Schizogalerix* Engesser, 1980

Diagnosis (emended): Van den Hoek Ostende (2001: 686).

Differential diagnosis: Engesser (1980: 63) and comments in Van den Hoek Ostende (2001).

Type species: *Schizogalerix anatolica* Engesser, 1980.

Other species included: *S. zapfei* (Bachmayr & Wilson, 1970) (= *Galerix atticus* Rümke, 1976), *S. moedlingensis* (Raeder, 1973), *S. voesendorfensis* (Rabeder, 1973), *S. pasalarensis* Engesser, 1980, *S. anatolica* Engesser, 1980, *S. sinapensis* Sen, 1990, *S. macedonica* Doukas, 1995, *S. sarmatica* (Lungu, 1981), *S. duolebulejinensis* Bi et al. 1999, *S. intermedia* Selänne, 2003, *S. evae* de Bruijn et al. 2006.

‘*Schizogalerix*’ *iliensis* Kordikova, 2000 is transferred to the genus *Galerix* by Doukas & Van den Hoek Ostende (2006). De Bruijn et al. (2006) and Doukas & Van den Hoek Ostende (2006) consider *S. pristina* Ziegler, 2003 as an ancestor of *Parasorex* and not as *Schizogalerix*.

Schizogalerix voesendorfensis (Rabeder, 1973)
Fig. 2A-J

1973 *Galerix voesendorfensis* n. sp. – Rabeder, p. 430-433, figs. 1-10.
1980 *Schizogalerix voesendorfensis* (Rabeder). – Engesser, figs. 3d, 4b.
Part. 1993 *Galerix* aff. *socialis* (Rabeder). – Kälin, p. 54-56, fig. 23a.
2001 *Schizogalerix voesendorfensis* (Rabeder 1973). – Kälin & Engesser, p. 13-15, fig. 8.

Type locality: Vösendorf (Austria).

Stratigraphic correlation: early Late Miocene (MN9), Middle Pannonian “zone” D/E (“zonation” after Papp 1951).

Material und measurements: 67 isolated teeth, 22 mandibles, 7 maxillaries and 1 fragmentary skull (BSPG 2008 IV 1-27; LMJG 203.740, 984-999, 204.022, 024, 026-30, 043, 048, 104, 105, 138-143, 146, 208.732-737, 739-742). (Table 1).

Diagnosis: Since Rabeder (1973) did not give any diagnosis for his new species (only a differential diagnosis) and considered it part of the genus *Galerix*, a diagnosis is proposed herein: Medium sized *Schizogalerix* species having a continuous to slightly interrupted and clearly S-shaped mesostyle in the first two upper molars. The species does not fully develop the posterior cingulid/entoconid connection in the two first lower molars. The hypolophid is continuous.

Description and discussion. – Dental remains: the p2 is smaller than the p3; the well-developed paralophid of the p4 is continuous; the hypolophid of the m1 and m2 is continuous; the connection posterior cingulid/entoconid is variable, most often not fully achieved: in some specimens this connection is absent, as found in the German and Swiss *Parasorex socialis*, whereas in some teeth this cingulid reaches the top of the entoconid. The mesostyle of the first two upper molars is clearly S-shaped (‘Schlaufenbildung’ in German, Engesser 1980) and most often continuous with tapering of its middle part; in some specimens, this structure is interrupted, but without the development of a clear valley; there is no connection between metaconule and protocone; the posterior arm of the metaconule ends to the postero-labial corner of the M1 and M2 and the P3 has two

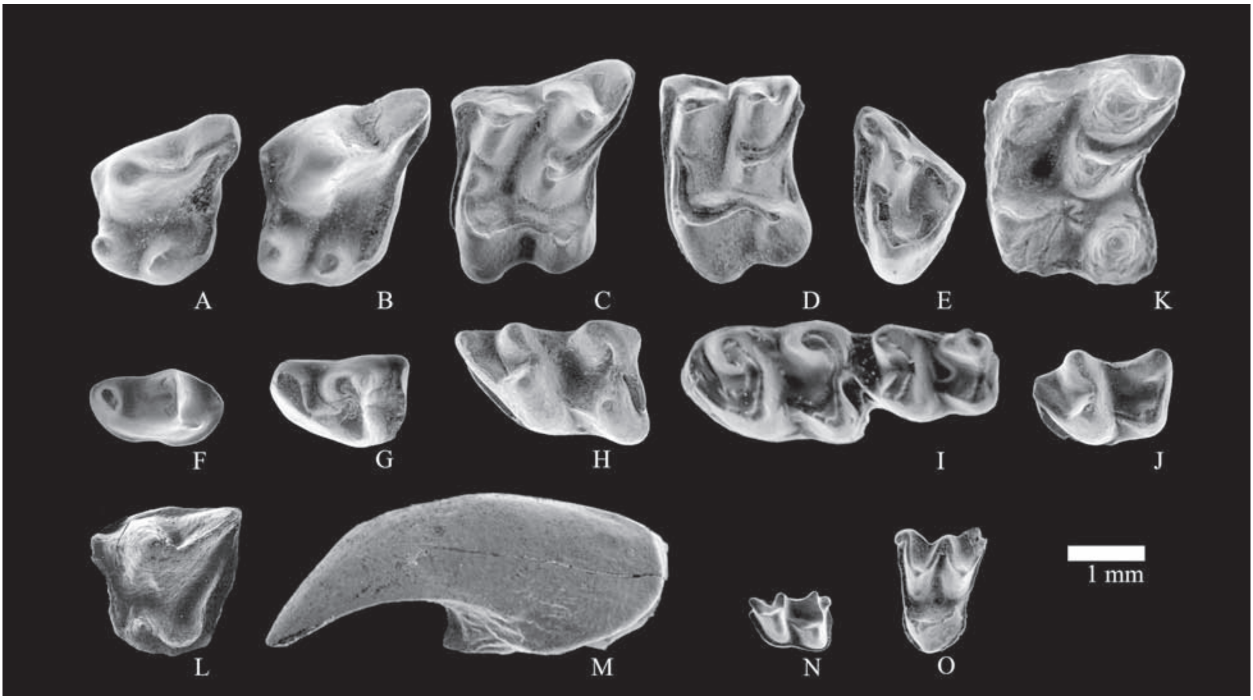
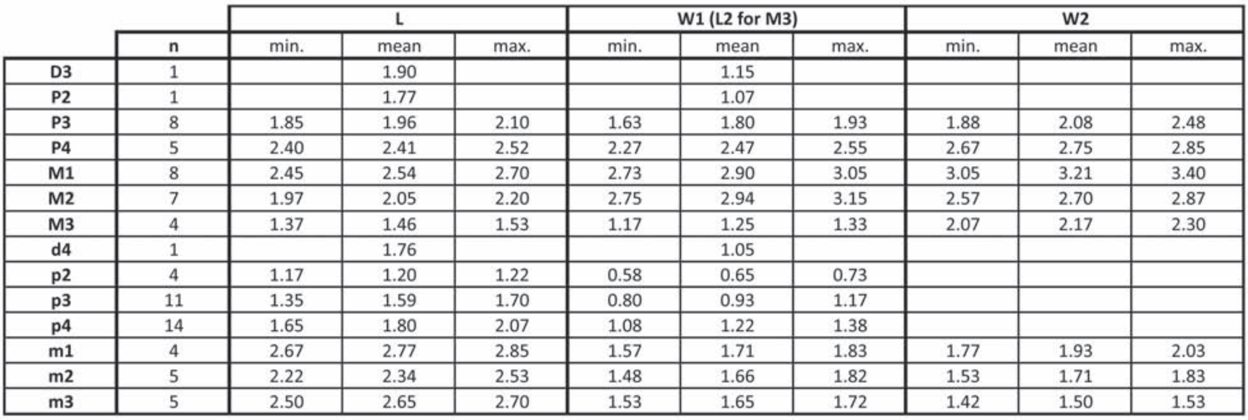


