Upper Miocene rodents from Pezinok in the Danube Basin, Slovakia

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Abstract: Rodent assemblages are described from two sampled sites at the Pezinok clay pit in the Danube Basin. Although these assemblages contain material poor in specimens, the following eleven rodent taxa are distinguished and described: *Progonomys hispanicus, Kowalskia* sp., *Microtocricetus molassicus, Anomalomys gaillardi, Graphiurops austriacus, Paraglirulus* sp., *Eomyops catalaunicus, Keramidomys* sp., *Spermophilinus* sp., *Albanensia* sp. and *Euroxenomys minutum*. The co-occurrence of very primitive Progonomys hispanicus with Microtocricetus molassicus confirms fauna age as Late Miocene, middle Vallesian (early MN10).

Key words: Danube Basin, Late Miocene, Vallesian, Mammalia, Rodentia, biostratigraphy

1. INTRODUCTION

Pannonian sediments are mostly known from Danube Basin boreholes; and although outcrops are rare due to the great thickness of fluvial Pliocene and Pleistocene deposits, the new brickyard clay pit in the Pezinok locality is an exception. This is located in the Blatné Depression at the eastern margin of the Danube Basin.

The Pezinok locality is typical for relatively high variability of sedimentary facies and their lateral instability. The uppermost part of the profile has massive or horizontally to cross bedded fine-to-medium grained sands, and rarely silts and variegated and spotted clays. These sediments are fluvial facies; most likely point-bar deposits from a meandering river (Pliocene/Pleistocene?). The middle part of the outcrop has variegated and spotted clays, lignite clays, lignite-rich and fine-to-medium grained sands with molluscs and silts while the lower part has more common massive, blue–gray clays rich in molluscs. This latter part of the profile is characterized by extremely variable sedimentary environments with limnic clays, alluvial sands and clays and also lagunar lignite clays and lignites. The age of the middle and lower parts (Ivánka Fm.) was proposed as the Late Miocene – Pannonian zone E (Holec et al., 1987; Fordinál, 1997; Pipík 1998).

Mollusc finds are commonly reported in sand–clay sediments, and are especially rich in both the old and new clay pits (Horusitzky, 1907; Lörenthey 1911; Pokorný 1946; Cílek 1960; Fordinál, 1991, 1997). The old pit is now recultivated, but it was formerly situated 100–150m NE of the newly-worked clay pit.

Vertebrate remains, especially large mammals are relatively rare here. These are limited to just one "*Hipparion primigenium* (von Meyer, 1829)" tooth and one tooth from *Deinotherium giganteum* Kaup, 1829 (Holec, 1981, 2005). These were surface findings without affiliation to a special layer.

The fauna described in this article came from a sandy layer rich in molluscs from the uppermost part of the "Miocene section"; a few meters below the fluvial complex (Fig. 1). The Pezinok

A and B samples reported here were collected a large distance apart, and although they are thought to come from the same sandy layer, precise lithological correlation is impossible. The sample from Pezinok A was collected in 2004–2005 from the southern wall of the new clay pit, but mining activity has now destroyed the original location. The rodent fauna from this site was described in my PhD thesis (Joniak, 2005) but not published in detail; Sabol et al. (2004) supplied only a preliminary list of discovered fauna.

Fauna was interpreted as upper Vallesian (MN10) in age. Stratigraphically the oldest part of the pit did not yield any valuable mammal remains. Only one enamel fragment of a rodent incisor was recovered from washing of more than 300kg of sediment. However, additional remains of small mammals were recovered from a sandy layer rich in molluscs in the upper part of the limnic section on the eastern wall of the pit (Fig. 1). This layer was bulk sampled in 2015 and Pezinok B fauna was recovered. Both Pezinok A and B rodent assemblages are described herein.

2. METHODS

At least 3 tons of sediment from each Pezinok A and B was sieved on a set of stable sieves (Daams & Freudenthal, 1988); with Pezinok A sampled in 2004–2005 and Pezinok B in 2015. The mesh size of the lower sieve was 0.5 mm, and the residue was subsequently dried and soaked in 10% acetic acid to reduce the high content of mollusc shell fragments. Fossil remains were then picked manually under the stereo-microscope; with more than 50 rodent teeth recovered from each sample. While insectivore material was also recovered, this is outside the scope of this article.

