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New data on Eomyidae and Gliridae (Rodentia, Mammalia) from the Late Miocene of Austria

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(With 21 figures and 15 table)

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Abstract

We report on three Eomyidae species and twelve Gliridae species from the Late Miocene of Austria. Among them are two new species, the eomyid *Keramidomys ermannorum* nov. spec. and the glirid *Paraglirulus schultzi* nov. spec. The fossils were recovered from eight localities in the Vienna Basin and the Austrian parts of the Northern Alpine Foreland Basin and the Pannonian Basin, ranging from the Early Vallesian (MN9 / Pannonian C) to the Early Turolian (MN11 / Pannonian H). They cover a time interval of three million years, i.e. from ~ 11.2 Ma to ~ 8.2 Ma. The diversity of Gliridae in the Late Miocene of Austria is relatively high, with highest species numbers in the Early Vallesian and the beginning of the Late Vallesian (8 species per assemblage). Towards the end of the Vallesian and in the Early Turolian (5-6 species per assemblage) the diversity decreased. Most Vallesian dormice were forest-dwellers, whereas in the Turolian a significant increase of ground-dwellers reflects the change from predominating forested wetland environments to open woodland and steppe-like environments. We assume increasing aridity and seasonality, most probably hot/dry summers and cool/wet but frost-free winters, from the Late Vallesian towards the Early Turolian.

Keywords: Taxonomy, Palaeoecology, Biostratigraphy, Neogene Basins, Pannonian.

Zusammenfassung

Aus dem späten Miozän von Österreich wurden drei Arten der Familie Eomyidae und zwölf Schlafmaus-Arten nachgewiesen. Darunter sind zwei Neubeschreibungen, die Eomyiden-Art *Keramidomys ermannorum* nov. spec. und die Gliriden-Art *Paraglirulus schultzi* nov. spec. Die Fossilien stammen aus acht Fundstellen des Wiener Beckens, aus den Österreichischen Anteilen des Nordalpinen Vorlandbeckens und des Pannonischen Beckens. Stratigraphisch reichen sie vom frühen Vallesium (MN9 / Pannonium C) bis zum frühen Turolium (MN11 / Pannonium H) und umfassen damit einen Zeitumfang von drei Millionen Jahren, von etwa 11.2 bis 8.2 Millionen Jahren vor heute. In Österreich war die Diversität von Schlafmäusen im späten Miozän relativ hoch, mit höchsten Artenzahlen (8 Arten pro Fauna) im frühen Vallesium und zu Beginn des späten Vallesium. Gegegen Ende des Vallesium und im frühen Turolium ging die Artenvielfalt zurück (auf 5-6 Arten pro Fauna). Die Schlafmäuse des Vallesium waren großteils Waldbewohner, während im Turolium die signifikante Zunahme von Bodenbewohnern eine Veränderung von Lebensräumen anzeigt, von vorwiegend bewaldeten Feuchtgebieten hin zu lichten Wäldern und steppenähnlichen offenen Landschaften. Es wird eine Zunahme von trockenem Klima und jahreszeitlichen Schwankungen, höchst wahr-

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scheinlich in Richtung warmer, trockener Sommer und kühler, feuchter aber frostfreier Winter angenommen. Diese Entwicklung begann während des späten Vallesium und verstärkte sich im frühen Turolium.

Schlüsselworte: Taxonomie, Paläoökologie, Biostratigraphie, Neogene Becken, Pannonium.

Introduction

Austria has some of the richest known Late Miocene vertebrate faunas of Europe. Some of them yielded small and large mammals, others exclusively small mammals associated with amphibians, fishes and reptiles. From eight localities of the Northern Alpine Foreland Basin, the Vienna Basin and the Pannonian Basin, fossil remains of Gliridae and Eomyidae were recovered. The fossil sites are: Schernham and Mariathal located in the Northern Alpine Foreland Basin, Eichkogel, Richardhof-Wald, Richardhof-Golfplatz, Stixneusiedl and Götzendorf in the Southern Vienna Basin, and Kohfidisch in the Pannonian Basin (fig. 1).

In the second half of the 20th century, a range of field activities focussed on smaller mammals, among them the excavations of the Kohfidisch fauna conducted by the Museum of Natural History Vienna, Geological-Palaeontological Department, in the summer months from 1955 to 1984. The outcome of these excavations was a series of publications on molluscs (Bachmayer & Zapfe 1969), amphibians and reptiles (Bachmayer & Mlynarski 1977, 1983; Bachmayer & Szyndlar 1985, 1987; Tempfer 2005), and mammals (Bachmayer & Wilson 1970, 1978, 1980, 1983, 1985, 1990; Bachmayer & Zapfe 1960, 1969, 1972; Beaumont 1984; Daxner-Höck 2004 b; van Weers & Montoya 1996; Vislobokova 2004, 2005, 2006, 2007). During two field seasons (1968 to 1969) the small mammal fauna from Eichkogel was excavated by the Palaeontological Institute, University of Vienna. The investigated fossils from Eichkogel include numerous gastropods (Harzhauser & Binder 2004) and small mammals (Daxner 1967; Daxner-Höck 1970, 1972a, 1972b, 1975, 1977, 1980, 2004; Daxner-Höck & Rabeder 1970; Daxner-Höck & de Bruijn 1981; Rabeder 1970, 1972; Ziegler 2004). The first mammal fossils from the primate locality Götzendorf were collected by the private collectors H. Schwengersbauer and P. Ullrich, and in several field seasons (1988 to 1992) a rich vertebrate and invertebrate collection was made by the Museum of Natural History and the University of Vienna. Rögl et al. (1993) published an overview of the fauna, and Harzhauser & Tempfer (2004) provided a palaeoenvironmental interpretation based on molluscs and amphibians. Some taxonomic studies on selected small mammal groups followed (Rabeder 1998; Daxner-Höck 2004b; Ziegler 2006). The recent field investigations, organized by the first author since 1992, have yielded some new Late Miocene micromammal faunas, including diverse glirid and eomyid assemblages, i.e. Stixneusiedl, Götzendorf 2, Richardhof-Golfplatz, Richardhof-Wald, Mariathal and Schernham (Daxner-Höck 1996, 2004a, 2004b; Ziegler 2006; Ziegler & Daxner-Höck 2005).

Study area

Geological framework

The deposition of limnic and fluvial sediments, and the respective mammal locations, is closely related with the history of of the Northern Alpine Foreland Basin (Molasse Basin), the Vienna Basin and the Pannonian Basin, and with the origin and development of Lake Pannon. At the Middle/Late Miocene-transition (= Sarmatian/Pannonian boundary), i.e. at about 11.6 Ma, a glacioeustatic sea-level drop caused the final disintegration of the Paratethys Sea (HILGEN et al. 2000; LIRER et al. 2002; HARZHAUSER et al. 2004). The Paratethys split geographically into the Eastern Paratethys and, west of the Pannonian basin system, Lake Pannon arose. Lake Pannon attained a maximum length of 860 km (from the Karlovac Basin close to Zagreb in the west to the Transsylvanian Basin in Romania in the east) and a width of 550 km (from the Vienna Basin in the north to Belgrade in the south), covering an area of about 290,000 km² (MAGYAR et al. 1999; HARZHAUSER et al. 2004; HARZHAUSER & MANDIC 2008). In Austria, Lake Pannon covered the northern and southern Vienna Basin and parts of the Pannonian Basin system, the Styrian Basin included.

In the Early Pannonian the fluvial system Palaeo-Danube arose, and its huge delta prograded into Lake Pannon. The Palaeo-Danube was fed by a drainage system of the Northern Alpine Foreland Basin and can be traced from Krems via Hollabrunn to the Mistelbach area by the characteristic gravels, sand and pelites of the Hollabrunn-Mistelbach Formation (NEHYBA & ROETZEL 2004). In this area, associated wetland environments display plant-, mollusc- and vertebrate-bearing fossil sites such as Pellendorf, Atzelsdorf, Gaiselberg, Obersulz, Mistelbach, Mariathal and Magersdorf (BERNOR et al. 1988; DAXNER-HÖCK 1975, 2004b; HARZHAUSER et a. 2003; ZAPFE 1948).

During the Middle Pannonian the level rise of Lake Pannon mostly destroyed these wetlands. However, in the Late Pannonian and probably towards the end of the Middle Pannonian, a fringe of freshwater lakes became established along the margin of the Eastern Alps, when the backstepping of the shoreline of Lake Pannon towards the basin began (HARZHAUSER & TEMPFER 2004). In the Late Pannonian, Lake Pannon retreated from the Vienna Basin and established its northwestern coast in the Hungarian Basin (MAGYAR et al. 1999). Consequently, the drainage systems from the Alps and the Molasse Basin entered the Vienna Basin and formed extended floodplains with oxbows, rivulets and floodplain-lakes (HARZHAUSER & TEMPFER 2004), as reconstructed for the localities Götzendorf, Stixneusiedl and Neusiedl am See. These freshwater lakes had no connection to Lake Pannon; ultimately, the extended wetland environments vanished from the Vienna Basin. Along the slopes of the Alps, however, the swampy lakes persisted under more or less stagnant conditions throughout the Late Pannonian, spanning a time of about two million years (HARZHAUSER & BINDER 2004). From this area, three vertebrate faunas of different ages were recovered, i.e. Richardhof-Golfplatz, Richardhof-Wald and Eichkogel.

Simultaneously, in the West, a huge drainage system from the Alps entered the Molasse Basin of Upper Austria, depositing gravels and sands of the Kobernaußer Wald and Hausruck. The highest and youngest member of this sequence is the "Hausruck Schotter" on top of the lignite-bearing deposits of the Hausruck. Here, sandy-silty layers

interbeded in gravels of the "Hausruck Schotter" yielded the very diverse Late Pannonian vertebrate fauna of Schernham.

Stratigraphy of the fossil sites

The eight investigated localities span a time of around three million years from the Early to the Late Pannonian, with Mariathal being the eldest and Eichkogel the youngest. Correlations are based on biostratigraphic data of molluscs (Harzhauser & Tempfer 2004; Harzhauser & Binder 2004) and of mammals (Daxner-Höck 1996a, 2001, 2004b), as well as on the age-model elaborated by Harzhauser et al. (2004).

The locality Mariathal (Mat) is well known because of the occurrence of the primate *Dryopithecus* (Thenius 1982). The small fauna stems from a sand pit east of Hollabrunn, Lower Austria (N48°33'49", E16°07'43"). The fossils were recovered from a gray siltlayer above gravels of the Hollabrunn-Mistelbach Formation. The biostratigraphic correlation with the lowermost Vallesian (MN9) and the Early Pannonian (letter zone C; Papp 1951) is indicated by the presence of the horse *Hippotherium* and the bivalve *Mytilopsis hoernesi.* This correlates with an age of 11.2 to 11.1 Ma (Harzhauser et al. 2004).

Richardhof-Golfplatz (RH-A) is an artificial outcrop near Gumpoldskirchen, Lower Austria (N48°03'23", E16°16'08"). Note that Richardhof-Golfplatz and Richardhof-Wald are two different sections a few hundred meters apart laterally. For localization see fig. 1 and Harzhauser & Binder (2004: fig. 2). The about 7-m thick section of Richardhof-Golfplatz (RH-A) comprises marly sandy silt and silty clay with three main fossil layers (RH-A/2, RH-A/7, RH-A/11) yielding a rich smaller vertebrate- and gastropod fauna (Daxner-Höck 2004b; Ziegler 2006; Harzhauser & Tempfer 2004; Harzhauser & Binder 2004). The fauna stems from swampy freshwater lake deposits that developed along the easternmost slopes of the Alps. The biostratigraphic correlation with the Early Vallesian is indicated by a number of rodents such as *Microtocricetus molassicus*, *Albanensia grimmi*, *Pliopetaurista kollmanni*, *Myoglis ucrainicus*, *Muscardinus vallesiensis*, and *Muscardinus hispanicus*. The presence of *Megacricetodon* and the lack of the murid *Progonomys* (with its first abundant occurrence in Europe in MN10) evidence mammal Zone MN9 for Richardhof-Golfplatz. The evolutionary level of the rodent fauna points to a stratigraphic position between Götzendorf and Borský Svatý Jur, with Götzendorf being slightly younger and Borský Svatý Jur slightly older (Joniak, unpublished thesis). The rodent assemblage from Borsý Svatý Jur in Slowakia (NE part of the Vienna Basin) stems from Middle Pannonian sediments of Lake Pannon (letter zone E; Papp 1951) as indicated by ostracods (e. g. *Candona mutans*, *C. elongata*, *Cyprideis heterostigma*, *Hemicytheria biornta*) and molluscs (e.g. *Melanopsis vindobonensis*, *Congeria subglobosa*) (Pipik & Holec 1998; Joniak, unpublished thesis). This fauna is time-equivalent with the faunas from Vösendorf, Inzersdorf and Hennersdorf (western margin of the Vienna Basin) as indicated by the characteristic mollusc-assemblage. In Vösendorf (= Brunn-Vösendorf), large mammals and lower vertebrates are well represented, whereas the small mammal record is very poor (Papp & Thenius 1954; Daxner 1967; Rabeder 1973).

Richardhof-Golfplatz is slightly younger than Vösendorf and Borsý Svatý Jur. The estimated age is 10.2 to 10.1 Ma (Harzhauser et al. 2004).

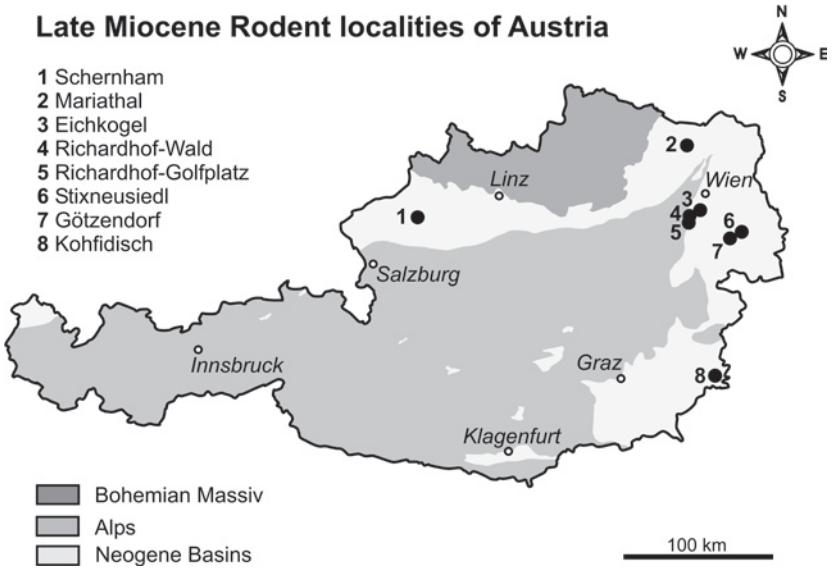


Fig. 1. Sketch map of Austria showing the topographic position of the investigated localities.

Götzendorf (Gö1 and Gö2) is a sandpit in Sandberg near Mannersdorf in Lower Austria (N48°00'26", E16°34'55"). The locality is well known due to the occurrence of the primate *Anapithecus* (formerly described as *Dryopithecus* by ZAPFE 1989). A detailed description of the locality and the section and a stratigraphic correlation is given in RÖGL et al. (1993: figs. 1-2). Götzendorf is situated at the eastern margin of the southern Vienna Basin close to the Leitha Mountains. The sections (Gö1 and Gö2) display floodplain deposits. The outcrop (Gö1) starts with a basal unit of silty clay with scattered lignites covered by about 5 m of bedded clay, silt and fine sand with intercalations of cross-bedded silt. An up to 1-m-thick layer of poorly sorted gravel and mud clasts follows, containing the vertebrate fauna and molluscs (BACHMAYER & WILSON 1984; BERNOR et al. 1993; DAXNER-HÖCK 1996a, 2004b; HARZHAUSER & TEMPFER 2004; RABEDER 1998; RÖGL et al. 1993; ZIEGLER 2006). The second section (Gö2) within about 70 m distance from the former, displays silt and fine sand with interbedded layers of fossiliferous clay and sand. The rodent faunas of Gö1 and Gö2 are similar and considered time equivalent. They are slightly more advanced than in Richardhof-Golfplatz and indicate zone MN9. The mollusc fauna indicates a correlation with the *Mytilopsis neumayri/ Mytilopsis zahalkai* Zone (= letter zone F of PAPP 1951) of the lowermost Late Pannonian. The magnetostratigraphic correlation is Chron C5n1n/C4Ar3r (DAXNER-HÖCK 2001). The estimated age is 9.9 to 9.8 Ma (HARZHAUSER et al. 2004).

Stixneusiedl (Stix) is a sandpit near Bruck a.d. Leitha in Lower Austria (N48°03'21", E16°23'18"). The section consists of 20 m of clay, silt, sand and gravel with some intercalated small lenses containing molluscs and isolated teeth of small mammals (RÖGL et al. 1993; DAXNER-HÖCK 1996a; ZIEGLER 2006). The sedimentary succession points to repeated shifts from fluvial settings to lacustrine environments (HARZHAUSER et al.

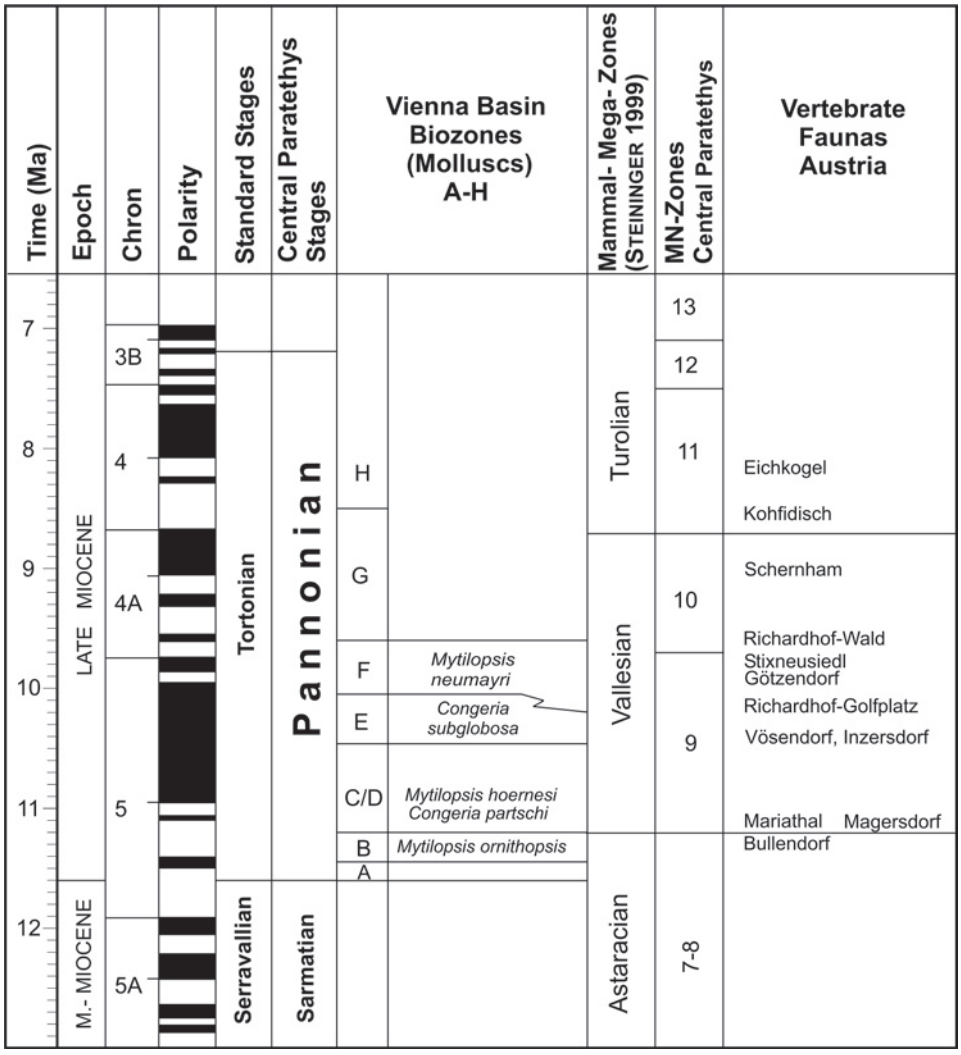


Fig. 2. Chronostratigraphy and biostratigraphy of the Pannonian; modified after MAGYAR et al. (1999) and DAXNER-HÖCK (2004).

2004: fig. 7). Biostratigraphically the small rodent fauna gives evidence of an Early Vallesian (MN9) age. The estimated age is around 9.8 Ma (HARZHAUSER et al. 2004).

Richardhof-Wald (Rh) is an artificial outcrop near Richardhof-Golfplatz near Gumpoldskirchen in Lower Austria (N48°03'45", E16°16'15"). For a detailed localization and the gastropod data of the locality see HARZHAUSER & BINDER (2004: fig. 2). The section (Rh) comprises marly sandy silt and silty clay with three main fossil layers (Rh-1, Rh-3, Rh-5) yielding a rich small mammal fauna (DAXNER-HÖCK 1996a, 2004b; ZIEGLER 2006). The sediments represent a swampy freshwater environment that developed along the easternmost slopes of the Alps during the Late Pannonian when Lake Pannon re-

treated from the Vienna Basin. The biostratigraphic correlation with the Late Vallesian (lower part of MN10) is indicated by the first abundant occurrence of the murid *Progonomys* and the hamster *Kowalskia*, and by a great number of last occurrences (LOD), i.e. *Albanensia*, Glirinae gen.et spec. indet., *Muscardinus vallesiensis*, *Eumyarion*, *Democricetodon*, *Microtocricetus* and *Anomalomys*. *Pliopetaurista kollmanni*, *Paraglirulus werenfelsi* and *Muscardinus hispanicus* had their last appearances (LAD). The dental morphology of these rodents from Götzendorf and Richardhof-Wald is almost identical. This hints at a relatively short time interval (< 200,000 years) between the deposition of the two faunas. The normal magnetisation of the Richardhof-Wald fossil beds (SCHOLGER, oral communication) rather corresponds to Chron C4Ar2n than to C4Ar1n (DAXNER-HÖCK 2001). The estimated age is 9.7 to 9.6 Ma (HARZHAUSER et al. 2004).

Schernham (Sch) is a sand and gravel pit west of Haag am Hausruck in Upper Austria (N48°10'40", E13°36'38"). Above lignite-bearing deposits, the section comprises gravels and conglomerates with intercalated sand layers and lenses of gray, yellow and reddish colour. One of these sand layers yielded a very rich vertebrate fauna comprising smaller and large mammals (DAXNER-HÖCK 2004a, 2004b; ZIEGLER 2006) and many different lower vertebrates. The Late Miocene sediments represent a fluvial environment. There is no immediate connection with the Pannonian Basin system. However, correlation with the Late Pannonian is most probable. The biostratigraphic correlation with the Late Vallesian (upper part of MN10) is characterized by the first appearances (FAD) of the flying squirrel *Pliopetaurista bressana*, *Muscardinus pliocaenicus austriacus* and *Paraglirulus schultzi* nov. spec. Furthermore there are some FOD of *Pliopetes*, *Prospalax*, *Pseudocollimys*, and the LOD of *Myoglis.* The estimated age is around 9 Ma.