Fig. 2. The erinaceids, soricid and bat from Gratkorn. All teeth are shown in left orientation and in occlusal view (except M: labial view). **A-J:** *Schizogalerix voesendorfensis* (RABEDER, 1973): **A:** right P3 (reversed, LMJG 208.732); **B:** right P4 (reversed, LMJG 208.733); **C:** left M1 (LMJG 208.734); **D:** left M2 (LMJG 208.735); **E:** left M3 (LMJG 208.736); **F:** right d4 (reversed, LMJG 204.159); **G:** left p4 (LMJG 208.742); **H:** left m1 (LMJG 208.740); **I:** left mandible with m2-m3 (LMJG 203.986); **J:** left m3 (LMJG 208.741); **K:** Galericinae gen. et sp. indet.: right M1 (reversed, LMJG 208.738); **L-M:** *Dinosorex* sp.: **L:** left P4 (LMJG 204.161); **M:** left upper incisor (LMJG 204.160); **N-O:** cf. *Myotys* sp.: **N:** left m1 (LMJG 204.162); **O:** left M2 (LMJG 204.163).

lingual cusps. All these morphologic characters permit to attribute the teeth to the genus *Schizogalerix*.

The dental remains from Gratkorn fit best, in size and morphology, with the species *S. voesendorfensis* and *S. anatolica.* Following the differential diagnosis given by ENGESSER (1980: 70), the specimens from Gratkorn can be attributed to the Austrian species. This is especially clear in the trigonid basin of the lower molar, which is broader than in *S. anatolica*, and the absence of diagonal enlargement in the P4. The fossil record of *S. voesendorfensis* is, at present,

Table 1. Sample statistics of the *Schizogalerix voesendorfensis* (RABEDER, 1973) molars. n: number of specimens; min: minimum; max.: maximum; mean: arithmetic mean. For method and additional legend see Fig. 1.



		L			W1 (L2 for M3)			W2		
	n	min.	mean	max.	min.	mean	max.	min.	mean	max.
D3	1		1.90			1.15				
P2	1		1.77			1.07				
P3	8	1.85	1.96	2.10	1.63	1.80	1.93	1.88	2.08	2.48
P4	5	2.40	2.41	2.52	2.27	2.47	2.55	2.67	2.75	2.85
M1	8	2.45	2.54	2.70	2.73	2.90	3.05	3.05	3.21	3.40
M2	7	1.97	2.05	2.20	2.75	2.94	3.15	2.57	2.70	2.87
M3	4	1.37	1.46	1.53	1.17	1.25	1.33	2.07	2.17	2.30
d4	1		1.76			1.05				
p2	4	1.17	1.20	1.22	0.58	0.65	0.73			
p3	11	1.35	1.59	1.70	0.80	0.93	1.17			
p4	14	1.65	1.80	2.07	1.08	1.22	1.38			
m1	4	2.67	2.77	2.85	1.57	1.71	1.83	1.77	1.93	2.03
m2	5	2.22	2.34	2.53	1.48	1.66	1.82	1.53	1.71	1.83
m3	5	2.50	2.65	2.70	1.53	1.65	1.72	1.42	1.50	1.53

