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# Flying Squirrels (Pteromyinae, Mammalia) from the Upper Miocene of Austria

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(With 3 Textfigures, 5 Plates, 6 Tables)

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**Abstract**

Eight flying squirrels are reported from the upper Miocene (Pannonian C-H / Vallesian-Turolian / MN9-11) of Austria. There are two new descriptions: *Neopetes* nov. gen. and *Pliopetaurista kollmanni* nov. spec. Large-sized representatives are *Albanensia grimmi* (BLACK, 1966) and *Miopetaurista* sp. Species of middle size are *Neopetes hoeckarum* (DE BRUIN, 1998), *Pliopetaurista kollmanni* nov. spec., *Pliopetaurista bressana* MEIN, 1970 and Pteromyinae indet. *Pliopetes* cf. *hungaricus* KRETZOI, 1959 and *Blackia miocaenica* MEIN, 1970 are the smallest. The high species-diversities (5-6 species) indicate that the Pannonian fluvial environments of Götzendorf (MN9) and Schernham (MN10) were very favourable for flying squirrels. In the Vienna Basin the last occurrence of the Giant Flying squirrel *Albanensia* is isochronous with the first occurrence of Muridae (Late Vallesian /MN10).

**Zusammenfassung**

Aus dem Ober-Miozän von Österreich (Pannonium C-H / Vallesium-Turolium / MN9-11) wurden acht Flughörnchen nachgewiesen. Darunter sind zwei Neubeschreibungen: *Neopetes* nov. gen. und *Pliopetaurista kollmanni* nov. spec. Die großwüchsigen Formen sind: *Albanensia grimmi* (BLACK, 1966) und *Miopetaurista* sp. Mittelgroße Arten sind *Neopetes hoeckarum* (DE BRUIN, 1998), *Pliopetaurista kollmanni* nov. spec., *Pliopetaurista bressana* MEIN, 1970 und Pteromyinae indet. Am kleinsten sind *Pliopetes* cf. *hungaricus* KRETZOI, 1959 und *Blackia miocaenica* MEIN, 1970. Die Artenvielfalt (5-6 Arten) lässt darauf schließen, dass die Pannonen Flusslandschaften von Götzendorf (MN9) und Schernham (MN10) ideale Lebensräume für Flughörnchen boten. Im Wiener Becken fällt das letzte Vorkommen des Riesen-Flughörnchens *Albanensia* zeitlich mit dem Erstauftreten der Muridae zusammen (spätes Vallesium / MN10).

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## Introduction

For a long time, our knowledge about extinct Pteromyinae was rather poor. MEIN (1970) was the first to write a monograph on flying squirrels from the Neogene of Western Europe. During recent decades, the fossil record has increased considerably in Southeastern Europe, Anatolia and Central Europe. Although much of the material was neither described nor figured, the available knowledge was summarized and interpreted by de BRUIJN (1999).

Neogene flying squirrels differ considerably in molar morphology and size. They may be grouped into large-, middle- and small-sized genera:

1. Large: *Miopetaurista* and *Albanensia*
2. Middle: *Aliveria, Forsythia, Neopetes* nov. gen., *Pliopetaurista*
3. Small: *Blackia, Pliopetes*

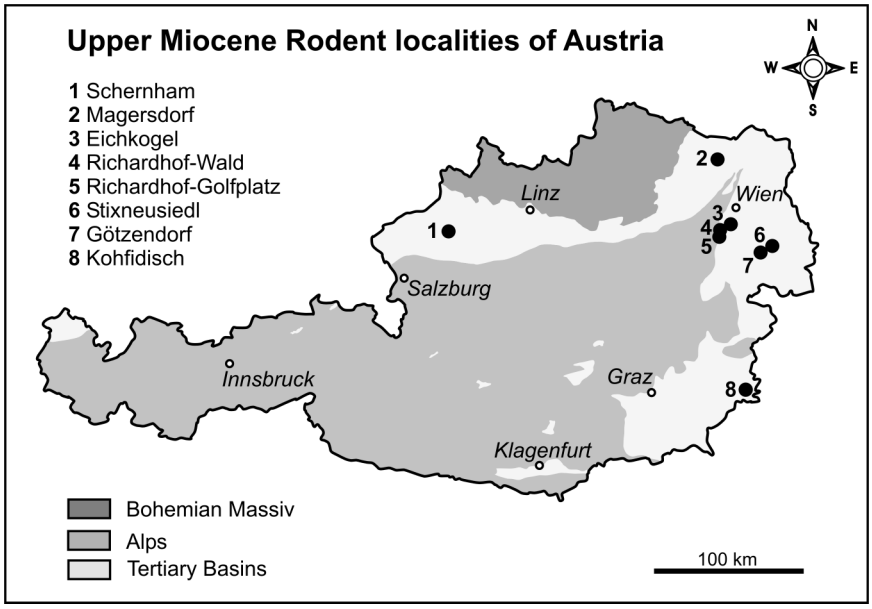
Except for *Aliveria* and *Forsythia,* all genera are represented in the Miocene of Austria. Quite a number of Upper Miocene fossil sites have yielded flying squirrels, which as a rule are rich in species but poor in individual numbers. The findings stem from the Vienna Basin (localities: Richardhof-Golfplatz, Götzendorf, Stixneusiedl, Richardhof-Wald, Eichkogel / all in Lower Austria), from the Austrian part of the Pannonian Basin (locality: Kohfidisch / Burgenland), and from the Molasse Basin (localities: Magersdorf / Lower Austria, Schernham / Upper Austria). Three of these Pteromyidae-assemblages were investigated years ago, i.e. Kohfidisch (BACHMAYER & WILSON 1970, 1978), Magersdorf and Eichkogel (DAXNER-HÖCK 1975). Others were listed (RÖGL et al. 1993, DAXNER-HÖCK 1996, DAXNER-HÖCK 2004) but so far not carefully studied (Fig. 1).

## Methods

The fossil sites are artificial outcrops that were investigated by the NHMW. Large sediment samples were washed using sieves with mesh sizes of 0.5, 2.0 and 5.0 mm. SEM-photos of the fossils were taken with a Philips XL 20 scanning electron microscope at the Biocenter/University of Vienna. The measurements were made with a Leica WILD M8 stereo microscope. For classification of rodents I follow MC KENNA & BELL (1997).

For comparative studies, skulls and mandibles of extant flying squirrels were available: *Glaucomys volans* (Pennsylvania, USA; Coll. NHMW*), *Pteromys volans* (Baikal Mountains, Sibiria; Coll. NHMW*), *Petinomys hageni* (Indonesia; Coll. NHMW*), *Hylopetes phayrei* (Thailand; Coll. NHMW*), *Belomys pearsoni* (Thailand; Coll. NHMW*), *Eoglaucomys fimbriatus* ( Kaschmir; Coll. NHMW*), *Petaurista petaurista* (unknown locality; Coll. NHMW**).

Fossil originals and casts: *Albanensia grimmi, Pliopetaurista kollmanni, Neopetes hoeckarum, Blackia miocaenica* (Rudabanya, Hungary; U. Miocene - MN9; Coll. Geological Institute of Hungary, Budapest), *Neopetes macedoniensis, Pliopetaurista dehneli, Miopetaurista thaleri* (Maramena, Greece; Miocene/Pliocene - MN13/14; Coll. NHMW**), *Miopetaurista dehmi, Blackia miocaenica, Neopetes hoeckarum* (Oberdorf, Austria; L. Miocene – MN4; Coll. NHMW **).




Textfig. 1: Localisation of fossil sites in Austria: Molasse Basin: 1. Schernham near Haag a. Hausruck in Upper Austria, 2. Magersdorf near Hollabrunn in Lower Austria. Southern Vienna Basin – Lower Austria: 3. Eichkogel, 4. Richardhof-Wald, 5. Richardhof-Golfplatz, 6. Stixneusiedl, 7. Götzendorf. Pannonian Basin – Burgenland: 8. Kohfidisch

Abbreviations:

NHMW – Natural History Museum = Naturhistorisches Museum, Vienna (* department of mammals = Säugetierabteilung, ** department of geology and paleontology = Geologisch-Paläontologische Abteilung

PIUW – Paleontological Institute of the University, Vienna

L. Miocene – Lower Miocene
M. Miocene – Middle Miocene
U. Miocene – Upper Miocene

MN – Neogene Mammal zones
P3-M3 – upper teeth
p4-m3 – lower teeth

## Taxonomy

Family Sciuridae FISCHER DE WALDHEIM, 1817

Subfamily Pteromyinae BRANDT, 1855

### *Albanensia* DAXNER-HÖCK & MEIN, 1975

1970 *Miopetaurista* KRETZOI – MEIN: 11-22, Figs. 1-14.
1975 *Albanensia* nov. gen. – DAXNER-HÖCK. & MEIN: 76.

T y p e s p e c i e s : *Albanensia albanensis* (MAJOR, 1893) – La Grive-Saint-Alban M (France; M- Miocene / MN7)

European fossil species - type localities and stratigraphic correlations:
*A. sansaniensis* (LARTET, 1851) – Sansan (France; M. Miocene / MN6)
*A. albanensis* (MAJOR, 1893) – La Grive-Saint-Alban M (France; M. Miocene / MN7)
*A. albanensis quiricensis* (VILLALTA, 1950) – San Quirze de Galliners (France; M. Miocene / MN7-8)
*A. grimmi* (BLACK, 1966) – Marktl (Germany; U. Miocene / MN9)

Remarks: *Albanensia* is a large-sized flying squirrel and differs from *Miopetaurista* by a more complicated molar pattern. The depressions are strongly granulated, partly undulated and narrow. The lophs/lophids and cones/conids are undulated and ornamented with additional conules/conulids; in lower molars a pronounced anterolophid extends to the base of the protoconid; the posterolophid is buffed up and tends to build a strong hypoconulid; the V-pattern of the converging protoloph and metaloph is characteristic for *Albanensia*. This character is also reminiscent of the middle-sized flying squirrels *Aliveria* and *Forsythia*.

### *Albanensia grimmi* (BLACK, 1966)
(Plate 1, Figs. 1-9)

1975 *Albanensia grimmi* – DAXNER-HÖCK: 60-61, Taf. 7, Figs. 8-11.
1984 *Albanensia grimmi* – BACHMAYER & WILSON: 321f, Taf. 2, Figs. 9-10.
1993 *Albanensia grimmi* – RÖGL et al.: 510.
1996 *Albanensia grimmi* – DAXNER-HÖCK: 3.

Type locality of *A. grimmi*: Marktl (Germany, Molasse Basin / U. Miocene / MN9)

Occurrences in Austria – stratigraphy (U. Miocene): Magersdorf (Vienna Basin; lower Pannonian / MN9), Richardhof-Golfplatz (Vienna Basin; middle Pannonian / MN9), Götzendorf a.d. Leitha (Vienna Basin; upper Pannonian / MN9), Stixneusiedl (Vienna Basin; upper Pannonian / MN9) and Richardhof-Wald (Vienna Basin; upper Pannonian / MN10)

Other occurrences in Europe - stratigraphy: Rudabanya (Hungary; U. Miocene / MN9), Nebelbergweg (Switzerland; U. Miocene / MN9).

References: KRETZOI et al. (1974), BERNOR et al. (2004), KÄLIN & ENGESSER (2001)

Stratigraphic range: Upper Miocene (lower-upper Pannonian, Vallesian, MN9-10)

Investigated material:

Richardhof-Golfplatz (RH-A/2) - (Inv. Nr. NHMW2004z0056/0001): 1 M1/2 right, 1 p4 right, 1 m1left, 2 m2 right, 1 m3 right, 7 fragmentary teeth

Götzendorf (Gö 1, Gö 2):

Gö 2 - (Inv. Nr.NHMW1990/27/1): 1 M1/2 left

Gö 1 - (Inv. Nr.NHMW1990/15/2/191-270): 4 fragmentary mandibles (with m1-3 left, p4-m1 right, i-p4 right, p4 left), 3 p4 left, 1 p4 right, 2 m1 left, 1 m1 right, 2 m2 left, 1 m2 right, 1 m3 left, 2 m3 right, 1 P3, 1 P4 right, 1 P4 left, 5 M1/2 left, 4 M1/2 right, 3 M3 left, 1 M3 right, numerous tooth fragments

Stixneusiedl (St.): M fragm.

Richardhof-Wald (Rh-1) - (Inv. Nr. NHMW2004z0057/0001): Rh-1: 1 P4 left, 1 M1/2 left, 1 M3 left, 1 M – fragm., 4 fragmentary incisors.

Magersdorf: 1 left mandible with I and m3. Coll. W.Andrä in Windpassing near Hollabrunn, Lower Austria (DAXNER-HÖCK, 1975).