Kohfidisch (Ko), a famous locality of the Late Pannonian, is situated in the Austrian part of the Pannonian Basin near Kirchfidisch in Burgenland (N47°08'52", E16°20'39"). This locality yielded one of the richest vertebrate faunas of Europe where bones, partly articulated skeletons and teeth from different vertebrate groups accumulated in karst fissures (Ko II, III, IV, V, VI, Cm) and a cave (Ko I) in Palaeozoic limestones (BACHMAYER & MLYNARSKI 1977, 1983; BACHMAYER & SZYNDLAR 1985, 1987; TEMPFER 2005; BACHMAYER & WILSON 1970, 1978, 1980, 1983, 1985, 1990; BACHMAYER & ZAPFE 1960, 1969, 1972; BEAUMONT 1984; DAXNER-HÖCK 2004 b; VAN WEERS & MONTOYA 1996; VISLOBOKOVA 2004, 2005, 2006, 2007). The biostratigraphic correlation with the Lower Turolian (MN11) is indicated by the FOD of *Progonomys woelferi*, *Epimeriones austriacus*, *Kowalskia fahlbuschi*, *Vasseuromys pannonicus*, *Hystrix parvae* and *Parapodemus lugdunensis.* As outlined in DAXNER-HÖCK (2004b) the small mammal fauna from Kohfidisch is similar to that from Eichkogel (MN11) concerning the composition and first occurrences of taxa and the relative specimen-abundances. Furthermore, the dental morphology of species occurring in both faunas is very similar also. These data indicate a relatively short time interval between Kohfidisch and Eichkogel (see figs 2 to 3). However, there are major differences towards the next elder fauna, namely Schernham (upper part of MN10). Consequently, Kohfidisch should be correlated with the Early Turolian and not with the Late Vallesian as previously thought (DE BRUIJN et al. 1992; DAXNER HÖCK 1996a, 2001). The estimated age is 8.6 to 8.5 Ma.

Eichkogel (E) is an artificial outcrop near Mödling in Lower Austria (N48°03'55", E16°17'32"). For the localization see HARZHAUSER & BINDER (2004: fig. 2). The sec-

tion comprises marly sandy silt and silty clay with different fossil layers. In the upper part of the section, below of the limestone forming the top of Eichkogel, an extremely high concentration of terrestrial and aquatic gastropoda was observed. This eyecatching mollusc-layer also yielded a rich small mammal fauna (Daxner 1967; Daxner-Höck 1970, 1972a, 1972b, 1975, 1977, 1980, 2004; Daxner-Höck & de Bruijn 1981; Daxner-Höck & Rabeder 1970; Rabeder 1970, 1972; Ziegler 2004). Lithologically a swampy freshwater lake is indicated – one of the lakes that developed along the slopes of the Alps during the Late Pannonian. The biostratigraphic correlation with the Early Turolian (MN11) is indicated by the occurrences of *Parapodemus lugdunensis*, *Kowalskia skofleki* (= ? *K. schaubi*), *Vasseuromys pannonicus*, *Epimeriones austriacus* and by the occurrences of other taxa typical for the Early Turolian. The estimated age is 8.3 to 8.0 Ma (Harzhauser et al. 2004).

Material & Methods

Numerous mandibles and about 2500 isolated teeth of Eomyidae and Gliridae were sampled from these eight localities. They are listed in detail in the Systematic part. The collecting method was screen washing of large sediment samples in the field with water followed by drying by sun and wind. The washing equipment consists of sieves of 0.5, 2.5 and 5.0 mm mesh sizes, an electric water pump and a generator. The residue was dried, and the smaller molluscs, bones and teeth of lower vertebrates and small mammals were picked out of the residue and studied using head-lenses and light microscopes (Leica – Wild M3B and Leica – Wild M8). The measurements were taken using the Leica – Wild M8 light microscope. The teeth were coated with gold, and SEM-photos were taken with a Philips XL 20 scanning microscope at the Biocenter, University of Vienna. To facilitate easier comparisons all right side teeth are figured as mirror images, and their figure numbers are underlined, e.g fig. 4/1 (= right D4).

All collected fossils are integrated in the collections of the NHMW, except for most of the Eichkogel-fauna, which was excavated by the Palaeontological Institute, University of Vienna, in the 1960s and stored in the collection of the PIUW. For comparisons, skulls of living dormice from the Museum of Natural History Vienna, Mammal Department, and fossils from the Institute of Earth Sciences, University of Utrecht, were available.

For classification and terminology of dental structures of Eomyidae and Gliridae, we follow Engesser (1990) and Daams & de Bruijn (1995), respectively.

Abbreviations

NHMW	Museum of Natural History Vienna, Geological-Palaeontological Department
PIUW	University Vienna, Geocenter, Department of Palaeontology
Mat	Mariathal
RH-A	Richardhof-Golfplatz
Gö	Götzendorf
Stix	Stixneusiedl
Rh	Richardhof-Wald
Sch	Schernham

Ko	Kohfidisch
E	Eichkogel
FAD	first appearance datum
FOD	first occurrence datum
LAD	last appearance datum
LOD	last occurrence datum
Ma	million years
MN	Neogene Mammal Zone
D4, P4, M1-3	maxillary teeth
d4, p4, m1-3	mandibular teeth
l	from the left side
r	from the right side
Inv. Nr.	repository number

Systematic Part

Family Eomyidae DEPERET & DOUXAMI, 1902

Dental terminology: fig. 3

Dental formula: 1 0 1 3 / 1 0 1 3

Genus *Keramidomys* HARTENBERGER, 1966

***Keramidomys ermannorum* nov. spec.**
(fig. 4, tab. 1)

1977	*Keramidomys* aff. *mohleri* ENGESSER, 1972. – DAXNER-HÖCK: 26-27; pl. 4, figs 18-20.
1978	*Keramidomys* sp. – BACHMAYER & WILSON: 147, pl. 3, fig. 10; pl. 5, fig. 20.
1980	*Keramidomys* sp. – BACHMAYER & WILSON: 353.
1985	*Keramidomys* sp. – BACHMAYER & WILSON: 105.
1995	*Keramidomys* cf. *karpathicus* (SCHAUB & ZAPFE, 1953). – DE BRUIJN: 100; pl. 3, figs 22-41.
1996a	*Keramidomys* sp. – DAXNER-HÖCK: 3-4.
1996a	*Keramidomys* aff. *mohleri* ENGESSER. – DAXNER-HÖCK: 4.
2004a	*Keramidomys* sp. – DAXNER-HÖCK: 3.

D e r i v a t i o n o m i n i s : In honour of Friederike† and Oskar Ermann, who provided financial support for the Richardhof field-investigations.

T y p e l o c a l i t y : Richardhof-Golfplatz (RH-A/2, 7) near Mödling, Lower Austria (Vienna Basin).

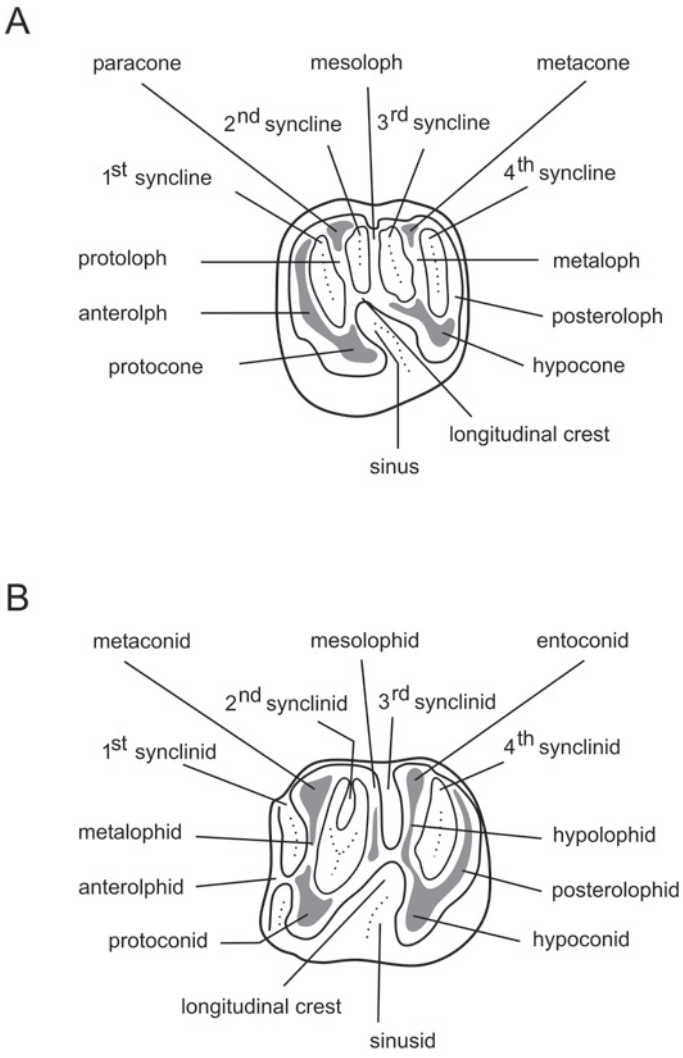


Fig. 3. Dental terminology of Eomyidae modified after ENGESSER (1990:17).

S t r a t u m t y p i c u m : marls of the Bzenec Fm. deposited in a swampy lake adjacent to Lake Pannon; Late Miocene, Middle Pannonian, Early Vallesian, mammal Zone MN9.

O t h e r o c c u r r e n c e s in Austria: Stixneusiedl (MN9), Richardhof-Wald (MN10), Schernham (MN10), Kohfidisch (MN11), Eichkogel (MN11).

H o l o t y p e : m1 r (RH-A/7). Museum of Natural History Vienna, Geological-Palaeontological Department (2008z0110/0013); fig. 4/18.

Description and measurements of the holotype: The m1 is wide, has a plane occlusal surface, and five pronounced lophids. The 1st, 2nd and 4th synclinids are labially and

Tab. 1. Measurements (in mm):

		length					width			
		min	mean	max	stdev	n	min	mean	max	stdev
D4	Rh		0.78			1		0.75		
	Ko		0.83			1		0.73		
P4	RH-A	0.65	0.69	0.72	0.0382	3	0.73	0.74	0.78	0.0289
	Rh	0.70		0.70		2	0.78		0.80	0.0177
	Sch		0.83			1		0.80		
	Ko	0.83		0.85	0.0177	2	0.80		0.88	0.0530
	E		0.72			1		0.72		
M1	RH-A	0.70	0.77	0.80	0.0339	8	0.80	0.86	0.90	0.0345
	Rh	0.75	0.83	0.88	0.0404	12	0.83	0.89	0.95	0.0530
	Sch		0.83			2		0.88		
	Ko	0.83	0.87	0.93	0.0447	5	0.83	0.91	0.95	0.0483
	E		0.82			1		0.92		
M2	RH-A	0.63	0.66	0.68	0.0289	3	0.80	0.83	0.85	0.0250
	Rh	0.65	0.69	0.73	0.0265	10	0.80	0.83	0.88	0.0250
	Sch	0.70	0.75	0.80	0.0408	4	0.88	0.92	0.93	0.0239
	Ko	0.73	0.76	0.80	0.0315	4	0.80	0.85	0.90	0.0456
M3	RH-A		0.45			1		0.65		
	Rh		0.55			1		0.65		
	Ko	0.60		0.63	0.0520	2	0.68		0.88	0.1155
	E		0.52			1		0.72		
d4	Ko		0.93					0.63		
p4	RH-A	0.65	0.72	0.83	0.0647	5	0.55	0.65	0.70	0.0671
	Stix		0.65			1		0.60		
	Rh	0.65	0.78	0.93	0.0794	16	0.65	0.75	0.85	0.0540
	Sch		0.68			1		0.58		
m1	RH-A	0.75	0.82	0.90	0.0499	8	0.73	0.78	0.83	0.0299
	Rh	0.80	0.86	0.90	0.0377	14	0.70	0.83	0.95	0.0723
	Sch	0.83	0.85	0.88	0.0250	3	0.83	0.86	0.90	0.0382
	E		0.84			1		0.82		
m2	RH-A	0.75	0.76	0.78	0.0144	3	0.70	0.72	0.73	0.0144
	Rh	0.60	0.72	0.80	0.0725	10	0.60	0.72	0.83	0.0789
	E		0.72			1		0.78		
m3	Rh	0.63		0.70	0.0530	2	0.63		0.70	0.0530

lingually closed. The 3rd synclinid is lingually open. Its position is opposite to the deep sinusid, which extends across the median line of the tooth. The longitudinal crest is short and very thin; it is almost interrupted. No roots are present.

Measurements: length = 0.80 mm, width = 0.78 mm

P a r a t y p e s : 28 teeth (RH-A/2) and 3 teeth (RH-A/7).(NHMW 2008z0110/0002 to 0012) and (NHMW 2008z0110/0014 to 0033). figs 4/2, 5, 9, 12, 14, 17.

R e f e r r e d m a t e r i a l :

2. Stixneusiedl (Stix): 1 tooth. (NHMW 2008z0111/0001).

3. Richardhof-Wald (Rh = Rh-1, 3, 5): 56 teeth (Rh-1), 4 teeth (Rh-3), 9 teeth (Rh-5). (NHMW 2008z0112/ 0001 to 0070).

4. Schernham (Sch): 10 teeth. (NHMW 2008z0113/0001 to 0010).

5. Kohfidisch (Ko = Ko, Ko IIIu): 20 teeth (Ko), 1 tooth (Ko IIIu). (NHMW 2008z0114/0001 to 0021) and 1 tooth. (Bachmayer & Wilson 1978: 147).

6. Eichkogel (E): 3 teeth. (NHMW 2008z0115/0001 to 0003) and 3 teeth. (PIUW 1953/8/1 to 3) (Daxner-Höck 1977: 26).

D i a g n o s i s : Teeth are characterized by: five loph(id)s; pronounced lophodonty; labial and lingual connections of loph(id)s; labial connection of protoloph and metaloph occasionally weak; deep sinus(id) extending across the medial line of the tooth; plane occlusal surface; large p4; wide m1-2; 1st, 2nd and 4th syncline of M1-2 and 1st, 2nd and 4th synclinid of d4-m2 labially and lingually in most cases closed.

D i f f e r e n t i a l d i a g n o s i s : *Keramidomys ermannorum* nov. spec. combines dental characters of *K. thaleri* Hugueney & Mein, 1968, *K. carpathicus* (Schaub & Zapfe, 1953) and *K. mohleri* Engesser, 1972. However, it differs from all known species by: a tendency to develop lophodonty, a deeper sinus(id), the plane occlusal surface, the labial and lingual connections of loph(id)s, and wider lower molars. *K. ermannorum* is intermediate in size between the larger species *K. mohleri* and the two smaller species *K. thaleri* and *K. carpathicus*. From *K. anwilensis* Engesser, 1972, *K. pertesunatoi*

Fig. 4. *Keramidomys ermannorum* nov. spec. from Richardhof-Golfplatz (RH-A), Richardhof-Wald (Rh), Schernham (Sch) and Kohfidisch (Ko); holotype (H), paratypes (P). Magnifications: 30 x; all specimens in the NHMW colln. ►

4/1 right D4; Rh-5; 2008z0112/0009.
4/2 right P4 (P); RH-A/2; 2008z0110/0002.
4/3 right P4; Rh-1; 2008z0112/0002.
4/4 left P4; Sch; 2008z0113/0001.
4/5 right M1 (P); RH-A/2/; 2008z0110/0006.
4/6 left M1; Rh-1; 2008z0112/0003.
4/7 right M1; Rh-1; 2008z0112/0011.
4/8 right M3; Rh-1; 2008z0112/0006.
4/9 left M2 (P); RH-A/2; 2008z0110/0005.
4/10 left M2; Rh-1; 2008z0112/0004.
4/11 right M2; Rh-1; 2008z0112/0007.
4/12 right M3 (P); RH-A/2; 2008z0110/0008.
4/13 right d4; Ko; 2008z0114/0011.
4/14 left p4 (P); RH-A/7; 2008z0110/0010.
4/15 right p4; Rh-1; 2008z0112/0019.
4/16 left m3; Rh-1; 2008z0112/0014.
4/17 left m2 (P); RH-A/2; 2008z0110/0012.
4/18 right m1 (H); RH-A/7; 2008z0110/0013.
4/19 left m1; Rh-1; 2008z0112/0018.

(HARTENBERGER, 1966) and *K. reductus* BOLLIGER, 1992, *K. ermannorum* differs by less reduced dental characters. It differs from the Chinese species *K. fahlbuschi* QIU, 1996 by its closed synclin(id)s and the deeper sinus(id).

D e s c r i p t i o n of paratypes and referred material from Austria:

D4: trapezoidal; anteroloph present; protoloph short; mesoloph long and oblique; longitudinal crest interrupted; sinus and 2nd syncline fused; 1st and 4th synclines closed.

P4: square outline with rounded corners; protoloph frequently absent; mesoloph varying from absent to long; longitudinal crest complete or weak; 1st syncline absent or closed or fused with the sinus; 2 nd and 3rd synclines fused or separated by the mesoloph, labially open; 4th syncline closed.

M1: square outline; largest of upper teeth; 1st syncline closed, smaller than 2nd – 4th synclines; longitudinal crest mostly weak or interrupted; in the latter case, 2nd syncline and sinus fused; mesoloph long; anterior arm of hypoconus oblique; 2nd syncline labially open or closed; 3rd syncline labially open; 4th syncline closed.

M2: smaller than M1; longitudinal crest complete or interrupted; mesoloph long; 1st and 4th synclines closed and narrow; 2nd syncline and sinus sometimes fused; 3rd syncline labially open.

M3: rounded; sinus lingually closed; mesoloph present; longitudinal crest interrupted; 1st and 4th syncline closed.

d4: with five distinct lophids, mesolophid long; 1st and 4th synclinids closed.

p4: four to five lophids (anterolophid and metalophid sometimes fused); 1st, 2nd and 4th synclinids closed; 3rd synclinid lingually open, opposite to the sinusid.

m1: wide; five distinct lophids; anterolophid, metalophid, mesolophid lingually connected; longitudinal crest sometimes constricted; 1st, 2nd and 4th synclinids closed; 3rd synclinid lingually open.

m2: similar but smaller than m1; tendency towards reduction of metalophid and 1st synclinid

m3: five lophids with lingual connections similar to m1-2; mesolophid sometimes constricted or interrupted in its middle part.

Root numbers and positions: The maxillary D4, P4, M1-3 have three roots, a lingual and two labial ones. The mandibular m3 has also three roots, a posterior and two anterior ones; d4 and p4 have two roots, a posterior and an anterior one; m1-2 have four roots, two anterior and two posterior ones.

R e m a r k s : *K. ermannorum* is an advanced species of *Keramidomys*. All occurrences show a wide variability of dental characters. However, from the Vallesian through the Early Turolian, certain morphological and metric changes are visible, i.e. increase of size and lophodonty, the larger and deeper the sinus(id) and flattening of the occlusal surface.

K. aff. *pertesunatoi* from Giggenhausen and Marktl (Germany: FAHLBUSCH 1975: fig. 11) seems similar in dental pattern. Whether these specimens are identical with *K. er-*

mannorum remains to be established. In our opinion, *K.* cf. *karpathicus* from Maramena (Greece: DE BRUIJN 1995) is *K. ermannorum.*

Other occurrences in Europe: Maramena (Greece: DE BRUIJN 1995; MN13/14) and Stanjantsi (Bulgaria: under investigation; Meotian). The stratigraphic range is: Late Miocene to the Miocene/Pliocene transition (MN9-13/14).

Keramidomys cf. *pertesunatoi* (HARTENBERGER, 1966)

(fig. 5, tab. 2)

Type locality: Can Llobateres (Spain); Late Miocene (MN9)

Occurrences in Austria: Richardhof-Golfplatz (Late Miocene; MN9)

Referred material:

1. Richardhof-Golfplatz (RH-A/2): 1 P4. (NHMW 2008z0116/0001); 1 M1/2. (NHMW 2008z0116/0002); 1 m1/2. (NHMW 2008z0116/0003).

Dental characters: Lophodont, relatively high-crowned teeth; occlusal surface plane and square in outline; some dental structures reduced.

P4: square outline with rounded corners; protoloph absent; mesoloph long; longitudinal crest weak; 1st syncline absent; 2nd syncline closed; 3rd syncline labially open; 4th syncline closed; three roots, one in lingual and two in labial position.

M1/2: square outline; 1st and 2nd synclines absent; 3rd syncline labially open; 4th syncline closed; longitudinal crest extremely short; protoloph absent; mesoloph absent; anteroloph and metaloph strong; anterior arm of hypocone strong, oblique; no roots present.

m1/2: almost square in outline; anterolophid and metalophid partly fused; mesolophid reduced; longitudinal crest oblique; sinusid almost symmetrical; 1st synclinid in labial position; 2nd synclinid reduced; sinusid and 3rd synclinid in opposite position; 4th synclinid closed; no roots present.

Remarks: Conspicuous reductions in dental pattern are described from three *Keramidomys* species, i.e. *K. pertesunatoi*, *K. reductus* and *K. anwilensis*. The few specimens from Richardhof-Golfplatz do not allow clear species-identification. However, they show closest affinities with *K. pertesunatoi*.

Other occurrences in Europe: Can Llobateres (Spain: HARTENBERGER 1966; MN9); Lissieu (France: HUGUENEY & MEIN 1968; MN13). The stratigraphic range is: Late Miocene (MN 9-13).

Tab. 2. Measurements (in mm):

	length	width
P4l	0.63	0.73
M1/2l	0.70	0.83
m1/2r	0.73	0.80

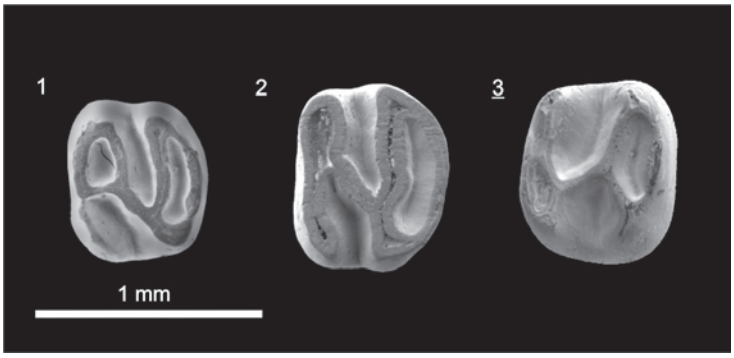


Fig. 5. *Keramidomys* cf. *pertesunatoi* (HARTENBERGER, 1966) from Richardhof-Golfplatz (RH-A). Magnifications: 30 x.

5/1 left P4; RH-A/2; NHMW 2008z0116/0001.
5/2 left M1/2; RH-A/2; NHMW 2008z0116/0002.
5/3 right m1/2; RH-A/2; NHMW 2008z0116/0003.

Genus *Eomyops* ENGESSER, 1979

Eomyops catalaunicus (HARTENBERGER, 1966)
(fig. 6, tab. 3)

1980 *Leptodontomys* sp. – BACHMAYER & WILSON: 372; pl. 1, fig. 1.
1985 *Leptodontomys* sp. – BACHMAYER & WILSON: 105.
1993 *Eomyops catalaunicus* (HARTENBERGER). – RÖGL et al.: 510.
1996a *Eomyops catalaunicus* (HARTENBERGER). – DAXNER-HÖCK: 3.
1996a *Eomyops* sp. – DAXNER-HÖCK: 3, 4.
2004a *Eomyops catalaunicus* (HARTENBERGER, 1966). – DAXNER-HÖCK: 3.

Type locality: Can Llobateres (Spain); Late Miocene (MN9).

Occurrences in Austria: Richardhof-Golfplatz (MN9), Götzendorf (MN9), Stixneusiedl (MN9), Richardhof-Wald (MN10), Schernham (MN10), Kohfidisch (MN11).

Referred material:

1. Richardhof-Golfplatz (RH-A = RH-A/2, 7): 133 teeth. (NHMW 2008z 0117/0001 to 0133).

2. Götzendorf (Gö = Gö1): 9 teeth. (NHMW 1990/0015/0161 to 0169).

3. Stixneusiedl (Stix): 1 tooth. (NHMW 2008z0118/0001).

4. Richardhof-Wald (Rh = Rh-1, 3, 5A): 171 teeth. (NHMW 2008z0119/0001 to 0167, 0171 to 0174).

5. Schernham (Sch): 20 teeth. (NHMW 2008z0120/0001 to 0020).

6. Kohfidisch (Ko = Ko, KoIII, KoIIIu, KoCm): 55 teeth. (NHMW 2008z0121/0001 to 0055) and 1 tooth (BACHMAYER & WILSON 1980: 372).

