Ruminantia from the Grund Formation: correlation of continental and marine deposits and climatic development during early Middle Miocene of the Central Paratethys (Austria)

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Abstract: The Badenian marine littoral Grund Formation at Grund in the Molasse Zone of Lower Austria provided marine and terrestrial faunas in the same strata. They allowed correlation between continental and marine biozonations of the European Middle Miocene. In the present paper for the first time the included fossil remains of Ruminantia are described in detail. Six isolated teeth and nine postcranial skeletal elements are determined as Ruminantia indet., Pecora indet., cf. *Micromeryx flourensianus* Lartet, 1851, *Micromeryx* cf. *styriacus* Thenius, 1950, and cf. *Eotragus clavatus* (Gervais, 1850). The biochronological age indicated by cf. *M. flourensianus*, *M.* cf. *styriacus* and cf. *E. clavatus* is restricted to the European mammal zones late MN5 to MN6. Consequently the hitherto identified age of late MN5 for these sediments is confirmed by the occurrence of the Ruminantia represented. The taxonomic composition further indicates paleoecological conditions compatible with earlier reconstructions of the environment as either islands or the elevated parts of a peninsula or rising terrain of the hinterland. In any of these settings groundwater levels would have been low and the vegetation a covering of woods, bushes and shrubs. Comparisons with Austrian ruminant faunas of the early MN5/late Karpatian (Obergänserndorf and Teiritzberg) support the interpretation of a change during MN5 towards a drier climate under more or less stable temperatures in Central Europe.

Key words: Middle Miocene, Lower Badenian, Molasse Zone, Grund Formation, paleoecology, biostratigraphy, taxonomy, dry wooded habitat, Ruminantia.

Introduction

Excavations in the type area of the Lower Badenian marine littoral Grund Formation at Grund near Hollabrunn in Lower Austria (Fig. 1) by the Institute of Paleontology of Vienna University from 1998 to 2000 provided a vertebrate assemblage poor in specimens but diverse in species (Roetzel 2003; Daxner-Höck et al. 2004). Its outstanding character is the syn-occurrence of marine and terrestrial vertebrates in isochronous sediments. Biostratigraphically the Grund-Formation belongs to the regional Lower Lagenid Zone (Lower Badenian) based on the evolutionary level of *Praeorbulina glomerosa circularis* and therewith to the top of the Planktonic Foraminifera Zone M5b/Mt5b (Rögl & Spezzaferri 2003) (Fig. 2). The co-occurrence of the nannofossils *Sphenolithus heteromorphus* and *Helicosphaera waltrans* in the section Mühlbach of the Gaindorf Formation (Ćorić 2003), which is a lateral equivalent (Roetzel 2003) indicates the Calcareous Nannoplankton Zone NN5 (Harzhauser et al. 2002) (Fig. 2). According to Daxner-Höck (2003) the terrestrial vertebrate assemblages are representative for the later part of the European Land Mammal Zone MN5. A major part of the vertebrate remains have been investigated and are already published in a special volume of "Annalen des Naturhistorischen Museums in Wien, 104/A". The remains of Ruminantia and a preliminary determination were hitherto only briefly mentioned in Daxner-Höck et al.

(2004). In the present paper the ruminant specimens from Grund are described in detail, determined as exactly as possible, and assessed biochronologically.

Material and methods

The available material of Ruminantia from Grund comprises six isolated teeth and nine postcranial specimens. Determination at species level can be attempted for the teeth, based on extensive and reliably determined material from different European localities. Comparisons of the postcranial specimens are difficult or even impossible, because postcranials have been described more rarely than dentitions and because reliable species determination of postcranials in taxonomically diverse collections have not been done. Therefore the ruminant postcranials from Grund are described and compared within these limitations, mainly based on material housed in the Bavarian State Collection of Paleontology and Geology Munich, and are determined only at a higher systematic level. The Grund fossils are housed in the collection of the Geological-Paleontological Department, Museum of Natural History, Vienna (NHMW).

All measurements are given in mm. Manner of measurement in teeth and tooth crown terminology is according to Rössner (1995).
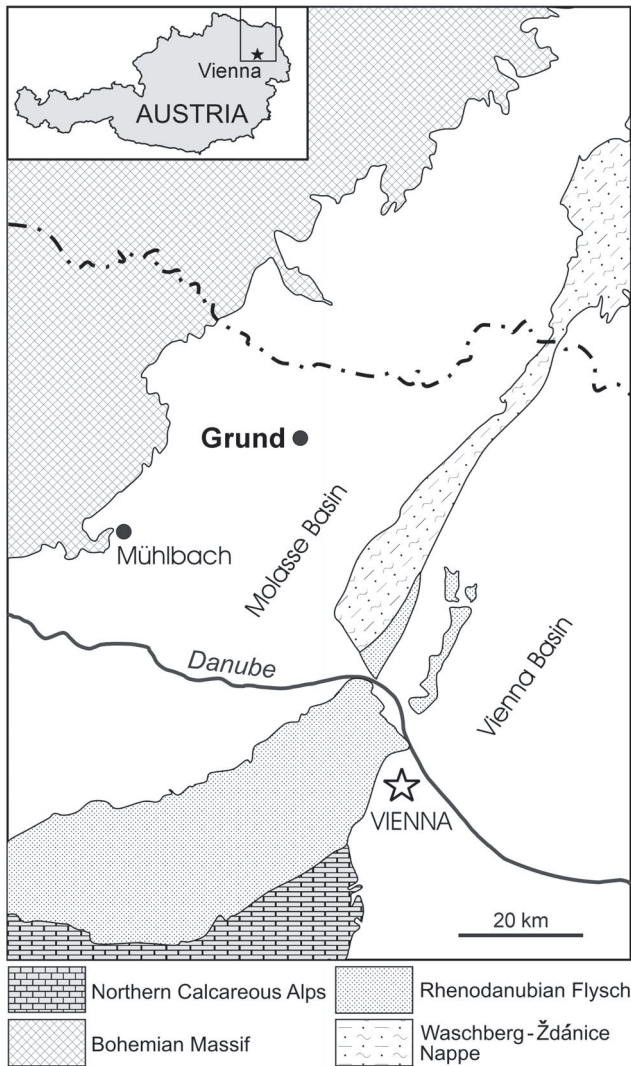
Fig. 1. Geological sketch of the Alpine-Carpathian Foredeep in northeastern Austria, and the position (asterisk) of the investigated site (taken from Harzhauser et al. 2003).