Measurements: Tab. 1

| | | L | | | n | W | | |
|---|---|---|---|---|---|---|---|---|
| | | range | mean | stdev | | rang | mean | stdev |
| RH-A/2 | M2 | | 3,50 | | 1 | | 4,20 | |
| | p4 | | 3,25 | | 1 | | 3,35 | |
| | m1 | | 3,50 | | 1 | | 3,50 | |
| | m2 | 3,70 - 3,75 | | 0,035 | 2 | 3,40 - 3,80 | | 0,283 |
| | m3 | | 4,35 | | 1 | | 3,65 | |
| GÖ 1 | P4 | 4,20 - 4,35 | | 0,106 | 2 | 4,35 - 4,65 | | 0,212 |
| | M1 | 3,10 | 3,10 | | 4 | 3,85 - 4,25 | 4,10 | 0,178 |
| | M2 | 3,45 -3,50 | 3,49 | 0,025 | 4 | 4,15 - 4,45 | 4,30 | 0,129 |
| | M3 | 3,50 - 3,85 | 3,68 | 0,155 | 4 | 3,55 - 4,00 | 3,80 | 0,196 |
| | p4 | 3,25 - 3,70 | 3,52 | 0,135 | 7 | 3,30 - 3,70 | 3,46 | 0,138 |
| | m1 | 3,40 - 3,90 | 3,58 | 0,192 | 5 | 3,40 - 3,80 | 3,60 | 0,170 |
| | m2 | 3,65 - 4,15 | 3,90 | 0,208 | 4 | 3,50 - 4,00 | 3,69 | 0,239 |
| | m3 | 4,25 - 4,65 | 4,38 | 0,231 | 3 | 3,35 - 3,75 | 3,52 | 0,208 |
| GÖ 2 | M2 | | 3,40 | | 1 | | 4,15 | |
| Rh-1 | P4 | | 4,00 | | 1 | | 4,40 | |
| | M2 | | 3,50 | | 1 | | 4,00 | |
| | M3 | | 3,25 | | 1 | | 3,35 | |

Description:

Upper dentition (Pl.): P3 has a single cusp. The occlusal pattern of P4-M2 is similar. There are three main cusps, the protocone, the metacone and the paracone. Two more large cusps, the protoconule and metaconule, are almost equal to the main cusps in size. The protoloph and the metaloph are reduced to sharp zigzag crests. They converge towards the protocone to form a V-pattern. The lingual slope of the protocone is rugose. The anterior and posterior arms of the protocone are connected with the cingulum, which surrounds the anterior, lingual and posterior part of the tooth. The paracone and the mesostyle are connected by a sharp and curved mesostyle-crista. Additional sharp crests of variable shape, number and position complete the ornamentation of the teeth. The P4 is the largest upper tooth. It is subtriangular due to the pronounced parastyle. The parastyle is as large as the main cusps. The P 4 has no hypocone, but an additional conule between the parastyle and the paracone. The M1 is the shortest tooth. It has only a small hypocone, which is fused with the cingulum in the posterior lingual corner of the tooth. The M2 is longer, and its hypocone is more pronounced. The M3 is relatively short. Only the protoloph is well developed in M3. The metaloph turns backwards and may be undulated. The protoconule and the metaconule are smaller than in P4-M2, or may be almost absent. P4-M3 have three roots, one lingual and two labial ones.

Lower dentition: The occlusal pattern of the p4-m3 is generally similar. There are two lingual main cusps, the metaconid and the entoconid. The two labial main cusps

are the protoconid and the hypoconid. There are some pronounced additional cusps along the margin: the lingual mesostylid, the dominating posterior hypoconulid, and the labial mesoconid on the ectolophid. Deep notches are present between the mesostylid and the entoconid, and between the entoconid and the hypoconulid. The metalophid consists of a lingual and a labial arm which converge backwards to form a V-pattern. The labial arm is stronger than the lingual one. While the labial arm increases from p4 to m3, the lingual one decreases successively. The occlusal surface of all teeth is strongly rugose, in particular the talonid basin. The lophids are undulated. The entolophid is M-shaped. The metaconid-protoconid distance of p4 is smaller than in m1. The lingual and labial main cusps of p4 are in opposite position, while the oblique position of the main cusps increases from m1 to m3. The trigonid basin is closed by the metalophid and the anteroconid and anterolophid, respectively. The p4 has an anteroconid or a short anterolophid. The anterolophid is short in m1. In m2-3 it is strong and curved towards the anterior labial edge, and is attached with the base of the protoconid. The p4 has two roots, the molars four roots.

R e m a r k s : The type material of *A. grimmi* from Marktl (Germany) is limited to three associated lower teeth; the upper dentition was unknown so far. Therefore P4-M3 are described in detail here. The interpretation of investigated specimens from the upper Miocene faunas of the Vienna Basin (i.e. Magersdorf, Richardhof-Golfplatz, Götzendorf and Richardhof-Wald) requires better knowledge of the intraspecific variation of *A. grimmi*. The type specimens from Marktl are somewhat larger and their trigonid and talonid basins are less rugged. However, these differences are interpreted as species-variation. *A. grimmi* differs from *A. albanensis* by: the pronounced protoconulus and metaconulus of P4-M2; the zigzag-shaped protoloph and metaloph of P4-M2; the large P4; the dominating hypoconulid of p4-m3; the relatively short m3.

Rudabanya in Hungary yielded the richest collection of *Albanensia*. This material was first described as *A. albanensis* by KRETZOI et al. (1974), and finally revised and determined as *A. grimmi*. Furthermore, *Albanensia* sp. from Nebelbergweg in Switzerland (KÄLIN & ENGESSER 2001) most probably belongs to *A. grimmi*.

### *Miopetaurista* KRETZOI, 1962

1970 *Cryptopterus* nov. gen. – MEIN: 22-33, Figs. 15-32, 34-41.
1975 *Miopetaurista* KRETZOI – DAXNER-HÖCK & MEIN: 76.

T y p e s p e c i e s : *M. göriachensis* (HOFMANN, 1893) = Syn. *M. gibberosus* (HOFMANN, 1893) – Göriach (Austria; M. Miocene / MN5). Correction: In DAXNER-HÖCK & MEIN 1975: 76, *Sciurus gibberosus* (HOFMANN 1893: 42-44, Taf. II, Fig. 11 and Taf. III, Figs. 19-20) was thought to be type species. According to the page priority, however, *Sciurus Göriachensis* (HOFMANN 1893: 41-42, Taf. II, Fig. 12) has priority.

E u r o p e a n f o s s i l s p e c i e s - type localities and stratigraphic correlations:
*M. dehmi* DE BRIUJN et al., 1980 – Wintershof West (Germany; L. Miocene / MN3)
*M. lappi* (MEIN, 1958) – Vieux Collonges (France; L-M. Miocene /MN4 ? vel MN5)
*M. göriachensis* (HOFMANN, 1893) = Syn. *M. gibberosus* (HOFMANN, 1893) – Göriach (Austria; M. Miocene / MN5)
*M. gaillardi* (MEIN, 1970) – La Grive M (France; M. Miocene / MN7)
*M. neogrivensis* (MEIN, 1970) – La Grive L (France; M. Miocene / MN7-8)
*M. crusafonti* (MEIN, 1970) – Can Ponsich (Spain; U. Miocene / MN 9)

*M. thaleri* (MEIN, 1970) – Celleneuve (France; Pliocene / MN14)
*M. tobieni* MEIN ,1970 – Wölfersheim-Wetterau (Germany; Pliocene / MN15; according to DE BRUIJN (1995), *M. tobieni* is synonym of *M. thaleri*

R e m a r k s : The main morphological differences between the two large-sized flying squirrels *Miopetaurista* and *Albanensia* are: *Miopetaurista* has a more simple molar pattern than *Albanensia;* less granulated depressions and less undulated lophs/lophids and cones/conids; in lower molars there is a labial anterolophid, but no hypoconulid; protoloph and metaloph of *Miopetaurista* are ± parallel, whereas they are V-shaped in *Albanensia.*

### ***Miopetaurista* sp.**

(Plate 2, Figs. 1-4)

1993 *Miopetaurista* sp. – RÖGL et al.: 510.
1996 *Miopetaurista* sp. – DAXNER-HÖCK: 9.

O c c u r r e n c e s i n A u s t r i a – stratigraphy: Götzendorf near Mannersdorf, Lower Austria (Vienna Basin; upper Pannonian / MN9) and Schernham near Haag, Upper Austria (Molasse Basin; upper Pannonian / MN10)

M a t e r i a l : Götzendorf (Gö 1) - (Inv. Nr.NHMW1990/15/1 /1-3): 1 M1/2 left, P4 right, p4 right

Schernham (Sch) - (Inv. Nr. NHMW2004z0055/0001): m3 right

M e a s u r e m e n t s : (length x width in mm)

| | | |
|---|---|---|
| Gö1: | p4 r: | 3.80 x 3.80 |
| | M1/2 l: | 4.00 x 4.80 |
| | P4 r: | 4.10 x 4.15 |
| Sch: | m3r: | 4.65 x 4.20 |

D e s c r i p t i o n : There is no mesoloph in P4 and M1/2. The protoloph and the metaloph are parallel, oblique and slightly undulated ridges. The p4 and m3 have four main cusps: the protoconid, metaconid, hypoconid and entoconid. There is a wide central depression with granulated surface. In the m3 a short metalophid and a somewhat longer hypolophid are present. The measurements of M1/2, p4 from Götzendorf and m3 from Richardhof-Wald are intermediate between middle Miocene and Pliocene species; only P4 from Götzendorf is rather small and probably represents a smaller species.

R e m a r k s : Determination of *Miopetaurista* species is rather problematical because of the poor knowledge about interspecific variation. There is a tendency of increasing size and simplification of molar pattern (i.e. reduction of the mesoloph) from lower Miocene to Pliocene species. The morphological pattern of the investigated teeth from the upper Miocene of Austria is similar to *M. gaillardi, M. neogrivensis* and *M. crusafonti,* but is not identical with one of these middle to upper Miocene species. For the time being, the upper Miocene Austrian findings will be determined as *Miopetaurista* sp.

### ***Neopetes* nov. gen.**

D e r i v a t i o n o m i n i s : greek "neos"= new; Neogene flying squirrels

T y p e s p e c i e s : *Neopetes hoeckarum* (DE BRUIJN, 1998) – Oberdorf (Austria; L. Miocene / MN4)

D i a g n o s i s : Cheek teeth of medium size, extremely low-crowned, with low lophs and cones; ornamentation of enamel almost absent. Upper cheek teeth: protoloph and metaloph parallel; mesoloph absent; conules absent; mesosyle round and isolated; paracone, metacone and protocone pronounced. Lower cheek teeth: m1-2 rhomboidal in outline; metaconid, entoconid, protoconid and hypoconid pronounced; mesostylid present; mesoconid weak; metalophid weak or absent.

D i f f e r e n t i a l d i a g n o s i s : *Neopetes* differs from *Hylopetes* by extremely low tooth-crowns and by almost no sculptured enamel on unworn teeth; the upper teeth differ by the absence of mesoloph, protoconule and metaconule; the lower teeth differ considerably by their rhomboidal outline and by the presence of pronounced entoconids and mesostylids, separated by a wide notch. *Neopetes* differs from *Blackia* and *Pliopetes* by its significantly larger size and almost no ornamentation of the enamel; furthermore it differs from *Blackia* by the presence of a strong entoconid and mesostylid. *Neopetes* differs from *Pliopetaurista* by less pronounced cones(ids) and loph(id)s; upper teeth differ by the absence of a metaconule and by a symmetrical, convex lingual side; lower teeth differ by the more postero-lingual positioned entoconid and the straight and weak anterolophid. *Neopetes* differs from *Aliveria* and *Forsythia* by the absence of the sculptured enamel, the absence of conules, and by protoloph and metaloph not converging towards the protocone. *Neopetes* differs considerably from the large-sized flying squirrels *Albanensia* and *Miopetaurista* in size, in the low tooth crowns and in the extremely simple tooth pattern.

E u r o p e a n f o s s i l s p e c i e s - type localities and stratigraphic correlations:
*N. hoeckarum* (DE BRUIJN, 1998) – Oberdorf (Austria; L. Miocene / MN4)
*N. macedoniensis* (BOUWENS & DE BRUIJN, 1986) – Maramena (Greece; U. Miocene-Pliocene / MN13/14)
*N. debruijni* (REUMER & HOEK OSTENDE, 2003) – Tegelen (Netherlands; Pleistocene)

### *Neopetes hoeckarum* (DE BRUIJN, 1998)

(Plate 2, Figs. 5-13)

1998 *Hylopetes hoeckarum* n. sp. – DE BRUIJN: 107, Plate 4, Figs.11-14.
1975 *Pliopetaurista bressana* – DAXNER-HÖCK: 62, Taf. 7, Fig. 6.
1993 *Hylopetes* ? sp. – RÖGL et al.: 510.
1996 *Hylopetes* ? sp. - DAXNER-HÖCK: 3.
1996 *Hylopetes* sp. – DAXNER-HÖCK: 3.

O c c u r r e n c e s i n A u s t r i a – stratigraphy: Oberdorf (Styrian Basin, L. Miocene / MN4), Richardhof-Golfplatz (Vienna Basin, U. Miocene / MN9), Götzendorf (Vienna Basin, U. Miocene / MN9), Richardhof-Wald (Vienna Basin, U. Miocene / MN10), Schernham (Molasse Basin, U. Miocene / MN10), Eichkogel (Vienna Basin, U. Miocene / MN11)

O t h e r o c c u r r e n c e s i n E u r o p e - stratigraphy: Rudabanya (Hungary, U. Miocene / MN9), Anwil (Switzerland, M. Miocene / MN8).