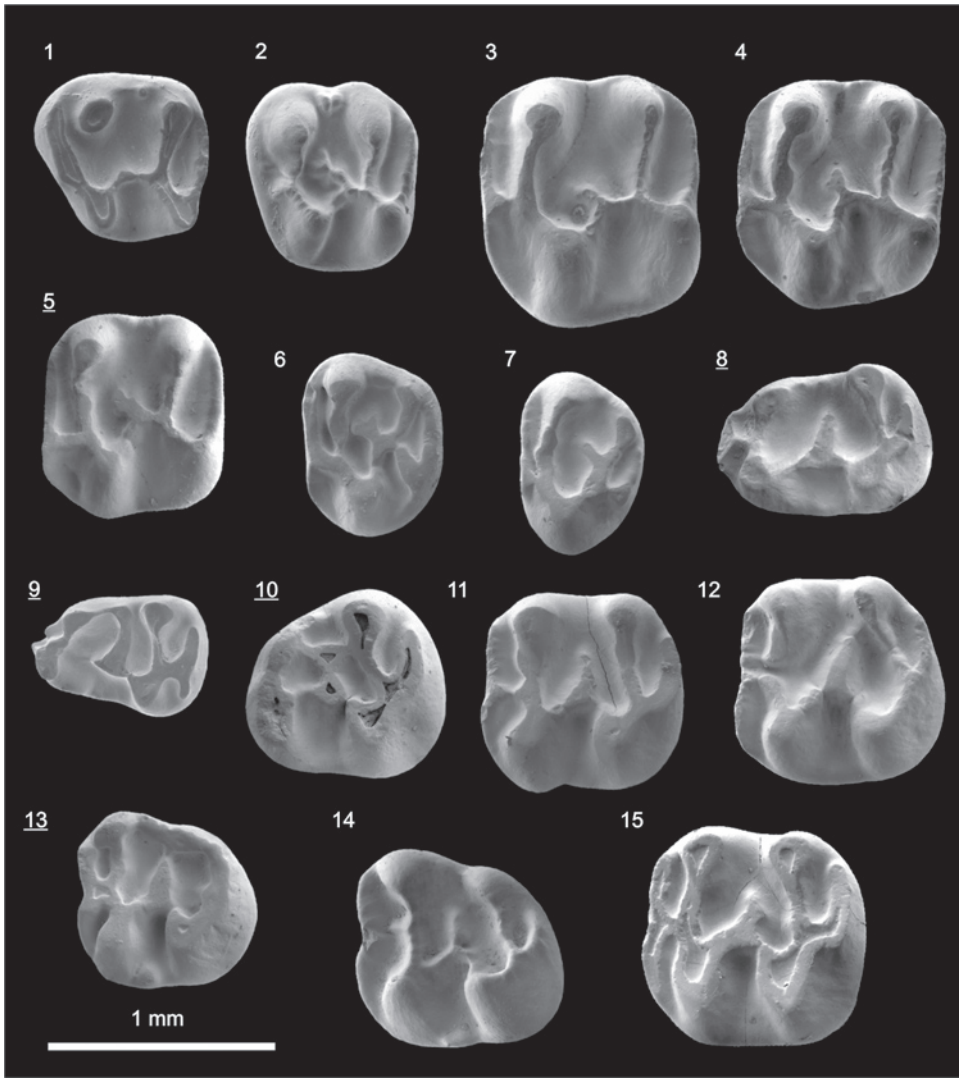


Fig. 6. *Eomyops catalaunicus* (HARTENBERGER, 1966) from Richardhof-Golfplatz (RH-A), Götzendorf (Gö), Richardhof-Wald (Rh), Schernham (Sch). Magnifications: 30 x; all specimens in the NHMW collection.

6/1 left D4; Rh-1; 2008z0119/0001.
6/2 left P4; Rh-1; 2008z0119/0002.
6/3 left M1; RH-A/7; 2008z0117/0004.
6/4 left M1; RH-A/7; 2008z0117/0003.
6/5 right M2; Rh-1; 2008z0119/0007.
6/6 left M3; RH-A/2; 2008z0117/0007.
6/7 left M3; Rh-1; 2008z0119/0005.
6/8 right d4; Sch; 2008z0120/0011.
6/9 right d4; Rh-1; 2008z0119/0019.
6/10 right p4; RH-A/2; 2008z0117/0010.
6/11 right m1/2; RH-A/2; 2008z0119/0014.
6/12 left m1/2; Sch; 2008z0120/0008.
6/13 right m3; RH-A/2; 2008z0117/0017.
6/14 left m3; Gö1; 1990/0015/0169.
6/15 left m1/2; Rh-1; 2008z0119/0012.

Tab. 3. Measurements (in mm):

		length					width			
		min	mean	max	stdev	n	min	mean	max	stdev
D4	Rh	0.75	0.81	0.90	0.0540	6	0.75	0.82	0.98	0.0828
P4	RH-A	0.75	0.85	1.00	0.0586	22	0.78	0.91	1.08	0.0744
	Gö		0.83			1		0.98		
	Stix		0.80			1		0.95		
	Rh	0.73	0.81	0.88	0.0434	21	0.80	0.89	1.05	0.0705
	Sch		0.78			1		0.83		
	Ko	0.83	0.83	0.85	0.0144	3	0.85	0.90	0.95	0.0500
M1	RH-A	0.83	0.90	1.05	0.0617	23	0.89	1.01	1.10	0.0327
	Gö	0.95		0.98		2	1.05		1.10	
	Rh	0.83	0.89	1.03	0.0473	22	0.88	0.99	1.13	0.0644
	Sch	0.88		1.05	0.1237	2	1.03		1.08	0.0354
M2	RH-A	0.78	0.85	0.95	0.0437	19	0.85	1.00	1.08	0.0573
	Gö		0.85			1			1.00	
	Rh	0.73	0.82	0.90	0.0501	19	0.83	0.91	1.00	0.0509
	Sch	0.85	0.90	0.95	0.0500	3	1.00	1.03	1.05	0.0250
M1/2	Ko	0.75	0.84	1.05	0.0752	21	0.85	0.93	1.13	0.0627
M3	RH-A	0.65	0.69	0.78	0.0518	6	0.80	0.85	0.88	0.0292
	Gö		0.80			1		0.85		
	Rh	0.58	0.67	0.90	0.0906	10	0.73	0.80	0.93	0.0575
	Ko	0.50	0.60	0.70	0.0641	8	0.70	0.74	0.80	0.0291
d4	RH-A	0.88		0.88		2	0.58		0.63	0.0354
	Rh	0.75	0.85	0.98	0.0768	8	0.50	0.57	0.68	0.5220
	Sch		1.00			1		0.63		
	Ko		0.80			1		0.60		
p4	RH-A	0.68	0.87	0.95	0.0797	11	0.70	0.76	0.88	0.0479
	Rh	0.70	0.79	0.90	0.0604	17	0.58	0.71	0.80	0.0672
	Sch	0.85	0.91	1.03	0.0737	5	0.70	0.87	0.85	0.0637
	Ko	0.85	0.90	0.95	0.0707	4	0.75	0.78	0.83	0.0354
m1	RH-A	0.93	1.03	1.15	0.0582	22	0.85	0.92	1.00	0.0475
	Stix		0.95			1		0.90		
	Rh	0.90	0.97	1.05	0.0358	21	0.83	0.90	1.05	0.0578
	Sch		1.10			1		0.95		
	Ko	0.88	0.94	1.00	0.0576	5	0.80	0.88	0.95	0.0463
m2	RH-A	0.88	0.98	1.05	0.0482	13	0.80	0.90	1.00	0.0586
	Rh	0.80	0.89	1.05	0.0514	29	0.68	0.82	0.93	0.0629
	Sch	0.95		0.89	0.0177	2	0.90		0.95	0.0354
	Ko	0.85	0.92	1.00	0.0688	4	0.83	0.89	0.98	0.0720
m1/2	Gö		1.00			1		0.90		
m3	RH-A	0.75	0.84	0.90	0.0513	11	0.70	0.81	0.88	0.0626
	Gö	0.85		0.93		2	0.83		0.85	
	Stix		0.85					0.75		
	Rh	0.83	0.85	0.88	0.0250	3	0.75	0.78	0.83	0.0382
	Sch	0.85	0.88	0.95	0.0577	3	0.68	0.77	0.88	0.1010
	Ko	0.73	0.76	0.80	0.0285	5	0.68	0.74	0.87	0.0418

D e s c r i p t i o n :

Dental characters: Bunodont dental pattern; four main cusps connected by lophs; M3/m3 reduced in the posterior part.

D4: trapezoidal in occlusal outline; anterior wall oblique; labial wall longer than lingual one; labial anteroloph continuous with anterior arm of protocone; no lingual anteroloph; protoloph absent or weak; mesoloph absent; strong metaloph connected to anterior arm of hypocone.

P 4: trapezoidal almost square in occlusal view; rounded corners; labial wall slightly longer than the lingual one; mesoloph short or of medium length and directed forwards; anteroloph weak or absent; lingual sinus transversely directed.

M1/M2: almost square in occlusal outline; rounded corners; M1 larger than M2; double anteroloph connected to anterior arm of protocone; labial anteroloph longer than the lingual one; protoloph and metaloph contacting the anterior arms of the protocone and hypocone, respectively; mesoloph short and directed forwards, sometimes bifurcated; V-shaped lingual sinus slightly directed forwards.

M3: smallest maxillary tooth; dental pattern similar to M1/2; wide variety of size and dental characters.

d4: long and slender; a small anteroconid or a labial or a lingual anterolophid may be present; pronounced protoconid anterior to the metaconid; metalophid short or absent; mesolophid variable from absent to long; longitudinal crest sometimes constricted; flat and open labial sinusid; pronounced posterolophid, occasionally isolated, sometimes with labial arm.

p4: wider than d4; anteroconid absent, sometimes small anterolophid; protoconid larger than metaconid; both cusps close to each other; metalophid almost absent; mesolophid long or of medium length; strong hypolophid extending transversally to posterior arm of hypoconid; posterolophid sometimes L-shaped; longitudinal crest sometimes constricted; sinusid transversal; 2nd, 3rd, 4th synclinids narrow.

m1/m2: rectangular in occlusal outline; rounded corners; lingual and labial cusps in opposite position; labial and lingual anterolophid almost equal; metalohid transversal; hypolophid transversal or backwards directed; short mesolophid transversal or backwards directed; sinusid transversal or backwards directed; pronounced posterolophid sometimes L-shaped.

m3: similar to m1/2, slightly smaller; hypolophid reduced in about 50 % of the specimens.

Root numbers and positions: The maxillary D4, P4-M3 have three roots, a lingual one and two labial ones. The mandibular d4 and p4 have two roots, an anterior and a posterior one. m1-3 have three roots, a posterior and two anterior ones.

R e m a r k s : Throughout its occurrence during the Neogene, the dental pattern of *Eomyops* remains very conservative. Species differentiation is mainly based on size. Among the four species, i.e. *E. catalaunicus*, *E. bodvanus* (JANOSSY, 1972), *E. hebeiseni* KÄLIN, 1997 and *E. oppligeri* ENGESSER, 1990, *E. hebeiseni* is largest and *E. oppligeri* smallest. *E. catalaunicus* is considerably smaller than *E. hebeiseni*, but slightly larger

than *E. oppligeri.* The morphological differences between *E. oppligeri*, *E. catalaunicus* and *E. bodvanus* are listed in ENGESSER (1990: 122).

The Austrian specimens share some characters with *E. oppligeri*, e.g. the sometimes L-shaped posterolophid of m1/2, the occasionally occurring hypolophid of m3. However, the more rounded dental structures, narrower valleys, the shorter, mostly simple mesoloph, the slightly backwards directed mesolophid, and the larger size identify the Austrian specimens as *E. catalaunicus.*

Other occurrences of *E. catalaunicus* in Europe: Can Llobateres (Spain: HARTENBERGER 1966; MN9), Soblay (France; GUÉRIN& MEIN 1971; MN10), Montredon (France: AGUILAR 1982; MN10), Ambérieu 1+2 (France: FARJANEL & MEIN 1984; MN9), Priay II (France: WELCOMME et al. 1991; MN9), Petersbuch 14 (Germany: BOLLIGER & RUMMEL 1994; MN9), Hammerschmiede (Germany: FAHLBUSCH 1975; MN9), Rudabanya (Hungary: DAXNER-HÖCK 2005; MN9), Maramena (Greece: DE BRUIJN 1995; MN13/14) and some *E.* cf./aff. *catalaunicus* occurrences, e.g. Lissieu (France: HUGUENEY & MEIN 1968; MN13), Podlesice (Poland: FAHLBUSCH 1978; MN14) and Nebelbergweg (Switzerland: KÄLIN & ENGESSER 2001; MN9). The stratigraphic range is Late Miocene to the beginning of the Pliocene (MN9-14).

Family Gliridae MUIRHEAD, 1819

Dental terminology: figs 7-8

Dental formula: 1 0 1 3 / 1 0 1 3

Subfamily Glirinae THOMAS, 1897

Genus *Muscardinus* KAUP, 1829

Muscardinus vallesiensis HARTENBERGER, 1966
(figs 8-9, tab. 4)

1966 *Muscardinus* (*Eomuscardinus*) *vallesiensis.* n. sp.– HARTENBERGER: 597, fig. 1.
1993 *Eomuscardinus* cf. *vallesiensis* HARTENBERGER. – RÖGL et al.: 510.
1996a *Eomuscardinus* cf. *vallesiensis* HARTENBERGER. – DAXNER-HÖCK: 3.
2005 *Muscardinus* cf. *vallesiensis* (HARTENBERGER, 1966). – DAXNER-HÖCK: 154.

Type locality: Can Llobateres (Spain); Late Miocene (MN9).

Occurrences in Austria: Richardhof-Golfplatz (MN9), Götzendorf (MN9), Richardhof-Wald (MN10).

Referred material:

1. Richardhof-Golfplatz (RH-A = RH-A/2, 7): 18 teeth. (RH-A/2), 1 tooth (RH-A/7). (NHMW 2008z0122/0001 to 0019).

2. Götzendorf (Gö = Gö1): 1 tooth. (NHMW 1990/0015/0187).

3. Richardhof-Wald (Rh = Rh-3): 2 teeth. (NHMW 2008z0123/0001 to 0002).

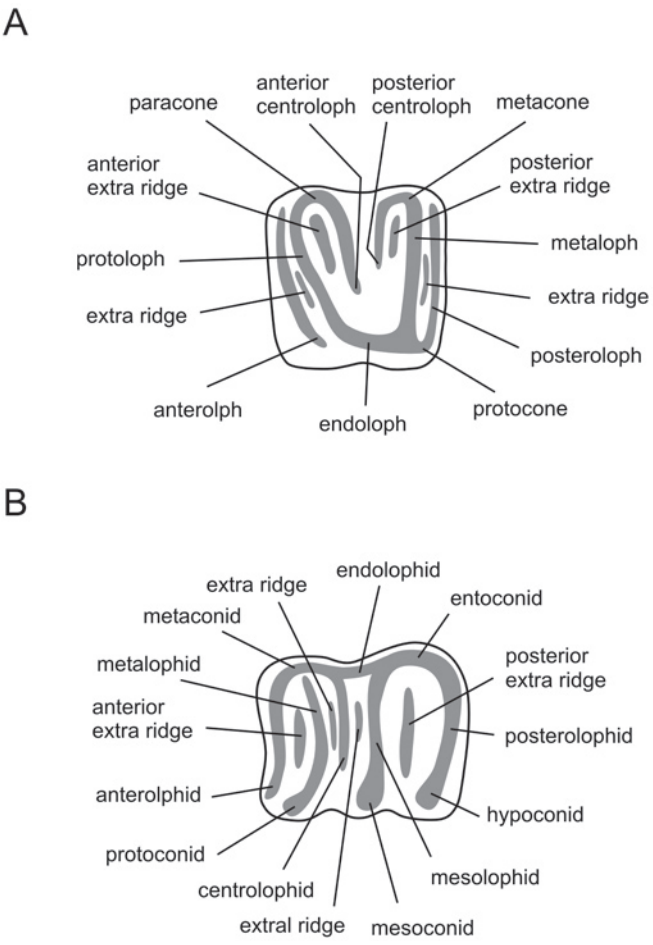


Fig. 7. Dental terminology of Gliridae modified after DAAMS & DE BRUIJN (1995: fig. 1). A: maxillary tooth, B: mandibular tooth.

D e s c r i p t i o n :

Dental characters: Large-sized species of *Muscardinus*; particular wide and short M1 and m1-2; high number of ridges in M2. Ridges of maxillary teeth are slightly tilted backwards, ridges of mandibular teeth are slightly tilted forwards. In order to facilitate the description of *Muscardinus*, the ridges have been numbered from anterior towards posterior (fig. 8).

D4: large, triangular in outline, five ridges; 1st ridge short, labial; 2nd ridge long, transversal; 3rd ridge of medium length, labial; 4th ridge of medium length, labial; 5th ridge short, labial, lingually connected with 4th ridge.

P4: relatively large, five ridges; 1st ridge long, 2nd and 4th ridge lingually connected, forming a U; 3rd ridge of medium length, labial; 5th ridge long.

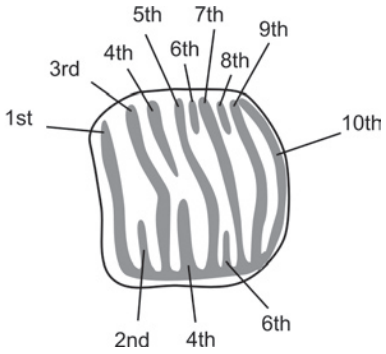


Fig. 8. Second upper molar (M2) of *Muscardinus*. The ridges have been numbered from anterior towards posterior. Modified after DAAMS (1985: fig. 6).

M1: largest tooth; wide and short; six long ridges; 1st ridge ending lingually free; 2nd – 6th ridge lingually connected to endoloph; 4th ridge sometimes constricted, in one specimen not connected with the endoloph (fig. 9/2).

M2: ten ridges (seven long ridges, three short accessory ridges); 1st, 3rd, 4th, 5th, 7th, 9th, 10th ridge long; 2nd ridge short, in lingual position; 6th ridge short, in labial and / or lingual position, 8th ridge short, in labial and / or lingual position; lingual connections of ridges to the endoloph.

M3: not available.

Tab. 4. Measurements (in mm):

		length				width		
		min	mean	max	n	min	mean	max
D4	RH-A/2		1.00		1		1.10	
P4	RH-A/2	1.35		1.40	2	1.05		1.15
M1	RH-A/2	1.45	1.70	1.75	7	1.40	1.45	1.55
	Gö1		1.70		1		1.45	
	Rh-3		1.70		1		1.50	
M2	RH-A/2		1.40		1		1.45	
M3	RH-A/2		1.35		1		1.55	
p4	RH-A/2		0.85		1		0.85	
m1	RH-A/2	1.40		1.50	2	1.30		1.40
m2	RH-A/2	1.25	1.35	1.40	3	1.20	1.45	1.50
m3	RH-A/2		1.40		1		1.35	

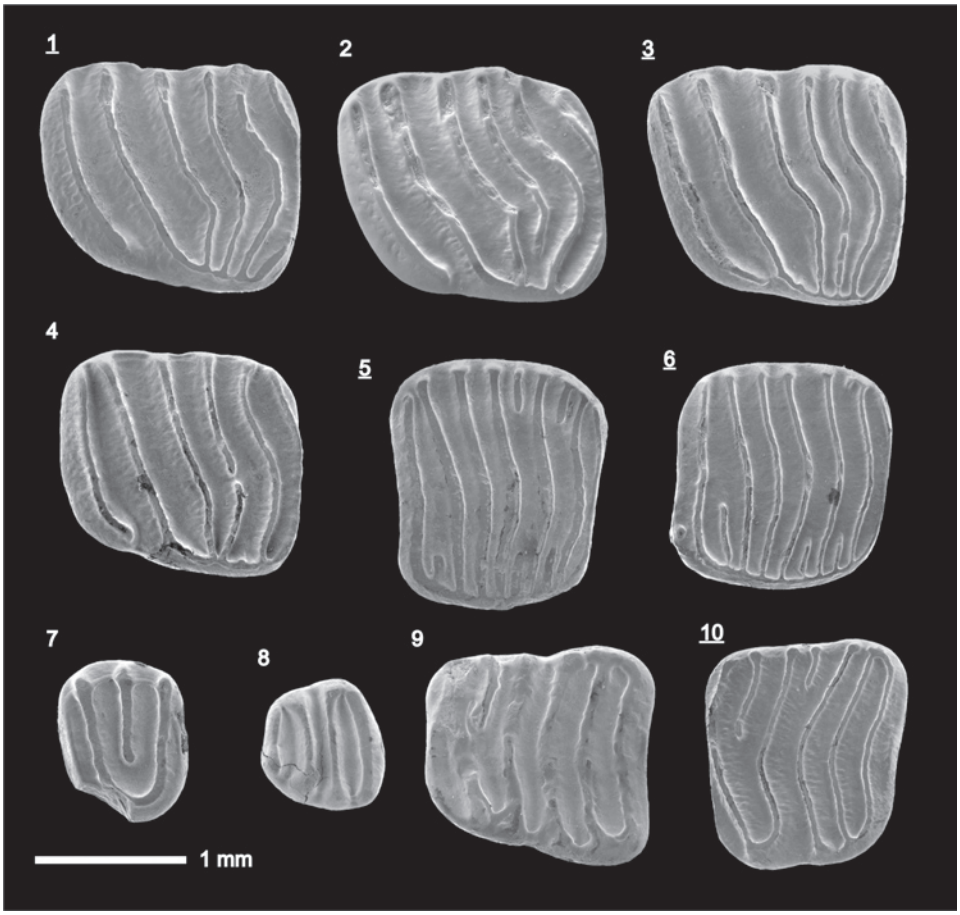


Fig. 9. *Muscardinus vallesiensis* HARTENBERGER, 1966 from Richardhof-Golfplatz (RH-A), Götzendorf (Gö), and Richardhof-Wald (Rh). Magnifications: 20 x; all specimens in the NHMW collection.

9/1 right M1; Rh-1; 2008z0123/0001.
9/2 left M1; Gö1; 1990/0015/0187.
9/3 right M1; RH-A/2; 2008z0122/0004.
9/4 left M1; RH-A/2; 2008z0122/0002.
9/5 right M2; RH-A/2; 2008z0122/0003.
9/6 right M2; RH-A/7; 2008z0122/0019.
9/7 left p4; RH-A/2; 2008z0122/0001.
9/8 left p4; RH-A/2; 2008z0122/0005.
9/9 left m1; RH-A/2; 2008z0122/0006.
9/10 left p2; RH-A/2; 2008z0122/0007.

p4: four parallel, long ridges; not connected.

m1: six main ridges slightly convex in anterior direction; 2nd ridge constricted; 1st – 6th ridge with labial connection; lingual connections of 1st + 2nd ridge and 5th + 6th ridge.

m2: seven ridges, slightly convex in anterior direction; 1st, 3rd, 5th, 6th, 7th ridge long; 2nd and 4th short accessory ridge in lingual position; labial connections of 1st + 3rd ridge and 5th + 6th + 7th ridge.

m3: not available.

Root numbers and positions: The maxillary P4 has three roots, a lingual and two labial ones. The mandibular m2 has four roots, two anterior and two posterior ones. The m3 has three roots, a posterior and two anterior ones. From D4, M1-3, p4-m1 no roots are available.

Remarks: *M. vallesiensis* is one of the large-sized *Muscardinus* species. It is larger than the middle Miocene *M. sansaniensis* (Lartet, 1851) and *M. thaleri* de Bruijn, 1966 and larger than the late Miocene *M. hispanicus* de Bruijn, 1966, *M. pliocaenicus austriacus* Bachmayer & Wilson, 1970 and *M. vireti* Hugueney & Mein, 1965. The typical dental characters, such as the wide and short M1/m1, the wide m2, and the high number of ridges in M2, indicate *M. vallesiensis* to be the immediate descendant of *M. sansaniensis*. These characters set *M. vallesiensis* apart from all other species from the Late Miocene to the present. So far, *M. vallesiensis* is a very rare species of the Vallesian.