Abbreviations: **apd** — largest anterior-posterior diameter distal; **app** — largest anterior-posterior diameter proximal; **aw** — anterior width; **l** — largest length; **pw** — posterior width; **td** — largest transversal diameter distal; **tp** — largest transversal diameter proximal; **w** — largest width.

Systematic Paleontology

Suborder **Ruminantia** Scopoli, 1777

Ruminantia indet. 1

Material: NHMW GRU-B/-1 13, atlas (l = 26.8; td = min. 42.3); Fig. 7A.
Description: Nearly completely preserved atlas of a small ruminant. The most lateral and most delicate parts of the wings are missing and the specimen is slightly corroded. The

shape is trapezoidal. The dorsocaudal Tuberculum dorsale is blunt. Dorsally laterocranially the Foramen alare and Foramen vertebrale laterale are close together and well rounded. There is no Foramen transversarium developed.
Discussion: The absence of a Foramen transversarium clearly indicates a member of the Ruminantia. A more precise determination is impossible.

Ruminantia indet. 2

Material: NHMW GRU-B/-1 15, left intermediale (l = 11.8; td = 14.5); Fig. 7D.
Description: The over all specimen is slightly corroded. The proximal articular surface extends far palmarly. It is differentiated into a large volar and a small palmar part, which consist both of a convex dorsal and a concave palmar morphology. The distal articular surface consists of a dorsal convex and a volar concave part. At the convex surface a blunt median crest separates the articular surfaces for Carpale 3 and Carpale 4. Generally the lateral and medial articular outlines are concave. The size is comparably small.
Discussion: All characters indicate Ruminantia. A more precise determination is impossible.

Infraorder **Pecora** Linné, 1758

Pecora indet. 1

Material: NHMW GRU-F 11, proximal phalange III or IV (l = 33.7; tp = 11.6; app = 13.4; td = 7.3; apd = 7.0); Fig. 7E.
Description: The small to medium sized phalange is robust. The surface of the internal side is very rough and marks the insertion of a strong interdigital ligament. The dorsal profile line is convex. The transversal diameter is relatively short and produces a slender shape. Respectively the proximal articular surface is slender with a wide incision for the metapodial Verticillus running from plantar/palmar to dorsal; interdigital as well as exterior part have the same width. Proximointerdigitally a shallow ligament groove for the proximal interdigital ligament is developed.