R e f e r e n c e s : BERNOR et al. (2004), ENGESSER (1972).

Stratigraphic range: Miocene (MN4-11)

Investigated material:

Richardhof-Golfplatz (Rh-A/2, HR-A/7) - (Inv. Nr. NHMW2004z0058/0000-0007):

RH-A/2: 1 P3, 1 D4 right, 2 D4 left, 2 M1/2 left, 1 M1/2 right, 1 d4 left, 1p4 right, 1 m1 left, 1 m1 right, 1 m2 right

Götzendorf (Gö 1) - (Inv. Nr. NHMW1990/15/4/1-5): 1 d4 right, 1 p4 left, 2 m1 left, 1 m2 right

Richardhof-Wald (Rh-1) - (Inv.Nr. NHMW2004z0059/0000-0001): 1 P4 left, 1 P4 right, 1 M1/2 left, 5 M1/2 right, 1 M3 left, 3 d4 right, 1 p4 right, 1 m1 right, 2 m2 right

Schernham (Sch) - (Inv. Nr. NHMW2004z0060/0000-0001): 2 D4 right, 1 P4 right, 4 M1 right, 3 M1 left, 4 M2 right, 1 M2 left, 1 M3 left, 2 d4 right, 3 m1 right, 4m1 left, 3 m2 right, 3 m2 left, 1 m3 right

Eichkogel (E): 1 m1/2 right (Inv. Nr.1993/0008/0017)

Measurements: Tab. 2

| | | L | | | n | W | | |
|---|---|---|---|---|---|---|---|---|
| | | range | mean | stdev | | range | mean | stdev |
| RH-A/2 | D4 | 1,55 - 1,75 | 1,67 | 0,104 | 3 | 1,50 - 1,60 | 1,55 | 0,050 |
| | M1/2 | 1,80 - 2,00 | 1,87 | 0,115 | 3 | 2,00 - 2,10 | 2,07 | 0,058 |
| | d4 | | 1,65 | | 1 | | 1,45 | |
| | p4 | | 1,70 | | 1 | | 1,50 | |
| | m1/2 | 1,85 - 1,95 | | 0,071 | 2 | 1,90 - 2,15 | 2,03 | 0,177 |
| Gö 1 | d4 | | 1,65 | | 1 | | 1,35 | |
| | p4 | | 1,65 | | 1 | | 1,65 | |
| | m1/2 | 1,80 - 1,85 | 1,82 | 0,029 | 3 | 1,85 - 1,95 | 1,90 | 0,050 |
| Rh-1 | P4 | 1,60 - 1,65 | | 0,035 | 2 | 1,65 - 1,80 | | 0,106 |
| | M1/2 | 1,85 - 1,90 | 1,89 | 0,025 | 4 | 2,10 - 2,25 | 2,14 | 0,075 |
| | d4 | 1,55 - 1,60 | | 0,035 | 2 | 1,25 - 1,30 | | 0,035 |
| Sch | D4 | | 1,50 | | 1 | | 1,45 | |
| | P4 | | 1,65 | | 1 | | 1,70 | |
| | M1/2 | 1,65 - 1,95 | 1,82 | 0,092 | 8 | 1,90 - 2,25 | 2,09 | 0,115 |
| | M3 | | 1,85 | | 1 | | 1,75 | |
| | d4 | 1,45 - 1,60 | | 0,106 | 2 | 1,15 - 1,20 | | 0,035 |
| | m1/2 | 1,65 - 2,00 | 1,83 | 0,116 | 12 | 1,75 - 2,05 | 1,93 | 0,101 |
| | m3 | | 2,00 | | 1 | | 1,85 | |
| E | m1/2 | | 2,00 | | 1 | | 1,95 | |

Description:

Upper dentition: D4 and P4 are triangular. The molars (M1/2) are almost square in outline. The labial side of the molars (M1/2) is somewhat longer than the lingual side. The parastyle in the antero-labial edge of the tooth is pronounced in D4 and P4; it is also present in most of the molars. The labial end of the anteroloph is separated from the paracone by a notch. The mesostyle is isolated and round, only rarely connected with

the paracone. The protocone is bulging and antero-posteriorly elongate. The hypocone is almost absent in D4, weak in and weak and rounded in M1/2. The paracone and the metacone are expanded .The protoloph and the metaloph are parallel, broadly separated lophs. Both lophs are directed slightly forwards. In some specimens the protoloph or the metaloph is thinned or constricted, in others not. The mesoloph is absent, except for one P4 (Rh-1) and one M1/2 from Oberdorf (O3) with a short mesoloph. As a rule the molars lack conules on protoloph and metaloph, although small nodules may occur on the metaloph of D4 and P4. M3 is of simple pattern. The parastyle is absent and the anteroloph is parallel to the protoloph. All upper teeth have three roots.

L o w e r d e n t i t i o n : The rectangular d4 and p4 are wider posteriorly than anteriorly. The anteroconid of d4 is small and may be connected with the metaconid or the protoconid. The hypoconid and the entoconid are connected by the posterolophid. The mesoconid and the mesostylid are small conulids. The p4 is slightly wider than d4. The metalophid is short. The small anteroconid is connected with the protoconid. The molars (m1-2) are rhomboidal in outline. The metaconid, entoconid, protoconid and hypoconid are pronounced cones. A mesostylid is always present. The mesoconid is weak or absent. The anterolophid and the metalophid are distinct in m1, weak or absent in m2.

R e m a r k s : De Bruijn (1998: 106-107; Pl. 4, figs. 11-14) incorporated the middle-sized flying squirrel from Oberdorf (*N. hoeckarum*) in the genus *Hylopetes* because of the morphological affinities: "the characteristic hummocky surface of the enamel of unworn teeth, the shape of these teeth, the presence of a parastyle in P4-M2 and of a rather well-developed entoconid in the p4-m3." At that time, *N. macedoniensis* (Greece; Miocene/Pliocene transition; MN13/14) was thought to be an extinct species of *Hylopetes* (De Bruijn, 1995). *N. hoeckarum* (Austria; L. Miocene; MN4) was assumed to be a close relative of *N. macedoniensis*, and the oldest record of *Hylopetes* from the Neogene of Europe (De Bruijn, 1998). In the meantime the fossil record of this middle-sized European flying squirrel has increased. New findings from Central Europe demonstrate that *N. hoeckarum* did not change throughout at least ten million years, neither in size nor in tooth pattern. In my opinion *N. hoeckarum* is similar but definitely not identical with the extant flying squirrel *Hylopetes*. On the contrary, most of the "affinities" mentioned by De Bruijn (1998: 106-107) characterise Pteromyinae in general, not only *Hylopetes*. However, the long-time stability in tooth pattern and size, and the existing differences from other flying squirrels – living and extinct – warrant identification of a separate genus *Neopetes* nov. gen. with the type species *N. hoeckarum*, whereby *N. macedoniensis* is its younger relative. I agree with De Bruijn (1998) that *Sciuropterus* spec. (Engesser 1972: 180, Abb. 63) from the middle Miocene of Anwil is close in line with *N. hoeckarum*. Three teeth from Rudabanya (Bernor et al. 2004) determined as *Hylopetes* sp. turned out to be *N. hoeckarum*. Recently Reumer & Hoek Ostende (2003) described *Hylopetes debruijni* from the Pleistocene of Tegelen. This species most probably belongs to the genus *Neopetes* rather than to *Hylopetes* because of its general tooth-pattern. It is significantly larger than *N. hoeckarum* and *N. macedoniensis*.

**Pteromyinae indet.**
(Plate 2, Fig. 14)

M a t e r i a l and M e a s u r e m e n t s : 1 m3 left; length = 2.70 mm, width = 2.40 mm Inv. Nr. NHMW2004z0061/0001)

L o c a l i t y : Schernham (Molasse Basin of Upper Austria; U. Miocene / MN10)

D e s c r i p t i o n and r e m a r k s : The m3 is of middle size, intermediate between *Miopetaurista* and *Pliopetaurista* from Schernham. The metaconid, entoconid, protoconid and hypoconid are prominent. The entoconid and the hypoconid are thickened and separated from each other only by a narrow, shallow notch. A mesostylid is present and is connected with the metaconid. The mesostylid and the entoconid are separated by a narrow, deep notch. The mesoconid is weak. The anterolophid and the metalophid are distinct. They enclose a small trigonid-basin. The talonid-basin is not smooth but has irregular and weak ornamentation.

This tooth does not fit to any other Sciuridae from Schernham. It is larger and differs in tooth pattern from *Spermophilinus* and the middle-sized Pteromyinae, but is much smaller than *Miopetaurista*. Its taxonomy remains open.

### *Pliopetaurista* KRETZOI, 1962

T y p e s p e c i e s – t y p e l o c a l i t y : *P. pliocaenica* (DEPERET,1897) – Perpignan (France ; Pliocene / MN15)

E u r o p e a n f o s s i l s p e c i e s – type localities and stratigraphic correlations:
*P. pliocaenica* (DEPERET,1897) – Perpignan (France ; Pliocene / MN15)
*P. bressana* MEIN, 1970 – Soblay (France; U. Miocene / MN10)
*P. dehneli* (SULIMSKI, 1964) – Weze 2 ( Poland; Pliocene / MN15)
*P. schaubi* (SULIMSKI, 1964) – Weze 1 ( Poland; Pliocene / MN15)
*P. raui* DAHLMANN, 2001 – Wölfersheim (Germany; Pliocene /MN15)
*P. meini* BLACK & KOWALSKI, 1974 – Zalesiaki (Poland; Pleistocene)

### *Pliopetaurista kollmanni* nov. spec.

(Plate 3, Figs. 1-5, 11-15)

D e r i v a t i o n o m i n i s : in honour of Hofrat Dr. H.A. Kollmann, Director of the Geol.-Paleontol. Department.

T y p e l o c a l i t y : Götzendorf a.d. Leitha (Vienna Basin, U. Miocene / MN9)

H o l o t y p e : M2 left (Gö 1) - Inv. Nr. NHMW1990/15/2/3; (Plate 3, Fig. 4).

P a r a t y p e s : M1 left (Plate 3, Fig.3), M3 right (Plate 3, Fig.5), p4 left (Plate 3, Fig.12), m1 right (Plate 3, Fig.13), m2 right (Plate 3, Fig.14), m3 left (Plate 3, Fig.15).

D i a g n o s i s : Small to middle-sized flying squirrel. So far eldest, smallest and most primitive species of *Pliopetaurista*. Protoloph of D4, P4, M1-3 transversal and continuous, lingually connected anterior to the protocone; metaloph directed slightly forwards; small metaconule on M2; metaconule on M1 tiny or absent; metaloph connected posterior to the protocone or constricted between metaconule and protocone; short mesoloph present (holotype; Pl. 3, Fig. 4) or absent (Pl. 3, Fig. 3); lophules connecting metaloph and posteroloph weak or absent; mesostyle absent; on the lingual side of M1-3 shallow depressions anterior and posterior to the protocone; p4 with anteroconid; m1-3 with pronounced anterolophid; metalophid and trigonid-basin present; metastylid distinct and connected with metaconid; talonid-basin with slightly granulated enamel surface or smooth.

Differential diagnosis: *P. kollmanni* nov. spec., *P. raui* and *P. meini* are the smallest among all species of *Pliopetaurista*. *P. meini* and *P. raui* differ from *P. kollmanni* nov. spec. by age and by morphological features: So far *P. raui* is known from the Pliocene of Wölfersheim (Germany), and *P. meini* from the Pleistocene of Zalesiaki (Poland), whereas *P. kollmanni* nov. spec. is evidenced from the upper Miocene of Austria and Hungary. Morphologically, *P. meini* and *P. raui* differ from *P. kollmanni* nov. spec. by higher and more pronounced cones(ids) and loph(id)s, a large metaconule, a more reduced metaloph, and by no mesoloph.

*P. kollmanni* nov. spec. – *P. bressana – P. dehmi – P. pliocaenica* are in an evolutionary line (U. Miocene-Pliocene) which reflects size-increase and successively changing morphological characters: e.g. enamel ornamentation disappears; depressions anterior and posterior to the protocone on the lingual side of P4-M3 become accentuated; cone(id)s and loph(id)s become higher and more accentuated; metaconule grows while metaloph becomes curved and reduced; lophules connecting posteroloph and metaconus and/or metaconulus develop; mesoloph disappears; size of P4 increases; anterolophid thickens and becomes more pronounced; metalophid decreases; trigonid-basin and talonid-basin fuse; mesostylid fuses with metaconid; sulcus between entoconid and mesostylid-metaconid enlarges; length of m3 increases; a hypolophid develops.

Occurrences in Austria – stratigraphy: Götzendorf (Vienna Basin; U. Miocene / MN9), Richardhof-Golfplatz (Vienna Basin; U. Miocene / MN9), Richardhof-Wald (Vienna Basin; U. Miocene / MN10).

Stratigraphic range: Miocene (MN9-10)

Other occurrences in Europe - stratigraphy: Rudabanya (Hungary, M. Miocene / MN9).

References: KRETZOI et al. (1974), BERNOR et al. (2004).