Occurrences outside of Austria: Can Llobateres (Spain: Hartenberger 1966; MN9). *M.* cf. *vallesiensis* occurrences are: Rudabanya (Hungary: Daxner-Höck 2005; MN9) and Castell de Barbera (Spain: Agiular et al. 1979; MN?7/8-9). The stratigraphic range of *M. vallesiensis* is the Late Miocene (MN 9). *M. cf. vallesiensis* occurrences range from MN?7/8 to MN9.

Muscardinus hispanicus de Bruijn, 1966
(fig. 10, tab. 5)

1966 *Muscardinus* (*Muscardinus*) *crusafonti* n. sp. – Hartenberger: 598-599, fig. 2.
1993 *Muscardinus* cf. *hispanicus* De Bruijn – Rögl et al.: 510.
1996a *Muscardinus* cf. *hispanicus* De Bruijn. – Daxner-Höck: 3.
2005 *Muscardinus hispanicus* – Daxner-Höck: 154.

Type locality: Pedregueras IIC (Spain); Late Miocene (MN9).

Occurrences in Austria: Mariathal (MN9), Richardhof-Golfplatz (MN9), Götzendorf (MN9), Richardhof-Wald (MN10).

Referred material:

1. Mariathal (Mat): 1 tooth (fragmentary). (NHMW 2008z0124/0001).

2. Richardhof-Golfplatz (RH-A = RH-A/2, 7): 29 teeth (RH-A/2). (NHMW 2008z0125/0001 to 0029); 7 teeth (RH-A/7). (NHMW 2008z0126/0001 to 0007).

3. Götzendorf (Gö = Gö1): 1 tooth. (NHMW 1990/0015/0186).

4. Richardhof-Wald (Rh = Rh-1, 3, 5): 40 teeth (Rh-1). (NHMW 2008z0127/0001 to 0040); 5 teeth (Rh-3). (NHMW 2008z0128/0001 to 0005); 10 teeth (Rh-5). (NHMW 2008z0129/0001 to 0010).

Description:

Dental characters: Small-sized species of *Muscardinus*, relatively long teeth. Ridges of maxillary teeth are slightly tilted backwards, ridges of mandibular teeth are slightly tilted forwards.

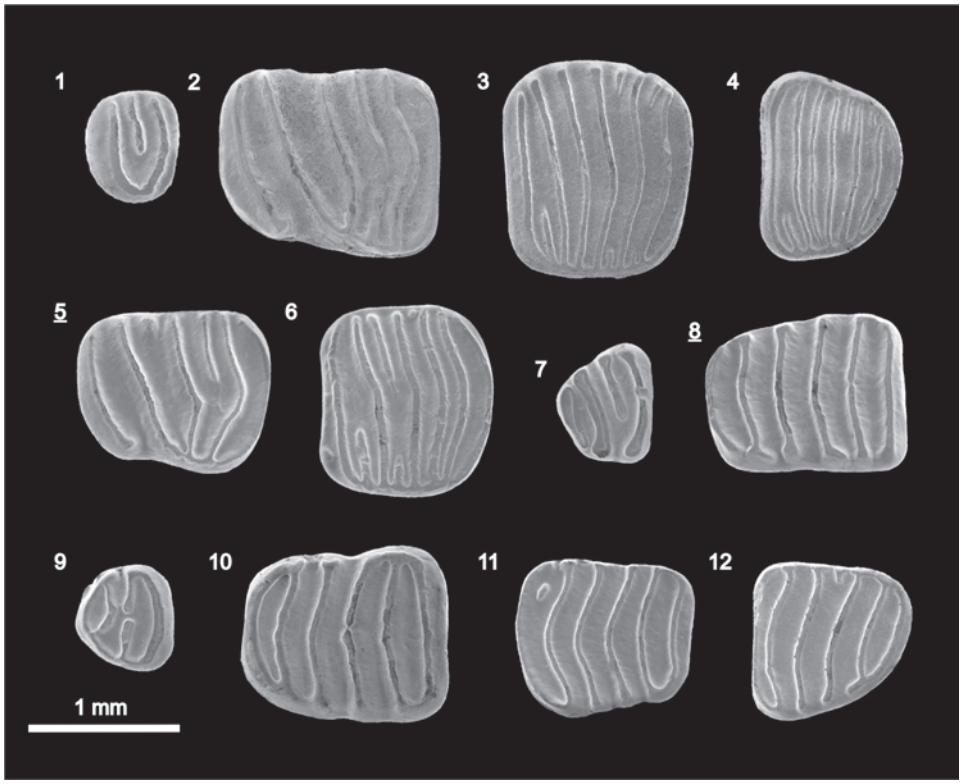


Fig. 10. *Muscardinus hispanicus* DE BRUIJN, 1966 from Richardhof-Golfplatz (RH-A) and Richardhof-Wald (Rh). Magnifications: 30 x; all specimens in the NHMW collection.

10/1 left P4; RH-A/7; 2008z0126/0001.
10/2 left M1; Rh-1; 2008z0127/0001.
10/3 left M2; Rh-1; 2008z0127/0002.
10/4 left M3; Rh-1; 2008z0127/0003.
10/5 right M1; RH-A/2; 2008z0125/0003.
10/6 left M2; RH-A/7; 2008z0126/0002.
10/7 left p4; Rh-3; 2008z0128/0001.
10/8 right m1; Rh-1; 2008z0127/0013.
10/9 left p4; Rh-1; 2008z0127/0008.
10/10 left m1; RH-A/2; 2008z0125/0006.
10/11 left m2; RH-A/2; 2008z0125/0007.
10/12 left m3; Rh-1; 2008z0127/0010.

P4: small; three significant ridges; 1st ridge weak or absent, 2nd and 4th ridge lingually connected, forming a U; 3rd ridge of medium length; 5th ridge weak.

M1: largest tooth; long; five to seven ridges; anteroloph (= 1st ridge) ending lingually free; 2nd, 4th, 6th, 7th ridge long, connected to endoloph; 3rd ridge short or absent; 5th ridge of medium length or long.

M2: eight (up to ten) ridges; 1st,3rd, 5th, 7th, 9th , 10th ridge long; 2nd ridge short in lingual position, 4th ridge interrupted or long; 6th and 8th ridge short or absent; all ridges lingually connected to endoloph.

M3: six long ridges, and three to four short ridges of variable position and length; lingual connection of ridges to endoloph.

p4: four parallel ridges, partly constricted.

m1: rectangular outline; six main ridges slightly convex in anterior direction; frequently labial and lingual connections of 1st and 2nd ridge, and 5th and 6th ridge; anterior part of the tooth more narrow than posterior part.

m2: shorter than m1; molar pattern similar to m1; anterior part more wide than posterior part.

m3: triangular outline; seven ridges; 1st, 3rd, 5th, 6th, 7th ridge long; 2nd ridge of medium length or long; 4th ridge short.

Root numbers and positions: P4 / p4 have one root. The maxillary M1-3 have three roots, a lingual and two labial ones. The mandibular m1-2 have two roots, an anterior and a posterior root; m3 has three roots, a posterior and two anterior ones.

R e m a r k s : *M. hispanicus* differs from *M. thaleri*, *M. sansaniensis* and *M. vallesiensis* by relatively long and slender teeth, and by the reduction of ridges. M1 is longer in relation to M2. *M. topachevskii* Nesin & Kowalski, 1997 from Grytsiv (Ukraine) is very close in size and molar pattern, and has identical root numbers. In our opinion *M. topachevskii* is a junior synonym of *M. hispanicus.*

Tab. 5. Measurements (in mm):

		length					width			
		min	mean	max	stdev	n	min	mean	max	stdev
P4	RH-A	0.60	0.66	0.75	0.0629	4	0.70	0.73	0.75	0.0288
	Rh	0.50	0.57	0.60	0.0577	3	0.60	0.68	0.85	0.1444
M1	RH-A	1.20	1.31	1.45	0.0861	6	1.00	1.08	1.25	0.0987
	Rh	1.30	1.43	1.50	0.0707	9	0.95	1.16	1.45	0.1309
M2	RH-A	1.20	1.23	1.30	0.0447	5	1.20	1.23	1.25	0.0274
	Rh	1.20	1.23	1.25	0.0288	3	1.20	1.27	1.40	0.1155
M3	RH-A	0.85		1.05		2	1.10		1.30	
	Rh	0.90	0.97	1.00	0.0408	6	1.10	1.17	1.30	0.0753
p4	Rh	0.60	0.63	0.70	0.0447	5	0.55	0.64	0.70	0.0652
m1	RH-A	1.15	1.25	1.35	0.0607	7	0.90	1.01	1.15	0.0802
	Gö1		1.30			1		1.10		
	Rh	1.20	1.29	1.45	0.0927	10	0.95	1.08	1.25	0.1059
m2	RH-A	1.15	1.18	1.25	0.0447	5	1.00	1.05	1.15	0.0707
	Rh	1.15	1.27	1.35	0.0790	9	1.10	1.17	1.25	0.0565
m3	RH-A	0.85	1.03	1.15	0.1254	5	0.85	1.03	1.15	0.1500
	Rh	0.95	1.05	1.30	0.1414	5	0.95	1.08	1.30	0.1351

Noteable is the co-occurrence of *M. vallesiensis* and *M. hispanicus* from several localities of the Late Miocene (MN9-10), i.e. Richardhof-Golfplatz, Götzendorf, Richardhof-Wald (Austria), Rudabanya (Hungary), Can Llobateres (Spain). In the Late Vallesian (upper part of MN10) and the Early Turolian (MN 11) of Austria, *M. hispanicus* was replaced by the larger species *M. pliocaenicus austriacus*.

Occurrences outside of Austria: *M. hispanicus* is known from the Late Miocene of Southwest- , and West-, to Central-, Eastern-, and Southeastern Europe (DAXNER-HÖCK 2005: 154) and probably traces back to the late Middle Miocene (CASANOVAS-VILAR 2007: 121): e.g. Castell de Barbera, San Quierze (Spain: MN7/8-9), Pedregueras 2C, Carrilanga 1, Can Llobateres (Spain; MN9), Peralejos, Masia del Barbo (Spain: MN10), Montredon (France; MN10), Marktl, Hammerschmiede (Germany: MN9), Belchatow A (Poland: MN9), Rudabanya (Hungary: MN9), Borský Svatý Jur (Slovakia: MN9), Grytsiv (Ukraine: = *M. topachevskii* NESIN & KOWALSKI, 1997; MN9), Comanesti 2b (Romania: MN9), and Kastellios Hill (Greece: MN10). The stratigraphic range is late Middle Miocene to Late Miocene (MN?7/8-10).

Muscardinus pliocaenicus austriacus BACHMAYER & WILSON, 1970
(fig. 11, tab. 6)

1970 *Muscardinus pliocaenicus austriacus* nov. subspec. – BACHMAYER & WILSON: 563-564, figs 14, 71.
1978 *Muscardinus pliocaenicus austriacus* BACHMAYER & WILSON 1970. – BACHMAYER & WILSON: 147-148, pl. 3, fig. 11.
1980 *Muscardinus austriacus* BACHMAYER & WILSON, 1970. – BACHMAYER & WILSON: 363-365.
1980 *Muscardinus pliocaenicus* KOWALSKI, 1963. – DAXNER-HÖCK : 148, tab. 1.
1981 *Muscardinus pliocaenicus* KOWALSKI, 1963. – DAXNER-HÖCK & DE BRUIJN: 163-165, fig. 3.
1983 *Muscardinus austriacus* BACHMAYER & WILSON, 1970. – BACHMAYER & WILSON: 130.
1996a *Muscardinus austriacus* BACHMAYER & WILSON. – DAXNER-HÖCK: 4.
1996a *Muscardinus pliocaenicus* KOWALSKI. – DAXNER-HÖCK: 4.
2004a *Muscardinus* sp. – DAXNER-HÖCK: 3.

Type locality: Kohfidisch (Austria); Late Miocene (MN11)

Occurrences in Austria: Schernham (MN10), Kohfidisch (MN11), Eichkogel MN(11).

Referred material:

1. Schernham (Sch): 93 teeth. (NHMW 2008z0130/0001 to 14, 2008z0130/0021 to 0059, 2008z0130/0061 to 0100).

2. Kohfidisch (Ko = Ko IIIu, IIIo, IV, Cm): 250 jaws, tooth rows and isolated teeth. (NHMW 2008z0131/0001 to 0250); and type material (BACHMAYER & WILSON 1970, 1978, 1980, 1983).

3. Eichkogel (E): 43 teeth and fragments. (NHMW 2008z0246/0001 to 0043); and 85 teeth. (PIUW 1953/23/1 to 85) (DAXNER-HÖCK & DE BRUIJN 1981: 163-165).

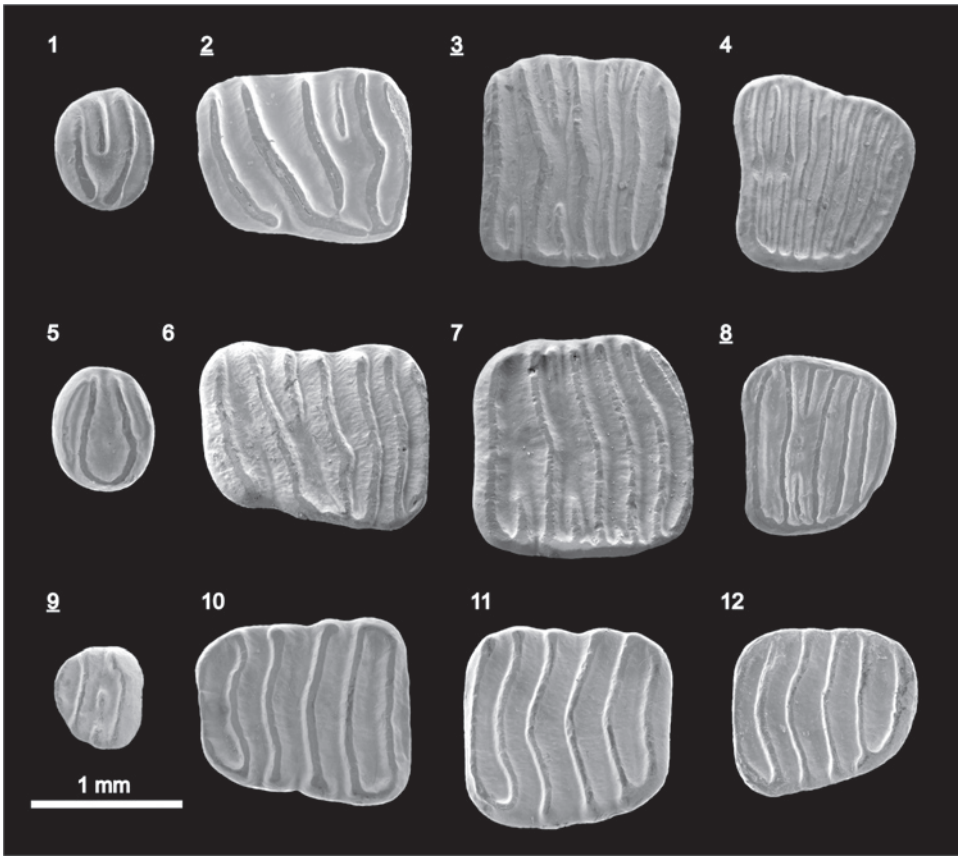


Fig. 11. *Muscardinus pliocaenicus austriacus* BACHMAYER & WILSON, 1970 from Schernham (Sch), Kohfidisch (Ko) and Eichkogel (E). Magnifications: 30 x; all specimens in the NHMW collection.

11/1 left P4; E; 2008z0246/0002.
11/2 right M1; E; 2008z0246/0008.
11/3 right M2; Ko; 2008z0131/0004.
11/4 left M3; Ko; 2008z0131/0006.
11/5 left P4; Sch; 2008z0130/0006.
11/6 left M1; Ko; NHMW2008z0131/0003.
11/7 left M2; Sch; 2008z0130/0002.
11/8 right M3; Ko; 2008z0131/0007.
11/9 right p4; E; 2008z0246/0004.
11/10 left m1; Sch; 2008z0130/0008.
11/11 left m2; Sch; 2008z0130/0009.
11/12 left m3; Sch; 2008z0130/0010.

D e s c r i p t i o n :

Dental characters: Middle-sized, relatively long teeth; ridges of maxillary teeth are slightly tilted backwards, ridges of mandibular teeth are slightly tilted forwards; increasing root numbers.

P4: smallest tooth; from three to five ridges; 1st ridge weak or absent; 2nd and 4th ridge lingually connected, forming a U; 3rd ridge of medium length, short or absent; 5th ridge mostly long, sometimes weak or absent.

M1: largest tooth; five to seven ridges; 1st ridge (= anteroloph) long, ending lingually free; 2nd, 4th, 6th, 7th main ridge long, lingually connected with endoloph; 3rd ridge varying from absent to long; if present in labial position; 5th ridge in labial position, as a rule longer than 3rd ridge, varying in length from short to long, sometimes interrupted; endoloph sometimes interrupted.

M2: square outline; eight to ten ridges; 1st, 3rd, 5th, 7th, 9th and 10th ridge long; 2nd ridge short, lingual, 4th ridge interrupted or long; short 6th and 8th ridge possible; mostly lingual connection of ridges with endoloph.

Tab. 6. Measurements (in mm); Published measurements from DAXNER-HÖCK & DE BRUIJN (1981: 163), BACHMAYER & WILSON (1970: 564), BACHMAYER & WILSON (1978: 148), BACHMAYER & WILSON (1980: 364) and BACHMAYER & WILSON (1983: 130) are not included in this table.

		length					width			
		min	mean	max	stdev	n	min	mean	max	stdev
P4	Sch	0.60	0.65	0.65	0.0288	3	0.75	0.77	0.80	0.0288
	Ko	0.50	0.54	0.65	0.0607	7	0.65	0.71	0.85	0.0731
	E	0.55	0.61	0.65	0.0376	6	0.60	0.70	0.80	0.0836
M1	Sch	1.35	1.48	1.60	0.0693	13	1.05	1.16	1.25	0.0681
	Ko	1.35	1.47	1.60	0.0687	58	1.05	1.16	1.35	0.0595
	E	1.35	1.47	1.65	0.1125	6	1.10	1.14	1.20	0.0376
M2	Sch	1.20	1.33	1.45	0.0674	24	1.15	1.30	1.40	0.0607
	Ko	1.15	1.26	1.40	0.0646	51	1.15	1.27	1.40	0.0633
	E	1.20	1.25	1.30		3	1.20	1.22	1.25	
M3	Sch	1.05	1.09	1.15	0.0478	4	1.10	1.20	1.30	0.0912
	Ko	0.75	1.00	1.25	0.0925	39	1.00	1.14	1.30	0.0646
	E	0.85	0.90	1.05		3	1.05	1.10	1.25	
p4	Ko	0.40		0.45		2	0.50		0.55	
	E	0.55	0.58	0.60	0.0288	4	0.50	0.61	0.65	0.0750
m1	Sch	1.15	1.37	1.50	0.0840	15	1.00	1.15	1.25	0.0667
	Ko	1.15	1.35	1.45	0.0689	31	1.00	1.10	1.25	0.0637
	E		1.45			1		1.20		
m2	Sch	1.25	1.36	1.50	0.0680	16	1.00	1.24	1.35	0.0898
	Ko	1.20	1.28	1,45	0.0674	24	1.15	1.22	1.30	0.0461
	E	1.15	1.28	1.35	0.1154	3	1.10	1.13	1.15	0.0288
m3	Sch	1.10	1.18	1.25	0.0516	6	1.00	1.13	1.30	0.1169
	Ko	0.95	1.06	1.25	0.0911	24	0.90	1.05	1.15	0.0683

M3: high variability in size and molar pattern; six long ridges and three to four short ridges of variable position and length; lingual connection of ridges with endoloph; narrow valleys.

p4: very small; three to four parallel ridges, not connected.

m1: narrow in its anterior part; six main ridges slightly convex in anterior direction; 1st and 2nd ridge and 5th and 6th ridge with labial and partially with lingual connections.

m2: widest in its anterior part; labially slightly convex; six main ridges slightly convex in anterior direction; 1st and 2nd ridge and 5th and 6th ridge with labial and partially with lingual connections.

m3: triangular outline; six long ridges.

Root numbers and positions: P4/p4 have one root. The maxillary M1 has four roots, two labial and two lingual ones; M2 has three or four roots (Schernham: three roots, i.e. two labial, one lingual; Kohfidisch, Eichkogel: three to four roots), M3: has three roots, a lingual and two labial ones. The mandibular m1 has two or three roots (Schernham: one anterior, one or two posterior; Kohfidisch and Eichkogel: one anterior, two posterior); m2 has two or four roots (Schernham: one anterior and one posterior (bifurcated) root; Kohfidisch and Eichkogel: two anterior, two posterior roots); m3 has three roots, a posterior and two anterior ones.

R e m a r k s : Previous investigations of *M. pliocaenicus austriacus* from Kohfidisch (Bachmayer & Wilson 1970, 1978) and Eichkogel (Daxner-Höck & de Bruijn 1981: 164-165) include detailed illustrations and taxonomic discussions. *M. pliocaenicus austriacus* combines dental characters of *M. hispanicus* and *M. pliocaenicus pliocaenicus* Kowalski, 1963. It is intermediate between these species in tooth-pattern and size, and in root numbers. *M. pliocaenicus austriacus* from Austria is considerably older (Late Miocene, MN10-11) than *M. pliocaenicus pliocaenicus* from Poland (Pliocene, MN 14-16). In our opinion there is a close relationship between *M. hispanicus*, *M. pliocaenicus austriacus* and *M. pliocaenicus pliocaenicus*. Most probably, *M. pliocaenicus austriacus* derived from *M. hispanicus*.

So far, occurrences outside of Austria are unknown. The stratigraphic range of *M. pliocaenicus austriacus* is Late Miocene (MN10-11).

Glirinae gen. and spec. indet.
(fig. 12, tab. 7)

O c c u r r e n c e s in Austria: Richardhof-Golfplatz (MN9), Richardhof-Wald (MN10).

R e f e r r e d m a t e r i a l :

1. Richardhof-Golfplatz (RH-A/2): 1 tooth. (NHMW 2008z0132/0001).

2. Götzendorf (Gö1): 1 tooth. (NHMW 1990/0015/0188).

3. Richardhof-Wald (Rh-1): 2 teeth. (NHMW 2008z0133/0001 to 0002).

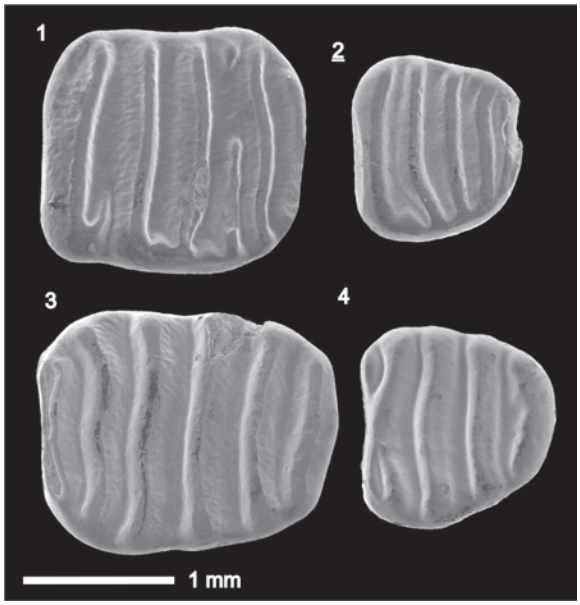


Fig. 12. Glirinae gen. and spec. indet. from Richardhof-Golfplatz (RH-A), Götzendorf (Gö), and Richardhof-Wald (Rh). Magnifications: 20 x.

12/1 left M2; RH-A/; NHMW 2008z0132/0001.
12/2 right M3; Gö1; NHMW 1990/0015/0118.
12/3 left m2; Rh-1; NHMW 2008z0133/0001.
12/4 left m3; Rh-1; NHMW 2008z0133/0002.

Dental characters: Large teeth; occlusal surface flat; ridges robust, transverse, parallel; ridges of maxillary molars slightly tilted backwards; ridges of mandibular molars slightly tilted forwards.