The described material is housed in the collections of Department of Geology and Paleontology, Comenius University in Bratislava, Slovakia. The upper cheek teeth are indicated by upper case (P4, M1, M2, M3) and lower cheek teeth by lower case (p4, m1, m2, m3). Where distinction between first and
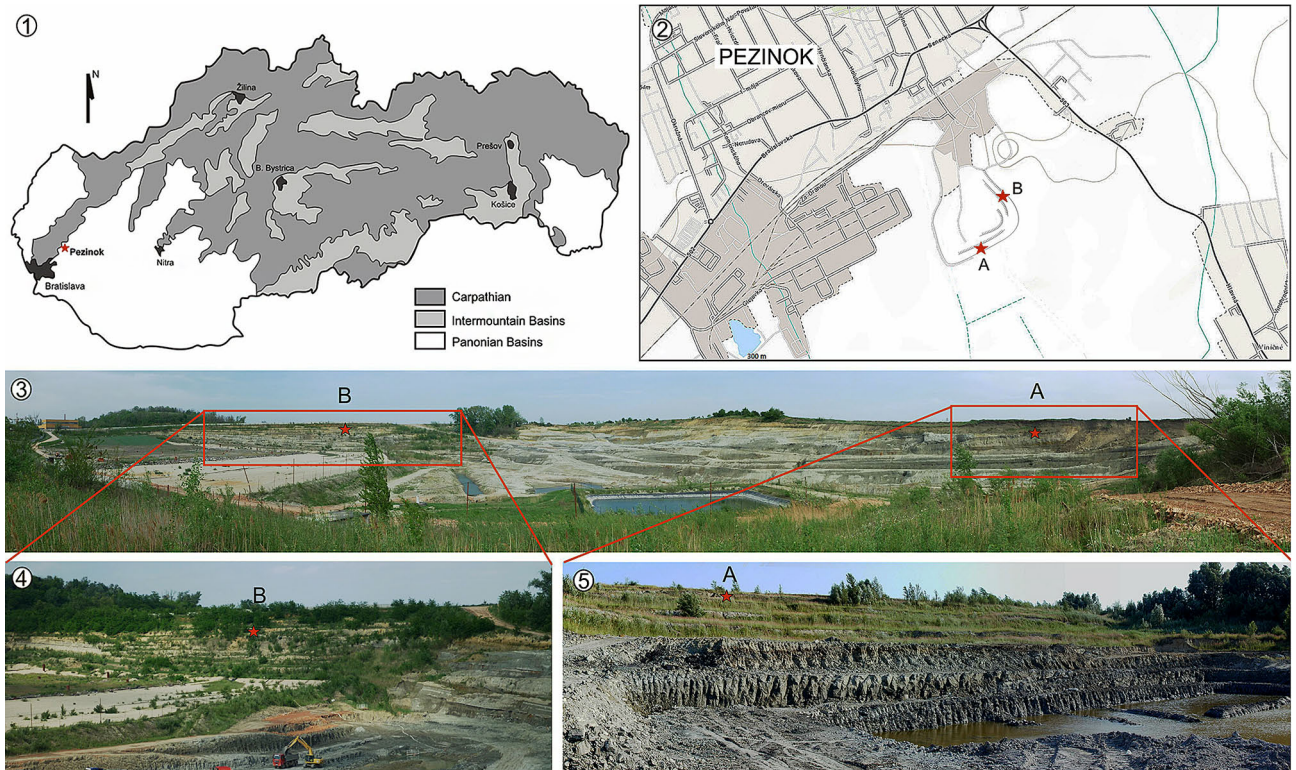
Fig. 1. 1 - Sketch map of Slovakia with the location of Pezinok; **2** - Location of Pezinok A and Pezinok B in the clay pit; **3** - Panorama view of Pezinok outcrop (2014) with assumed position of original Pezinok A locality and precise position of Pezinok B locality; **4** - Photo (2015) of eastern wall with position of the B locality; **5** - Photo (2004) of southern wall with precise position of the original A locality.

second molars is questionable, these are indicated as m1/2 or M1/2. Teeth measurements in mm were taken by calibrated micrometer eyepiece on a Leica MZ7.5 stereomicroscope; providing cheek teeth occlusal surface maximum length (L) and width (W); unless otherwise stated. Terminology used for teeth parts follows van de Weerd (1976) for Murinae; Daams & Freudenthal (1988) and Freudenthal et al. (1994) for Cricetidae; de Bruijn (1967) for Gliridae; Engesser (1990) for Eomyidae; Cuenca Bescós (1988) for Sciuridae; and Hugueney (1999) for Castoridae. Taxa were studied by direct comparison with specimens held at the Department of Geology and Paleontology, Comenius University in Bratislava, the Naturhistorisches Museum Wien, Utrecht University, and also from published data of type materials.