Interdigital and exterior part of the distal articular surface are of the same size. The interdigital part extends a little more dorsally than the exterior part. The median groove runs slightly from exterior to interdigital. The lateral outline of the pulley is well rounded volarly/plantarly and distally, but flat dorsally. The exterior ligament groove is shallow and rounded, the interdigital one is deeper and elongated.
Discussion: The morphology differs clearly from tragulids in which the incision for the metapodial Verticillus does not reach the dorsal edge as well as the pulley is relatively shorter and wider and has a different shape of the articular surface. Within higher pecoran groups Cervidae show the most similar morphotype (see Köhler 1993). The exterior part of the proximal articular surface clearly extends more proximally than in the small to medium sized Cervidae *Procervulus dichotomus* (Rauscheröd, Germany, MN4, Rössner 1995) and *Heteroprox* (Sandelzhausen, Germany, MN5, Rössner 1997, 2002, 2004). The distal articular surface is distally less wide, possibly a result of corrosion but this is not certain. For the
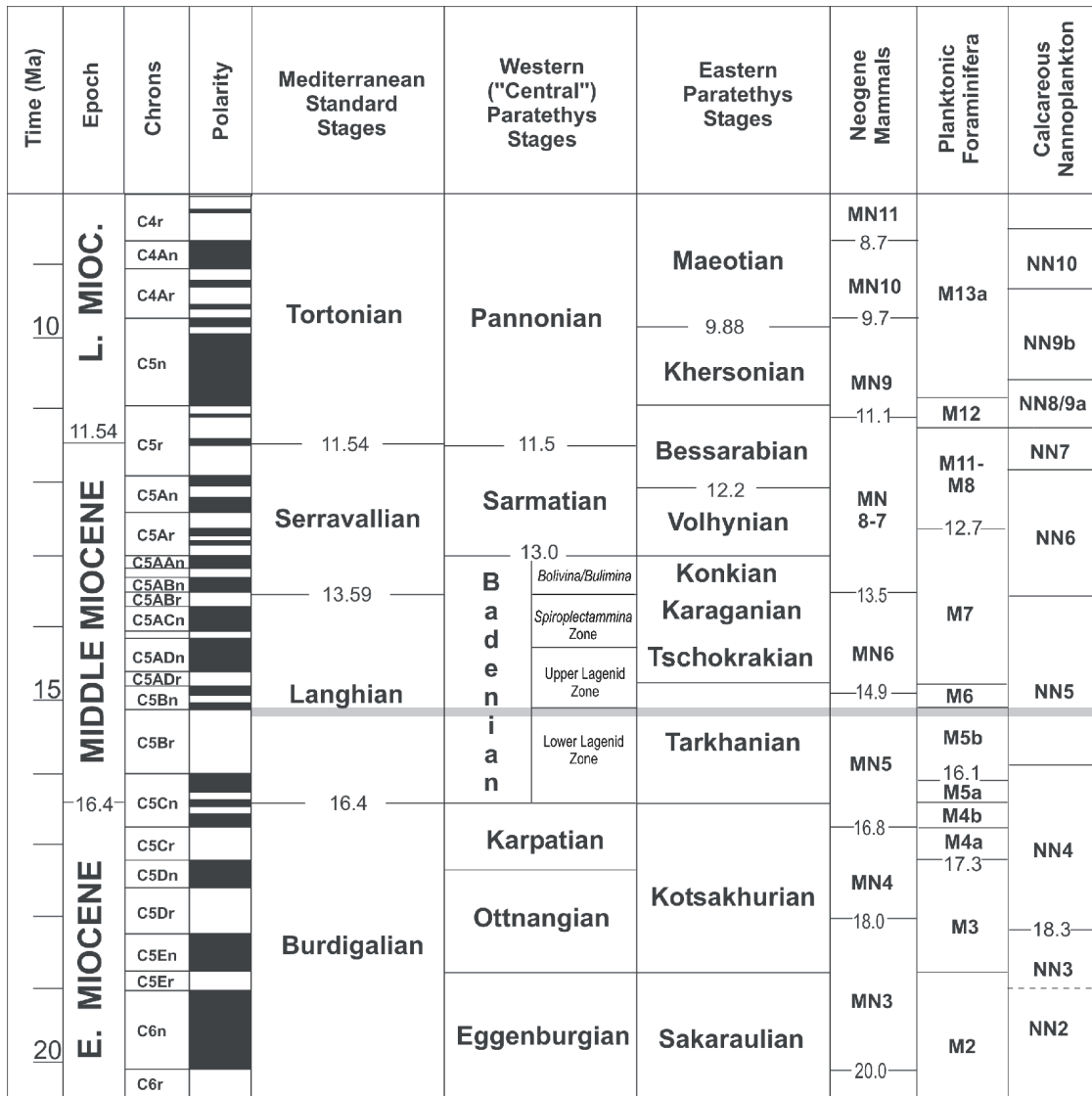
Time (Ma)	Epoch	Chrons	Polarity	Mediterranean Standard Stages	Western ("Central") Paratethys Stages	Eastern Paratethys Stages	Neogene Mammals	Planktonic Foraminifera	Calcareous Nannoplankton
	L. MIOC.	C4r					MN11		
		C4An			Pannonian	Maeotian	— 8.7 —	M13a	NN10
10		C4Ar		Tortonian			MN10		NN9b
		C5n				— 9.88 — / Khersonian	— 9.7 — / MN9		NN8/9a
11.54	MIDDLE MIOCENE	C5r		— 11.54 —	— 11.5 — / Bessarabian	— 11.1 —	M12	NN7
		C5An			Sarmatian	— 12.2 —	MN 8-7	M11-M8	
		C5Ar		Serravallian		Volhynian		— 12.7 —	NN6
		C5AAn / C5ABn / C5ABr / C5ACn		— 13.59 —	— 13.0 — / Badenian — Bolivina/Bulimina / Spiroplectammina Zone	Konkian / Karaganian	— 13.5 —	M7	
15		C5ADn / C5ADr / C5Bn		Langhian	Upper Lagenid Zone	Tschokrakian	MN6 — 14.9 —	M6	NN5
		C5Br			Lower Lagenid Zone	Tarkhanian	MN5	M5b — 16.1 — M5a	
16.4		C5Cn		— 16.4 —			— 16.8 —	M4b / M4a — 17.3 —	NN4
	E. MIOCENE	C5Cr			Karpatian	Kotsakhurian	MN4		
		C5Dn					— 18.0 —	M3	— 18.3 —
		C5Dr		Burdigalian	Ottnangian				NN3
		C5En					MN3		
		C5Er			Eggenburgian	Sakaraulian		M2	NN2
20		C6n					— 20.0 —		
		C6r							

Fig. 2. Early to Late Miocene geochronology and biostratigraphy (taken from Daxner-Höck 2004 after Harzhauser et al. 2003). The shaded area indicates the stratigraphic position of vertebrate-bearing samples from the Grund Formation.

time being the most precise determination possible is Pecora indet.

Pecora indet. 2

Material: NHMW GRU-F 12, distal fragment of proximal phalange (tp = 14.4; app = 11.9); Fig. 3.

The interdigital part of the distal articular surface is wider than the exterior part and extends more distally and dorsally. The facet of the distal articulation is well visible from the dorsal aspect. The outline of the pulley is flattened from the distal and the volar aspect. The exterior ligament groove is shallow and rounded, the interdigital one is deeper and elongated. The dorsal transversal diameter of the pulley is wider than in specimen GRU-F 11.

Discussion: In tragulids the pulley is proximally shorter. The size is similar to *Heteroprox* n. sp. from Sandelzhausen (Germany, MN5, Rössner 1997, 2002, 2004), but the

specimen is too incomplete to allow a more detailed comparison. Hence within Pecora a precise determination is not yet possible.

Pecora indet. 3

Material: NHMW GRU-B/-1 10, proximal fragment of right ulna; Fig. 7B.

Description: The specimen is slightly corroded and belonged to a small ruminant. The proximal Tuber olecrani is absent. It is not possible to decide, if this either might indicate an immature stage or simply an incomplete preservation. Cranially the articular area is characterized by a prominent proximocranial ridge, by a shallow lateral groove in the middle part, by a prominent laterodistal appendage, and a small non-prominent mediodistal articular surface.

Discussion: The morphology differs by a less prominent laterodistal appendage from small tragulids.

Fig. 3. NHMW GRU-F 12, Pecora indet. 2, distal fragment of proximal phalange. **A** — external view, **B** — internal view, **C** — distal view, **D** — dorsal view. Scale bar 5 mm.

Pecora indet. 4

Material: NHMW GRU-B/-1 14 proximal fragment of proximal phalange, (td = 7.7; apd = 6.8); Fig. 7C.

Description: The specimen is slightly corroded and medium sized. The transversal diameter is comparably small and produces a slender proximal articular surface. The incision for the metapodial Verticillus is shallow and wide. The interdigital part of the articular surface is slender and shows the strongest palmo/plantointerdigital extension of the whole articulation area. Laterally no articulation surface is developed. Laterodorsally a ligament groove is present. This proximal phalange differs clearly from specimen GRU-F 11, Pecora indet. 1, in morphology and a little larger size.