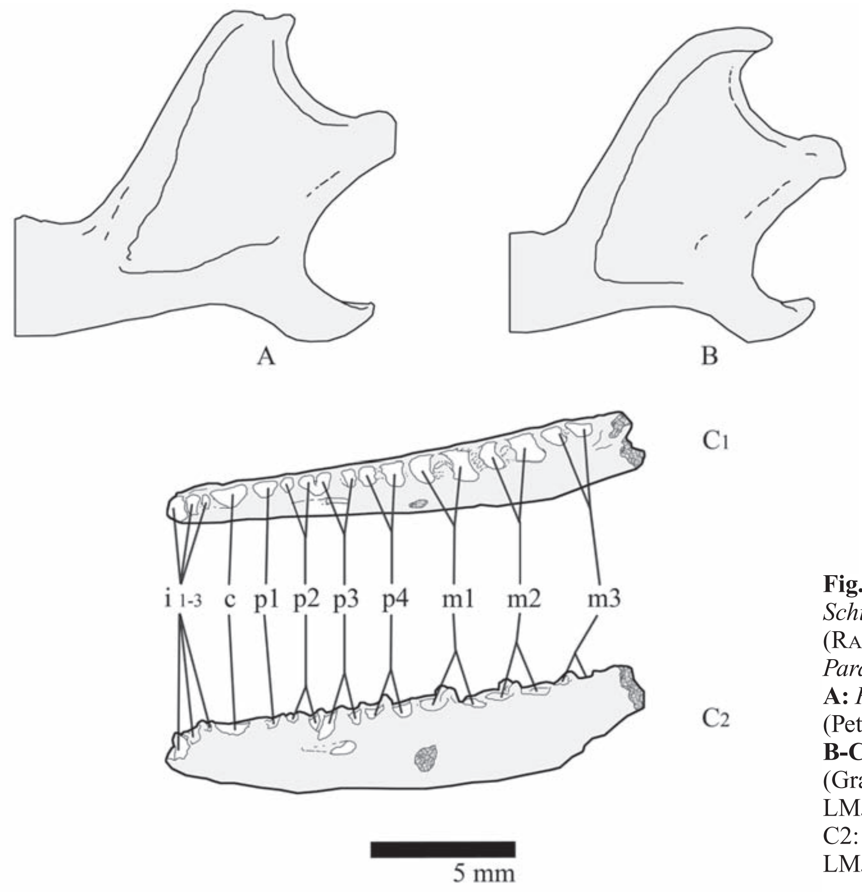


Fig. 3. Mandible fragments of *Schizogalerix voesendorfensis* (Rabeder, 1973) and *Parasorex socialis* (von Meyer, 1865): **A:** *Parasorex socialis*, labial view (Petersbuch 6, BSPG 1993 IV 653); **B-C:** *Schizogalerix voesendorfensis* (Gratkorn): B. labial view (reversed, LMJG 204.239); C1: occlusal view; C2: labial view (both reversed, LMJG 204.104).

restricted to Austria and Switzerland. In addition to the Austrian type locality Vösendorf (Rabeder 1973), the species is also reported in Nebelbergweg (Kälin & Engesser 2001). Metrically these assemblages are very similar, though the teeth from Gratkorn are slightly smaller.

Mandible: the mental foramen is found under the p3; in general, the mandibles from Gratkorn resemble *Parasorex socialis* mandibles (figures in Engesser 1980, Novacek et al. 1985, and Ziegler 2005a). Nevertheless, some significant differences can be observed (Fig. 3): the p1 and the preceding anterior teeth are clearly deeply slanted forwards in *P. socialis*; furthermore the anterior part of the mandible tapers from the p3 onwards in *P. socialis*, but more anteriorly (p2) in Gratkorn. Based on the large size of the premolars from Vösendorf, Kälin & Engesser (2001: 15) hypothesize a low reduction level of the mandible of the Swiss species, which is a primitive character state within the genus. This is confirmed by the fossils from Gratkorn.

Galericinae gen. et sp. indet.
Fig. 2K

Material: Partly damaged right M1 (LMJG 208.738).

Description and discussion: The single M1 is corroded but can be clearly differentiated from the *Schizogalerix voesendorfensis* molar sample due to its larger size and the presence of a straight and undivided mesostyl. Furthermore, the posterior arm of the metaconule does not join the postero-labial margin of the tooth and the hypocone is very conical, due to the absence of an anterior arm. A small crest is developed between the two lingual cusps in the direction of the metaconule.

The overall morphology of the M1 fits well with *Parasorex socialis* even though the molar is too large to be attributed to this species. In addition to *S. voesendorfensis*, Kälin & Engesser (2001) report a second and larger *Schizogalerix* species in Nebelbergweg. Unfortunately this species is a rare element of the Swiss fauna (four teeth) and the M1 is not represented in the sample. The M2 displays a divided mesostyle, and such a character should be present in the M1 or at least the mesostyle has to be S-shaped. This is not the case in Gratkorn. Therefore, due to the lack of diagnostic characteristics the molar cannot be determined.

Order Soricomorpha Gregory, 1910
Family Talpidae Fischer, 1814
Subfamily Talpidae incertae sedis
Genus *Desmanodon* Engesser, 1980

Diagnosis: See Engesser (1980: 116), differential diagnosis in Engesser (1980: 116-117).