Investigated material:

Götzendorf (Gö 1 and Gö 2):

Gö 1 - (Inv. Nr. NHMW1990/15/2/1-17) – type material: 1 M1 left, 1 M1 right, 1 M2 left (Holotype), 1 M2 right, 1 M3 right, 1 p4 left, 2 m1 right, 1 m1 left, 1 m2 right, 1 m3 left, 4 fragmentary molars

Gö 2 - (Inv. Nr. NHMW 1990/22/ 21-22): 1 m2 left, 1 m3 right

Richardhof-Golfplatz (RH-A/2) - (Inv. Nr. NHMW2004z0065/0000-0006): 2 D4 left, 1 P4 right, 2 M3 right, 2 d4 left, 1 d4 right, 1 p4 left, 1 p4 right, 2 m1 right, 1 m1 left, 1 m2 right, 1 m3 right

Richardhof-Wald (Rh-1) - (Inv. Nr. NHMW2004z0066/0000): 1 M1 right, 1 M2 right, 1 M3 left, 2 p4 right, 1 m1 left, 1 m2 left, 1 m3 right

Description of the type material from Götzendorf:

Upper molars including the holotype: M1-2 are almost square in outline. The protocone is antero-posteriorly elongate. The contact of its anterior arm and the anteroloph is rectangular. The hypocone is indistinct. The protoloph is continuous, transversal and lingually connected anterior to the protocone. The metaloph is directed slightly forwards; at the lingual connection posterior to the protocone it is very thin. The

metaconule of M1 is tiny; it is small in M2. A very low lophulus connects the metaloph and the posteroloph. One M2 (= holotype) has a short mesoloph. The anterior part of M3 is almost equal to M2. The hypocone and the metaloph are absent. On the lingual side of M1-3 there are shallow depressions anterior and posterior to the protocone.

L o w e r d e n t i t i o n : The p4 is similar with m1. The p4 has an anteroconid, but no anterolophid. The anterolophid is pronounced in m1-3. In all lower teeth the metalophid and the trigonid-basin are present. The distinct metastylid is connected with the metaconid. A distinct notch separates the metastylid and the entoconid. A mesoconid is present in p4-m3. The talonid-basins of unworn teeth are ornamented with indistinct granulation and undulation.

M e a s u r e m e n t s : Tab. 3

| | | L | | | n | W | | |
|---|---|---|---|---|---|---|---|---|
| | | range | mean | stdev | | range | mean | stdev |
| RH-A/2 | D4 | 1,25 - 1,30 | | 0,035 | 2 | 1,25 - 1,30 | | 0,035 |
| | P4 | | 1,55 | | 1 | | 1,80 | |
| | M3 | 1,80 - 1,85 | | 0,035 | 2 | 1,75 | | |
| | d4 | 1,35 - 1,40 | 1,37 | 0,029 | 3 | 1,10 | 1,10 | |
| | p4 | 1,55 - 1,60 | 1,58 | 0,035 | 2 | 1,40 - 1,50 | 1,45 | 0,071 |
| | m1 | 1,70 - 1,75 | 1,72 | 0,029 | 3 | 1,70 - 1,75 | 1,73 | 0,029 |
| | m2 | | 1,75 | | 1 | | 1,85 | |
| | m3 | | 1,50 | | 1 | | 1,90 | |
| Gö 1 | M1 | 1,55 - 1,65 | | 0,071 | 2 | 1,90 - 2,00 | | 0,035 |
| | M2 | 1,70 | | | 2 | 1,85 - 1,95 | | 0,071 |
| | M3 | | 1,80 | | 1 | | 1,90 | |
| | p4 | | 1,80 | | 1 | | 1,65 | |
| | m1 | 1,60 - 1,70 | 1,65 | 0,050 | 3 | 1,60 - 1,65 | 1,62 | 0,029 |
| | m2 | | 1,80 | | 1 | | 1,75 | |
| | m3 | | 2,30 | | 1 | | 2,00 | |
| Gö 2 | m2 | | 1,80 | | 1 | | 1,70 | |
| | m3 | | 2,15 | | 1 | | 1,85 | |
| Rh-1 | M1 | | 1,50 | | 1 | | 2,00 | |
| | M2 | | 1,65 | | 1 | | 2,00 | |
| | M3 | | 1,65 | | 1 | | 1,80 | |
| | p4 | 1,60 - 1,65 | | 0,035 | 2 | 1,45 - 1,55 | | 0,071 |
| | m1 | | 1,85 | | 1 | | 1,70 | |
| | m2 | | 1,90 | | 1 | | 1,95 | |

D e s c r i p t i o n of material other than the type materials:

U p p e r d e n t i t i o n : The D4 and P4 from Richardhof-Golfplatz are rather small. The outline of D4 and P4 is subtriangular due to its large unicuspid parastyle. The protoloph of D4 and P4 is transverse. In one out of two P4 a small protoconule is present. A metaconule is present in P4 and in one out of two D4. All molars are similar with the type material, except for M1 and M2 with a very tiny metaconule from the locality Richardhof –Wald.

Lower dentition: The d4 from the locality Richardhof-Golfplatz are smaller than p4 but of similar shape. The p4 and m1-3 are similar with the type material but the ornamentation of the trigonid-basin is more distinct. The lower molars from the slightly younger fauna Richardhof-Wald seem more advanced in having smooth enamel surfaces and wide notches between the entoconid and the mesostylid.

Remarks: So far *P. kollmanni* nov. spec. has been reported from Richardhof-Golfplatz, Götzendorf and Richardhof-Wald in Austria, and from Rudabanya in Hungary (= earlier determined as *Pliopetes* sp. by KRETZOI et al. 1974; and parts of *Hylopetes* sp. listed in BERNOR et al., 2004). According to our present knowledge, Richardhof-Golpfplatz (MN9), Rudabanya (MN9), Götzendorf (MN9) and Richardhof -Wald (lower MN10) are close in age. Younger faunas from Austria, Schernham (upper MN10), Kohfidisch (lower MN11) and Eichkogel (MN11) yielded the more advanced species *P. bressana.* However, *P. kollmanni* nov. spec. (MN9-10) is in an evolutionary line with *P. bressana* (MN10-11), *P. dehneli* (MN13-15) and *P. pliocaenica* (MN15), and represents the eldest and most primitive species of *Pliopetaurista.* The primitive features of *P. kollmanni* nov. spec. are: smaller sizes of all teeth (P4 is significantly smaller), protoconule of P4 absent, metaconule of P4-M2 small or absent, short mesoloph of M2 sometimes present, lingual distance of protoloph and metaloph wider than in more advanced species of *Pliopetaurista.* Note that these features differ considerably from *Forsythia.* Consequently, *Forsythia* most probably was not an ancestor of *Pliopetaurista* as suggested by MEIN (1970) and DE BRUIJN (1999).

### *Pliopetaurista bressana* MEIN, 1970

(Plate 3, Figs. 6-10 and 16-19; Plate 4, Figs. 1-4)

1970 *Pliosciuropterus* prob. nov. spec. – BACHMAYER & WILSON: 563.
1975 *Pliopetaurista bressana* – DAXNER-HÖCK: 61-62, Taf. 7, Fig. 1-5, 7.
1978 *Pliopetaurista* cf. *P. bressana* – BACHMAYER. & WILSON: 145-146, Taf. 3, Fig. 9.
1980 *Pliopetaurista bressana* – DAXNER- HÖCK: 184.
1996 *Pliopetaurista bressana* – DAXNER- HÖCK: 4.
1996 *Pliopetaurista* cf. *bressana* – DAXNER- HÖCK: 4.
2004 *Pliopetaurista bressana* – DAXNER- HÖCK: 3

Occurrences in Austria – stratigraphy: Schernham (Molasse Basin; U. Miocene / MN10), Kohfidisch (Vienna Basin; U. Miocene / MN11), Eichkogel (Vienna Basin; U. Miocene / MN11)

Stratigraphic range: Miocene (MN10-11)

Other occurrences in Europe - stratigraphy: Soblay (France; U. Miocene / MN10), Mollon (France; U. Miocene / MN11), Dorn-Dürkheim (Germany; U. Miocene / MN11).

References: MEIN (1970), FRANZEN & STORCH (1975, 1999).

Investigated material:

Schernham (Sch) - (Inv. Nr. NHMW2004z0067/0000-0026): 1 maxilla P4-M1 left, 3 D4 left, 1 D4 right, 5 P4 right, 1 P4 left, 5 M1/2 left, 1 M1/2 right, 1 M3 left, 1 M3 right, 3 d4 left, 1 p4 left, 2 p4 right, 2 m1 left, 1 m1 right, 4 m2 left, 2 m2 right

Kohfidisch (Ko, Ko-IIIo, Ko-IIIu ) – (Inv. Nr. NHMW2004z0068/0000-0012):

Ko: 1 max. P3-M3 left (AO; BACHMAYER & WILSON 1978; Taf. 3, Fig. 6), 1 m2-3 right, 1 m2 left, 1 m3 left

Ko-IIIo: 1 max. P4-M3 right, 1 m2 left, 1 m3 right

Ko-IIIu: 1 max. P3-M3 right, 1 max. P3-M2 right, 1 M1 left, 1 max. P4-M2 right

Eichkogel (E): 1 D4 right, 1 M3 left (Inv. Nr. 1993/0008/0014)

M e a s u r e m e n t s : Tab. 4

| | | L | | | n | W | | |
|---|---|---|---|---|---|---|---|---|
| | | range | mean | stdev | | range | mean | stdev |
| Sch | D4 | 1,40 - 1,45 | | 0,035 | 2 | 1,50 - 1,55 | | 0,035 |
| | P4 | 1,65 - 1,80 | 1,75 | 0,063 | 6 | 1,85 - 1,95 | 1,90 | 0,045 |
| | M1 | 1,75 - 1,85 | 1,80 | 0,050 | 3 | 1,90 - 2,00 | 1,95 | 0,050 |
| | M2 | 1,90 - 1,95 | | 0,035 | 2 | 2,00 - 2,05 | | 0,035 |
| | M3 | 1,75 - 1,80 | | 0,035 | 2 | 1,80 - 1,85 | | 0,035 |
| | d4 | 1,50 - 1,55 | 1,53 | 0,029 | 3 | 1,20 - 1,40 | 1,28 | 0,104 |
| | p4 | 1,75 - 1,85 | 1,78 | 0,058 | 3 | 1,50 - 1,60 | 1,53 | 0,058 |
| | m1 | 1,85 - 1,90 | | 0,035 | 2 | 1,80 - 1,85 | | 0,035 |
| | m2 | 2,00 - 2,20 | 2,10 | 0,100 | 5 | 1,90 - 2,00 | 1,93 | 0,045 |
| Ko | P4 | 1,70 - 1,95 | 1,85 | 0,117 | 5 | 1,75 - 1,95 | 1,82 | 0,084 |
| | M1 | 1,65 - 1,90 | 1,76 | 0,102 | 6 | 2,00 - 2,10 | 2,04 | 0,038 |
| | M2 | 1,75 - 1,95 | 1,84 | 0,102 | 5 | 2,00 - 2,15 | 2,09 | 0,065 |
| | M3 | 1,75 - 1,85 | 1,82 | 0,058 | 3 | 1,90 - 2,00 | 1,95 | 0,050 |
| | m2 | 1,80 - 2,20 | 2,00 | 0,200 | 3 | 1,80 - 2,00 | 1,92 | 0,104 |
| | m3 | 2,25 - 2,35 | 2,30 | 0,050 | 3 | 1,90 - 1,95 | 1,92 | 0,029 |

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

U p p e r d e n t i t i o n : The protoloph of D4 is transverse. The protoloph of P4 is directed forwards and interrupted by a protoconule, except for one P4 from Schernham without a protoconule. The metaloph is directed forwards in D4 and P4. A metaconule is present in D4 and in P4. All molars have a transversal protoloph and a forwards directed metaloph. The metaloph is undulated and partly replaced by a strong metaconule. It is very thin or incontinuous at the connection with the protocone. One or two small lophuli connect the metaloph and the posteroloph. The anterior part of the M3 is almost equal to M2. The hypocone and the metaloph are absent. The lingual side of M1-3 shows shallow depressions anterior and posterior to the protocone.

L o w e r d e n t i t i o n : The d4 is smaller and more slender, but of similar morphological pattern as p4. The p4 has an anteroconid, but no anterolophid. The anterolophid is pronounced in m1-3. In all lower teeth the metalophid and the trigonid-basin are present. The metastylid is present and connected with the metaconid. A distinct notch separates the metastylid from the entoconid. A mesoconid is present in p4-m3. The enamel surface is almost smooth.

R e m a r k s : *P. bressana* was identified from the Austrian localities Schernham, Kohfidisch and Eichkogel. Only small morphological differences (i.e. more primitive D4 and P4) are recognisable between specimens from Schernham (MN10) and the younger

ones from Kohfidisch and Eichkogel (MN11). Some other occurrences of *P. bressana* in France (Mollon, Soblay) and Germany (Dorn-Dürkheim) confirm the species to range from MN10 to MN11. P. *bressana* so far was thought to be the eldest and most primitive species of *Pliopetaurista,* and *Forsythia* (M. Miocene / MN7-8) to be its ancestor (MEIN, 1970 and DE BRUIJN,1999). However, since *P. kollmanni* nov. spec. (U. Miocene / MN9-10) has been shown to be an ancestor of *P. bressana*, the *Pliopetaurista*-descendance requires reconsideration.