3. SYSTEMATIC PART

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Order Rodentia Bowdich, 1821
Family Muridae Illiger, 1811
Subfamily Murinae Illiger, 1811
Genus *Progonomys* Schaub, 1938
Progonomys hispanicus Michaux, 1971
(Figs. 2.1–2.7)

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Type species: *Progonomys cathalai* Schaub, 1938
Type locality: Montredon (Héraut, France), Late Miocene (MN10).

Material – Pezinok A: 3 M2 (PK040101-03), 1 M3 (PK040104), 1 m1 (PK040105), 3 m2 (PK040107-09). Pezinok B: 10 M1 (PK150101–05, PK150110–14), 9 M2 (PK150120–24, PK150130–33), 1 M3 (PK150139), 10 m1 (PK150140–43, PK150150–55), 9 m2 (PK150160–63, PK150170–74).

Description: M1 – these molars are available only from Pezinok B. The t1 is posterior to t2 and t3, and t1 cusp is elongated while t2 and t3 are rounded. The connection between t2 and t3 is low with a deep valley between the cusps. t1bis and t2bis are absent. Three of the ten specimens have a small tuberculum between t3 and t5. The valley between t1–t2–t3 and t4–t5–t6 is continuous, but very narrow between t2 and t5. While t5 is

Tab. 1. Measurements of *Progonomys hispanicus* from Pezinok A and B [in mm].

		Length			N	Width		
		Min	Mean	Max		Min	Mean	Max
Pezinok A	M2	1.32	1.36	1.38	3	1.6	1.11	1.13
	M3		0.92		1		0.73	
	m1	1.74	1.75	1.75	2/1		1	
	m3	1.3	1.32	1.34	3	1.3	1.8	1.13
Pezinok B	M1	1.74	1.96	2.6	10	1.6	1.15	1.19
	M2	1.22	1.3	1.4	9	1.1	1.16	1.22
	M3		0.9		1		0.82	
	m1	1.66	1.71	1.8	10	1	1.4	1.8
	m2	1.2	1.25	1.28	9	1.2	1.7	1.12

situated more anteriorly than t6, t4 is elongated and connected to t5 by a shallow ridge. The t6 and t9 are not connected, but t4 is connected to t8 by a low ridge. The t9 is considerably smaller than the t8 and placed laterally to it. One specimen has a small tuberculum between t6 and t9. The t12 is short, ridge–like and connected only to t8. The M1 roots are not preserved.

M2 – all specimens are uniform in morphology. The t3 is a small cusp placed more posteriorly than the t1. While t1bis is undeveloped, t1 is elongated and curved. The t3 and t1 are connected by a low ridge to the anterior base of t5. The t4 has a posterior spur that reaches t8, and t5 and t8 are similar in size. The t6 and t9 are separated in all specimens. The t12 is ridge–like and connected to t8. The roots are not preserved.

M3 –the Pezinok A specimen is complete, but the Pezinok B specimen has damage to the central occlusal surface. The t1 is bigger than t3. The t4, t5 and t6 are connected. The t8 is separated and t12 is not developed. The tooth has no preserved roots.

m1 – the m1 occlusal surface has a sub–elliptical outline. The labial cusp and the lingual cusp of the anteroconid are approximately equal in size (9/11) or the lingual cusp is slightly larger (2/11). The antero–central cusp (tma) is absent (9/11) or is developed as a very small tuberculum (2/11). While a low ridge connects the lingual anteroconid and metaconid, connection between the labial anteroconid and protoconid is absent in all specimens. The labial and lingual anteroconid are divided by a shallow valley, and connection is developed in more worn specimens. The protoconid and metaconid, and the hypoconid and entoconid are connected by low ridges. The longitudinal ridge is absent. The c1 is developed as a small independent cusp and connected to the base of the hypoconid by a low ridge. The low accessory labial cusps are present in all specimens. While most specimens have a small elongated cusp incorporated in the antero–labial cingulum, some specimens (5/11) have only a cingulum descending from the anteroconid to the protoconid. All specimens have a small tuberculum at the labial border of the occlusal surface next to the base of the protoconid and the oval terminal heel is well–developed. The m1 has two roots.