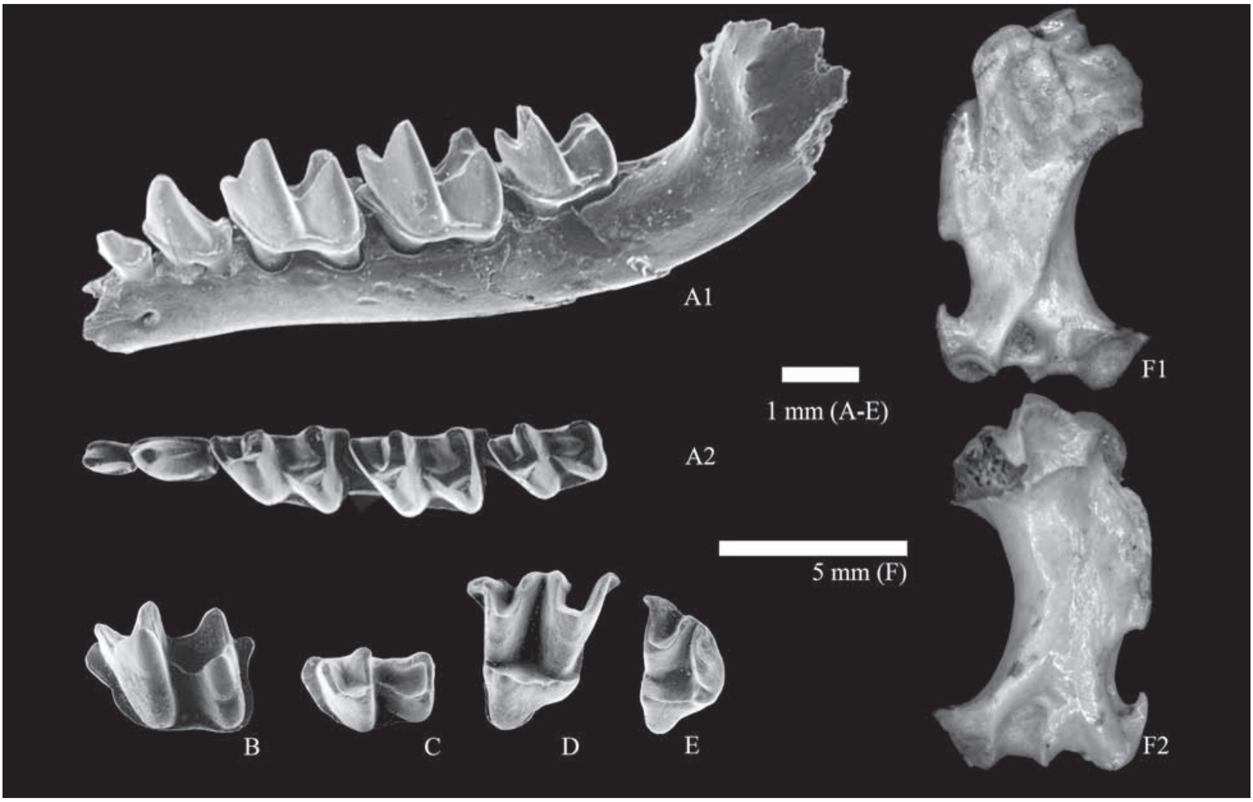


Fig. 4. *Desmanodon fluegeli* n. sp. All specimens are shown in left orientation; A2-E: occlusal view. **A:** Holotype, left lower mandible with p3-m3 (LMJG 204.164, A1: labial view, A2: occlusal view); **B:** right m2 (reversed, LMJG 204.165); **C:** right m3 (reversed LMJG 204.166); **D:** left M2 (LMJG 204.167); **E:** right M3 (reversed, LMJG 204.168); **F:** left humerus (F1: cranial view, F2: caudal view, LMJG 204.056).

Type species: *Desmanodon major* Engesser, 1980.

Other species included: *D. minor* Engesser, 1980, *D. antiquus* Ziegler, 1985 (= *D. meuleni* Doukas, 1986 in Doukas & Van den Hoek Ostende 2006), *D. daamsi* Van den Hoek Ostende, 1997, *D. ziegleri*, Van den Hoek Ostende 1997, *D burkarti* Van den Hoek Ostende, 1997, *D. crocheti* Prieto, in press.

Desmanodon fluegeli n. sp.
Fig. 4

In press *Desmanodon* sp. from Gratkorn. – Prieto.

Etymology: In honour of Helmut W. Flügel, for his intensive geologic work in the Graz area.

Holotype: Right lower jaw fragment with c, p3-m3 (LMJG 204.164, Fig. 3A); measurements: c: 0.90x0.60; p3: 0.83x0.55; p4: 1.23x0.63; m1: 1.93x(1.10x1.28); m2: 1.97x(1.28x1.32); m3: 1.63x1.13.

Paratypes: 2 fragmentary lower molars (trigonid), 2 m1, 3 m2, 4 m3, 2 M1, 2 M2, 2 M3, left humerus (LMJG 204.056, 165-180). Measurements of teeth: m2: 2.13x (1.33x1.35); m3: 1.80x(0.92x0,72); 1.60x(0.97x0.80); 1.60x(0.95x0.80); M2: 1.90x2.15; 2.02x2.13; M3: 1.55x(1.10x1.72); 1.70x(1.10x1.73). Measurements of humerus: Diameter of the shaft: 3.00; distal width: 5,65; distal with without epicondyles: 4.65.

Type locality: Gratkorn (Austria).

Type horizon: Clay pit of the company Wietersdorfer & Peggauer Zementwerke AG, 10 Km NW from Graz (15°20’55”E/47°08’15”N). Mottled and intensively bioturbated paleosoil at the base of the profile (Gross et al. 2007: 180); late Middle Miocene, late Sarmatian (upper *Ervilla* Zone; *Porononion granosum* Zone).

Diagnosis: Medium-sized *Desmanodon* species morphologically close to *D. minor*; single-rooted p3; lower molars with a short entoconid and continuous labial cingulid.

Differential diagnosis: *Desmanodon fluegeli* n. sp. differs from:

- *Desmanodon antiquus* (= *D. meuleni*) in the more divided mesostyl of the upper molars and in the broader pectoral crest of the humerus (compared with the specimen from Rauscheröd in Ziegler 1985: fig. 16).
- *Desmanodon crocheti* in the broader trigonid of the lower molars (Prieto in press).
- *Desmanodon daamsi* in being larger, having less inflated cusps in the lower molars and the complete division of the mesostyle of the upper molars.
- *Desmanodon ziegleri* in being larger, having a more divided mesostyle and reduced / absent metaconule / paraconule in the upper molars and in the longer and straighter teres tubercle of the humerus.
- *Desmanodon burkarti* in the position of the mental foramen (under the p3, under p4 in *D. burkarti*), the less developed paraconule of the M2.

The new species is morphologically close to the Anatolian lineage *D. minor* / *D. major*. It differs from:

- *Desmanodon major* in its smaller size, the position of the foramen mentale (under the p3), the more lingually positioned paraconid of the m1 and m2, the continuous labial cingulid of the m1 and m2, the interrupted metacingulum of the M2 and the more divided mesostyle of the upper molars.
- *Desmanodon minor* in the single-rooted p3, the shorter entoconid of the lower molars, the continuous labial cingulid of the m1 and m2, the presence of narrow labial cinguli in the M1 and M2, the relatively longer teres tubercle of the humerus and the less strong and more curved mandible.

Description of the holotype: The anterior part of the mandible is broken somewhat 0.8 mm before the mental foramen; the ascending ramus preserves only its lowermost part; the thinner part of the horizontal ramus is found under the contact point of p4 and m1; the mental foramen lies under the p3; the p3, p4, m1, m2 and m3 are conserved *in situ*, whereas the anteriorste tooth fell out of the mandible and is conserved as isolated element; this tooth is difficult to interpret. Engesser (1980: 123) described a mandible fragment of *D. minor* in which the alveole of a small single-rooted p2 and a double-rooted tooth are found before the p3. He cannot specify the nature of this tooth, p1 or canine. In the mandible from Gratkorn a small alveole can be observed before the p3; it has originally supported a small single-rooted premolar; the ? p1/c lays originally before this alveole.