## *Blackia* MEIN, 1970

Type species: *B. miocaenica* MEIN 1970 – La Grive L7 (France ; M. Miocene / MN7)

European fossil species - type localities and stratigraphic correlations:
*B. miocaenica* MEIN, 1970 – La Grive L7 (France ; M. Miocene / MN7)
*B. parvula* BAUDELOT, 1972 – Sansan (France ; M. Miocene / MN6);
*B. ulmensis* WERNER, 1994 – Ulm Westtangente (Germany; L. Miocene MN2)
*B. woelfersheimensis* MEIN, 1970 – Wölfersheim (Germany; Pliocene MN15)
*B. polonica* BLACK & KOWALSKI, 1974 – Podlesice (Poland; Pliocene MN14)

### *Blackia miocaenica* MEIN, 1970
(Plate 5, Figs. 1-10)

1975 *Blackia miocenica* – DAXNER-HÖCK: 64-66, Taf. 8, Fig. 1-8
1980 *Blackia miocenica* – DAXNER-HÖCK: 148
1993 *Blackia* sp. – RÖGL, F. et al.: 510
1996 *Blackia* sp. – DAXNER-HÖCK: 3.
1996 *Blackia miocaenica* – DAXNER-HÖCK: 4.

Type locality of *B. miocaenica***:** La Grive L7 (France; M. Miocene / MN7)

Occurrences in Austria – stratigraphy: Oberdorf (Styrian Basin; L. Miocene / MN4), Richardhof-Golfplatz (ViennaBasin; U. Miocene / MN9), Götzendorf (Vienna Basin; U. Miocene / MN9), Richardhof-Wald (Vienna Basin; U. Miocene / MN10), Schernham (Molasse Basin; U. Miocene / MN10), Eichkogel (Vienna Basin; U. Miocene / MN11)

Stratigraphic range: Miocene (MN4-15)

Other occurrences in Europe - stratigraphy: Erkertshofen 1, Rembach, Forsthart (Germany, L. Miocene /MN4), Franzensbad (Czech Republic, L. Miocene / MN5), Puttenhausen (Germany, L.-M. Miocene / MN5), Neudorf- Spalte (Czech Republic, M. Miocene / MN6), Sansan (France, M. Miocene / MN6), Anwil (Switzerland, M. Miocene / MN8), Giggenhausen (Germany, M. Miocene / MN8), Rudabanya (Hungary, M. Miocene / MN9), Nebelbergweg (Switzerland, U. Miocene / MN9), Suchomasty (Czech Republic, U. Miocene / MN10), Wölfersheim (Germany, Pliocene /MN15).

References: ZIEGLER & FAHLBUSCH (1986), FEJFAR (1974), FRANZEN & STORCH (1999), KÄLIN & ENGESSER (2001), BERNOR et al. (2004), DAHLMANN (2001).

Investigated material:

Richardhof-Golfplatz (Rh-A/2, HR-A/7) - (Inv. Nr. NHMW2004z0069/0000-0012):

RH-A/2: 2 D4 left, 1 D4/P4 right, 1 M1/2 right, 1d4 left, 2 d4 right, 1 p4 left, 1 m1 right,

1m2 left, 4 m3 left, 3 fragments

RH-A/7: 1 P4 right, 1 P4 left, 1 M1/2 right

Götzendorf (Gö 1) - (Inv.Nr.NHMW1990/15/3/ 281-284): 1 p4 right, 1 p4 left, 2 M-fragments

Richardhof-Wald (Rh-1) - (Inv. Nr. NHMW2004z0070/0000-0007):

Rh-1: 2 D4 left, 1 P4 right, 2 P4 left, 2 M1 left, 1 M2 left, 2M2 right, 2 M3 left, 2 p4 left, 3 m1 right, 2 m2 right, 1 M-fragment

Rh-5: 2 M2 right, 3 fragments

Schernham (Sch) - (Inv. Nr. NHMW2004z0071/000-0015): 2 M1/2 left, 2 M1/2 right, 1 d4 left, 1 p4 left, 1 m1 left, 1 m1 right, 4 m2 right, 1 m3 right, 1 m3 left

Measurements: Tab. 5

| | | L | | | n | W | | |
|---|---|---|---|---|---|---|---|---|
| | | range | mean | stdev | | range | mean | stdev |
| RH-A | D4 | 1,00 - 1,15 | 1,08 | 0,076 | 3 | 1,00 - 1,25 | 1,13 | 0,126 |
| | P4 | 1,10 - 1,25 | 1,18 | 0,076 | 3 | 1,25 - 1,44 | 1,36 | 0,098 |
| | M1/2 | | 1,30 | | 1 | | 1,50 | |
| | d4 | 1,05 | 1,05 | | 3 | 0,85 - 0,90 | 0,87 | 0,029 |
| | p4 | | 1,25 | | 1 | | 1,00 | |
| | m1 | | 1,15 | | 1 | | 1,25 | |
| | m2 | | 1,25 | | 1 | | 1,35 | |
| | m3 | 1,55 - 1,75 | 1,68 | 0,096 | 4 | 1,35 - 1,50 | 1,43 | 0,065 |
| GÖ 1 | p4 | | 1,10 | | 1 | | 1,10 | |
| Rh-1-5 | D4 | | 1,00 | | 1 | | 1,00 | |
| | P4 | 1,05 - 1,10 | 1,08 | 0,029 | 3 | 1,15 - 1,20 | 1,18 | 0,029 |
| | M1/2 | 1,10 - 1,25 | 1,14 | 0,061 | 7 | 1,30 - 1,50 | 1,39 | 0,089 |
| | M3 | | 1,50 | | 1 | | 1,55 | |
| | p4 | 1,15 - 1,20 | | 0,035 | 2 | 1,00 - 1,05 | | 0,035 |
| | m1 | 1,10 - 1,15 | 1,12 | 0,029 | 3 | 1,15 - 1,30 | 1,20 | 0,087 |
| | m2 | 1,40 | | | 2 | 1,30 - 1,35 | | 0,035 |
| Sch | M1/2 | 1,25 | | | 2 | 1,40 - 1,55 | 1,48 | 0,106 |
| | d4 | | 1,20 | | 1 | | 0,90 | |
| | p4 | | 1,20 | | 1 | | 1,00 | |
| | m1 | 1,20 - 1,25 | | 0,035 | 2 | 1,30 - 1,35 | 1,33 | 0,035 |
| | m2 | 1,45 - 1,50 | | 0,035 | 2 | 1,40 - 1,45 | 1,43 | 0,035 |

Description/ remarks: *Blackia* has the smallest cheek teeth among all extinct flying squirrels. The teeth are extremely low crowned and of triangular (D4, P4) or rhomboidal (M / m) outline. The protoloph and metaloph of P4-M2 are parallel and oblique. M3 has no metaloph. The entoconid and metalophid of lower molars are absent or almost so. The small dimensions, the simple tooth-pattern and the granulated surface of the teeth are the most characteristic features. Both size and dental morphology have essentially remained unchanged between the lower Miocene and the Pliocene (MN2-MN15). There is only a minor size decrease with time. However, DE BRUIJN (1999) con-

siders *B. parvula* and *B. ulmensis* to be junior synonyms of *B. miocaenica*, and *B. polonica* as a junior synonym of *B. woelfersheimensis.* According to DAHLMANN (2001) *B. woelfersheimensis* is a synonym of *B. miocaenica.*

### *Pliopetes* KRETZOI, 1959

Type species: *P. hungaricus* KRETZOI, 1959 - Csarnota 2 (Hungary, Pliocene / MN15)

### *Pliopetes* cf. *hungaricus* KRETZOI, 1959
(Plate 5, Figs. 11-20)

1975 *Pliopetes* cf. *hungaricus* – DAXNER-HÖCK: 63 f.; Taf. 8, Fig. 9-10.
2004 *Pliopetes* cf. *hungaricus* – DAXNER-HÖCK: 3.

Occurrences in Austria – stratigraphy: Schernham (Molasse Basin; U. Miocene / MN10), Kohfidisch (Vienna Basin; U. Miocene / MN11), Eichkogel (Vienna Basin; U. Miocene / MN11)

Stratigraphic range: Miocene-Pliocene (MN 10-15)

Other occurrences in Europe - stratigraphy**:** Podlesice (Poland; Pliocene / MN14), Weze1 (Poland; Pliocene / MN15), Dorn-Dürkheim (Germany; U. Miocene / MN11), Douvre and Soblay (France; U. Miocene / MN10), Wölfersheim (Germany ; Pliocene /MN15).

References: SULIMSKY (1964), BLACK & KOWALSKI (1974), FRANZEN & STORCH (1975), MEIN (1984), DAHLMANN (2001).

Investigated material:

Schernham (Sch) - (Inv. Nr. NHMW2004z0062/0001-0004): 1 D4 right, 1 P4 left, 1 M1/2 left, 1 M1/2 right

Kohfidisch (Ko) - (Inv. Nr. NHMW2004z0063/0001): 1 M1/2 left

Eichkogel (E) - (Inv. Nr. NHMW2004z0064/0001-0002): 1 d4 left, 2 d4 right, and some specimens from Coll. PIUW (DAXNER-HÖCK, 1975): 1 D4 left (Inv. Nr. PIUW1953/7/1), 1 P4 right (Inv. Nr. PIUW 1953/7/3), 1 m1/2 right (Inv. Nr. PIUW 1953/7/5).

Measurements: Tab. 6

| | | D4 | D4 | P4 | P4 | M1/2 | M1/2 | M3 | M3 |
|---|---|---|---|---|---|---|---|---|---|
| | | L | W | L | W | L | W | L | W |
| Sch | D4r | 1,30 | 1,30 | | | | | | |
| | P4l | | | 1,40 | 1,50 | | | | |
| | M1/2l | | | | | 1,40 | 1,60 | | |
| | M1/2r | | | | | 1,45 | 1,70 | | |
| Ko | M1/2l | | | | | 1,50 | 1,80 | | |

| | | d4 | d4 | p4 | p4 | m1/2 | m1/2 | m3 | m3 |
|---|---|---|---|---|---|---|---|---|---|
| | | L | W | L | W | L | W | L | W |
| E | d4l | 1,30 | 1,00 | | | | | | |
| | d4r | 1,35 | 1,05 | | | | | | |

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

U p p e r d e n t i t i o n : D4 and P4 are triangular. The parastyle in the antero-lingual edge is as high as the paracone and the metacone. Between paracone and metacone there is a small isolated mesostyle. The protocone is rounded and antero-posteriorly elongate. The hypocone is almost absent in D4, weak in P4. The protoloph and the metaloph are parallel and oblique. The mesoloph of D4 and P4 is very weak and short. The molars (M1/2) are almost square in outline and of a molar pattern similar to P4. The mesostyle is connected with the paracone.

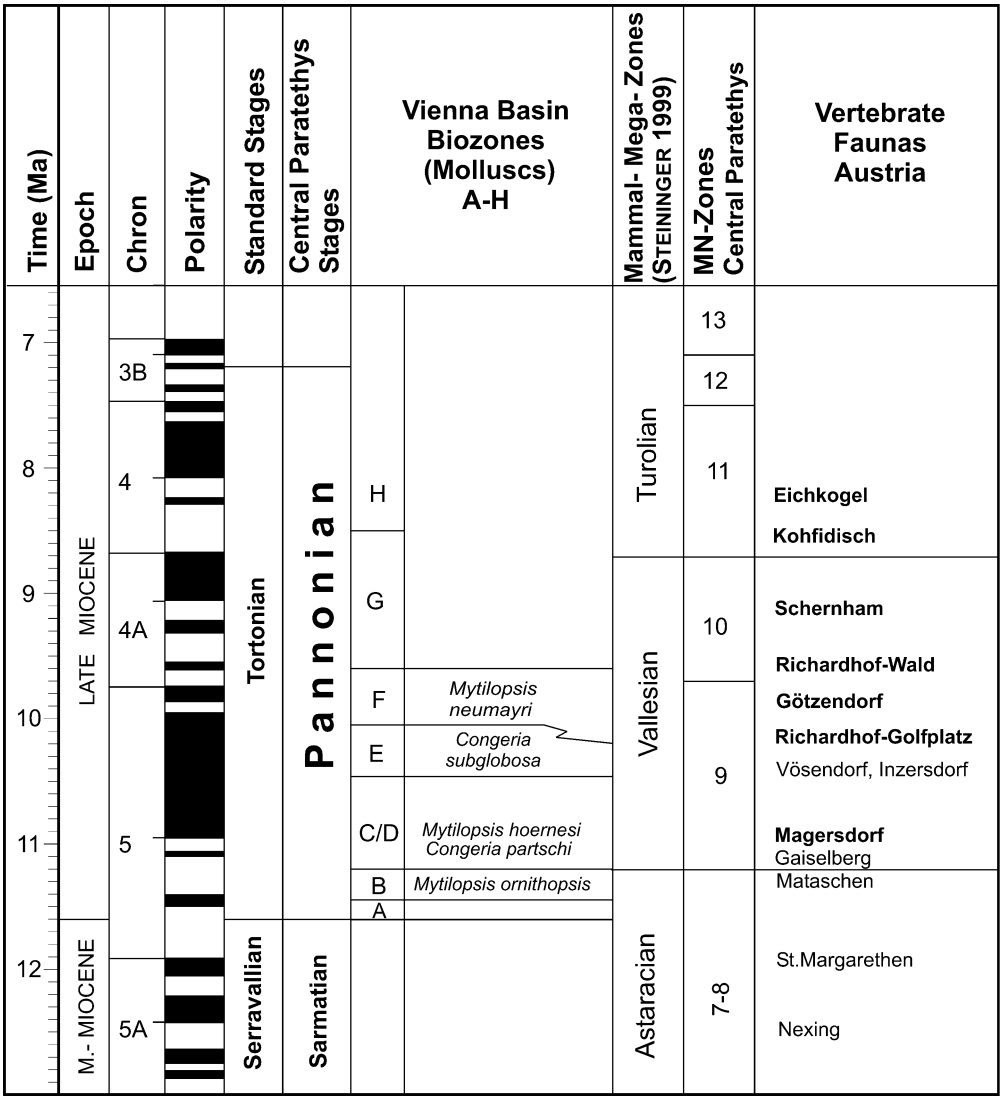
L o w e r d e n t i t i o n : Three lower deciduous teeth from the locality Eichkogel are intermediate between *Blackia* and *Pliopetaurista* in size. The morphological pattern of d4 is very simple. The tooth is elongate. Its wide basin is surrounded by a cingulum, which is interrupted by the metaconid, protoconid and some irregular small conulids. The right m1/2 with strongly ornamented enamel surface was figured by DAXNER-HÖCK (1975; Pl. 8, Figs. 11, 11a).