M2: rectangular outline, relatively long; five parallel long ridges and two ridges of secondary rank: 1st, 3rd, 4th, 6th, 7th ridge long, transversal; 2nd ridge short, in lingual position; 5th ridge interrupted, consisting of a long lingual and a short labial part; weak endoloph.

M3: considerably smaller than M2; five parallel long ridges and two ridges of secondary rank: 1st, 3rd, 4th, 6th, 7th ridge long, transversal; 2nd ridge short, in lingual position; 5th ridge short, in labial position; all ridges lingually connected by an endoloph.

m2: rectangular outline with rounded corners, relatively long; six strong transverse ridges without connections.

m3: considerably smaller than m2; four transverse ridges and a labial and a lingual anterolophid.

Tab. 7. Measurements (in mm):

		length	width
M2l	RH-A/2	1.80	1.60
M3r	Gö1	1.30	1.30
m2l	Rh-1	2.00	1.60
m3r	Rh-1	1.30	1.35

Root numbers and positions: The maxillary M2-3 have three roots, a wide lingual and two labial ones. The mandibular m2 has three roots, a posterior and two anterior ones; the roots of m3 are not preserved.

R e m a r k s : The teeth roughly resemble *Muscardinus* and *Glis*.

From *Muscardinus* they differ by:
- the relatively long M2/m2 and M3
- the robust straight and parallel ridges
- the divided anterolophid of m3
- the root numbers of m2 (three roots)

From *Glis* they differ by:
- tilted parallel and strongly transverse ridges
- no extra ridges between the main ridges, and neither labial nor lingual connections in mandibular teeth.

These teeth differ considerably from any other Glirinae genera or species. For the time being, the taxonomy remains open because of the poor record.

Till now, occurrences outside of Austria are unknown. The stratigraphic range of Glirinae gen. and spec. indet. is Late Miocene (MN9-10).

Genus *Glis* Brisson, 1762

Glis minor minor Kowalski, 1963
(fig. 13, tab. 8)

1983 *Glis* cf. *G. minor* Kowalski, 1963. – Bachmayer & Wilson: 133, pl. 1, fig. 1.
1996a *Glis* sp. – Daxner-Höck: 3.
2005 *Glis minor*. – Daxner-Höck: 157.

T y p e l o c a l i t y : Podlesice (Poland), Pliocene (MN14).

O c c u r r e n c e s in Austria: Richardhof-Golfplatz (MN9), Richardhof-Wald (MN10), Kohfidisch (MN11).

R e f e r r e d m a t e r i a l :

1. Richardhof-Golfplatz (RH-A/2): 2 teeth. (NHMW 2008z0134/0001 to 0002).

2. Richardhof-Wald (Rh-1): 1 tooth. (NHMW 2008z0135/0001).

3. Kohfidisch (Ko): 7 teeth. (NHMW 2008z0136/0001 to 0007) (originals from Bachmayer & Wilson 1983 included).

D e s c r i p t i o n :

Dental characters: Large, low crowned teeth with plane occlusal surface; thick main ridges that in unworn specimens have a symmetrical cross section with rounded apex. Maxillary teeth: protoloph and mealoph do not connect lingually; protoloph labially connected neither to the anteroloph nor to the anterior centroloph; long anterior centroloph of equal height and thickness as the protoloph and metaloph; posterior centroloph absent. Mandibular teeth: centrolophid does not reach lingual edge of tooth and is not

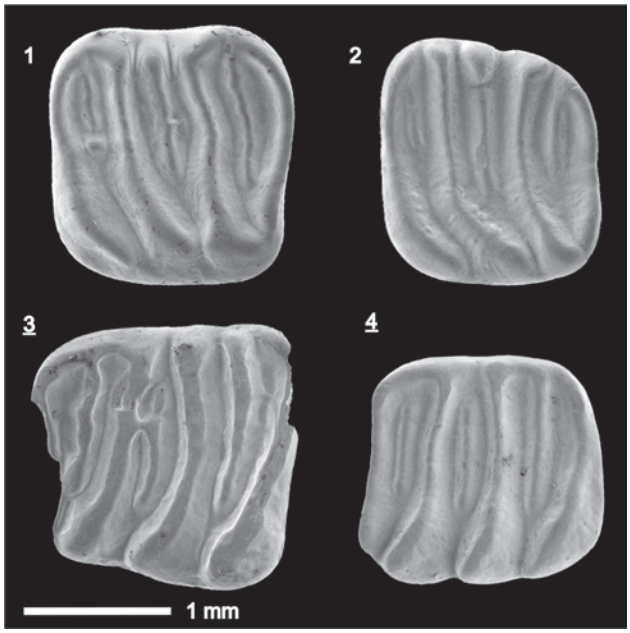


Fig. 13. *Glis minor minor* KOWALSKI, 1963 from Richardhof-Golfplatz (RH-A), Richardhof-Wald (Rh) and Kohfidisch (Ko). Magnifications: 20 x.

13/1 left M1; Rh-1; NHMW 2008z0135/0001.
13/2 left M2; Ko-IIIu; NHMW 2008z0136/0007.
13/3 right m1; RH-A/2; NHMW 2008z0134/0002.
13/4 left m2; Ko-IIIu; NHMW 2008z0136/0003.

connected to metaconid; mesolophid not always connected to entoconid; posterior extra ridge may be confluent with posterolophid lingually (DE BRUIJN 1998; 108-109).

M1-2: almost square in outline; four main ridges; anterior centroloph; relatively long anterior extra ridge and posterior extra ridge; variable labial connections of ridges; M2 widest in its anterior part.

m1-2: rectangular outline; four main ridges; long anterior extra ridge lingually connected with metaconid, anterolophid and metalophid; a centrolophid of medium length;

Tab. 8. Measurements (in mm):

		length				width		
		min	mean	max	n	min	mean	max
M1	RH-A	1.55	1.50		1		1.60	
	Rh-1		1.70		1		1.70	
	Ko	1.55		1.55	2	1.55		1.60
M2	Ko	1.45		1.55	2	1.60		1.70
m1	RH-A/2		1.70		1		1.70	
	Ko		1.50		1		1.45	
m2	Ko	1.55		1.60	2	1.50		1.55

long posterior extra ridge (without connection in m1, but connected to posterolophid in m2).

No roots preserved.

R e m a r k s : *Glis* is a very rare dormouse from the Miocene of Austria. The dental pattern and size is most similar to *G. minor minor* from the Pliocene of Poland (KOWALSKI 1963). *G. vallesiensis* AGUSTI, 1981 from Seu d' Urgell (Spain; MN9) differs by its larger size, by having no extra ridge between anteroloph and protoloph of M2, no centrolophid in m3 and a more or less square outline of m2 (AGUSTI 1981). *Glis* cf. *minor* from the Late Miocene of Rudabanya (Hungary) is intermediate in morphology and size between the smaller *G. minor minor* and the larger *G. vallesiensis*, but definitely resembles the former more (DAXNER-HÖCK 2005: 152). The younger *G.* cf. *minor* from Maramena (Greece) is slightly larger, but the molar pattern resembles *G. minor minor* (DAXNER-HÖCK 1995: 109). In our opinion, *G. vallesiensis* from Grytsiv (Ukraine; NESIN & KOWALSKI 1997) and from Belchatov A (Poland; KOWALSKI 1997) resemble *G. minor minor* more than *G. vallesiensis*. Possible relationships with *G. minor minor* were not discussed by KOWALSKI (1997) and NESIN & KOWALSKI (1997).

O c c u r r e n c e s outside of Austria: Rudabanya (Hungary: DAXNER-HÖCK 2005; MN9), Belchatov A (Poland: KOWALSKI 1997; MN9), Grytsiv (Ukraine: NESIN & KOWALSKI 1997; MN9), Maramena (Greece: DAXNER-HÖCK 1995; MN13/14), Podlesice, Rebielice, Weze (Poland: KOWALSKI 1963; MN14-16). The stratigraphic range is Late Miocene to Pliocene (MN9-16).

Genus *Myoglis* BAUDELOT, 1965

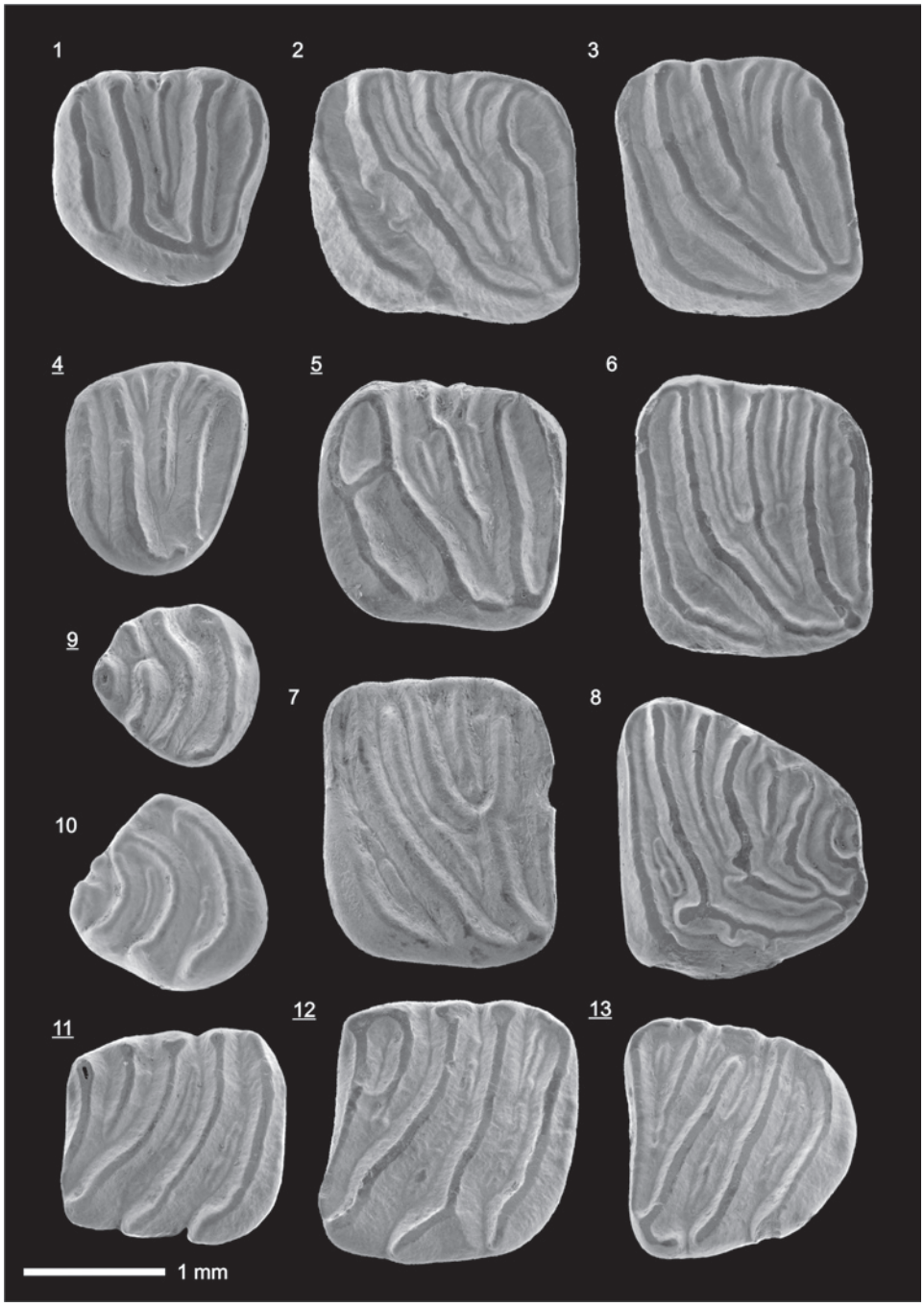
Myoglis ucrainicus NESIN & KOWALSKI, 1997
(fig. 14, tab. 9)

1993	*Myoglis meini* (DE BRUIJN). – RÖGL et al.: 510.
1996a	*Myoglis meini* (DE BRUIJN). – DAXNER-HÖCK: 3.
2003	*Myoglis meini* (DE BRUIJN, 1995[1996]). – NEMETSCHEK & MÖRS: 404.
2004a	*Myoglis* sp. – DAXNER-HÖCK: 3.
2005	*Myoglis ucrainicus*. – DAXNER-HÖCK: 160.

T y p e l o c a l i t y : Grytsiv (Ukraine); Late Miocene (MN9).

Fig. 14. *Myoglis ucrainicus* NESIN & KOWALSKI, 1997 from Richardhof-Golfplatz (RH-A), Götzendorf (Gö), Richardhof-Wald (Rh) and Schernham (Sch). Magnifications: 20 x. ►

14/1	left P4; Gö; 1990/0015/0183; all specimens in the NHMW collection.
14/2	left M1; RH-A/2; 2008z0137/0002.
14/3	left M2; RH-A/2; 2008z0137/0003.
14/4	right P4; Sch; 2008z0139/0008.
14/5	right M1; Sch; 2008z0139/0007.
14/6	left M2; Rh-1; 2008z0138/0002.
14/7	left M2; Sch; 2008z0139/0009.
14/8	left M3; Rh-1; 2008z0138/0004.
14/9	right p4; Sch; 2008z0139/0014.
14/10	left p4; Sch; 2008z0139/0010.
14/11	right m1; Sch; 2008z0139/0016.
14/12	right m2; Sch; 2008z0139/0015.
14/13	right m3; Sch; 2008z0139/0011.



Occurrences in Austria: Richardhof-Golfplatz (MN9), Götzendorf (MN9), Richardhof-Wald (MN10), Schernham (MN10).

Referred material:

1. Richardhof-Golfplatz (RH-A = RH-A/2): 21 teeth. (NHMW 2008z0137/0001 to 0021).

2. Götzendorf (Gö = Gö 1): 4 teeth. (NHMW 1990/0015/0181 to 0184).

3. Richardhof-Wald (Rh = Rh-1, 3, 5A): 22 teeth (partly fragments). (NHMW 2008z0138/0001 to 0022).

4. Schernham (Sch): 36 teeth. (NHMW 2008z0139/0001 to 0036).

Tab. 9. Measurements (in mm):

		length					width			
		min	mean	max	stdev	n	min	mean	max	stdev
P4	Gö	1.20		1.50		2	1.30		1.55	
	Rh		1.45			1		1.55		
	Sch	1.25	1.28	1.30	0.0288	4	1.35	1.40	1.45	0.0408
M1	RH-A	1.65	1.70	1.75	0.0500	3	1.55	1.68	1.75	0.1154
	Rh	1.40	1.70	1.75	0.1600	4	1.60	1.70	1.75	0.0629
	Sch	1.60	1.66	1.75	0.0495	8	1.50	1.63	1.70	0.0801
M2	RH-A	1.50	1.56	1.60	0.0418	4	1.70	1.78	1.85	0.0570
	Rh	1.55	1.63	1.70	0.0645	4	1.75	1.85	1.90	0.0750
	Sch	1.50	1.52	1.55	0.0288	3	1.65	1.78	1.90	0.1258
M3	RH-A		1.60			1		1.70		
	Rh	1.40		1.60		2	1.60		1.80	
	Sch	1.35	1.45	1.55	0.0912	4	1.50	1.60	1.70	0.0816
p4	RH-A		1.30			1		1.35		
	Gö		1.30			1		1.20		
	Rh	0.80	1.20	1.25	0.2466	3	0.80	1.20	1.20	0.2309
	Sch	1.10	1.19	1.30	0.0865	4	1.05	1.11	1.25	0.0946
m1	RH-A	1.60	1.68	1.75	0.0763	3	1.45	1.48	1.50	0.0288
	Gö		1.80			1		1.60		
	Rh		1.65			1		1.55		
	Sch	1.55	1.63	1.70	0.0570	5	1.40	1.46	1.50	0.0547
m2	RH-A	1.65	1.65	1.65		3	1.60	1.72	1.80	0.1040
	Sch	1.55	1.67	1.80	0.0908	5	1.55	1.66	1.75	0.1024
m3	RH-A	1.70		1.80		2	1.70		1.80	
	Sch		1.60			1		1.55		

D e s c r i p t i o n :

Dental characters: Large, low crowned teeth with plane occlusal surface; four oblique main ridges and a varying number of extra ridges in upper and lower teeth; ridges tilted backwards in upper teeth, and forwards in lower teeth; V-shaped valleys between ridges; ridges with structured enamel surface mainly on the flat slope of the ridges: i.e. anterior slope of upper teeth and posterior slope of lower teeth; extra ridges of upper teeth in labial position; anterior centroloph of maxillary teeth and anterior extra ridge of mandibular teeth as high as the main ridges; trend towards increasing size and towards a more complex dental pattern with time.

P4: of variable size and shape; four main ridges (anteroloph, protoloph, metaloph, posteroloph); anterior centroloph of medium length and one or two short extra ridges; except for the anteroloph the main ridges may be connected lingually.

M1: rectangular outline; four main ridges, two or three extra ridges; anterior centroloph as high as main ridges; extra ridges anterior and posterior to anterior centroloph; a third extra ridge between metaloph and posteroloph only in two specimens; extra ridge anterior to anteroloph in one specimen; protoloph mostly without lingual connection; lingual connection of protoloph, metaloph and posteroloph only in two specimens; metaloph and posteroloph lingually connected in five specimens.

M2: square outline; four main ridges, two or three short extra ridges; anteroloph free; protoloph, metaloph and posteroloph lingually connected; anterior centroloph and anterior extra ridge longer than in M1.

M3: highest number of ridges; extra ridges almost as high as main ridges; protoloph of semicircular extend from the antero-labial to the postero-lingual corner, similar arrangement of the other ridges; high variability of the M3-pattern.

p4: four transversal ridges; anterolophid smallest.

m1: rectangular outline, anterior narrower than posterior; four long main ridges (anterolophid, metalophid, mesolophid, posterolophid); anterior extra ridge of medium length, as high as main ridges; two or three posterior low extra ridges.

m2: rectangular outline; wider in its anterior than posterior part; four long main ridges; anterior extra ridge of medium length, as high as main ridges; two or three posterior low extra ridges.

m3: similar to m2 but narrower in its posterior part.

Root numbers and positions: The maxillary P4 has two or three roots, two labial and one or two in lingual position; M1-2 have four roots, two labial and two lingual ones. The mandibular p4 has one root; m1-2 have three roots, one in posterior, two in anterior position. From M3/m3 no roots are available.

R e m a r k s : *M. ucrainicus* is the largest and youngest species of *Myoglis*. It differs from *M. meini* (DE BRUIJN, 1996a) by its larger teeth, higher root-numbers, longer extra ridges and by the trend to lose the lingual connection of protoloph and metaloph in M1, and the small extra ridge posterior to the posterolophid of m1-2. Note that the youngest occurrences from Schernham (MN10) show some complications of the molar pattern: e.g. one M1 with connection of anteroloph and protoloph by a longitudinal ridge (fig.

14/5) and one M2 with an unusual connection between anterior centroloph and metaloph labial to the longitudinal axis of the tooth (fig. 14/7). *M. ucrainicus* most probably descended from the Middle Miocene *M. meini.*

The locality Schernham (late MN10) provides not only the youngest occurrence of *M. ucrainicus* but also of the genus *Myoglis.*

O c c u r r e n c e s outside of Austria: Grytsiv (Ukraine: Nesin & Kowalski 1997; MN9) and Rudabanya (Hungary: Daxner-Höck 2005; MN9). The stratigraphic range is Late Miocene (MN9-10).

Subfamily Dryomyinae de Bruijn, 1967

Genus *Paraglirulus* Engesser, 1972

Paraglirulus werenfelsi Engesser, 1972
(fig. 15, tab. 10)

1996a *Paraglirulus werenfelsi* Engesser. – Daxner-Höck: 3.
1998a *Paraglirulus werenfelsi* Engesser 1972. – Daxner-Höck: 379-380, fig. 7; pl. 4, fig. 1-8, tab. 14.
2003a *Paraglirulus werenfelsi* Engesser, 1972. – Daxner-Höck, G.: 294, tab. 1.

T y p e l o c a l i t y : Anwil (Switzerland), Middle Miocene (MN7/8).

Early and Late Miocene o c c u r r e n c e s in Austria: Obergänserndorf (MN5; Daxner-Höck 1998a), Richardhof-Golfplatz (MN9), Götzendorf (MN9), Richardhof-Wald (MN10).

R e f e r r e d m a t e r i a l :

1. Richardhof-Golfplatz (RH-A = RH-A/2, 7): 64 teeth. (NHMW 2008z0140/0001 to 0064).

2. Götzendorf (Gö = Gö1): 5 teeth. (NHMW 1990/0015/0171 to 0175).

3. Richardhof-Wald (Rh = Rh-1, 3, 5): 30 teeth. (NHMW 2008z0141/0001 to 0030).

D e s c r i p t i o n :

Dental characters: Medium-sized cheek teeth with concave occlusal surface; relatively simple dental pattern; main ridges higher than extra ridges; wide valleys between main ridges; mostly nine ridges in maxillary molars and ten ridges in mandibular molars.

Maxillary molars: Five main ridges (anteroloph, protoloph, anterior centroloph, metaloph, posteroloph) and four extra ridges between main ridges; continuous endoloph; ornamented lingual border; labial border not concave; weak paracone and metacone; frequent connections of anteroloph to protoloph and metaloph to posteroloph; anterior centroloph lingually ending free (some P4, M1, M3), or connected to endoloph (all M2), labially sometimes connected to protoloph + anteroloph or ending free; transverse ridges run parallel and at right angles to the endoloph (especially in M2).

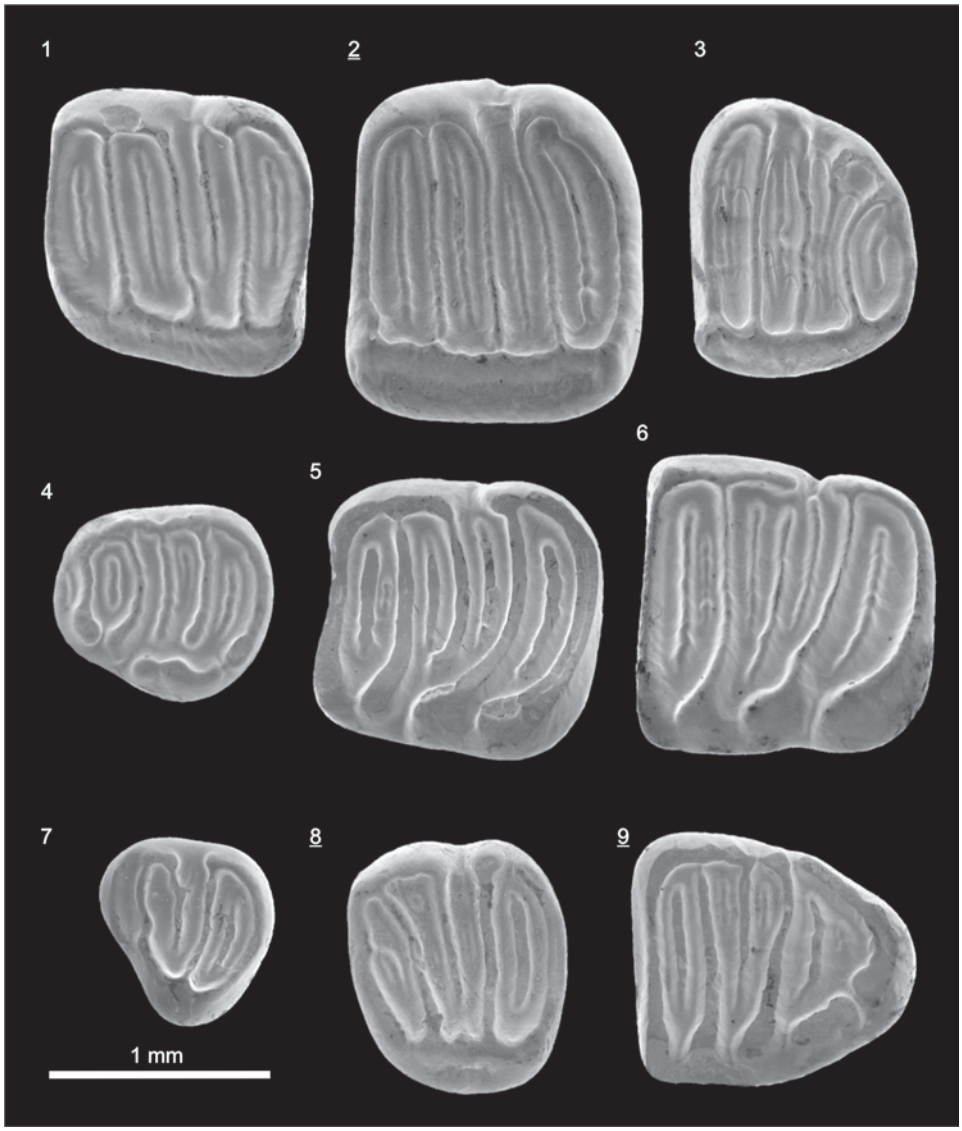


Fig. 15. *Paraglirulus werenfelsi* ENGESSER, 1972 from Richardhof-Golfplatz /RH-A) and Richardhof-Wald (Rh). Magnifications: 30 x; all specimens in the NHMW collection.