m2 – all specimens have the same morphology. The antero–labial cusp is elongated and connected to the ridge between the metaconid and protoconid, and the hypoconid and entoconid are also connected. The c1 accessory cusp is developed as an isolated cusp and one small cusp is also developed at the labial border of the occlusal surface next to the base of the protoconid. The sinusid is continuous from the labial to the lingual border because the longitudinal crest is absent. The terminal heel is oval. The m2 has two roots.

Comments: The *Progonomys* from Pezinok A and B corresponds perfectly in length to *P. hispanicus* from Masia de la Roma (Spain). However, the Pezinok teeth are slightly larger than those in *P. hispanicus* from Masia del Barbo 2B (Spain), and the upper molars approximate those of *P. cathalay* from Montredon (France) in length but they are more slender. The W/L ratio in M1 is 0.59. Van Dam (1997) described Spanish populations of *Progonomys* species in great detail and highlighted the clear evolutionary trend of increased width in successive *P. hispanicus* populations.

The Pezinok first upper molars have all morphological characteristics typical in *P. cathalai* and *P. hispanicus* populations, but they are variable (van de Weerd, 1976; van Dam, 1997). These are: connection between the t1 and t2, absence of t1bis, medium-high connection between t4 and t5, t4 connected to t8 by a low ridge, absence of t7, separation of t6 and t9 in M1 and M2 and well developed t12. In addition, the lower molars are characteristic in absence of a longitudinal spur, a large c1 in m1 and m2 and absence of the antero–central cusp in most specimens. These characters are typical for *P. cathalay* and the oldest *P. hispanicus* populations. All specimens have connection between the antero–lingual cusp and the metaconid, but connection between the labial anteroconid and the protoconid is always absent. There are only small morphological differences between *P. hispanicus* and *P. cathalay*; with overlap both in size and morphology (Michaux, 1971; van de Weerd, 1976; van Dam, 1997; Daxner–Höck & Höck, 2015). The relative positions of t8 and t9 was used by van Dam (1997) to discriminate between the earliest *P. hispanicus* and *P. cathalay*; where t9 is lateral to t8 in *P. hispanicus,* but t9 is more anterior in *P. cathalay.* When all these characteristics are considered, the Pezinok material resembles a primitive form of *P. hispanicus.*

Occurrences of *Progonomys* in central Europe are limited to Austria and Hungary. In Austria, *P. hispanicus* occurs at Richardhof–Wald (MN10) and Neusiedl am See (MN10) and *P. woelferi* Bachmayer & Wilson, 1970 is found at Kohfidish (MN10) and Eichkogel (MN11; Daxner–Höck & Höck, 2015); and in Hungary, *P.* cf. *cathalay* is reported from Sümeg (MN11; Bernor et al. 1999).

Subfamily Cricetinae Fischer de Waldheim, 1817
Genus *Kowalskia* Fahlbusch, 1969
Kowalskia sp.
(Figs. 2.10–2.12)

Type species: *Kowalskia polonica* Fahlbusch, 1969
Type locality: Podlesice (Poland), Lower Pliocene (MN 14).
Material: Pezinok A: 1 m2 (PK040201 1.63x1.36) and 2 m3 (PK040202 1.60x1.16; PK040204 1.48x1.24). Pezinok B: 2 m3 (PK150401 1.45x1.19; PK150402 –x1.20).