The two-rooted ? p1/c is larger than the p3; the high protoconid is directed forwards; a very low crest descends along its posterior wall; the tooth is surrounded by a cingulum, which becomes stronger on the posterior border of the canine.

The overall morphology of the single-rooted p3 does not differ from the ? p1/c; the protoconid is clearly lower and the cingulid surrounding the tooth is relatively stronger; an extremely reduced parastylid is present.

The protoconid of the two-rooted p4 is situated in the anterior part of the tooth; a cingulum is present all around the p4, forming a small parastylid at its anterior border; the height of the protoconid of the p4 corresponds to the height of the hypoconid of the m1.

The talonid of the m1 is broader than its trigonid; the thin paracristid is higher than the postcristid; the thin precingulid extends on the lingual wall of the paraconid; labially the cingulids are continuous; the postcingulid ends lingually in a strong entostylid; the crista oblica strongly descends from the hypoconid to the base of the posterior wall of the protocristid.

The m2 mainly differs from the m1 in trigonid and talonid having about the same width; the trigonid basin is also antero-posteriorly narrower than in m1 and the precingulid is stronger.

In the m3, the paraconid is not aligned with the meta- and entoconid like in m1 and m2, but positioned somewhat more centrally; the precingulid is as strong as in m2; the labial walls of the proto- and hypoconid have no cingulid (in the Figure 4 A1, the ectocingulid seems to be complete, but this is not correct); the crista oblica descends strongly from the hypoconid to the base of the posterior wall of the protocristid, almost parallel to the entocristid.

Description of the paratypes: Humerus: The humerus is broken around the head but preserved in full length; the teres tubercle forms a long straight crest; the small pectoral tubercle is situated in the middle of the shaft; the scalopine ridge extends from the head to the medial side of the lesser tubercle.

The lower molars basically do not differ from the holotype.

M1: The two M1 are either broken or corroded; the labial border of the molar is strongly oblique; the mesostyle is strongly divided; the metaconule is present; a cingulum is present on both anterior and posterior walls of the protocone; three roots.

M2: The M2 differs from the M1 in its labial border, which is not oblique; the parastyle is slightly more labially positioned than the others labial styles; the mesostyle is strongly divided; the metaconule is present; the paracingulum and metacingulum are missing; reduced cingula are found on both the anterior and posterior sides of the protocone; a very weak paraconule is present in unworn specimens.

M3: The labial border of the molar is oblique backwards; the metacrista is missing; the mesostyle is clearly divided; the metacingulum is missing; an extremely reduced cingulum is present on the posterior wall of the protocone of one M3 (out of four).

Discussion: The differences between *Desmanodon* and *Paratalpa* were extensively discussed by Van den Hoek Ostende (1997). The teeth and humerus from Gratkorn clearly belong to *Desmanodon*. Furthermore, only one mole species is present in the locality and the attribution of the humerus to the tooth sample is confident.

The overall morphology of the specimens clearly links *D. fluegeli* to the lineage *D. minor* / *D. major* as defined by

Engesser (1980). The new species shares characteristics found either in *D. minor* (specifically the size, the entoconid length) or *D. major* (especially the humerus, the single-rooted p3, the form of the mandible). Nevertheless, it is not possible to interpret *D. fluegeli* as intermediate stadium between the two Anatolian species. Finally, it cannot be excluded that the differences observed in the new species are correlated to geographical differentiation.

Family Soricidae Fischer, 1814
Subfamily Heterosoricinae Viret & Zapfe, 1952
Genus *Dinosorex* Engesser, 1972

Diagnosis: Engesser (1972: 80-81), Differential diagnosis: Engesser (1972: 78-80), comments in Engesser (1975: 662-663).

Type species: *Sorex sansaniensis* Lartet, 1851.

Other species included: *D. pachygnathus* Engesser, 1972, *D. zapfei* Engesser, 1975, *D. anatolicus* Van den Hoek Ostende, 1995, *D. grycivensis* Rzebik-Kowalska & Topachevsky, 1997, *D. engesseri* Rabeder, 1998.

Dinosorex sp.
Figs. 2L-M, 5

Material und measurements: Right mandible with incisor, a(?), m1-m3, left upper incisor, left P4 (LMJG 204.004, 160, 161): lower incisor: 8x2.1; a(?): 1.45x1.22; m1: 2.5x(1.47x1.73); m2: 2.07x(1.67x1.63); m3: 1.68x (1.58x1.05); upper incisivor: 4.9x2.78x2.35; P4: 2.01x2.

Description and discussion: Heterosoricinae are not well represented in the Gratkorn sample but a very well-preserved mandible was discovered. This mandible has a divided massetic fossa and an acuspulate incisor. Therefore, the lower jaw belongs to *Dinosorex*. The two other isolated teeth are also attributed to the genus. In the jaw, the lower incisor, the anteriormost antemolar and all the molars are *in situ*. The posterolophid extends to the postero-labial (m1) or labial (m2) wall of the entoconid. The teeth are coloured, suggesting an original pigmentation. The posterior margin of the incisor extends below the rear of the m1 trigonid. The mental foramen is situated under the protoconid of the m2, in the upper half of the horizontal ramus. A small post-symphyseal foramen is preserved below the rear of the m3, slightly above the ventral margin of the jaw. The condyl is divided into two facets, the ventral one being clearly larger. The facets are connected by a narrow ridge.

The differences with *Dinosorex sansaniensis, D. grycivensis, D. anatolicus* and *D. zapfei* are clear:

- *D. sansaniensis* has a less robust mandible with four antemolars (see Engesser 1972: fig. 18b, 1975: pl. 3, fig. 3, 1980: pl. 8, fig. a) and isolated condylar facettes. The lower molars are without entocristid. Furthermore, the postero-lingual valley of the P4 is more developed.
- *D. zapfei* has 4 antemolars (including p4, Engesser 1975: pl. 5, fig. 3b), a smaller m3 and lower molars without entocristid.
- *D. grycivensis* has four antemolars and lower molars without entocristid (Rzebik-Kowalska & Topachevsky 1997).
- *D.anatolicus* has a foramen mentale lying under the anterior root of the m2 and the first two lower molars have a large valley separating the posterolophid from the entoconid.