15/1 left M1; RH-A/2; 2008z0140/0003.
15/2 right M2; RH-A/2; 2008z0140/0005.
15/3 left M3; RH-A/2; 2008z0140/0007.
15/4 left p4; RH-A/7; 2008z0140/0011.
15/5 left m1; RH-A/7; 2008z0140/0012.
15/6 left m2; RH-A/7; 2008z0140/0014.
15/7 left D4; Rh-1; 2008z0141/0001.
15/8 right P4; RH-A/7; 2008z0140/0001.
15/9 right m3; RH-A/2; 2008z0140/0017.

D4: triangular; short anteroloph; protoloph labially continuous with anterior centroloph; labial and lingual connection of metaloph to posteroloph; posterior extra ridge.

P4: molariform; subquadrate in outline; rounded corners; anterior centroloph long, connected to paracone, irregular lingual connection to endoloph; anterior and posterior extra ridges present; small extra ridges anterior and / or posterior of the anterior centroloph.

M1-2: almost square in outline; extra ridges long or of medium length.

M3: trapezoidal outline; pattern similar to M1-2; minor reductions in the posterior part.

Mandibular molars: without continuous endolophid; four long and strong main ridges (anterolophid, metalophid, mesolophid, posterolophid); centrolophid strong but shorter than main ridges; four or five lower extra ridges; centrolophid separate from mesolophid but lingually connected to anterolophid + metalophid; in most of the specimens

Tab. 10. Measurements (in mm):

		length					width			
		min	mean	max	stdev	n	min	mean	max	stdev
D4	Rh		0.80			1		0.85		
P4	OG2	0.80	0.80	0.80		2	0.94	0.95	0.96	0.0141
	RH-A	0.85	0.93	1.00	0.0597	8	0.95	1.04	1.15	0.0821
	Rh		0.85			1		1.00		
M1	RH-A	1.20	1.22	1.25	0.0258	8	1.15	1.24	1.35	0.0678
	Gö	1.20		1.25		2	1.30		1.35	
	Rh	1.15	1.20	1.25	0.0500	3	1.20	1.27	1.30	0.0577
M2	RH-A	1.15	1.24	1.30	0.0475	7	1.25	1.36	1.45	0.0787
	Gö		1.25			1		1.40		
	Rh	1.15	1.25	1.35	0.0790	5	1.25	1.36	1.45	0.1031
M3	RH-A	0.90	0.96	1.00	0.0478	4	1.05	1.18	1.25	0.0866
	Gö		1.05			1		1.40		
	Rh	1.00	1.03	1.10	0.0408	6	1.20	1.23	1.30	0.0408
p4	RH-A	1.00	1.01	1.05	0.0224	5	0.85	0.90	0.95	0.0500
	Rh	0.90	0.96	1.00	0.0479	4	0.60	0.73	0.85	0.1443
m1	RH-A	1.20	1.26	1.30	0.0376	6	1.10	1.16	1.20	0.0376
	Rh	1.20		1.25		2	1.05		1.15	
m2	RH-A	1.20	1.28	1.35	0.0510	14	0.05	1.26	1.40	0.0874
	Gö		1.35			1		1.30		
	Rh	1.25	1.28	1.30	0.0289	3	1.20	1.25	1.30	0.0500
m3	RH-A	1.00	1.16	1.25	0.1109	4	1.00	1.10	1.15	0.0707

no labial connection of anterolophid to metalophid; lingual connection of mesolophid to posterolophid.

p4: large; endolophid continuous or interrupted; small anteroconid in some specimens; three or four extra ridges.

m1: narrow in its anterior part; four pronounced extra ridges of medium length or long; a second anterior extra ridge is possible.

m2: wide in its anterior part; four pronounced extra ridges of medium length or long; a second anterior and /or posterior extra ridge is possible.

m3: relatively long; similar with m2 but smaller.

Root numbers and positions: P4 / p4 have two roots. The maxillary molars have three roots, a wide lingual and two labial ones. The mandibular molars have two roots, one in posterior and one in anterior position.

R e m a r k s : *Paraglirulus* and *Glirulus* are similar in dental pattern. However, there are significant differences in size between the larger *Paraglirulus* species and the smaller *Glirulus* species. The original diagnosis of *Paraglirulus* includes: the connection of the anterior centroloph to the endoloph, the free labial end of the anterior centroloph, the absence of an endolophid, and two roots in lower molars. However, the continuous endolophid, and three roots in lower molars, are *Glirulus*-characters. Note the long evolutionary independence of smaller species and larger species within the *Glirulus* – *Paraglirulus* group. From the Early Miocene (MN4) to the Late Miocene (MN10), large and small species co-occur. The problem of genus-identification and attribution of certain species to *Paraglirulus* or *Glirulus* was extensively discussed in previous years (ENGESSER 1972; MAYR 1979; DAXNER-HÖCK & DE BRUIJN 1981; MEULEN VAN DER & DE BRUIJN 1982). As a result, MEULEN VAN DER & DE BRUIJN (1982: 490) distinguished only one genus *Glirulus* and two subgenera *Glirulus* (*Paraglirulus*) and *Glirulus* (*Glirulus*). In our opinion, however, *Paraglirulus* and *Glirulus* should retain generic rank.

From the Miocene of Europe, two species of *Paraglirulus* are known, i.e. *P. agelakisi* MEULEN VAN DER & DE BRUIJN, 1982 (range: MN4) and *P. werenfelsi* ENGESSER, 1972 (range: MN5-10). The first record of *Paraglirulus* in Austria is *P*. sp. from Oberdorf (MN4; DE BRUIJN 1998: 117, pl. 5, figs 8-9). The first record of *P. werenfelsi* in Austria is Obergänserndorf (MN5; DAXNER-HÖCK 1998a: 379-380, pl. 4, figs 1-8). From MN5 to MN10, minor changes of dental pattern – expressed by increasing dominance and increasing number of extra ridges – go along with size increase. A third species is described in this volume, i.e. *P. schultzi* nov. spec. from Schernham (MN10).

O c c u r r e n c e s outside of Austria: Maßendorf, Schönenberg (Germany: SCHÖTZ 2002; MN5), Anwil (Switzerland: ENGESSER 1972; MN7/8), Sansan (France: ENGESSER 1972; MN6), Wiesholz (Switzerland: BOLLIGER 2000; MN6), Belchatov B, A (Poland: KOWALSKI 1997; MN5/6-9), Kleineisenbach, Giggenhausen, Marktl (Germany: MAYR 1979; MN7/8-9), Rudabanya (Hungary: DAXNER-HÖCK 2005; MN9), Can Llobateres (Spain: ENGESSER 1972; MN9). The stratigraphic range is Early to Late Miocene (MN5-10).

***Paraglirulus schultzi* nov. spec.**
(fig. 16, tab. 11)

2004a *Glirulus* sp. – DAXNER-HÖCK: 3.

D e r i v a t i o n o m i n i s : In honour of our colleague and friend Dr. Ortwin SCHULTZ.

T y p e l o c a l i t y : Schernham (Sch) near Haag am Hausruck, Upper Austria (Northern Alpine Foreland Basin).

S t r a t u m t y p i c u m : silt and sand of the Hausruck Schotter; Late Miocene, Late Pannonian, Late Vallesian, mammal Zone MN10.

H o l o t y p e : Left M1 (Sch). Museum of Natural History Vienna, Geological-Palaeontological Department (NHMW 2008z0142/0001); fig. 16/1.

D e s c r i p t i o n of the holotype: Outline of M1 square. Posterior side wider than anterior side. Lingual border ornamented. Five main ridges and eight ridges of secondary rank intercalated in the valleys. Five transverse main ridges (anteroloph, protoloph, anterior centroloph, metaloph and posteroloph) lingually connected to the endoloph. Endoloph constricted posterior to the anteroloph. Labial connection of anteroloph and protoloph. Eight second-rank ridges (1st – 8th) of almost the same height and thickness as the main ridges, i.e. 1st a long extra ridge between anteroloph and protoloph, 2nd the long anterior extra ridge accompanied by 3rd – 4th shorter extra ridges anterior and posterior of it, 5th an extra ridge between anterior and posterior centroloph, 6th the long posterior centroloph, 7th the posterior extra ridge, 8th a long extra ridge between metaloph and posteroloph. The posteroloph is elongated and turns from the posterior border to the labial border as far as the posterior centroloph. The posteroloph is not connected to the transversal ridges. The labial end of the anterior centroloph is free. The holotype has three roots.

P a r a t y p e s : 2 M1l (fragmentary), 1 M2r, 1 M3l, 3 m1l, 1 m2l. (NHMW 2008z0142/0002 to 0009); figs 16/2-5.

D i a g n o s i s : *Paraglirulus* species with many ridges and narrow valleys. Extra ridges are mostly long and almost as high and thick as the main ridges. Anterior centroloph of M1-2 is connected to the endoloph. M3 is small. Maxillary molars have three, mandibular molars have two roots.

Tab. 11. Measurements (in mm):

pos. nr.		length	width
1 holotype	M1l	1.20	1.20
3 paratype	M2r	1.30	1.20
2 paratype	M3l	0.95	1.10
4 paratype	m1l	1.30	1.10
8 paratype	m1l	1.20	1.10
9 paratype	m1l	1.30	1.10
5 paratype	m2l	1.35	1.20

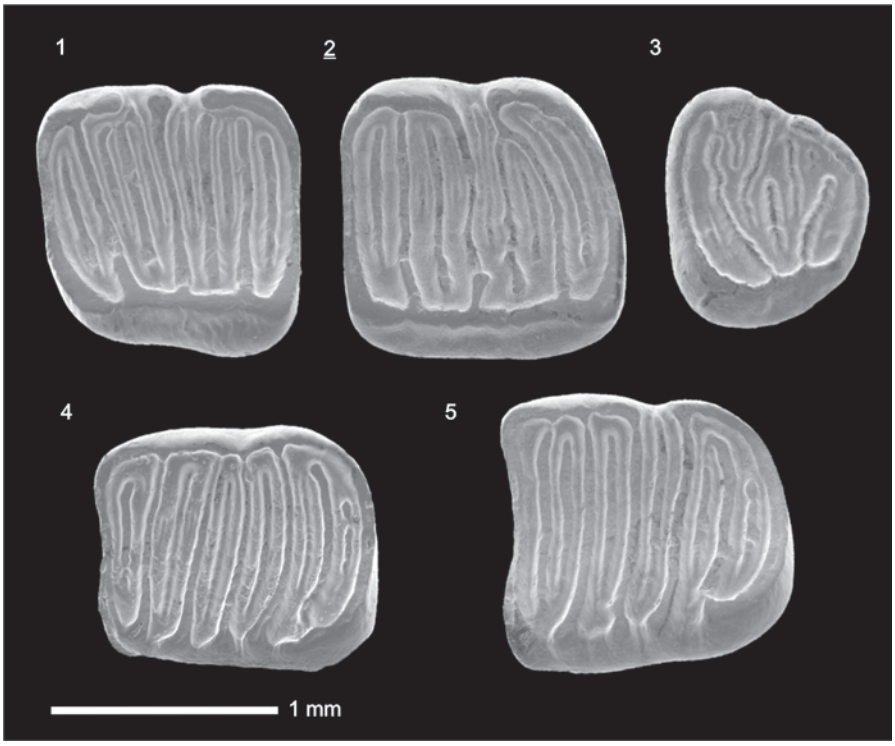


Fig. 16. *Paraglirulus schultzi* nov. spec. from Schernham. Magnifications: 30 x; all specimens in the NHMW collection.

16/1 left M1 (H); Sch; 2008z0142/0001.
16/2 right M2 (P); Sch; 2008z0142/0003.
16/3 left M3 (P); Sch; 2008z0142/0002.
16/4 left m1 (P); Sch; 2008z0142/0004.
16/5 left m2 (P); Sch; 2008z0142/0005.

D i f f e r e n t i a l d i a g n o s i s : *P. schultzi* nov. spec. differs from *P. agelakisi* and *P. werenfelsi* by narrow valleys, by the numerous thin ridges and by the small M3. *P. schultzi* is slightly larger than *P. agelakisi* and *P. werenfelsi* from the Early Miocene, yet the Late Miocene occurrences of *P. werenfelsi* and *P. schultzi* are almost equal in size, and differ in dental pattern only. *P. schultzi* is significantly larger than the various *Glirulus* species.

D e s c r i p t i o n of the paratypes: The lingual border of maxillary molars is ornamented. The endoloph is well developed.

M1 (fragmentary): pattern identical with the holotype.

M2 (fig. 16/2): outline almost square, slightly longer than wide; five main ridges and eight ridges of secondary rank as in M1 (holotype); main ridges lingually connected to the endoloph; anteroloph and anterior centroloph join in a labial loop to which the protoloph is attached; a second labial loop is formed by the posteroloph and metaloph, to which the posterior centroloph is attached.

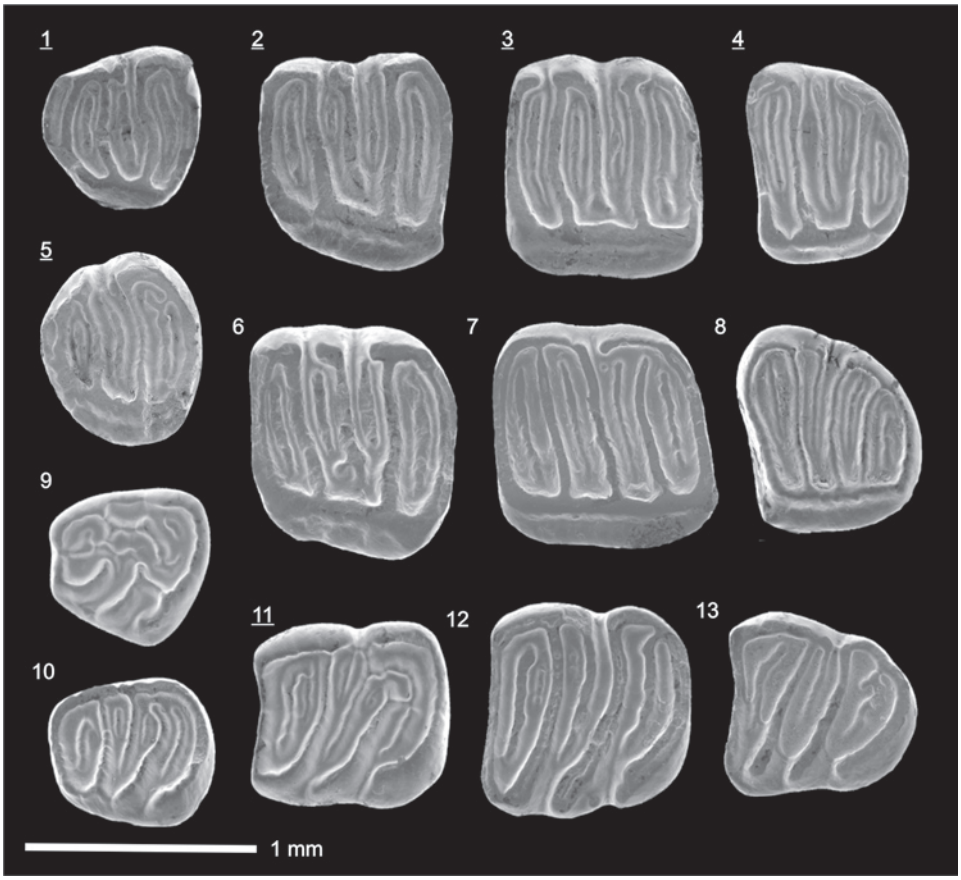


Fig. 17. *Glirulus lissiensis* Hugueney & Mein, 1965 from Richardhof-Golfplatz (RH-A), Richardhof-Wald (Rh), Schernham (Sch), Kohfidisch (Ko) and Eichkogel (E). Magnifications: 30 x; all specimens in the NHMW collection.

17/1 right P4; RH-A/2; 2008z0143/0001.
17/2 right M1; RH-A/2; 2008z0143/0002.
17/3 right M2; Rh-1; 2008z0144/0002.
17/4 right M3; RH-A/2; 2008z0143/0004.
17/5 right P4; Ko; 2008z0146/0005.
17/6 left M1; Sch; 2008z0145/0001.
17/7 left M2; Ko; 2008z0146/0001.
17/8 left M3; Sch; 2008z0145/0002.
17/9 left p4; Rh-5A; 2008z0144/0008.
17/10 left p4; Sch; 2008z0145/0003.
17/11 right m1; Rh-1; 2008z0144/0006.
17/12 left m2; E; 2008z0147/0004.
17/13 left m3; RH-A/2; 2008z0143/0007.

M3 (fig. 16/3): outline rounded; relatively small; anteroloph, protoloph, metaloph and posteroloph connected to the oblique endoloph; labial and lingual free ends of anterior and posterior centrolophs; five extra ridges partly rudimented.

Mandibular molars with at least five long ridges (anterolophid, metalophid, centrolophid, mesolophid, posterolophid) and seven to nine ridges of secondary rank. Out of the latter the anterior extra ridge and posterior extra ridge are longest and can reach

the labial and / or lingual border. Five to seven more extra ridges of variable length do not reach the labial and lingual border. The endolophid can be complete or incomplete consisting of two parts separated by a notch.

m1: rectangular outline; posterior part widest; at least thirteen ridges; two m1 with incomplete endolophid; one m1 with complete endolophid (fig. 16/4) to which six ridges are connected (anterolophid, anterior extra ridge, metalophid, centrolophid, mesolophid, posterolophid); labial connection of anterolophid to anterior extra ridge.

m2 (fig. 16/5): rectangular outline; anterior part widest; twelve parallel ridges; incomplete endolophid; anterolophid, metalophid and centrolophid lingually connected to the incomplete endolophid (anterior part); long extra ridge between centrolophid and mesolophid; mesolophid lingually connected to the elongated posterolophid; additionally six middle to long extra ridges.

Root numbers and positions: The maxillary molars have three roots, a wide lingual and two labial ones. The mandibular molars have two roots, an anterior and a posterior one.

R e m a r k s : *P. schultzi* from the Late Miocene is the youngest known member in the *Paraglirulus*-lineage. From the Early Miocene to the Late Miocene, *Paraglirulus* remained very conservative in size and dental pattern. *P. schultzi*, however, shows significantly modified molar structures, i.e. the originally wide valleys between the dominating main ridges are filled up by extra ridges of increasing number, length and height. This may be interpreted as a reaction to a changed food supply and environmental conditions at end of the Vallesian. An alternative explanation could be that *P. schultzi* is not a descendent of *P. werenfelsi*, but stems from an unknown side branch of the *Paraglirulus*-line.

No occurrences outside of Austria known. The stratigraphic range is Late Miocene (MN10).

Genus *Glirulus* THOMAS, 1906

Glirulus lissiensis HUGUENEY & MEIN, 1965
(fig. 17, tab. 12)

1970 *Glirulus* sp. – DAXNER-HÖCK: 600.
1970 *Glirulus* sp. – DAXNER-HÖCK & RABEDER: 3.
1980 *Glirulus lissiensis* HUGUENEY & MEIN, 1965. – DAXNER-HÖCK: 148, tab.1.
1980 *Paraglirulus* cf. *P. lissiensis* (HUGUENEY & MEIN, 1965). – BACHMAYER & WILSON: 366.
1981 *Glirulus lissiensis* HUGUENEY & MEIN, 1965. – DAXNER-HÖCK & DE BRUIJN: 166-168, fig. 4.
1983 *Paraglirulus* cf. *P. lissiensis* (HUGUENEY & MEIN, 1965). –BACHMAYER & WILSON: 132.
1998 *Glirulus* (*Glirulus*) *lissiensis* HUGUENEY & MEIN, 1965. – DE BRUIJN: 116, pl. 6, figs 1-7.
1998b *Glirulus* (*Glirulus*) *lissiensis*. – DAXNER-HÖCK: 478, tab. 1.
1996a *Paraglirulus* cf. *lissiensis* (HUGUENEY & MEIN, 1965). – DAXNER-HÖCK: 4.
1996a *Glirulus lissiensis* HUGUENEY & MEIN – DAXNER-HÖCK: 4.

T y p e l o c a l i t y : Lissieu (France), Late Miocene (MN13).

O c c u r r e n c e s in Austria: Richardhof-Golfplatz (MN9), Richardhof-Wald (MN10), Schernham (MN10), Kohfidisch (MN11), Eichkogel (MN11).

R e f e r r e d m a t e r i a l :

1. Richardhof-Golfplatz (RH-A = RH-A/2, 7): 30 teeth. (HMW 2008z0143/0001 to 0030).

Tab. 12. Measurements (in mm). *Measurements from DAXNER-HÖCK (1981: 167) included.

		length					width			
		min	mean	max	stdev	n	min	mean	max	stdev
P4	RH-A	0.60		0.75		2		0.70		
	Ko	0.70	0.75	0.80	0.0500	3	0.75	0.80	0.85	0.0500
	E*		0.68			1		0.73		
M1/2	RH-A	0.75	0.84	0.95	0.0579	10	0.75	0.85	0.95	0.0745
	Rh	0.90	0.90	0.95		3	0.90	0.95	1.00	
	Sch		0.90			1		0.95		
	Ko	0.80	0.89	1.00	0.0453	53	0.80	0.9	1.00	0.0592
	E*	0.80	0.85	0.96		11	0.85	0.94	1.05	
M3	RH-A	0.75		0.80		2	0.85		0.90	
	Rh	0.75		0.90		2	0.80		0.90	
	Sch		0.75			1			0.90	
	Ko	0.70	0.77	0.85	0.0480	13	0.75	0.84	0.90	0.0463
	E*	0.82	0.84	0.85		5	0.90	0.95	1.07	
p4	Rh		0.75			2	0.65		0.70	
	Sch		0.75			1		0.65		
	Ko	0.70	0.73	0.75	0.0288	4	0.55	0.59	0.60	0.0250
m1	RH-A	0.80	0.88	0.95	0.0524	6	0.75	0.78	0.85	0.0408
	Rh	0.85		0.90		2	0.80		0.85	
	Ko	0.80	0.89	1.00	0.0736	6	0.75	0.78	0.80	0.0258
	E*	0.93		0.94		3	0.83		0.91	
m2	RH-A	0.85	0.90	0.95	0.0353	5	0.85	0.87	0.90	0.0273
	Rh		0.90			2		0.85		
	Sch		1.00			1		1.00		
	Ko	0.90	0.96	1.00	0.0418	5	0.85	0.90	0.95	0.0500
	E*	0.93	0.95	1.01		6	0.90	0.93	1.05	
m3	RH-A	0.80	0.87	0.90	0.0447	5	0.80	0.84	0.85	0.0223
	Rh	0.80	0.80	0.95		3	0.75	0.80	0.95	
	Ko	0.85	0.92	1.00	0.0758	6	0.80	0.83	0.90	0.0418
	E*	0.85		0.89		2	0.85		0.87	

2. Richardhof-Wald (Rh = Rh-1, 5A): 14 teeth. (NHMW 2008z0144/0001 to 0014).

3. Schernham (Sch): 4 teeth. (NHMW 2008z0145/0001 to 0004).

4. Kohfidisch (Ko = Ko I, Ko II, KoIII, KoIIIu, KoCm): 90 teeth. (NHMW 2008z0146/0001 to 0019, 0021 to 0091) and originals from BACHMAYER & WILSON (1980, 1983).