Description: m2 – one extremely worn specimen was recovered; with a long mesolophid, reaching the labial margin of the tooth. The posterolopid is strong and not connected to the entoconid and the ectomesolophid is developed as a very low but long and distinctive crest. The tooth has two roots.

m3 – two specimens are available from both Pezinok A and B. They have almost the same morphology, and the teeth have a narrow posterior portion. Both labial and lingual anterolophid are well developed, with the lingual slightly shorter. The metalophid is connected to the anterolophid approximately in the median line of the tooth, and the mesolophid is long and reaches the lingual cingulum. The hypolophid runs parallel to the mesolophid. The posterolophid is strong, forming the posterior part of the tooth and connected to the entoconid. This latter is smaller than other main cusps, but well developed. The teeth have two roots.
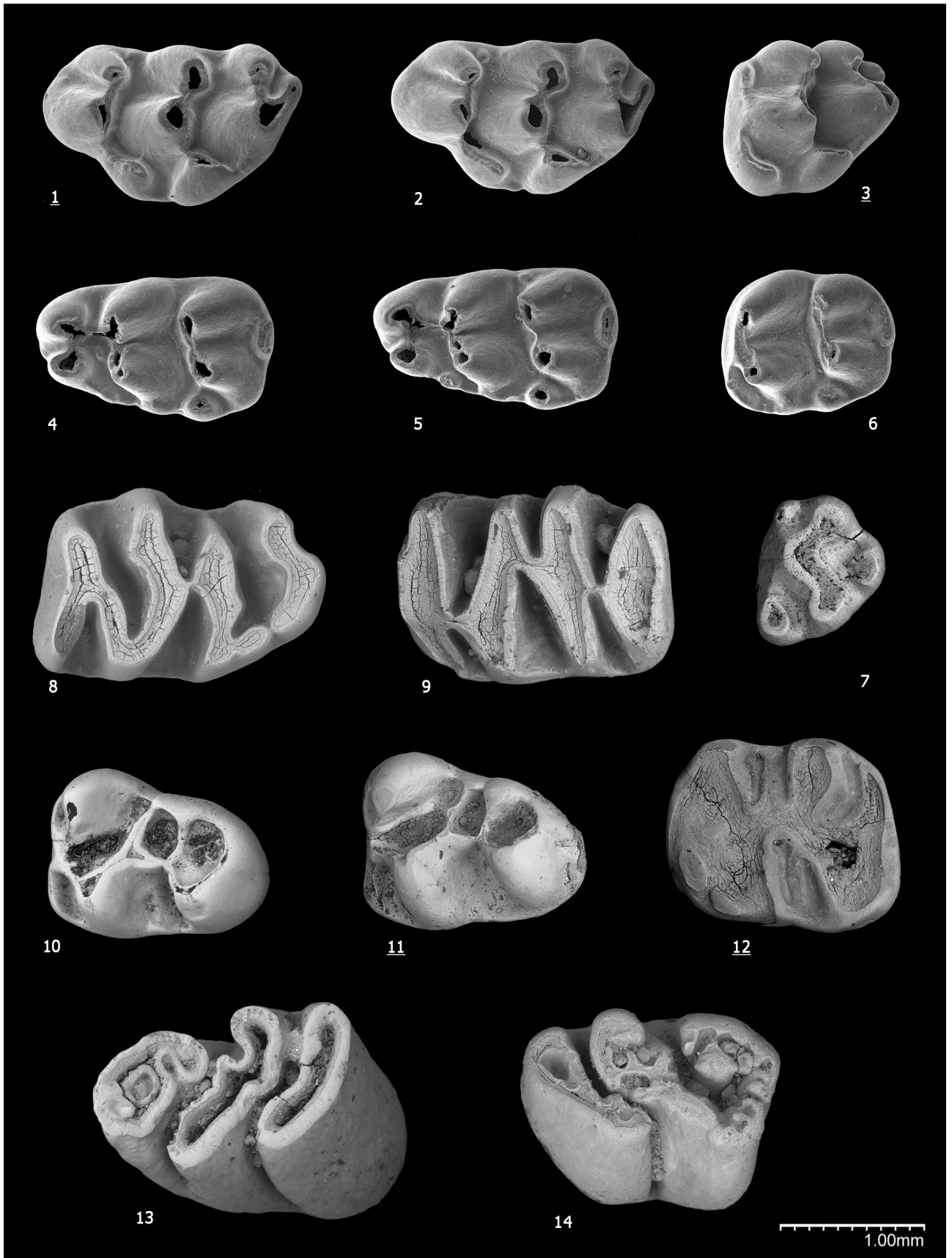
Fig. 2. 1–7. *Progonomys hispanicus*: 1. M1 (PK150111), 2. M1 (PK150104), 3. M2 (PK150131), 4. m1 (PK150141), 5. m1 (PK150140), 6. m2 (PK150161), 7. M3 (PK040104); 8–9. *Microtocricetus molassicus*: 8. M2 (PK040302), 9. m2 (PK040304); 10–12. *Kowalskia* sp.: 10. m3 (PK040202), 11. m3 (PK040204), 12. m2 (PK040201); 13–14. *Anomalomys gaillardi*: 13. m1 (PK040810), 14. M1 (PK040807). Underlined numbers indicate reversed specimens.