Discussion: The subdivided articular surface is typical for pecorans in contrast to the tragulids with an incompletely divided articular surface. The lack of marginal articular surfaces is untypical for moschids, cervids, bovids and palaeomerycids. This might indicate a phalange of a side digit (II or V), what further would indicate a large individual, considered the medium size of the specimen and consequently larger phalanges of ray III or IV. For the time being the specimen can only be set in Pecora indet.

Family **Moschidae** Gray, 1821
Genus *Micromeryx* Lartet, 1851

cf. *Micromeryx flourensianus* Lartet, 1851

Material: NHMW GRU-F 1, sin M1 (l = 6.1; aw = 6.8; pw = 6.8); Fig. 6A. NHMW GRU-F 2, dex M2 (l = 6.4; aw = 7.0; pw = 6.8); Fig. 6B. NHMW GRU-F 3, sin m1 (l = –; aw = –; pw = 4.3); Fig. 6C. NHMW GRU-F 4, dex P4 (l = 4.2; w = 5.2); Fig. 6D.

Description: Specimens GRU-F 1 and GRU-F 2 are medium worn. Their morphology is seleno-brachyodont and their size is relatively small. Parastyle, mesostyle and the paracone column are strong and they are not connected at the base. There are weak anterior cingula and entostyles. Specimen GRU-F 1 shows a spur of the posthypocrista and a neocrista.

GRU-F 3 and GRU-F 4 are strongly worn and have lost their morphological details. Moreover specimen GRU-F 3 lacks its most anterior part and specimen GRU-F 4 lacks its most lingual part.

Discussion: Based on the small size those teeth might belong to the selenodont-brachyodont European ruminants *Pomelomeryx gracilis* (Pomel, 1853) (Moschidae) (Rössner & Rummel 2001), *Tuscomeryx huerzeleri* Abbazzi, 2001 (Moschidae), *Micromeryx flourensianus* Lartet, 1851 (Moschidae), *Micromeryx styriacus* Thenius, 1950 (Moschidae), *Hispanomeryx aragonensis* Azanza, 1986 (Bovoidea), *Hispanomeryx duriensis* Morales, Moyà-Solà et Soria, 1981 (Bovoidea), *Lagomeryx pumilio* Roger, 1896 (Cervidae), and *Lagomeryx parvulus* (Roger, 1898) (Cervidae). Distinctive morphological details are no longer preserved except for the shape of the teeth. Compared with *P. gracilis*, *L. pumilio* and *H. duriensis* the teeth show a different shape in the upper molars (less square) and the P4 (more symmetrical). Moreover *L. pumilio* is smaller than the specimens from Grund. In *Micromeryx styriacus*, *Tuscomeryx huerzeleri*, and *L. parvulus* the shape is the same, but the size is larger. *Hispanomeryx aragonensis* is only known from lower teeth, but estimated from those, it might come close in size. *M. flourensianus* show the same shape and size. Hence several of the postcranial elements differ from *Hispanomeryx* but resemble *M. flourensianus* therefore the specimens GRU-F 1, GRU-F 2, GRU-F 3, and GRU-F 4 most likely belong to *M. flourensianus*. But because of further missing morphological species characters (crown height, closed anterior valley in p4, third lingual conid of m3, dorsodistally closed gulley of the metatarsal III + IV; Gentry et al. 1999) the present determination is cf. *M. flourensianus*.

Material: NHMW GRU-Kroh 9, middle phalange (l = 13.5; tp = 4.7; td = 3.1); Fig. 4A.