5. Eichkogel (E*): 7 teeth. (NHMW 2008z0147/0001 to 0007) and 24 teeth. (PIUW 1953/24/1 to 32) (DAXNER-HÖCK 1981: 167).

D e s c r i p t i o n :

Dental characters: Small-sized cheek teeth with concave occlusal surface; extra ridges almost as high as main ridges, valleys narrow; mostly nine ridges in maxillary molars and nine or ten ridges in mandibular molars.

Maxillary molars: four main ridges (anteroloph, protoloph, metaloph, posteroloph) lingually connected to endoloph; five extra ridges, i.e. long anterior centroloph, shorter posterior centroloph, anterior extra ridge, posterior extra ridge, and extra ridge between protoloph and anterior centroloph; mostly labial connections of anteroloph to protoloph and metaloph to posteroloph; anterior centroloph lingually ending free or connected to endoloph, anterior centroloph labially ending free or connected to anteroloph+metaloph; posterior centroloph sometimes connected to metaloph+posteroloph.

P4: molariform; four main ridges; three or four extra ridges.

M1/2: square outline; four main ridges, five extra ridges (anterior centroloph always long); in specimens from Kohfidisch, tendency towards increasing length of extra ridges and connection of anterior centroloph to endoloph.

M3: similar to M1/2, but narrow in its posterior part.

Mandibular teeth: four long main ridges (anterolophid, metalophid, mesolophid, posterolophid); relatively long centrolophid; variable number of additional extra ridges (one to five); occasionally labial connection of anterolophid and metalophid; endolophid continuous or interrupted posterior to the centrolophid.

p4: nine or ten ridges, in some specimens irregularly arranged (fig. 17/9).

m1-2: four main ridges; long centrolophid and increasing number and length of extra ridges; increasing tendency towards complete endolophid (from Vallesian towards Turolian occurrences).

m3: similar to m1-2; four main ridges and three to six extra ridges.

Root numbers and positions: The maxillary teeth have three roots, a wide lingual and two labial ones. The mandibular teeth have two roots, an anterior and a posterior one.

R e m a r k s : As outlined above there are no reliable morphological differences between *Glirulus* and *Paraglirulus* cheek teeth, but time equivalent species of *Glirulus* are considerably smaller than *Paraglirulus* species. Three species of Gliridae have been defined from the Miocene of Europe, i.e. *G. diremptus* (MAYR, 1979) (range: NM4-5), *G. minor* WU, 1993 (range: MN4), *G. lissiensis* HUGUENEY & MEIN, 1965 (range: MN4-13). *Paraglirulus conjunctus* MAYR, 1979 (range: MN4-9) is thought to be a synonym of

G. lissiensis (Daxner-Höck & de Bruijn 1981: 168). *G. ekremi* Ünay, 1994 has been reported from the Early Miocene of Anatolia.

Occurrences outside of Austria: Lissieu (France: Hugueney & Mein 1965; MN13), Sansan (France: Engesser 1972; MN6), Anwil (Switzerland: Engesser 1972; MN7/8), Can Llobateres (Spain: Engesser 1972; MN9), Rudabánya (Hungary: Daxner-Höck 2005; MN9), Belchatów A (Poland: Kowalski 1997; MN9), Belchatów B (Poland: Kowalski 1997; MN5/6), part of "*P. diremptus-conjunctus*" and the "*P. diremptus*"- occurrences in Germany (Mayr 1979: 302; MN5-9). The stratigraphic range is Early to Late Miocene (MN4–13).

Genus *Graphiurops* Bachmayer & Wilson, 1980

Graphiurops austriacus Bachmayer & Wilson, 1980
(fig. 18, tab. 13)

1978 Gliridae, indeterminant. – Bachmayer & Wilson: 151, pl. 3, fig. 14.
1980 *Graphiurops austriacus* nov. spec. – Bachmayer & Wilson: pl. 3, figs 1-12.
1980 Gliride gen. et spec. indet. – Daxner-Höck: 148, tab. 1.
1981 Gliride gen. et spec. indet. – Daxner-Höck & de Bruijn: 170-171, fig. 6.
1983 *Graphiurops austriacus* Bachmayer & Wilson, 1980. – Bachmayer & Wilson: 132-133.
1985 *Graphiurops austriacus* Bachmayer & Wilson. – Bachmayer & Wilson: 105.
1985 Glirid, gen. and sp. indet. – Bachmayer & Wilson: 104.
1990 ? *Graphiurops austriacus* Bachmayer & Wilson, 1980. – Bachmayer & Wilson: 2-3; pl. 1/2a, 2b.
1995 *G. austriacus* Bachmayer & Wilson, 1980. – Daams & de Bruijn: 10.
1995 *Graphiurops austriacus* Bachmayer & Wilson, 1980. – Daams & de Bruijn: 42.
1996a *Graphiurops austriacus* Bachmayer & Wilson. – Daxner-Höck: 4
1996b *Graphiurops austriacus*. – Daxner-Höck: 263, fig. 21.1.
1999 *Graphiurops austriacus* Bachmayer & Wilson, 1980. – Daams: 307, tab. 29.2.

Type locality: Kohfidisch (Austria), Late Miocene (MN11).

Occurrences in Austria: Richardhof-Golfplatz (MN9), Richardhof-Wald (MN10), Schernham (MN10), Kohfidisch (MN11), Eichkogel (MN11).

Referred material:

1. Richardhof-Golfplatz (RH-A = RH-A/2): 1 tooth. (NHMW 2008z0148/0001).

2. Richardhof-Wald (Rh = Rh-1): 2 teeth. (NHMW 2008z0149/0001 to 0002).

3. Schernham (Sch): 2 teeth. (NHMW 2008z0150/0001 to 0002).

4. Kohfidisch (Ko): right maxilla with p4-M3. (NHMW 2008z0151/0001); 2 right fragmentary mandibles with m2. (NHMW 2008z0151/0020, 0022); 21 teeth. (NHMW 2008z0151/0002 to 0018, 0023 to 0026); and type material: right fragmentary mandible with m1 (holotype). (NHMW1980/0053/0001); left fragmentary mandible with m2. (NHMW 1980/0053/0002); right m1. (NHMW 1980/0053/0003) (Bachmayer & Wilson 1980: 367, pl. 3, figs 11-12) and right M1. (NHMW 1989/0073/0001) (Bachmayer & Wilson 1990: pl. 1 / 2A, 2B.

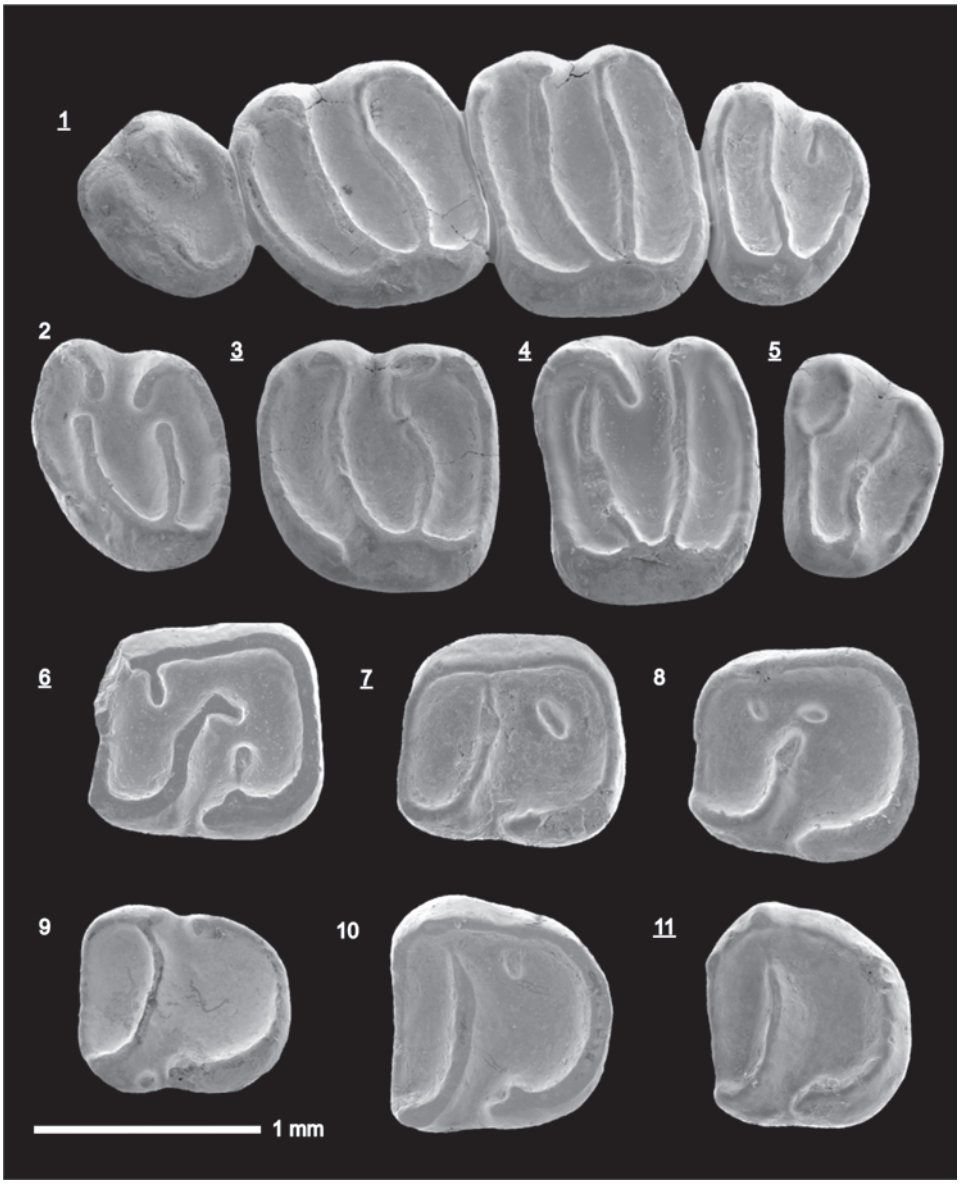


Fig. 18. *Graphiurops austriacus* BACHMAYER & WILSON, 1980 from Kohfidisch (Ko) and Eichkogel (E). Magnifications: 30 x; all specimens in the NHMW collection.

18/1 right P4-M3; Ko-IIIu; 2008z0151/0001.
18/2 left P4; Ko-IIIo; 2008z0151/0005.
18/3 right M1; Ko; 2008z0151/0007.
18/4 right M2; Ko-IIIu; 2008z0151/0011.
18/5 right M3; Ko-IIIu; 2008z0151/0002.
18/6 right m1 (H); Ko; 1980/0053/0001.
18/7 right m1 (P); Ko; 1980/0053/0003.
18/8 left m1; Ko-IIIu; 2008z0151/0016.
18/9 left m2; (E); 2008z0249/0001.
18/10 left m2 (P); Ko; 1980/0053/0002.
18/11 right m3; Ko-IIIu; 1980/0053/0002 (= 2008z0151/0017).

5. Eichkogel (E): 1 tooth. (NHMW 2008z0249/0001); and 2 teeth. (PIUW 1953/29/1 to 2) (Daxner-Höck & de Bruijn 1981: 170-171).

D e s c r i p t i o n :

Dental characters: Teeth small-medium sized; occlusal surface concave; strongly reduced dental structures; wide valleys enclosed by marginal ridges.

Maxillary teeth: labial margin concave; three wide valleys surrounded by four main ridges (anteroloph, protoloph, metaloph, posteroloph); lingual connections of the ridges to the endoloph can be notched or constricted; frequently, labial connections of anteroloph, paracone and protoloph, and labial connections of metaloph, metacone and posteroloph.

P4: three or four transversal ridges, partly connected to endoloph, partly constricted or short.

M1/2: four long main ridges mostly connected to endoloph; anteroloph-endoloph connection can be notched or constricted (fig. 18/3); short anterior centroloph connected to paracone in M1/2 (fig. 18/4): anterior and posterior valleys completely or almost completely enclosed by ridges; median valley open in labial direction.

M3 (fig. 18/1, 18/5): anterior valley small or large, enclosed by anteroloph and protoloph; metaloph variable in length and shape.

Tab. 13. Measurements (in mm). * measurements from Bachmayer & Wilson (1980: 367) and ** measurements from Daxner-Höck & De Bruijn (1981: 171) included.

		length				width		
		min	mean	max	n	min	mean	max
P4	Rh-1	0.75		0.60	2		0.70	
	Ko	0.60	0.65	0.85	3	0.75	0.80	1.00
	E**		0.68		1		0.70	
M1	Ko	0.95	1.00	1.05	5	1.00	1.00	1.05
	E**		0.88		1		0.82	
M2	Ko	0.90	1.00	1.00	7	1.10	1.17	1.25
M3	RH-A/2		0.65		1		0.80	
	Sch		0.70		1		0.80	
	Ko	0.70	0.75	0.90	5	0.90	0.95	1.00
m1	Ko*	0.95	1.02	1.05	4	0.85	0.90	0.91
m2	Ko*	1.03	1.03	1.05	4	1.00	1.05	1.09
	E		1.00		1		0.80	
m3	Ko		0.90		1		0.95	

Mandibular teeth: wide trigonid- and talonid-basins surrounded by marginal ridges; trigonid-basin partly or completely enclosed by the anterolophid, metalophid and anterior part of the endolophid; talonid-basin separated from the trigonid-basin by the metalophid, surrounded by the endolophid and the posterolophid, which is elongated to the labial side; one or two small extra ridges of variable length and position can occur.

m1: trigonid basin completely enclosed by metalophid, anterolophid and endolophid (fig. 18/7) or partly open (fig. 18/8; 18/6 = holotype); one or two rudimentary ridges in the talonid-basin possible.

m2: trigonid-basin closed (fig. 18/9), wide talonid-basin surrounded by a marginal ridge; one rudimentary extra ridge possible.

m3 (fig. 18/11): similar to m2.

Root numbers and positions: The maxillary teeth (P4-M3) have three roots, a wide lingual and two labial ones. The mandibular m1 has two roots, an anterior and a posterior one. The m2 and m3 have three roots, two in anterior and one in posterior position.

R e m a r k s : *Graphiurops* is most similar to *Myomimus* in size, in shape of teeth, in number and position of roots, but has a simplified dental pattern. It differs considerably from all fossil Gliridae of Europe by the strongly reduced dental structures. As mentioned by DAXNER-HÖCK & DE BRUIJN (1981: 171), BACHMAYER & WILSON (1980: 368-369), MONTGELARD et al. (2003: 1954), there are remote morphological similarities with the living African genus *Graphiurus*. However, as opposed to *Graphiurus*, the lower molars are longer than wide. The phylogenetic relations of *Graphiurops* are unknown.

We follow the opinion of DAAMS & DE BRUIJN (1995) to include *Graphiurops* into the subfamily Dryomyinae. *Graphiurops* is a monospecific genus that has so far been recognized only from the Late Miocene of Europe: i. e. *G. austriacus* (range: MN9-11).

O c c u r r e n c e s outside of Austria: Suchomasty (Czech Republic: FEJFAR 1989; MN10), Pezinok (Slovakia: JONIAK / unpublished Thesis; MN10), Dionay (France: MEIN 1984; MN11). The stratigraphic range is Late Miocene (MN9-11).

Genus *Myomimus* OGNEV, 1924

Myomimus dehmi (DE BRUIJN, 1966)
(fig. 19, tab. 14)

1970 *Peridyromys* sp. – DAXNER-HÖCK: 600.
1970 *Peridyromys* sp. – DAXNER-HÖCK & RABEDER: 3.
1970 *Peridyromys compositus* nov. spec.(in part) – BACHMAYER & WILSON: 564-566, figs 72, 74.
1978 *Myomimus* cf. *M. dehmi* (DE BRUIJN 1966). – BACHMAYER & WILSON: 148.
1980 *Myomimus dehmi* (DE BRUIJN, 1966). – DAXNER-HÖCK: 148, tab. 1.
1980 Cf. *Myomimus dehmi*. – BACHMAYER & WILSON: 353.
1981 *Myomimus dehmi* (DE BRUIJN, 1966). – DAXNER-HÖCK & DE BRUIJN: 168-170, fig. 5.
1983 *Myomimus dehmi* (DE BRUIJN, 1966). – BACHMAYER & WILSON: 132.
1996a *Myomimus dehmi* (DE BRUIJN). – DAXNER-HÖCK: 4.

Type locality: Pedregueras II C (Spain), Late Miocene (MN9)

Occurrences in Austria: Kohfidisch and Eichkogel (MN11)

Referred material:

1. Kohfidisch (Ko = Ko IIIu, IIIo, IV, Cm): more than 600 maxillas, mandibles, and isolated teeth. (NHMW 2008z0152/0001 to 0600) and material published by BACHMAYER & WILSON (1978: 151)

2. Eichkogel (E): 40 teeth. (NHMW 2008z0247/0001 to 0040); and 40 teeth. (PIUW 1953/ 25/1 to 49) (DAXNER-HÖCK & DE BRUIJN 1981: 168-170).

Description:

Dental characters: Teeth of small-medium size; concave occlusal surface; few ridges, shallow flat valleys between ridges.

Maxillary molars: square outline; paracone and metacone distinct; labial margin concave; four main ridges (anteroloph, protoloph, metaloph and posteroloph), protoloph,

Tab. 14. Measurements (in mm). * Measurements from Eichkogel (DAXNER-HÖCK & DE BRUIJN 1981: 170) included. Measurements from Kohfidisch (BACHMAYER & WILSON 1978: 151) not included.

		length					width			
		min	mean	max	stdev	n	min	mean	max	stdev
D4	Ko	0.65	0.65	0.65		4	0.75	0.78	0.80	0.0288
P4	Ko	0.55	0.64	0.70	0.0351	30	0.60	0.81	0.90	0.0626
	E		0.59			1		0.76		
M1/2	Ko	0.85	0.95	1.10	0.0494	116	0.90	1.10	1.25	0.0653
	E	0.85	0.98	1.05	0.0866	23	1.00	1.13	1.25	0.1443
M3	Ko	0.70	0.81	0.88	0.0463	28	0.85	0.96	1.05	0.0438
	E	0.80	0.85	0.90	0.0418	10	0.90	0.96	1.12	0.0418
d4	Ko		0.75			1		0.60		
p4	Ko	0.60	0.68	0.75	0.0498	12	0.60	0.64	0.70	0.0428
	E	0.70	0.73	0.75	0.0353	2	0.70		0.70	
m1	Ko	0.90	1.00	1.10	0.0482	64	0.85	0.95	1.05	0.0450
	E	0.95	1.00	1.10	0.0534	12	0.90	0.94	1.00	0.0378
m2	Ko	0.90	1.01	1.10	0.0372	56	0.90	1.00	1.10	0.0383
	E	0.95	1.03	1.10	0.0516	12	0.96	1.02	1.05	0.0258
m3	Ko	0.80	0.86	0.95	0.0545	13	0.75	0.85	1.00	0.0577
	E	0.88	0.90	0.95	0.0523	6	0.83	0.90	1.00	0.0353

Fig. 19. *Myomimus dehmi* (DE BRUIJN, 1966) from Kohfidisch (Ko) and Eichkogel (E). Magnifications: 30x; all specimens in the NHMW collection.

19/1 left P4; Ko; 2008z0152/0006.
19/2 left M1/2; E; 2008z0247/0004.
19/3 right M1/2; E; 2008z0247/0015.
19/4 right M3; E; 2008z0247/0019.
19/5 right P4-M2; Ko; 2008z0152/0007.
19/6 left M3; Ko; 2008z0152/0002.
19/7 right p4; E; 2008z0247/0021.
19/8 left m1; E; 2008z0247/0023.
19/9 left m2; E; 2008z0247/0030.
19/10 left m3; E; 2008z0247/0031.
19/11 left p4; Ko; 2008z0152/0021.
19/12 left m1-3; Ko; 2008z0152/0012.

metaloph and posteroloph lingually connected to the endoloph; anteroloph labially and lingually free ending, or lingually connected to endoloph, or / and labially connected to paracone; posteroloph labially frequently connected to metacone; anterior centroloph longer, shorter or equal in length to posterior centroloph; centrolophs sometimes with Y-shaped connection; one or two short extra ridges exclusively in the middle part, not in the anterior or posterior valley.

D4: triangular outline; long anteroloph with labial connection to paracone, but no lingual connection; protoloph long, oblique, labial connection to paracone; posteroloph transversal, labial connection to metacone; lingual connection of protoloph and posteroloph; metaloph of medium length, connected to protoloph; anterior centroloph of medium length or absent; posterior centroloph short or absent; no additional extra ridges.

P4: triangular or oval; rounded corners; three or four ridges; anteroloph short; anterior centroloph short or absent.

M1/2: square outline; high variability in dental pattern.

M3: similar to M1/2 but slightly smaller.

Mandibular molars: Rectangular outline; four long main ridges (anterolophid, metalophid, mesolophid and posterolophid), a centrolophid of medium length and a pronounced posterior extra ridge. Additional extra ridge rare. Pattern of trigonid varable.

p4: mesolophid and posterolophid long, with lingual connection to entoconid; anteroconid or short anterolophid present; metalophid absent; centrolophid short or absent; frequently with posterior extra ridge.

m1-2: narrow in its anterior part; anterolophid labially connected to metalophid, lingually connected to metaconid; metalophid and centrolophid of variable shape; centrolophid can be connected to mesolophid in its middle part (fig. 19/9); m2 similar to m1 but wide in its anterior part.

m3: similar to m2 but smaller.

Root numbers and positions: The maxillary D4 has three widely spreading roots. P4 has one, two or three roots. M1-3 have three roots, a larger lingual and two smaller labial ones. The mandibular p4 has one root. The lower molars (m1-3) have three roots, two in anterior and one in posterior position.

R e m a r k s : The Austrian occurrences of *M. dehmi* are highly variable in dental pattern and size. Due to the longer accumulation time in the fissure fillings of Kohfidisch, the variability of dental characters from that locality is even higher than from the lacustrine deposits of Eichkogel.

Furthermore, the Austrian specimens differ from the type material from Pedregueras IIC by:

a) frequently occurring labial connection of the anteroloph to the paracone and

b) posteroloph connections to protocone and metacone of the maxillary teeth (Daxner-Höck & de Bruijn 1981: 170).

M. dehmi has a more complicated dental pattern than other *Myomimus* species from the Miocene/Pliocene-transition to the recent (Daams 1981; Daxner-Höck 1995).

Occurrences outside of Austria: Nombrevilla, Pedregueras II C, Pedregueras 1A, Pedregueras 2A, Peralejos 4, Peralejos D (Spain: de Bruijn 1966; Daams 1981; MN9), Lefkon (Greece: Daxner-Höck 1995; MN10), Pikermi-Chomateri (Greece: de Bruijn 1976; MN 11-12). The stratigraphic range is Late Miocene-Miocene (MN9-12).

Genus *Vasseuromys* Baudelot & Bonis, 1966

Vasseuromys pannonicus (Kretzoi, 1978)
(fig. 20, tab. 15)

1970 *Glirudinus* sp. – Daxner-Höck: 601.
1970 *Microdyromys* ? sp. – Daxner-Höck & Rabeder: 3.
1970 *Peridyromys compositus* nov. spec. – Bachmayer & Wilson: 564-566, figs 15, 73.
1978 *Myomimus* cf. *M. multicristatus* (de Bruijn 1966). – Bachmayer & Wilson: 149-151, pl. 3, fig. 12, 13, pl. 5, fig. 19.
1980 *Myomimus* cf. *M. multicristatus* (de Bruijn, 1966). – Bachmayer & Wilson: 366.
1980 *Vasseuromys thenii* Daxner-Höck & de Bruijn. – Daxner-Höck: 148, tab. 1.
1981 *Vasseuromys thenii* nov. spec. – Daxner-Höck & de Bruijn: 158-162, fig. 1-2.
1983 Cf. *Vasseuromys thenii* Daxner-Höck & de Bruijn, 1981. – Bachmayer & Wilson: 131-132, pl. 1, figs 2-3; pl. 2, figs 4-5.
1985 *Vasseuromys thenii* Daxner-Höck. – Bachmayer & Wilson: 104.
1985 Cf. *Vasseuromys thenii* Daxner-Höck. – Bachmayer & Wilson: 105.
1996a *Vasseuromys pannonica* (Kretzoi). – Daxner-Höck: 4.
1995 *Vasseuromys pannonicus* (Kretzoi, 1978). – Daams & de Bruijn: 50.
1999 *Vasseuromys pannonicus* (Kretzoi, 1978). – Daams: 317, tab. 29.2.