The specimens from Gratkorn differ from *Dinosorex pachygnathus* in the clearly longer and narrower lower incisor; the lingual borders of the lower molars from Gratkorn are convex, whereas they are almost straight in *D. pachygnathus*; the horizontal ramus of the mandible is also narrower; the m2 does not cover the postcingulid of the m1, as is usually the case in *Dinosorex*; the ascending ramus shows clear differences with the specimen figured by Engesser (1972: fig. 18a), especially in its anterior border which is less convex. It is not possible to estimate precisely the original number of antemolars, probably two with the p4. The P4 differs clearly from the premolar of *D. pachygnathus* in the postero-lingual part of the tooth, with extends more lingually. This characteristic is also noticed by Kälin & Engesser (2001) for *D.* aff. *pachygnathus* of Nebelbergweg (see below).

The main characteristic of *D. engesseri* from the Upper Miocene of Austria is the crest developed between hypocone and metacone in the M1 and M2 (Rabeder 1998). These elements are not preserved in Gratkorn. Rabeder (1998: fig. 5) figures a fragmentary mandible from Götzendorf which shares some morphologic similarities with the mandible from Gratkorn although the processus angularis is better developed. Ziegler (2005a, 2006a) reports the presence of the species in the Upper Miocene localities Schernham, Richardhof-Wald, Neusiedl am See, Richardhof-Golfplatz (all Austria) and Rudabánya (Hungary). The incisor from Gratkorn is larger than in these localities, whereas the molars are somewhat smaller. Furthermore, the hypolophid of the m1 and m2 joins the entoconid on its postero-labial wall, not clearly posteriorly like in *D. engesseri*. Indeed, this character can be slightly variable in the *Dinosorex* species.

Kälin & Engesser (2001) report *Dinosorex* in Nebelbergweg (Switzerland). They notice some differences with *D. engesseri* but refrain from describing a new species. The incisor from Gratkorn, though also long, is nevertheless shorter than those from Nebelbergweg. The molars are also smaller, but, in the overall morphology, the specimens from Gratkorn share great similarities with the material from Nebelbergweg.

In size and morphology the Austrian lower molars are not basically different from *Dinosorex* sp. from Sari Çay (Turkey, Engesser 1980), but the tooth sample of this locality is also very small.

The specimens from Gratkorn, in spite of the presence of the especially well-preserved mandible, do not allow one to reach confident conclusions regarding their specific attribution.

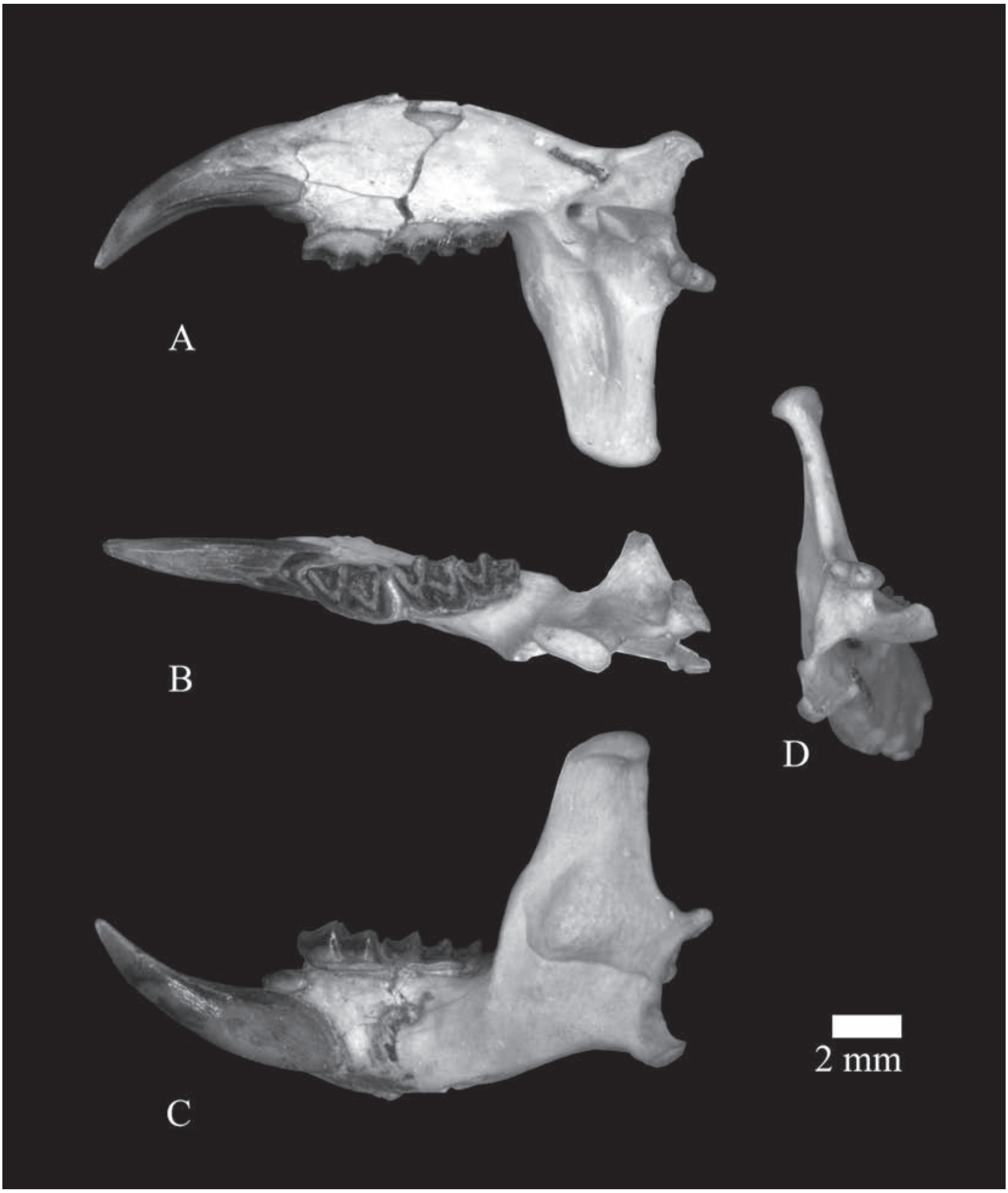


Fig. 5. *Dinosorex* sp. from Gratkorn. Right mandible (reversed, LMJG 204.004). **A:** lingual view; **B:** occlusal view; **C:** labial view; **D:** distal view.