Description: The phalange is small as well as comparatively long and slender within ruminants (see Köhler 1993). In exterior view the proximal articular surface is strongly concave. The "Plateau Postarticulaire" (Heintz 1970) is proximally elongated. The dorsal extensor process is short. In interdigital view the outline of the distal articular surface is well rounded. Volarly it extends only a little and dorsally strongly. The interdigital part of the distal articulation is slightly elongated. The volar surface includes distally a shallow sagittal groove.
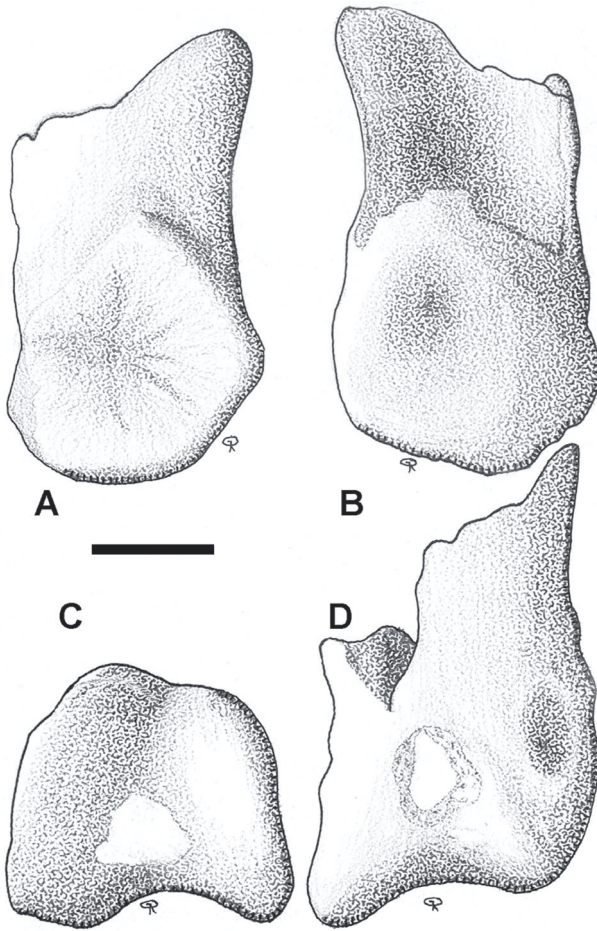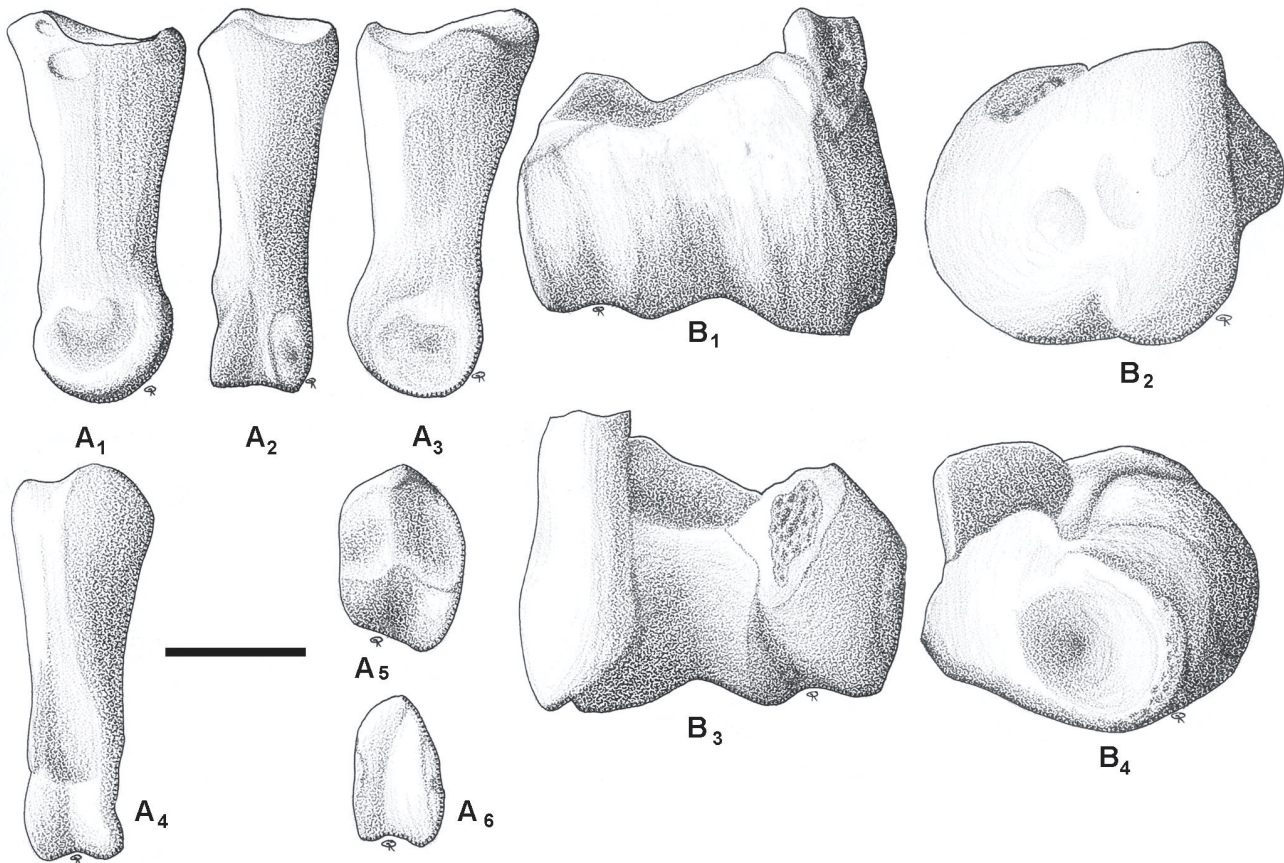
Fig. 4. cf. *Micromeryx flourensianus*. **A** — NHMW GRU-Kroh 9, middle phalange. A₁ — external view, A₂ — dorsal view, A₃ — internal view, A₄ — plantar or palmar view, A₅ — proximal view, A₆ — distal view. **B** — NHMW GRU-Kroh 8, right Condylus humeri. B₁ — cranial view, B₂ — medial view, B₃ — caudal view, B₄ — lateral view. Scale bar 5 mm.

The outstanding slenderness of the proximal articular surface fits with the slenderness of the distal articular surface of specimen GRU-F 11. But the size is a little bit too small. Possibly specimen GRU-Kroh 9 is an anterior phalange and specimen GRU-F 11 is a posterior phalange of the same species.

Discussion: Generally this specimen differs from Tragulidae by its slenderness. Moreover in Tragulidae the proximal articular surface does not have an elongated "Plateau Postarticulaire". Its delicate size combined with its slenderness is comparable to a phalange of *Micromeryx flourensianus* figured by Filhol (1891, Pl. 25, Figs. 1–2), but unlike *Hispanomeryx duriensis* Morales et al. 1981 (Pl. 1, Fig. 7). All Middle Miocene Bovidae can be eliminated, because of a general larger body size. The smaller cervids from that time might be a possible source. *Lagomeryx parvulus* as well as *Lagomeryx pumilio* from Sandelzhausen (Germany, MN5, Rössner 1997, 2002, 2004) show little differences in size and significant in shape. From *Euprox minimus* (Toula, 1884) no middle phalange is known, but it would be probably most similar to *L. parvulus*. Therefore the most precise determination what can be given is cf. *Micromeryx flourensianus*.

Material: NHMW GRU-Kroh 7, distal fragment of left humerus (td = 13.9; apd = 11.4); Fig. 7F. NHMW GRU-Kroh 8, right Condylus humeri (td = 13.5; apd = 10.3); Fig. 4B.

Description: The specimens belong to a comparatively small ruminant. The body is slender without prominent crests or obvious rough areas. The mediodistal Epicondylus medialis is strong with a sagittal ligament groove distally. The Condylus humeri shows medially a narrow rounded shallow ligament groove and the Capitulum humeri shows laterally a wide rounded deep ligament groove. The diameter of the Trochlea medially is twice as large as the one of the Capitulum laterally. The sagittal crest of the Condylus is rounded.