R e m a r k s : The dimensions and proportions of the teeth are identical with the extant flying squirrel *Glaucomys volans.* They are intermediate between *Blackia miocaenica* and *Pliopetaurista kollmanni* among extinct flying squirrels. However, *Pliopetes* and *Blackia* are the smallest extinct genera. Unworn teeth of both genera have strongly ornamented occlusal surfaces, which can be lost after usage. *P. hungaricus* was first recorded from the Pliocene of Csarnota 2 in Hungary (KRETZOI, 1959) and from the Polish localities Weze and Podlesice (SULIMSKY, 1964; BLACK & KOWALSKI, 1974). Some findings from Eichkogel, Kohfidisch and Schernham in Austria, and Douvre and Soblay in France, enlarge the stratigraphic range back to the Miocene (DAXNER-HÖCK, 2004; MEIN, 1984). The detailed descriptions of SULIMSKY (1964; 181-183; Fig. 10), BLACK & KOWALSKI (1974; 473-474; Pl. XVI, Fig. 9) and DAXNER-HÖCK (1975; 63-64; Taf. 8, Figs. 9-10) show that *Pliopetes* differs from *Blackia* by more rounded major cusps, by a weak mesoloph, and by a distinct mesoconid and entoconid. In contrast to *Blackia*, the protoloph and the metaloph may be ornamented with tiny wrinkles and nodules. A morphological relationship of *Pliopetes* with the extant genus *Hylopetes* was already mentioned by KRETZOI (1959; 354), SULIMSKY (1964; 183) and VAN DE WEERD (1978;132). Finally, BOUWENS & DE BRUIJN (1986; 118-119) synonymized *Pliopetes* with *Hylopetes*, arguing that the two genera cannot be distinguished based on their dentitions. In my opinion there is no full agreement between these two genera, not in molar morphology and definitely not in size. I therefore retain the genus name *Pliopetes* for the extinct flying squirrel which occurred very rarely in Europe from the late Miocene to the Pliocene. In accordance with KRETZOI (1959) and FRANZEN & STORCH (1975), *Pliopetes* is thought to be a potential ancestor of the living *Hylopetes*.

## Stratigraphy and Correlations

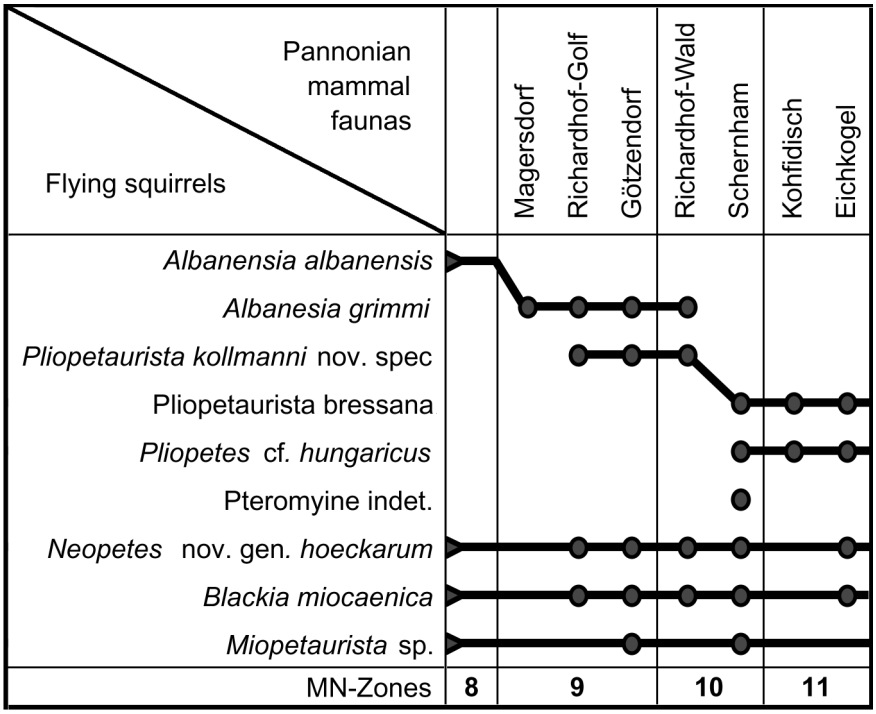
(Textfigs. 2-3)

In Austria, flying squirrels have been recorded from eight fossil sites throughout the Pannonian, i.e. Magersdorf, Richardhof-Golfplatz, Götzendorf, Stixneusiedl, Richardhof-Wald, Schernham, Kohfidisch and Eichkogel. These localities are situated in the Vienna Basin, in the Pannonian Basin and in the Molasse Basin (Fig. 1).




Textfig. 2: Correlation of Upper Miocene mammal faunas from Austria modified after DAXNER-HÖCK (2004)

The position of the locality Magersdorf is in the Molasse Basin of Lower Austria near Hollabrunn. There, gravels and sands of the Hollabrunn-Mistelbach-Formation (ROETZEL et al. 1999) are exposed in surface outcrops. They indicate a fluvial system which can be traced from Krems in the West through the Molasse Basin of Lower Austria towards the East; it entered the Vienna Basin near Mistelbach, prograding a deltaic system into the northern Vienna Basin (HARZHAUSER et al., in press). Fossil mammals (*Hippotherium primigenium, Albanensia grimmi*) and molluscs (*Mytilopsis hoernesi*) indicate the lower Vallesian / Mammal zone MN9 and the Lower Pannonian / letter- zone C (PAPP 1951).




Textfig. 3: Stratigraphic ranges of flying squirrels recorded from Pannonian mammal faunas in Austria.

The fossil sites Richardhof-Golfplatz, Götzendorf, Stixneusiedl, Richardhof-Wald and Eichkogel are located in the southern part of the Vienna Basin. They yielded vertebrate faunas which represent a stratigraphic sequence within the Upper Pannonian / letter-zones F-H. The lithology of the Upper Pannonian is characterized by thin lignite seams in the basal parts and sands and marls in the upper part. These sediments were deposited from a fluvial and lake system. This system established in the entire Vienna Basin in the Upper Pannonian, when the Pannonian Lake retreated to the East after its last high-stand in the Middle Pannonian (letter-zone E). Consequently, drainage systems coming from the Alps and the Molasse Basin developed in the Southern Vienna Basin and formed extended floodplains, rivulets and oxbow lakes (HARZHAUSER & TEMPFER 2004). Along the slope of the Alps, stagnant lakes and swamps, indicated by the faunas of the Richardhof and Eichkogel sections, established. The mammal faunas from Richardhof-Golfplatz, Götzendorf and Stixneusiedl are dated to the upper part of MN9 / Lower Vallesian. Within that zone, the evolutionary level of the rodents indicates a position of Richardhof-Golfplatz below Götzendorf (letter-zone F) but above Vösendorf, Inzersdorf, Hennersdorf (letter-zone E / Middle Pannonian). The Richardhof-Wald section is dated as lowermost MN10 / Upper Vallesian, indicated by the first murids (*Progonomys* nov. spec.) in Central Europe. Finally, the Eichkogel mammals are typical for MN11 / Lower Turolian, and the molluscs indicate the Upper Pannonian / letter-zone H (DAXNER-HÖCK 1996, 2001).

The section Schernham is situated in the Molasse Basin of Upper Austria near Haag a. Hausruck. The lithology of the sediments, i.e. gravels and sands of the Hausruckschotter, point to a fluvial system. The mammal fauna indicates the upper part of MN10 / uppermost Vallesian (DAXNER-HÖCK 2004).

The Kohfidisch fauna, finally, stems from cave and fissure fillings of the Austrian part of the Pannonian Basin. The very rich fauna of smaller mammals is most similar with the Eichkogel assemblage and therefore indicative for MN11 / Lower Turolian.

All these fossil sites yielded flying squirrels, which turned out to be of stratigraphic and ecological importance. As shown in Fig. 3, some long-lived species (i.e. *B. miocaenica* and *N. hoeckarum*) – known to range from the Lower Miocene to the Upper Miocene (MN4-11) – are very well represented in Austria throughout the Pannonian. Others are short-lived species which were replaced by descendent species after a range of one or two MN-zones. The Middle Miocene *Albanensia albanensis* (range: MN7-8) was replaced by the Upper Miocene *A. grimmi*, with the first appearance in MN9 (Lower Pannonian / Lower Vallesian) and the last occurrence in the lowermost MN10 (Upper Pannonian / Upper Vallesian). *Pliopetaurista bressana* (range: upper part of MN10-MN11) derived from the more primitive *P. kollmanni* nov. spec. (range: MN9 - lower part of MN10). Finally, *Pliopetes* cf. *hungaricus* – so far known to range from the Upper Miocene (MN11) to the Pliocene (MN15) – turned out to have its first occurrence already in the Upper Vallesian (MN10).

## Distribution and biology of extant Pteromyinae

Extant flying squirrels are restricted to the northern hemisphere, where they are distributed over three huge areas, i.e. North America, the northern part of Eurasia, and South- and Southeast Asia. There is only one genus, *Glaucomys* (small sized), known from wooded areas throughout the North American continent. A second genus, *Pteromys* (small to middle sized), inhabits boreal evergreen forests and mixed forests from Northern Europe throughout Siberia to Japan. The favourite habitats are high forests with many old hollow trees, coniferous forests mixed with birch, alder and aspen (OGNEV 1966) A third area of distribution is the tropical and subtropical zones of South- and East Asia. Quite a number of genera live from Pakistan across the Himalayan chain through India, Nepal, Burma, Malaysia, Indo-China and to northeastern China and Japan, ranging from the Giant Flying Squirrel *Petaurista* to the smallest genus *Petaurillus*. From Pakistan, ROBERTS (1977) reported that the Red Giant Flying Squirrel *Petaurista* occurs mainly in Himalayan moist temperate forest, which has a mixture of deciduous and coniferous tree species, whereas the coexisting Small Kashmir Flying squirrel *Hylopetes* is more adaptable to dryer conditions. This smaller form extends into more northern regions, where the forest is predominantly coniferous.

All living flying squirrels are arboreal and nocturnal in their habits, and all are excellent gliders (WALKER 1964; SULKAVA 1978; ROBERTS 1977; OGNEV 1966). They live in extended forested environments, from deep valleys up to hillside forests in altitudes above 2000 meters. In squirrel manner they leap from one tree-top to the next or glide if the tree is too distant. In this case they run up to a higher point and leap. Extending arms and legs – which spread the gliding membrane – they glide to the desired point. Being

nocturnal, flying squirrels spend the day curled up asleep in a tree-hole; during the night they are active. Their diet consists of young green fir and pine cones, leaves, young twigs and tree buds, and even eggs and young birds. When available in season, they also eat various fruits, acorns and nuts. Flying squirrels do not hibernate in winter, but can migrate to suitable forests in lower altitudes. In winter- and springtime they feed on buds, on immature cones and catkins of birch and alder. Little is known about their breeding habits but, as reported from different species, two litters a year varying from two to three young are raised in special nests in hollow trees. The main predators of young and adult flying squirrels are martens, cats and owls.