Comments: The cricetid material from Pezinok A and B is insufficient to be identified with certainty at the species level. The m3 dimensions and morphology most closely resemble the medium sized *Kowalskia* species. The extremely worn m2 provides only presence of an ectomesolophid. Daxner–Höck et al. (1996) supplied emended diagnosis for *Kowalskia,* declaring that an ectomesolophid is sometimes present, and also an extra ridge in the protosinusid. A developed ectomesolopid is present in some specimens from the Hungarian locality of Rudabánya (MN9) (Kretzoi & Fejfar, 2005) and also from Götzendorf (MN9) and Richardhof–Wald (MN10) in Austria (Daxner–Höck & Höck, 2015). Likewise, the ectomesolophid is a morphological character that can develop in some *Democricetodon* species. The size and morphology of *Democricetodon freisingensis* Fahlbusch, 1964 is similar to the material from Pezinok, and co-occurences of *Kowalskia* and *Democricetodon* are found in Suchomasty (MN10), Rudabánya (MN9), Götzendorf, Richardhof-Golfplatz (MN9) and Richardhof-Wald (MN10).

Although the material from Pezinok A and B is most likely an early *Kowalskia* form, it cannot be excluded that the material is an advanced species morphologically close to *D. freisingensis* or even both genera *Democricetodon* and *Kowalskia* are represented in the Pezinok material. The currently available specimens preclude unambiguous genus attribution, so I tentatively assign all m3 and the worn m2 to *Kowalskia* sp..

Genus *Microtocricetus* Fahlbusch & Mayr, 1975
Microtocricetus molassicus Fahlbusch & Mayr, 1975
(Figs. 2.8, 2.9)

Type species: *Microtocricetus molassicus* Fahlbusch & Mayr, 1975
Type locality: Hammerschmiede (Germany), Late Miocene (MN 9).
Material: Pezinok A – 3 M2 (PK040301 –x–, PK040302 2.00x1.53, PK040303 –x0.53), 1 m2 (PK040304 1.98x1.45). Pezinok B – 1 m2 (PK150201 1.74x1.30), 1 m3 (PK150202 1.78x1.34).

Description: M2 – available material includes one complete and almost unworn specimen, one heavily worn and slightly damaged on the posterior side and one posterior tooth portion. Morphologically, all molars are almost identical to type material. The metacone and mesoloph connection in the worn PK040303 specimen forms an enamel island, with a small labial syncline between these elements. The teeth have three roots.

m2 – the two molars are medium to heavily worn. The occlusal surface is flat and the synclines well-connected. The external transversal ridge (ectomesolophid) is well-developed. Morphologically, these are identical to type material. The specimen PK040304 has two preserved roots.

m3 – this specimen is heavily worn, with a flat occlusal surface and only enamel preserved. The protoconid is connected to the anterolophid and the mesolophid is joined to the entoconid. A small but distinctive 3rd labial syncline occurs behind the hypoconid. This tooth fits the type material, although it is slightly larger than the average described specimens.

Comments: *Microtocricetus molassicus* is relatively rare in rodent assemblages but it is easily recognizable. The Pezinok A and B material morphology conforms to Hammerschmiede type material. Although the size of available specimens approximates type material, one Pezinok B m3 is slightly larger.

M. molassicus is a representative of so-called "microtoid cricetid". This is a non–taxonomic term established by Schaub (1934). The higher–crowned molars are interpreted as adaptation to climatic controlled change to a "harder" diet. (Fejfar, 1999; Fejfar et al. 2011). *M. molassicus* was considered the oldest recorded cricetid rodent with mesodont prismatic molars known to spread in Europe during MN9 and persist to MN10. While this was distributed through southeastern, central and western Europe, Maridet et al. (2014) described the new microtoid cricetid *Primoprismus fejfari* from the early Miocene of China. These authors state that *Primoprismus* shares similar morphological features with *Microtocricetus*; including incomplete prismatic morphology, a flat occlusal surface, and presence of an ectomesolophid ("external transverse ridge" - sensu Fejfar, 1999). *Primoprismus* is considered a common ancestor of all Late Miocene microtoid cricetids.