Order Chiroptera Blumenbach, 1779
Family Vespertilionidae Gray, 1821
Genus *Myotis* Kaup, 1829

Remarks: The systematic rank of *Leuconoe* Boie, 1830, as genus or subgenus of *Myotis*, is a subject of debate. Thus the diagnosis/differential diagnosis of *Myotis* is dependent of the generic attribution of *Leuconoe*. The reader is referred to Baudelot (1972), Menu (1987), Ziegler (2000) and Horáček (2001) for emended diagnosis and discussion on this subject.

Type species: *Vespertilio myotis* Borkhausen, 1797.

Other species included (Oligocene-Pliocene species only):
M. insignis (von Meyer, 1845) (*nomen dubium* in Ziegler 2003b), *M. salodorensis* Revilliod, 1922, *M. wuesti* Kormos, 1934, *M. schaubi* Kormos, 1934, *M. steiningeri*

Kormos, 1934, *M. kormosi* Heller, 1936, *M. rapax* Heller, 1936, *M. aemulus* Heller, 1936, *M. gunderheimensis* Heller, 1936, *M. praevius* Heller, 1936, *M. delicatus* Heller, 1936 (?= *M. dasycneme subtilis* Kowalski, 1956), *M. exilis* Heller, 1936, *M. sanctialbani* Viret, 1951, *M. danutae* Kowalski, 1956, *M. helleri* Kowalski, 1962, *M. boyeri* Mein, 1964, *M. ziegleri* (Baudelot, 1972), *M. lavocati* Sigé & Menu, 1992, *M. minor* Ziegler, 2000, *M. intermedius* Ziegler, 2000, *M. major* Ziegler, 2000, *M. reductus* Ziegler, 2003, *M. bavaricus* Ziegler, 2003.

cf. *Myotis* sp.

Fig. 2N-O

Material and measurements: 1 m1 (LMJG 204.162): 1.10 x (0.63 x 0,71); 1 M2 (LMJG 204.163): ~1,4 x 1,7.

Description and discussion: Based on their size, the two teeth are considered to belong to a single species. The identification of chiropterian material based on isolated teeth is always extremely difficult and the two molars from Gratkorn are clearly insufficient to expect confident taxonomical conclusions. Nevertheless, based on the overall morphology of the upper molar, it should be possible to conclude that the two specimens are related to *Myotis*.

4. Biostratigraphic considerations

The insectivores are usually of minor interest regarding fine biostratigraphic correlations. However, at a larger scale the use of well defined insectivore lineages may be very useful. Such a lineage is reported for *Schizogalerix* in the Middle to Late Miocene from Turkey (Engesser 1980; Selänne 2003). *Schizogalerix voesendorfensis* is not directly integrated in this lineage, but in the morphologically close *S. voesendorfensis*-*S. zapfei*-*S. moedlingensis* lineage (in which Selänne (2003) includes the *Schizogalerix* species of the MN 12 and 13 from Greece).

The locality Vösendorf (type locality of *S. voesendorfensis*) belongs to Middle Pannonian sediments of the mollusc *Mytilopsis czjzeki* Zone (= *Congeria suglobosa*-“Zone” in Rögl & Daxner-Höck 1996) with an age between 10.3 and ~10.5 Ma (Harzhauser et al. 2004).

The Swiss locality Nebelbergweg, also containing this *Schizogalerix* species, cannot be at present dated with absolute accuracy. Based on the evolutionary level of the rodent *Collimys longidens*, this locality may be younger than Hammerschmiede in Germany (Mayr & Fahlbusch 1975, containing *C. hiri*), but slightly older than the Hungarian Felsötarkany 3/2 (containing *C. dobosi* Prieto & Rummel 2009), and may be similar in age as the fauna from Felsötarkany-Felnémet (Hír 2006, 2007).

Prieto et al. (in prep.) describe from Gratkorn a new species of Cricetodontinae which is interpreted as the ancestor of *Cricetodon klariankae* Hír, 2007 from Felsötarkany-Felnémet. Following this proposal, Gratkorn has to be older than Nebelbergweg. Based on terrestrial gastropod and geologic evidences, Harzhauser et al. (2008) date Gratkorn at around 12 Ma. Thus the Gratkorn specimens can be interpreted as the first occurrence of *Schizogalerix voesendorfensis*. This will imply that *Schizogalerix voesendorfensis* shows no major evolutionary changes between Gratkorn and Vösendorf, in a time-span ranging from ~10.5 to 12 Ma.

Desmanodon fluegeli is a new species which cannot be certainly integrated in the Anatolian lineage *D. minor* / *D. major* and its stratigraphic value is therefore limited.

Dinosorex sp. cannot be directly related to a previously described species, although some similarities with *D. engesseri* from the Upper Miocene (MN 9-10) of Austria and Hungary are evident. However, the material from Gratkorn also seems to be similar to the species from Nebelbergweg. The correlation of the Swiss locality is difficult but it is certainly older than the reported sites containing *D. engesseri*.

The bat cf. *Myotys* sp. does not provide any stratigraphic information.