## Pannonian Pteromyinae: considerations on paleoenvironments and climatic conditions

Fossil remains of flying squirrels are generally rare in faunas of the Neogene. This reflects the arboreal life and the low reproduction rates. As opposed to Muridae, Pteromyinae produce only a few young a year and have relatively long life expectances. As a result, these long-living and arboreal/scansorial/gliding rodents are under-represented in the fossil record. Nevertheless, in Austria the diversity of flying squirrels, concerning individual and species numbers, is unexpectedly high throughout the Pannonian. This diversity, not only in flying squirrels but in overall mammal records, hints at favourable environments. Favourable environments for flying squirrels were probably humid habitats with extended forests. Based on records of extant flying squirrels, the tropical and subtropical zones of South-, East and Southeast-Asia harbour the highest diversity in genera and species, including the large-sized genus *Petaurista,* which exclusively inhabits moist temperate forests. Smaller and middle-sized species tolerate dryer conditions (e.g. *Hylopetes*) or are adapted to boreal evergreen and mixed forests (*Pteromys*).

In the Pannonian of Austria (Fig. 3) the highest diversity of Pteromyinae-species is recorded from fluvial (Götzendorf / 5 species; Schernham / 6 species) and limnic deposits (Richardhof-Golfplatz, Richardhof-Wald, Eichkogel / 4 species in each fauna), whereas it is low in fissure fillings (Kohfidisch / 2 species). Furthermore, the large-sized *Albanensia grimmi*, known to be most abundant in Rudabanya (Hungary / MN9) and Götzendorf (Austria / MN9), has its last occurrence in Richardhof-Wald (lower part of MN10). The assemblages from Schernham (upper part of MN10), Kohfidisch and Eichkogel (MN11) almost exclusively yielded small- and middle-sized species, which hints at less favourable life-conditions. These could have been increasing cooling, and/or aridity, and/or seasonality (warm/cold- or wet/dry- seasonality), accompanied by changing of plant associations. In my opinion, increasing seasonality, e.g. wet winter- but dryer summer months, is most probable. As a result, changing vegetation and food supply affected the development of flying squirrels with regard to diversity and species compositions.

The Pteromyinae-data are in full agreement with the overall vertebrate faunas of the Pannonian: They indicate wetland and rather humid, forested environments with warm temperate climate along the western margin of Lake Pannon during the Early and Middle Pannonian (letter-zones C-E), and vast floodplains and stagnant lakes accompanied by extended mixed forests in the early Late Pannonian (letter-zone F). During the Late

Pannonian (letter-zones G-H), terrestrial and floodplain environments established in the Vienna and Molasse Basins. This last period started with dramatic changes in mammal assemblages, expressed in significant numbers of extinctions and first occurrences, known as the "Vallesian Crisis". These sudden extinctions of most Middle Miocene and lower Late Miocene (Early Vallesian) elements and the entry and rapid dispersal of murids and other "newcomers" was first recognised by AGUSTI & MOYÀ-SOLA (1990) in Spain. In Austria the faunas from Richardhof-Wald and Schernham (Late Vallesian / MN10) provide evidence of the "Vallesian Crisis".

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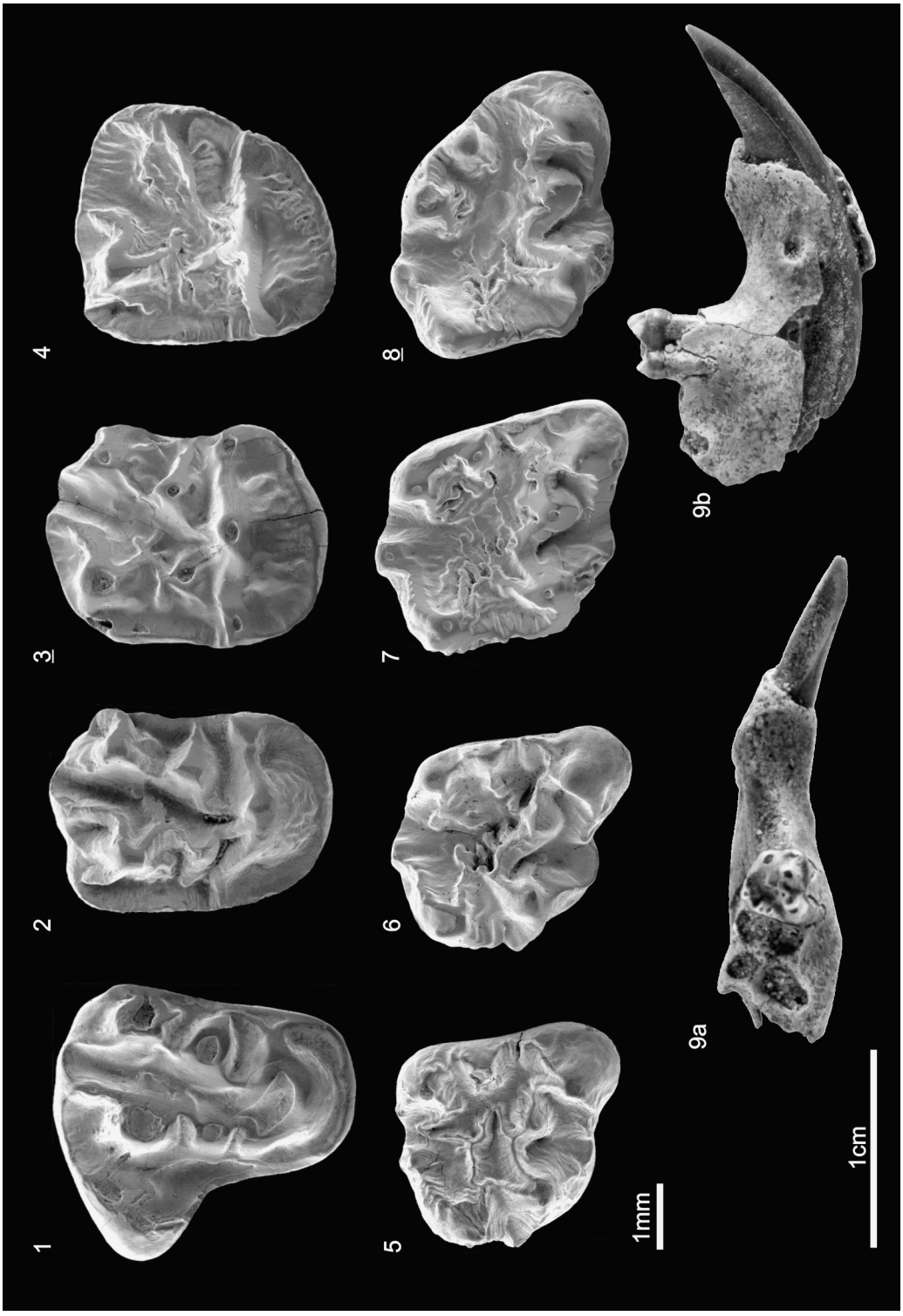
**Plate 1**

***Albanensia grimmi* (BLACK, 1966)** from Götzendorf near Mannersdorf in Lower Austria (Upper Miocene, MN9). Collection of the Natural History Museum, Department of Geology and Paleontology, Vienna (NHMW). All right side teeth are figured as if they were from the left side, and the figure-numbers are underlined (3, 8, 9). Magnifications: Fig. 1-8 = 10x and Fig. 9 = 3x.

1. left P4; Gö1; Inv. Nr. NHMW1990/15/236
2. left M1; Gö1; Inv. Nr. NHMW1990/15/244
3. right M2; Gö1; Inv. Nr. NHMW1990/15/248
4. left M3; Gö1; Inv. Nr. NHMW1990/15/266
5. left p4; Gö1; Inv. Nr. NHMW1990/15/259
6. left m1; Gö1; Inv. Nr. NHMW1990/15/297
7. left m2; Gö1; Inv. Nr. NHMW1990/15/204
8. right m3; Gö1; Inv. Nr. NHMW1990/15/214

9a. right mandible with p4 (occlusal); Gö1; Inv. Nr. NHMW1990/15/228

9b. right mandible with p4 (labial); Gö1; Inv. Nr. NHMW1990/15/228


1
2
3
4
5
6
7
8
9a
9b
1mm
1cm

## Plate 2

***Miopetaurista* sp.** from Götzendorf (Gö 1) near Mannersdorf, Lower Austria and Schernham (Sch) near Haag a. Hausruck, Upper Austria (Upper Miocene). All right side teeth are figured as if they were from the left side, and the figure-numbers are underlined (1, 3, 4). Magnifications: Fig. 1- 4 = 10x

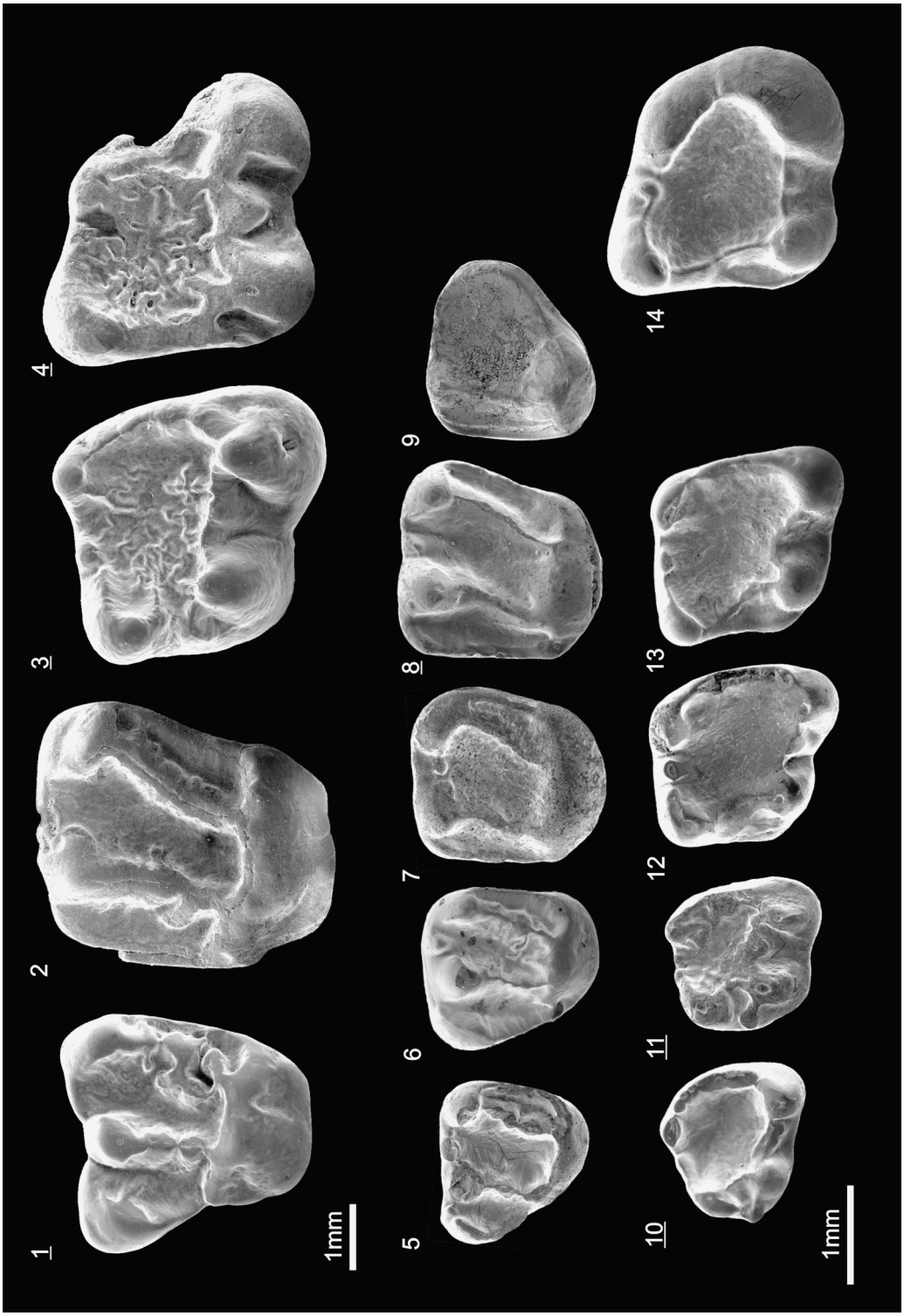
1. right P4; Gö 1; NHMW1990/15/276
2. left M1/2; Gö 1; NHMW1990/15/274
3. right p4; Gö1; NHMW1990/15/272
4. right m3; Sch; Inv. Nr. NHMW2004z0055/0001):

***Neopetes hoeckarum* (DE BRUIJN, 1998)** from Richardhof-Golfplatz (RH-A/2), Richardhof-Wald (Rh-1), Götzendorf (Gö 1) in Lower Austria and Schernham (Sch) in Upper Austria (Upper Miocene). All right side teeth are figured as if they were from the left side, and the figure-numbers are underlined (8, 10, 11). Magnifications: Fig. 5-13 = 15x

5. left D4; RH-A/2; Inv. Nr. NHMW2004z0058/0002
6. left P4; Rh-1; Inv. Nr. NHMW2004z0059/0001
7. left M1; RH-A/2; Inv. Nr. NHMW2004z0058/0004
8. right M2; RH-A/2; Inv. Nr. NHMW2004z0058/0005
9. left M3; Sch; Inv. Nr. NHMW2004z0060/0001
10. right d4; Gö 1; Inv. Nr.NHMW1990/15/1/0001
11. right p4; RH-A/2; Inv. Nr. NHMW2004z0058/0007
12. left m1; Gö 1; Inv. Nr. NHMW1990/15/1/0004
13. left m2; Gö 1; Inv. Nr. NHMW1990/15/10003