Discussion: The size of the specimen indicates a small ruminant. The small tragulid *Dorcatherium guntianum* Meyer, 1846 differs by a larger size and a different morphology of the Capitulum humeri (Hambach, Germany, MN5, Mörs 2000). The moschids *Pomelomeryx gracilis* and *P. boulangeri* (Pomel, 1853) as well as the cervids *Lagomeryx pumilio* and *L. parvulus* can be excluded from the determination: In *P. gracilis* and *P. boulangeri* from Wintershof-West (Germany, MN3, Rössner 1997, 2002) the Condylus medially has the same width but a larger height, in *L. pumilio* and *L. parvulus* from Sandelzhausen (Germany, MN5, Rössner 1997, 2002, 2004) the Condylus is morphologically identical, but larger. *Hispanomeryx duriensis* differs in morphology with a more pronounced Verticillus (Morales et al. 1981, Pl. I, Fig. 11). Morphologically and in size this specimen is most similar to *Micromeryx flourensianus* (Fihol,

1851, Pl. XXV, Figs. 3, 4) with some uncertainties left from the comparison with a figure.

Micromeryx cf. s*tyriacus* Thenius, 1950

Material: NHMW GRU-Kroh 5, dex M2 (l = 7.4; aw = 7.6; pw = 7.3); Fig. 5A.

Description: The seleno-brachyodont tooth is very well preserved and only weakly worn. It is relatively small. Its shape is nearly square and usur facets are developed anteriorly and posteriorly, which indicates an M2 (see Rössner 1995: Table 2). Its styles and the column of the paracone are slender and not connected at the base. A short but clear anterior cingulum is developed. The spur of the posthypocrista is strong and the Neocrista is poorly developed sitting at the end of the post-protocrista. The entostyle is small.

Discussion: This small-sized brachyodont ruminant is similar to the European Early to Late Miocene moschids *Pomelomeryx gracilis*, *Micromeryx flourensianus*, *Micromeryx styriacus*, and *Tuscomeryx huerzeleri*, the Early to Middle Miocene cervids *Lagomeryx parvulus* and *L. pumilio*, as well as the Middle and Late Miocene bovoids *Hispanomeryx aragonensis* and *H. duriensis*. It differs from *P. gracilis*, *L. parvulus* and *L. pumilio* by a slightly higher crown as well as more slender styles and paracone-column. The labial crown base is less bulging than in the latter species. Specimen GRU-Kroh 5 is a little bit larger than *M. flourensianus* from Sansan (type locality, France, MN6) and a little bit smaller than *T. huerzeleri* as well as *H. duriensis*. It might fit in the size class of *M. styriacus* from Göriach (type locality, Austria, MN5), which is slightly larger than *M. flourensianus*, but only recorded by an m3, an m2 and a p4 (Hofmann 1893; Thenius 1950) and still discussed as sexual dimorphism within *M. flourensianus*. Hence direct comparison is not possible for the time being specimen GRU-Kroh 5 is described as *Micromeryx* cf. *styriacus*. It can not be compared with incomplete remains of *H.*
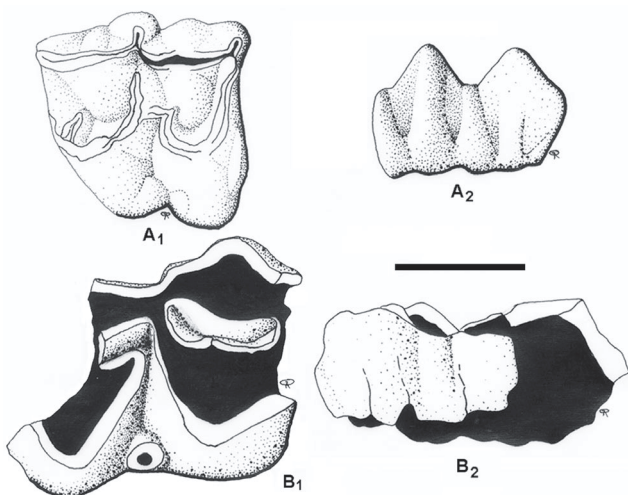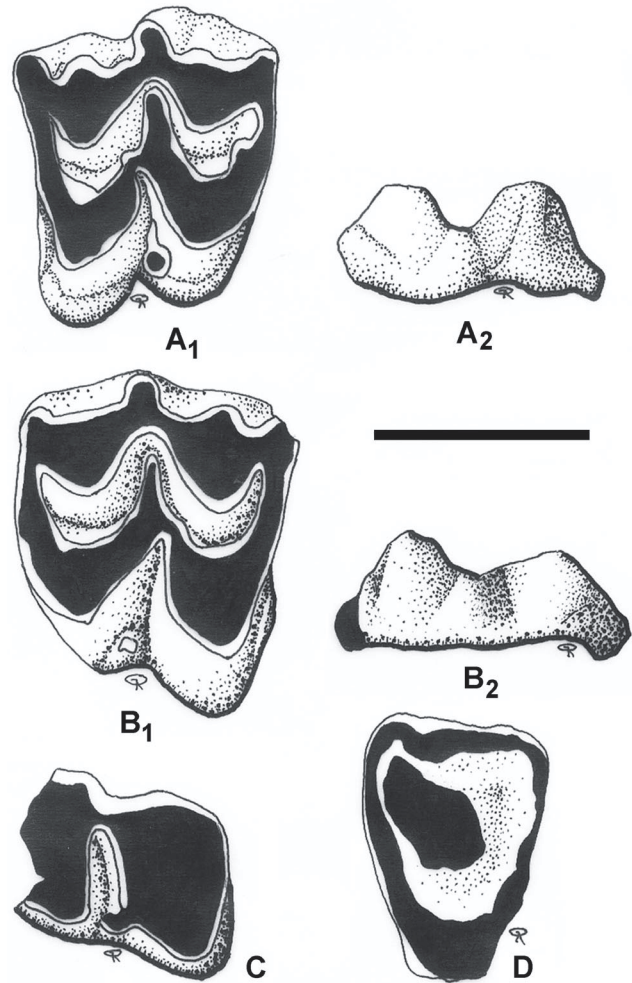

Fig. 6. A — NHMW GRU-F 1, cf. *Micromeryx flourensianus*, sin M1. A$_1$ — occlusal view, A$_2$ — labial view. **B** — NHMW GRU-F 2, cf. *Micromeryx flourensianus*, dex M2. B$_1$ — occlusal view, B$_2$ — labial view. **C** — NHMW GRU-F 3, cf. *Micromeryx flourensianus*, sin m1, occlusal view. **D** — NHMW GRU-F 4, cf. *Micromeryx flourensianus*, dex P4, occlusal view. Scale bar 5 mm.

aragonensis (see above), but the exclusively Spanish abundance of the latter one, makes this assessment improbable.