5. Geographical variations

The insectivore fauna from Gratkorn seems to be related to eastern European / Anatolian faunas. The most impressive species illustrating this observation is *Desmanodon fluegeli*, which shares several morphologic features with *D. minor* / *D. major* from the Turkey, although it cannot be directly integrated in this lineage. This can be interpreted as parallel evolution between lineages of the two regions, maybe as allo-or parapatric speciation modes. Indeed Engesser (1980) interprets the resemblance between Turkish and Austrian *Schizogalerix* as such a parallel evolution. In the NAFB, the first unequivocal occurrence of *Schizogalerix* is found in Nebelbergweg, a locality which can be confidently considered younger than Gratkorn. In the locality Hammerschmiede, also older than Nebelbergweg, *Schizogalerix* is absent. In the much older deposits of Anwil, Kleineisenbach and Giggenhausen (~13.2 My), the genus is missing, but another galericine, *Parasorex socialis* is present. At present, it can be hypothesised that *Schizogalerix* is an immigrant in the NAFB, from eastern origin, which might explain the resemblances of the Nebelbergweg specimen with the Austrian lineage.

6. Environmental and ecological implications

With four species, the α-diversity of the Gratkorn insectivores is low. The difference with Anwil, for example, is impressive (13 species, Engesser 1972). A bias due to insufficient collected material can be excluded since the chiropterans, which are generally extremely rare in the stratified deposits, are recorded in Gratkorn. This low diversity may be better explained by taphonomic bias. Indeed the small mammal remains in this locality were largely accumulated by owl, as proved by the find of fossilized pellet remains. Furthermore, these finds indicate that the pellets were not transported before fossilisation because even transport of small distance can rapidly disintegrated them and lead to the dispersal of the animal remains (for example Terry 2004). It may indicate that the prey accumulation illustrates local conditions, in which the alimentary preferences of the owls, size and abundance of the prey for example, are extremely reflected.

The ecological preferences of the galericines are still a subject of debate. Based on the ecology of extent gymnures from South-east Asia, Ziegler (2005b: 150) proposed that the galericines have preferred moist forested areas and explain their wide geographic distribution in the Miocene by a wide distribution of their habitat. By this, he challenges the interpretation of Van den Hoek Ostende (2001) who proposes a larger panel of ecologic adaptations for the Galericini.

The presence of large samples of *Parasorex socialis* in Middle Miocene fissure fillings of the Franconian Alb, fossil sites which are reputed to be dryer than the contemporary sites of the NAFB, is explained by Ziegler (2005b) by the hunting facilities of the owls in the basin. This seems somewhat exaggerated. Indeed the deposit place of isolated pellets can be extremely distant from the capture place of the prey (Kowalski 1990), but the accumulation of a large number of pellets is mostly found around the bird nests. Michelat & Giraudoux (1991) studied the hunting patch of *Tyto alba* during the nesting using radio senders. They conclude that the owl never exceed the distance 5.6 km for its hunt (1.5 km on average).

The northern limit of the NAFB deposit in Germany is found in Adelschlag (MN 5, Reichenbacher et al. 2004). If this limit is assumed to be the same at the time of fossil accumulation in Petersbuch, the minimal distance to attain the basin from Petersbuch would be 10 km, which seems to be too far for the owls compared with modern conditions. Alternative hypothesizes can be proposed to explain the presence of *Parasorex* in the Petersbuch fissures:

- *Parasorex socialis* could have been adapted to the environmental conditions of the Frankonian Alb (environmental differences between plateau and basin were not significant or the species was an ubiquiste).
- Temporary migrations of *Parasorex* in the Franconian Alb can also be hypothesized (dispersal phase period of the young for example, Prieto 2007).

Van den Hoek Ostende (2001) listed a series of dental characters in which *Parasorex* and *Schizogalerix* differ from *Galerix*. Since these characters lead in the enlargement of the grinding surface, he interprets them as an adaptation to a more herbivorous diet. Furthermore, he remarks on the high position of the condyle of the lower jaws of *Parasorex ibericus*. The high position of the condyle is in extant desman moles a character of more herbivorous diet (Rümke 1985). Indeed Van den Hoek Ostende uses for his observation two species of *Galerix* (*G. exilis* and *G. stehlini*) and one species of *Parasorex*. The ascending ramus is preserved in *P. socialis* mandibles of Petersbuch 6 (Fig. 5 and Ziegler 2005b: fig. 1B). In this species the condyle is higher positioned than in *G. exilis* but the height difference is clearly smaller than in *P. ibericus*. The resemblance between the *P. socialis* and *S. voesendorfensis* mandibles are impressive (Figure 3), which permits one to hypothesize that the two species could have had a comparable diet.

Schizogalerix is by far the most common small mammal in the Gratkorns sample, followed by a new Cricetodontinae species (Prieto et al. in prep.). Both species are relatively large small mammals and correspond in their size. From this observation we can conclude that they also corresponded in their ecology and abundance within the optimal prey type for the owls, which avoid close forested area during their hunt (Michelat & Giraudot 1993).

Desmanodon fluegeli n. sp. is the only mole recorded in Gratkorn. Although taphonomical biases have to be taken in account (see above), it is interesting to notice that *Desmanodon* is also the only talpid found in the Early and lower Middle Miocene of Spain (Van den Hoek Ostende 2003: 300). During this time (Spanish zone B to Da) relatively humid conditions are proposed (Van der Meulen & Daams 1992; Van den Hoek Ostende 2003). Prieto (in press) describes a new *Desmanodon* species from the late Middle Miocene from Germany. Based on faunal differences with the contemporaneous Swiss locality Anwil, where this species is missing, he concludes that the mole avoids lake environments. Furthermore, the morphology of the *Desmanodon* humerus indicates that the animal was not extremely adapted to fossorial life-style. The vertebrate producing layer at the base of the clay pit of Gratkorn corresponds to a paleosol showing root traces. Gross et al. (2007) interpreted these strata to be deposits of a vegetated alluvial plain with a moist soil cover and open areas. This reconstruction agrees with the hypothesized ecological preferences of *Desmanodon*.

7. Conclusions

The insectivores from Gratkorn illustrate a new faunal evolutionary level in Austria and are therefore of primary importance for the comprehension of the faunal evolution and exchanges in the late Middle Miocene of Central Europe. Furthermore, the excellent preservation of the bony and dental remains in this locality allows one to approach determining the ecology of these extant species. The fauna from Gratkorn contains a very large panel of vertebrates (small and big mammals, reptilians, amphibians, birds, Gross et al. 2009) and will, in the near future, permit greater understanding of environmental and climatic conditions in the Late Sarmatian of Central Europe.

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