**Pteromyinae indet.** from Schernham (Sch) in Upper Austria (Upper Miocene). Magnification: Fig. 14 = 15x

14. left m3; Sch; Inv. Nr. NHMW2004z0061/0001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1mm
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**Plate 3**

***Pliopetaurista kollmanni* nov. spec.** from Richardhof-Golfplatz (RH-A/2), Götzendorf (Gö 1) in Lower Austria and Schernham (Sch) in Upper Austria (Upper Miocene). All right side teeth are figured as if they were from the left side, and the figure-numbers are underlined (2, 5, 13, 14). Magnifications: 15x

1. left D4; RH-A/2; Inv. Nr. NHMW2004z0065/0002
2. right P4; RH-A/2; Inv. Nr. NHMW2004z0065/0003
3. left M1 (Paratype); Gö 1; Inv. Nr. NHMW1990/15/2/0002
4. left M2 (Holotype); Gö 1; Inv. Nr. NHMW1990/15/2/0003
5. right M3 (Paratype); Gö 1; Inv. Nr. NHMW1990/15/2/0005
11. left d4; RH-A/2; Inv. Nr. NHMW2004z0065/0006
12. left p4 (Paratype); Gö 1; Inv. Nr. NHMW1990/15/2/0006
13. right m1 (Paratype); Gö 1; Inv. Nr. NHMW1990/15/2/0007
14. right m2 (Paratype); Gö 1; Inv. Nr. NHMW1990/15/2/0010
15. left m3 (Paratype); Gö 1; Inv. Nr. NHMW1990/15/2/0011

***Pliopetaurista bressana* MEIN, 1970** from Schernham (Sch) in Upper Austria (Upper Miocene). All right side teeth are figured as if they were from the left side, and the figure-numbers are underlined (7, 10, 18). Magnifications: 15x

6. left D4; Sch; Inv. Nr. NHMW2004z0067/0002
7. right P4; Sch; Inv. Nr. NHMW2004z0067/0003
8. left M1/2; Sch; Inv. Nr. NHMW2004z0067/0004
9. left M1/2; Sch; Inv. Nr. NHMW2004z0067/0005
10. right M3; Sch; Inv. Nr. NHMW2004z0067/0008
16. left d4; Sch; Inv. Nr. NHMW2004z0067/0021
17. left p4; Sch; Inv. Nr. NHMW2004z0067/0023
18. right m1; Sch; Inv. Nr. NHMW2004z0067/0025
19. left m2; Sch; Inv. Nr. NHMW2004z0067/0026

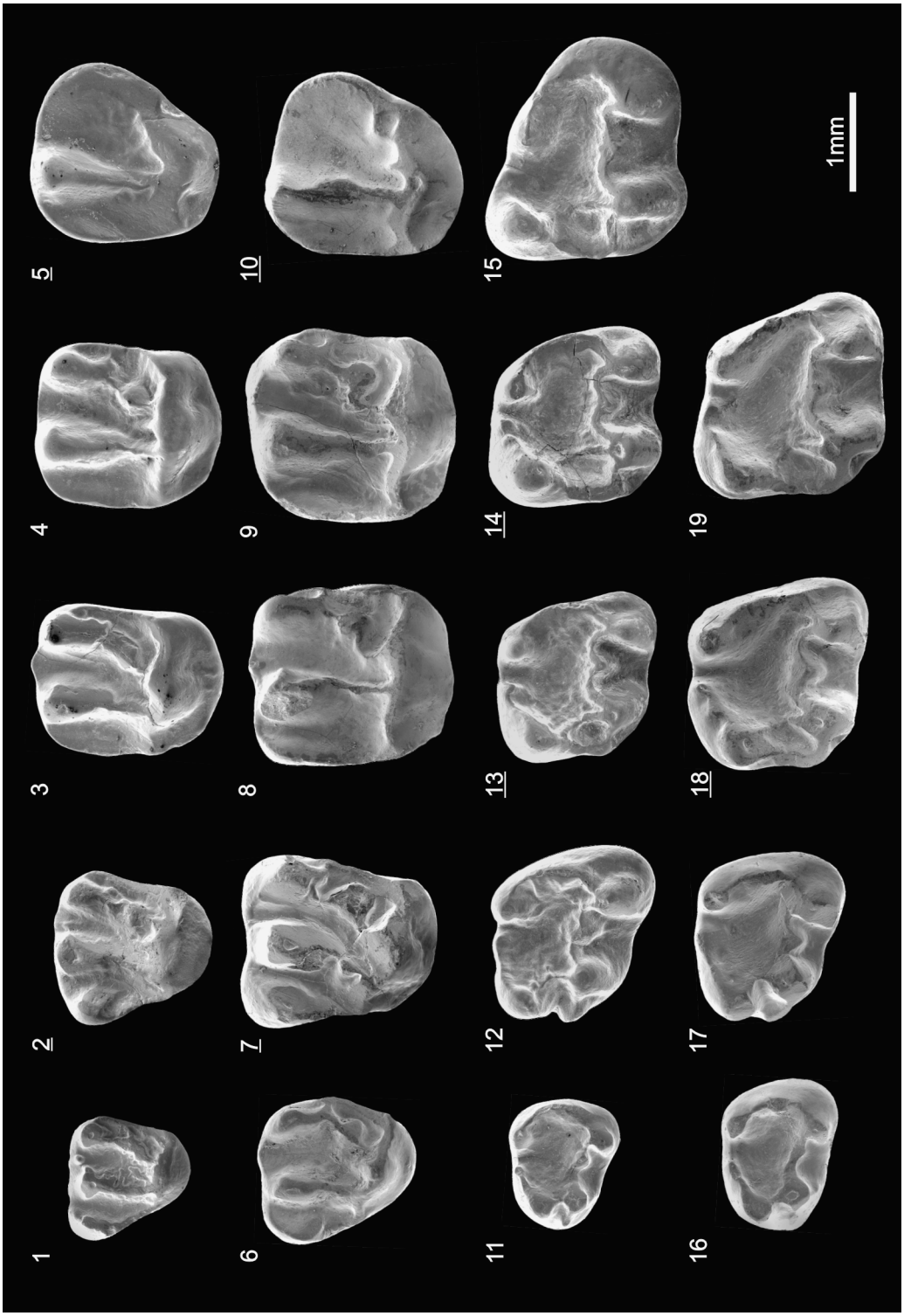
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**Plate 4**

***Pliopetaurista bressana* MEIN, 1070** from Kohfidisch (Ko) in Burgenland (Upper Miocene). All right side teeth are figured as if they were from the left side, and the figure-numbers are underlined (1, 2, 4). Magnifications: 15x

1. right maxilla, P3-M3; Ko-IIIu ; Inv. Nr. NHMW2004z0068/0002
2. right maxilla frag., P3-M2; Ko-IIIu; Inv. Nr. NHMW2004z0068/0006
3. left m2; Ko; Inv. Nr. NHMW2004z0068/0013
4. right mand. frag., m2-3; Ko; Inv. Nr. NHMW2004z0068/0012


1
2
3
4
1mm

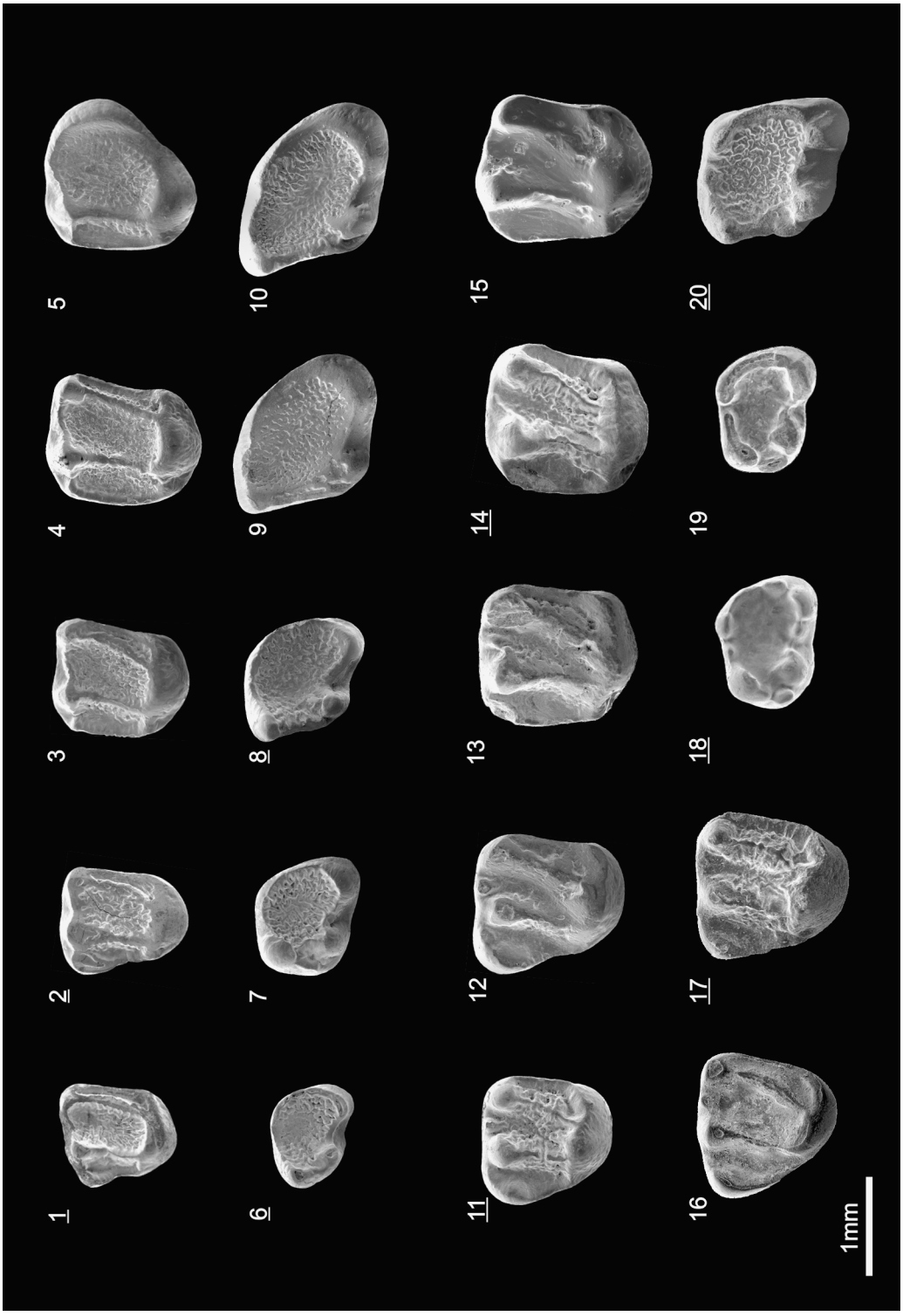
## Plate 5

***Blackia miocaenica* MEIN, 1970** from Richardhof-Golfplatz (RH-A/2), Richardhof-Wald (Rh-1), in Lower Austria and Schernham (Sch) in Upper Austria (Upper Miocene). All right side teeth are figured as if they were from the left side, and the figure-numbers are underlined (1, 2, 6, 8). Magnifications: 15x

1. right D4; Rh-1; Inv. Nr. NHMW2004z0070/0003
2. right P4; RH-A/2; Inv. Nr. NHMW2004z0069/0003
3. left M1; Rh-1; Inv. Nr. NHMW2004z0070/0007
4. left M2; Sch; Inv. Nr. NHMW2004z0071/0011
5. left M3; Sch.; Inv. Nr. NHMW2004z0071/0015
6. right d4; RH-A/2; Inv. Nr. NHMW2004z0069/0006
7. left p4; RH-A/2; Inv. Nr NHMW2004z0069/0008
8. right m1; RH-A/2; Inv. Nr. NHMW2004z0069/0009
9. left m2; RH-A/2; Inv. Nr. NHMW2004z0069/0010
10. left m3; RH-A/2; Inv. Nr. NHMW2004z0069/0012

***Pliopetes* cf. *hungaricus* KRETZOI, 1959** from Schernham (Sch) in Upper Austria, Kohfidisch (Ko) in Burgenland and Eichkogel (E) in Lower Austria (Upper Miocene). All right side teeth are figured as if they were from the left side, and the figure-numbers are underlined (11, 14, 17, 18, 20). Magnifications: 15x

11. right D4; Sch; Inv. Nr. NHMW2004z0062/0001
12. left P4; Sch; Inv. Nr. NHMW2004z0062/0002
13. left M1/2; Sch; Inv. Nr. NHMW2004z0062/0003
14. right M1/2; Sch; Inv. Nr. NHMW2004z0062/0004
15. left M1/2; Ko; Inv. Nr. NHMW2004z0063/0001
16. left D4; E; Inv. Nr. PIUW 1953/7/1
17. right P4; E; Inv. Nr. PIUW 1953/7/3
18. right d4; E; Inv. Nr. NHMW2004z0064/0002
19. left d4; E; Inv. Nr. NHMW2004z0064/0001
20. right m1/2; E; Inv. Nr. PIUW 1953/7/5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