Family **Bovidae** Gray, 1821
Genus *Eotragus* Pilgrim, 1939

cf. *Eotragus clavatus* (Gervais, 1850)

Material: NHMW GRU-Kroh 6, dex m1/2/3 (l = –; aw = 9.1; pw = –); Fig. 5B.

Description: The tooth is strongly worn and only partially preserved. The morphology is selenodont-brachyodont with a barely recognizeable metastylid characteristic for selenodont ruminants. There is no trace of a *Palaeomeryx*-fold.

Discussion: Compared to its wear stage the tooth is still relatively high crowned. Metastylid and praeentoconid are fused, which indicates also a relatively higher crown within the selenodont-brachyodont ruminants. Moreover, the lack of the *Palaeomeryx*-fold limits the possible determinations to the
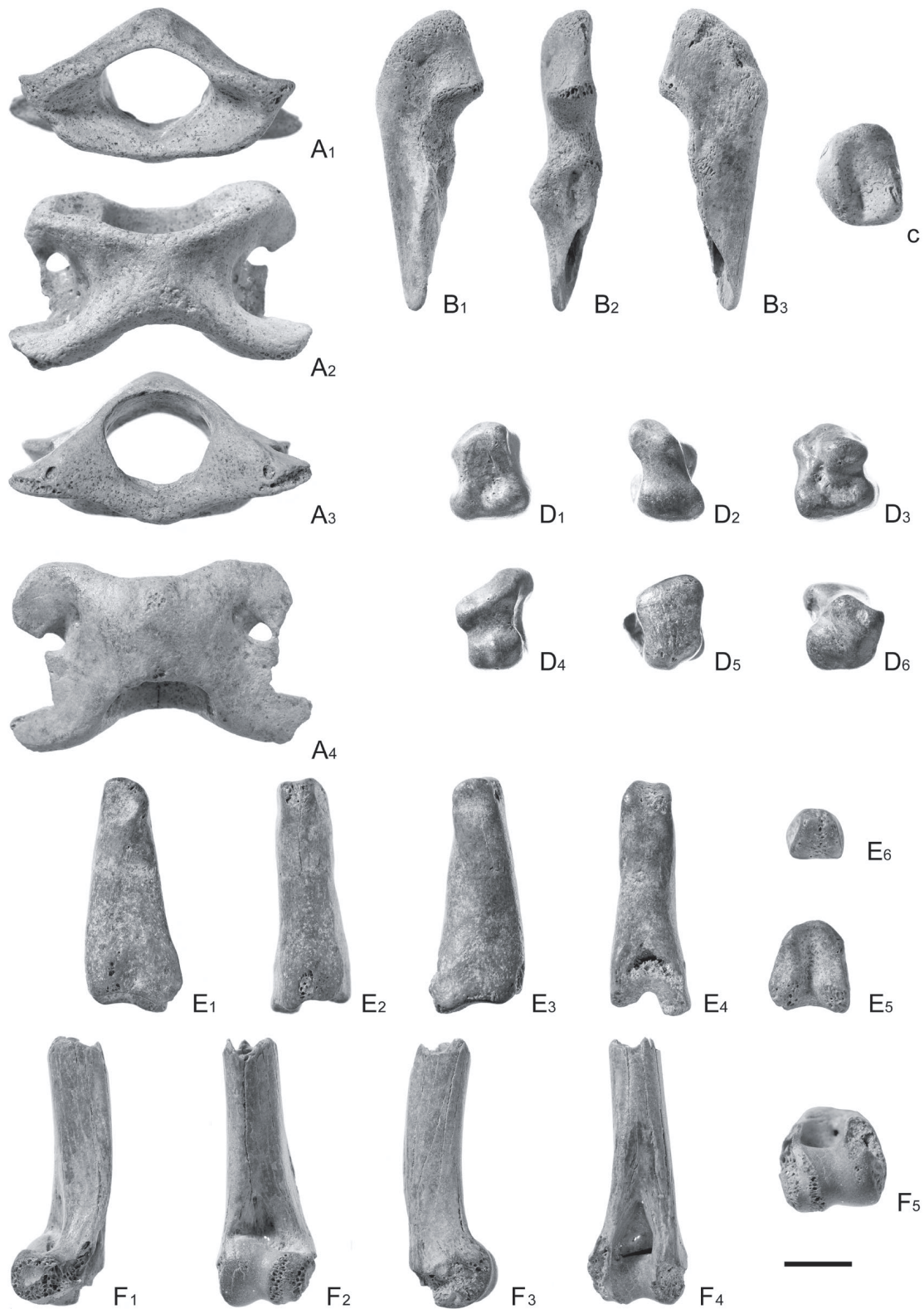

Fig. 5. A — NHMW GRU-Kroh 5, *Micromeryx* cf. s*tyriacus*, dex M2. A$_1$ — occlusal view, A$_2$ — labial view. **B** — NHMW GRU-Kroh 6, cf. *Eotragus clavatus*, dex m1/2/3. B$_1$ — occlusal view, B$_2$ — labial view. Scale bar 5 mm.