Type locality: Eichkogel (Austria), Late Miocene (MN11).

Occurrences in Austria: Eichkogel (MN11), Kohfidisch (MN11).

Referred material:

1. Kohfidisch (Ko = Ko IIIu, IIIo, IV, Cm): 350 maxillas, mandibles, and isolated teeth. (NHMW 2008z0153/0001 to 0350); and material published by Bachmayer & Wilson (1970, 1978, 1980, 1983, 1985).

2. Eichkogel (E): 59 teeth. (NHMW 2008z0248/0001 to 0059); and 56 teeth. (PIUW 1953/ 26/1 to 56 (Daxner-Höck & de Bruijn 1981: 158 – 160).

Description:

Dental characters: Medium-sized teeth with concave occlusal surface; numerous ridges; narrow valleys between the ridges; extra ridges slightly lower than main ridges; tendency towards disintegration of transversal ridges (mainly extra ridges) in undulated, partly fragmented ridges of irregular shape and extent.

Maxillary molars: extremely variable pattern; eight to ten ridges (a few specimens have up to twelve ridges); four long main ridges (anteroloph, protoloph, metaloph, posteroloph); anterior centroloph long but not connected to endoloph; posterior centroloph shorter than the anterior centroloph; anterior extra ridge longer than posterior extra ridge (frequently absent); up to four additional extra ridges possible; centrolophs and extra

ridges may be fragmented and irregular in shape; tendency to fill up narrow valleys by short extra ridges; main ridges (except for anteroloph) connected to endoloph; variable labial connections of ridges.

D4: triangular outline; long anteroloph with labial connection to paracone; protoloph long, oblique, labial connection to paracone; posteroloph transversal, labial connection to metacone; lingual connection of protoloph and posteroloph; metaloph of medium length, connected to protoloph; anterior centroloph short or absent; posterior centroloph short; three rudimentary diverging roots.

P4: rounded outline; larger than the deciduous tooth; four main ridges (anteroloph, protoloph, metaloph, posteroloph), and up to four extra ridges (anterior centroloph, posterior centroloph, anterior extra ridge, and short extra ridge anterior to posteroloph) of variable length; lingual connections of main ridges except for the anteroloph, which frequently has a free lingual and/or labial end.

M1-2: square or rhomboidal outline.

M3: trapezoidal outline; occasionally extra ridge between metaloph and posteroloph.

Mandibular molars: rectangular outline; seven to eleven ridges (anterolophod, metalophid, mesolophid, posterolophid, centrolophid, prominent anterior and posterior extra ridges and up to four small additional extra ridges); labial ends of main ridges curved anteriorly; no continuous endolophid.

p4: triangular-rounded outline; four to six ridges; high trend towards disintegration of ridges.

m1-2: rectangular outline; modification of ridges maximal in m1.

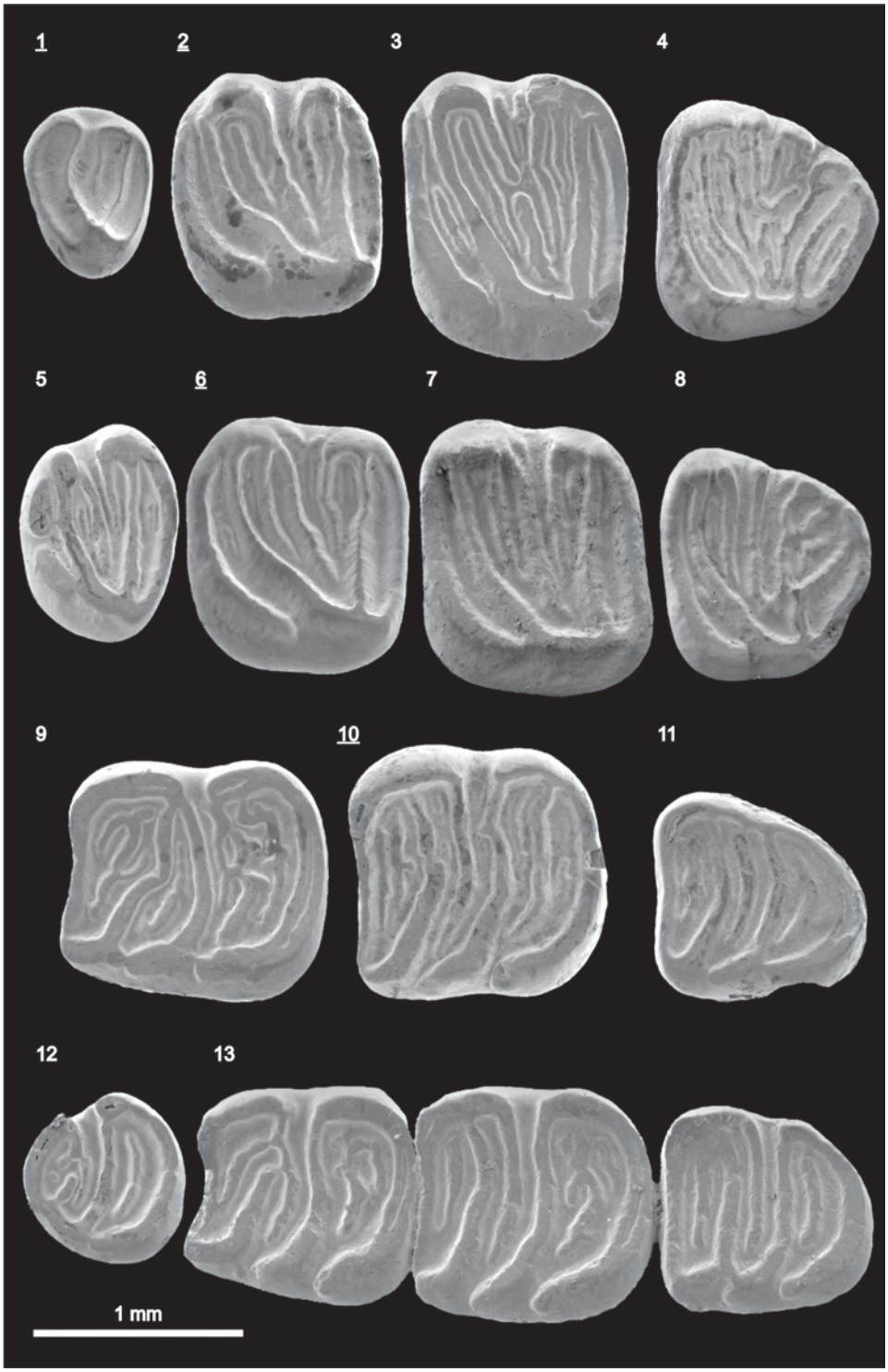
m3: similar to m2 but somewhat smaller and narrow in its posterior part; minimal modification of ridges.

Root numbers and positions: The maxillary D4, P4, M1-3 have three roots, a larger lingual and two smaller labial ones. The mandibular p4 has one root. The mandibular m1-3 have three roots, two in anterior and one in posterior position.

R e m a r k s : The dental pattern of *Vasseuromys* from Kohfidisch and Eichkogel is very complex and highly variable (tendency towards disintegration of ridges in undulated fragments of irregular direction and extent). Some dental characters resemble *Vasseuromys* Baudelot & Bonis, 1966, *Myomimus* Ognev, 1924, *Ramys* Garcia Moreno & Lopez Martinez, 1986, and *Szechenyia* Kretzoi, 1978. All these resemblances

Fig. 20. *Vasseuromys pannonicus* (Kretzoi, 1978) from Kohfidisch (Ko) and Eichkogel (E). ► Magnifications: 30 x; all specimens in the NHMW collection.

20/1 right D4; E; 2008z0248/0002.
20/2 right M1; E; 2008z0248/0058.
20/3 left M2; E; 2008z0248/0059.
20/4 left M3; E; 2008z0248/0028.
20/5 left P4; E; 2008z0248/0011.
20/6 right M1; Ko; 2008z0153/0002.
20/7 left M2; Ko; 2008z0153/0008.
20/8 left M3; Ko; 2008z0153/0005.
20/9 left m1; E; 2008z0248/0057.
20/10 right m2; E; 2008z0248/0052.
20/11 left m3; E; 2008z0248/0054.
20/12 left p4; E; 2008z0248/0034.
20/13 left m1-m3; Ko; 2008z0153/0011.



have caused several changes of genus-identification. The average dental pattern of the Eichkogel specimens is more complicated than in Kohfidisch. This can be interpreted as an intraspecific specialisation of molar pattern with time. For detailed descriptions and discussions see BACHMAYR & WILSON (1970: 565-566), BACHMAYR & WILSON (1978: 149-151), BACHMAYR & WILSON (1980: 366), BACHMAYR & WILSON (1983: 131-132), DAXNER-HÖCK & DE BRUIJN (1981: 158-162).

Vasseuromys from the Austrian localities is very similar to *Szechenyia pannonica* KRETZOI from the Széchenyi hills in Budapest (Hungary). The latter is a monospecific genus with unknown morphological variation because it was described (KRETZOI 1978: 348-349, pl. 1, figs 1-2) based on one tooth (left M1/2 = holotype) only.

According to DAAMS & DE BRUIJN (1995: 50), *Szechenyia* is a synonym of *Vasseuromys*, and *V. thenii* DAXNER-HÖCK & DE BRUIJN 1981 is considered a synonym of *V. pannonicus* (KRETZOI 1978).

Tab. 15. Measurements (in mm). Measurements from Kohfidisch (BACHMAYER & WILSON 1970: 566), (BACHMAYER & WILSON 1978: 151), (BACHMAYER & WILSON 1983: 132) and Eichkogel (DAXNER-HÖCK & DE BRUIJN 1981: 161) not included.

		length					width			
		min	mean	max	stdev	n	min	mean	max	stdev
D4	E	0.63		0.65		2	0.75		0.80	
P4	Ko	0.65	0.74	0.80	0.0351	38	0.75	0.91	1.05	0.0590
	E	0.70	0.74	0.85	0.0514	7	0.85	0.93	1.05	0.0698
M1/2	Ko	1.00	1.15	1.30	0.0571	66	1.20	1.29	1.45	0.0612
	E	1.05	1.17	1.40	0.0880	13	1.20	1.35	1.45	0.0877
M3	Ko	0.90	0.99	1.05	0.0534	13	1.05	1.12	1.18	0.0414
	E	0.95	1.04	1.10	0.0629	4	1.00	1.08	1.15	0.0645
d4	Ko		0.80			1		0.65		
	E		0.80			1		0.70		
p4	Ko	0.75	0.81	0.90	0.0452	11	0.70	0.77	0.80	0.0404
	E	0.75	0.82	0.90	0.0488	7	0.65	0.77	0.85	0.0636
m1	Ko	1.05	1.20	1.35	0.0695	33	0.95	1.08	1.20	0.0581
	E	1.20	1.28	1.35	0.0524	6	1.10	1.13	1.20	0.0408
m2	Ko	1.05	1.21	1.35	0.0589	48	1.05	1.16	1.35	0.0660
	E	1.20	1.23	1.25	0.0273	5	1.20	1.21	1.25	0.0223
m3	Ko	1.00	1.09	1.20	0.0548	19	0.85	1.03	1.15	0.0631
	E	1.05		1.15	0.0707	2	1.00		1.05	0.0353

O c c u r r e n c e s outside of Austria: Széchenyi hill (Hungary: KRETZOI 1978; Turolian). The stratigraphic range is Late Miocene (MN11?).

Conclusions

Three Eomyidae species and twelve Gliridae species from eight fossil sites of the Northern Alpine Foreland Basin, the Vienna Basin and the Pannonian Basin were discussed (fig. 21).

Eomyidae:
Keramidomys ermannorum nov. spec.
Keramidomys cf. *pertesunatoi* (HARTENBERGER, 1966)
Eomyops catalaunicus (HARTENBERGER, 1966)

Gliridae:
Muscardinus vallesiensis HARTENBERGER, 1966
Muscardinus hispanicus DE BRUIJN, 1966
Muscardinus pliocaenicus austriacus BACHMAYER & WILSON, 1970
Glirinae gen. et spec. indet.
Glis minor minor KOWALSKI, 1963
Myoglis ucrainicus NESIN & KOWALSKI, 1997
Paraglirulus werenfelsi ENGESSER, 1972
Paraglirulus schultzi nov. spec.
Glirulus lissiensis HUGUENEY & MEIN, 1965
Graphiurops austriacus BACHMAYER & WILSON, 1980
Myomimus dehmi (DE BRUIJN, 1966)
Vasseuromys pannonicus (KRETZOI, 1978)

Biostratigraphic feedback of the investigated taxa

All three Eomyidae species, *Keramidomys ermannorum* nov. spec., *K.* cf. *pertesunatoi* and *Eomyops catalaunicus* are indicative for the Late Miocene of Europe. The family Gliridae is represented in the Late Miocene of Austria by twelve species. Only a few of them clearly extend beyond this time interval; these include *Paraglirulus werenfelsi* and *Glirulus lissiensis*, known to range from the Early to the Late Miocene, and *Glis minor minor*, ranging from the Vallesian to the Pliocene. Four genera survived to the present, i.e. *Muscardinus*, *Glis*, *Glirulus* and *Myomimus.*

In Austria, *Keramidomys ermannorum* nov. spec. ranges from the Vallesian to the Turolian (MN9-11). It is very well represented in the Richardhof faunas, namely Richardhof-Golfplatz (MN9) and Richardhof-Wald (lower part of MN10). In younger faunas, i.e. Schernham (upper part of MN10), Kohfidisch and Eichkogel (both MN11), the number of individuals decreases. Outside of Austria the species is evidenced from the Meotian in Bulgaria and from the Miocene/Pliocene transition of Greece.

Keramidomys cf. *pertesunatoi* is documented from the Vallesian (MN9) in Austria; outside of Austria the species is known from the Vallesian (MN9) of Spain and the Turolian (MN13) of France.

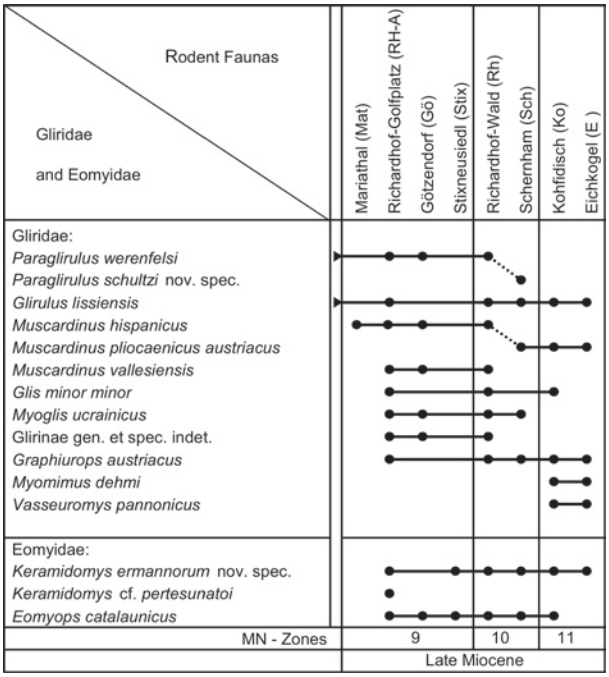


Fig. 21. Stratigraphic ranges of Eomyidae and Gliridae in the Late Miocene, namely the Vallesian (MN9-10) and Turolian (MN11) of Austria.

Eomyops catalaunicus is distributed all over Europe in the EarlyVallesian (MN9). Later occurrences are known from France, Greece and Poland (Late Vallesian to Pliocene). In Austria, *E. catalaunicus* ranges from the Vallesian to the Turolian (MN9-11) with highest specimen numbers in the two faunas from Richardhof (MN9 and lower part of MN10) and a decrease towards the Turolian. In Austria, it has the highest individual numbers among all Eomyidae- and Gliridae-species of the Vallesian.

Muscardinus vallesiensis and *Muscardinus hispanicus*, known as Late Miocene Gliridae, have their first records in the Late Astaracian (MN7/8) of Castell de Barbera in Spain (AGUILAR et al. 1979). In Austria, *M. vallesiensis* and *M. hispanicus* were recovered from Vallesian localities (MN9-10) only. *M. vallesiensis* is well represented in the locality Richardhof-Golfplatz (MN9), later occurrences are very rare. *M. hispanicus* is very well represented in both Richardhof-faunas (MN9-10), with a dramatic increase in abundance towards the lower part of MN10. Later it was replaced by *Muscardinus pliocaenicus austriacus* as documented from the assemblages Schernham (upper part of MN10), Eichkogel and Kohfidisch (MN11).

M. pliocaenicus austriacus (range MN10-11) is thought to be an immediate descendant of *M. hispanicus* (MN7/8-10) and the ancestor of *M. pliocaenicus pliocaenicus* of the Pliocene (MN14-16).

Glirinae gen. et spec. indet. is only known from the Late Miocene (MN9-10) of Austria, i.e. the localities Richardhof-Golfplatz, Götzendorf and Richardhof-Wald.

Glis minor minor is a very rare taxon. In Austria it sporadically occurs in Vallesian and Turolian faunas (MN9-11). Aside from that the species is known from Hungary, Greece, Ukraine and Poland, ranging from the Late Miocene to the Pliocene (MN9-16).

Myoglis ucrainicus is well represented throughout the Vallesian of Austria, with increasing individual numbers from MN9 to the uppermost MN10 (locality Schernham); then it disappeared. Furthermore, *M. ucrainicus* is known from the Vallesian (MN9) of Hungary and Ukraine.

Paraglirulus werenfelsi, known to range all over Europe from the Early to the Late Miocene (MN5-10), was also recognized in Austria in the Early Miocene (MN5) and in the Late Miocene (MN9-10). The Late Miocene fauna Richardhof-Golfplatz displays very high individual numbers of *P. werenfelsi*. The species is also well represented in Richardhof-Wald, just before its extinction.

Paraglirulus schultzi nov. spec. first appeared (FAD) in Austria in the upper part of MN10, replacing *P. werenfelsi* with its LAD in the lower part of MN10. In our opinion *P. schultzi* descended from *P. werenfelsi*. Occurrences outside of Austria are not known.

Glirulus lissiensis ranges from the Early to the Late Miocene (MN4-13), with a regional distribution from Spain in the SW to Poland in the NE of Europe. In Austria, *G. lissiensis* is documented in the Early Miocene (MN4), Middle Miocene (MN7/8) and Late Miocene (MN9-11).

Graphiurops austriacus is a very rare taxon. In Austria it sporadically occurs in Vallesian and Turolian faunas (MN9-11), but is well represented in Kohfidisch (MN11). Occurrences outside of Austria are also scarce, ranging from MN10 in the Czech Republic to MN11 in France.

Myomimus dehmi is very well represented in Spain in the Early Vallesian (MN9). From Greece, occurrences in the Vallesian and Turolian (MN10-12) are known. In Austria, *M. dehmi* first occurred in the Turolian (MN11) faunas Kohfidisch and Eichkogel, which is much later than the FOD in Spain.

Vasseuromys pannonicus is only known from the Early Turolian (MN11) of Austria and Hungary. The dormice *M. dehmi*, *V. pannonicus* and *M. pliocaenicus austriacus* of the Turolian faunas Kohfidisch and Eichkogel display very high individual numbers.

Distribution and biology of extant dormice – and reflections on extinct relatives.

Gliridae have an European origin (DAAMS & DE BRUIJN 1995) and a geographical range including Europe, Asia and Africa (fossil and extant). The stratigraphic range is Early Eocene (MP10) to the present. Throughout these fifty million years of evolution, dormice are represented by about 38 genera and 177 species (DAAMS & DE BRUIJN 1995: 5), a number which is permanently increasing.

The living representatives belong to eight genera, *Muscardinus*, *Glis*, *Glirulus*, *Eliomys*, *Dryomys*, *Myomimus*,*Chaetocauda* and *Graphiurus*. Today, dormice inhabit Europe and Asia from Great Britain in the West to Japan in the East, and from Scandinavia in the North to the Mediterranean Area, Asia Minor and Northern Africa in the South. A single genus, *Graphiurus*, ranges from the Sahara to the Cap in Africa. The easternmost occurrence is that of *Glirulus*, which inhabits certain Japanese islands.

The favoured environments of living Gliridae are deciduous forests, thickets and dense undergrowth or open woodlands with rocky substrate, ranging from lowlands to mountainous areas up to 2800 m elevation. Many dormice are squirrel like in some of their habits. They shelter in hollow trees and among rocks. Their nests are built of plant material and are located on the lower branches of trees, in bushes or in burrows of other animals. All extant dormice are nocturnal. In winter they hibernate in caves or in burrows. The diet of forest-dwelling dormice, such as *Muscardinus*, *Glis* or *Glirulus*, is mainly vegetarian, for example nuts, berries, seeds and leaves. They also occasionally feed on insects and even nestlings of birds. *Myomimus* species largely live as ground-dwellers in open country. They are omnivorous, preferring animal food, but also eat plants. *Dryomys* and *Eliomys*, however, live in a variety of habitats including cultivated areas, forests and even swamplands. Being omnivorous, they eat fruits, seeds and nuts, but also insects, young birds and small rodents.

As outlined above, four living genera are also known from the Late Miocene of Austria, *Glis*, *Muscardinus*, *Glirulus* and *Myomimus*. During the Late Miocene the diversity of Gliridae was very high, with highest species numbers in the Early Vallesian and beginning of the Late Vallesian (8 species per assemblage). Other than in SW Europe, there are no major extinction events between the Early and Late Vallesian. Based on the habits and the environmental requirement of extant relatives, we assume that most of the Vallesian dormice, i. e. *Glis minor minor*, *Muscardinus vallesiensis*, *M. hispanicus*, *M. pliocaenicus austriacus*, *Paraglirulus werenfelsi*, *P. schultzi*, *Myoglis ucrainicus*, *Glirulus lissiensis* and *Gliridae* gen. et spec. indet. lived arboreally in thickets and undergrowth of forests and woodlands. Note that *Glirulus* cf. *lissiensis* from Saint-Bouzile (France) was not only a forest-dweller but also a glider, as evidenced by a preserved gliding membrane (Mein & Romaggi 1991).

Towards the end of the Vallesian the diversity of the dormice begins to decrease (5 species per assemblage), and from Early Turolian faunas of Austria only 5 to 6 species are known. At that time, ground-dwelling (*Myomimus dehmi*, *Vasseuromys pannonicus* and *Graphiurops austriacus*) and forest-dwelling dormice (*Muscardinus pliocaenicus austriacus*, *Glirulus lissiensis* and *Glis minor minor*) were equal in species numbers, but the individual numbers of the ground-dwelling *M. dehmi* and *V. pannonicus* are significantly higher than of all other species. This shift towards a decrease of forest-dwellers and increase of ground-dwellers at the beginning of the Turolian reflects the change from predominating forested wetland environments to more open woodland and steppe-like environments, as is also indicated by flying squirrels and numerous small and large mammals (Daxner-Höck 1996a, 2004b; Harzhauser et al. 2004). Moreover, among the reptiles, gekkos and skinks point to climatic changes towards increasing aridity from the Late Vallesian towards the Early Turolian (Tempfer 2005). We assume increasing seasonality, most probably hot/dry summers and cool/wet but frost-free winters, which started during the Late Vallesian (upper part of MN10) and increased towards the Early Turolian (MN11).

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