Fig. 7. A — NHMW GRU-B/-1 13, Ruminantia indet. 1, atlas. A_1 — cranial view, A_2 — ventral view, A_3 — caudal view, A_4 — dorsal view. B — NHMW GRU-B/-1 10, Pecora indet. 3, proximal fragment of right ulna. B_1 — lateral view, B_2 — cranial view, B_3 — medial view. C — NHMW GRU-B/-1 14, Pecora indet. 4, proximal fragment of proximal phalange, proximal view. D — NHMW GRU-B/-1 15, Ruminantia indet. 2, left intermediale. D_1 — lateral view, D_2 — proximal view, D_3 — medial view, D_4 — distal view, D_5 — dorsal view, D_6 — plantar view. E — NHMW GRU- F 11, Pecora indet. 1, proximal phalange III or IV. E_1 — internal view, E_2 — dorsal view, E_3 — external view. E_4 — plantar or palmar view, E_5 — proximal view, E_6 — distal view. F — NHMW GRU-Kroh 7, cf. *Micromeryx flourensianus*, distal fragment of left humerus. F_1 — lateral view, F_2 — cranial view, F_3 — medial view, F_4 — caudal view, F_5 — distal view. Scale bar 10 mm.

group of early comparably low crowned European Bovidae: *Eotragus artenensis* Ginsburg et Heintz, 1968, *Eotragus clavatus* (Gervais, 1850), *Eotragus cristatus* (Biedermann, 1873), *Pseudoeotragus seegrabensis* van der Made, 1989. *E. artenensis* is a little smaller and lower crowned. *P. seegrabensis* and *E. cristatus* are smaller, too. *E. clavatus* is of the same size and therefore specimen GRU-Kroh 6 is assigned to it. However, the incompleteness of the tooth makes it necessary to restrict the determination to cf. *Eotragus clavatus*. The bovoid *Amphimoschus* can be excluded because of a stronger ectostylid.

Discussion

Determinations exact enough for biochronological interpretation of the Ruminantia from Grund comprise *Micromeryx* cf. *styriacus*, cf. *Micromeryx flourensianus*, and cf. *Eotragus clavatus*. *M. styriacus*, *M. flourensianus* and *E. clavatus* are known from the stratigraphical context of Europe from the Mammal Zone MN5 onwards (Gentry et al. 1999). However their total occurrence spans differ: while *M. flourensianus* is known in Europe until MN11, *E. clavatus* persisted only to MN6, and *M. styriacus* is restricted to late MN5. In a whole, the biochronological age indicated by the ruminant fossils from Grund is restricted from MN5 to MN6, if we are careful with the *M.* cf. *styriacus*, or even to late MN5. Consequently the hitherto identified age of late MN5 for the terrestrial vertebrate assemblage from Grund (Daxner-Höck 2003), mainly based on the micromammal elements, is confirmed by the occurrence of the Ruminantia represented.

The marine microfauna from Grund corresponds to the Calcareous Nannoplankton Zone NN5, based on the co-occurrence of *Sphenolithus heteromorphus* and *Helicosphaera waltrans* (Ćorić 2003), and more precisely to the top of Planktonic Foraminifera Zone M5b/Mt5b, based on the evolutionary level of *Praeorbulina glomerosa circularis* and therewith to the top of the regional Lower Lagenid Zone (Lower Badenian) (Rögl & Spezzaferri 2003). The co-occurrence with the mammal assemblage placed in late MN5 makes Grund a reference tie point for marine/continental correlation in the Middle Miocene of the Central Paratethys (Harzhauser et al. 2003; Daxner-Höck et al. 2004).

The allochthonous nature of the remains of terrestrial vertebrates in the studied marine sections of Grund (Roetzel 2003; Roetzel et al. 1999) limits paleoecological interpretations to purely taxonomically related evidence. Even the poor ruminant record, as much in specimens as in species number, from Grund gives an insight into the composition of this assemblage. *Micromeryx* and *Eotragus* are typical representatives for terrestrial faunas from the early Middle Miocene of Europe. *Micromeryx* is an extremely long legged moschid (Gentry et al. 1999) with relatively long metapodials, what is typical for bovids living in open country (Scott 1985). For *Eotragus* a duiker-like habitus and mode of life in more or less dense forests (Köhler 1993; Rössner 2002) can be reconstructed. Their abundance usually is rare to medium depending on the local habitat structure. But in the case of Grund, they seem to be the major faunal elements. Interestingly cervids, which usually are the major component in European Miocene forest

communities (Rössner 1997, 2004), are not recorded by teeth. Of course they might be represented within the Pecora indet. or Ruminant indet. specimens. Moreover tragulids are missing, which are usually also a major component in European Miocene forest communities, but indicate strongly moist ground conditions in a habitat with lots of small open standing waterbodies (Köhler 1993; Rössner 1997, 2004). Their absence might be due to dry ground conditions. Considering all that, the deduced environment agrees with the reconstruction of Daxner-Höck (2003). She suggested a habitat with low groundwater level at either an elevated region of a Peninsula or islands or small mountains of the hinterland, which are covered with woods, bushes and shrubs.

Significant differences in species composition among Austrian faunas of the early MN5/late Karpatian (Obergänserndorf and Teiritzberg) and the late MN5 /early Badenian (Grund) were demonstrated by Daxner-Höck (2003) for the rodents. These led to the conclusion of changes from a humid to a more dry climate under similar temperature conditions (subtropical climate with a mean annual temperature of 14–17, frost free winters, a minimal cold month temperature of 3–8 °C, annual precipitation of approximately 2000 mm, Harzhauser et al. 2002) in Central Europe. The ruminants of Obergänserndorf and Teiritzberg comprise remains of Ruminantia indet., the tragulid *Dorcatherium crassum* and a cervid Procervulinae indet. (Rössner 1998), which support the idea of a more humid environment with dense forests for the late Karpatian.

Conclusions

The extraordinary case of a locality yielding marine and terrestrial faunas in the same strata made Grund a reference tie point for marine/continental correlation in the early Middle Miocene Central Paratethys (Lower Badenian). The terrestrial fauna includes fossil remains of Ruminantia, which strengthen the biostratigraphical correlation. The identification of the species cf. *Micromeryx flourensianus*, *Micromeryx* cf. *styriacus* and cf. *Eotragus clavatus* indicates an age from European Land Mammal Zone MN5 to MN6 and strongly supports the already established ages of late MN5 (micromammals) and the top of Planktonic Foraminifera Zone M5/Mt5b (top of the Lower Lagenid Zone).

The interpretation of the preferred environment of the represented Ruminantia supports the reconstruction of a woodland habitat and the previously assumed successive drying during MN5 in Central Europe.

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