Subfamily Anomalomyinae Schaub, 1925
Genus *Anomalomys* Gaillard, 1900
Anomalomys gaillardi Viret & Schaub, 1946
(Figs. 2.13, 2.14)

Type species: *Anomalomys gaillardi* Viret & Schaub, 1946
Type locality: Montredon (France), Late Miocene (MN 10).
Material: Pezinok A: 12 isolated molars. 3 M1 (PK040801 2.21x2.01; PK040804 2.17x1.90; PK040807 2.05x1.51), 3 M2 (PK040802 1.84x1.99; PK040805 1.91x1.90; PK040808 1.60x1.82), 2 M3 (PK040803 1.37x1.53; PK040806 1.39x1.22), 3 m1 (PK040810 2.37x1.67; PK040811 2.34x1.67; PK040812 1.98x1.60), 1 m2 (PK040813 2.33x1.65). Pezinok B: 4 isolated molars. 1 M1 (PK150501 2.13x1.70), 1 M2 (PK150502 1.93x1.88), 1 M3 (PK150503 1.50x1.30), 1 m3 (PK150504 1.68x1.23).

Description: M1 – two worn (PK040801, PK040804) and two unworn teeth (PK040807, PK150501) were recovered. Their basic outline is sub-trapezoidal, slightly elongated and wider in the posterior portion. The anterior lobe of both unworn specimens is separated from the other lobes by the connected lingual and labial syncline. The dental pattern in the worn specimens is simplified; with a relatively deep lingual syncline and the remaining synclines reduced only to enamel islands or almost closed enamel folds. The teeth have three roots.

M2 – four specimens have a similar stage of wear. The outline is sub-rectangular and the dental pattern is simplified; with the two main deep labial and lingual synclines and forming a typical S–shape occlusal surface (resp. Z-shape). The anterior lobe is slightly narrower than the posterior lobe. One specimen has an indistinct enamel island in the paracone area. These teeth have three roots.

M3– the teeth outline is oval and rounded, with a variable occlusal surface and a distinct somewhat broader protocone

area. There is an enamel island between the protocone and the paracone. The unworn specimens have a small shallow syncline on the labial side separating the protocone and the hypocone. There is also a syncline between the paracone and metacone. The roots are not preserved.

m1– two unworn specimens and one moderately worn specimen are available. The outline is elongated and slightly broadened in the posterior portion. The dental pattern in the unworn PK040810 and PK040812 specimens appears more complex than in the slightly worn PK040811. The anterior lobe lies transverse, is wider than other lobes and has an irregular enamel islet. The three transverse lobes in the unworn specimens are separated, but connection is noted in one worn specimen between the second lobe (protoconid–metaconid?) and posterior lobe. The latter lobe is shorter and thinner. The roots are not preserved.

m2– one heavily worn specimen has a very simplified pattern. It has three transverse unconnected lobes. The anterior lobe is smaller than the other lobes. The second lobe has a small enamel islet preserved on its lingual side. Although there is no direct connection between the second and posterior lobes, they are lingually adjacent. The roots are not preserved.

m3 - is similar to m2 in morphology but reduced in its posterior portion. While the protosinusid is labially closed, both sinusid and posterosinusid are open. The entoconid is distinctive and the roots are not preserved.

Comments: The 5 specimens (PK040801-040805) are worn with similar abrasion pattern; so they most likely come from one animal. Although the *Anomalomys* material from Pezinok A and B is morphologically very close to *Anomalomys gaillardi* type material from Montredon (MN10), the Pezinok teeth have slightly more hypsodont crowns and deeper sinuses. This indicates that *A. gaillardi* from Pezinok is slightly more advanced than the type. In contrast, the occlusal pattern in unworn specimens is slightly more complex than the type material of *A. gaillardi*, but less so than *A. rudabanyensis* Kordos, 1989 from Rudabánya (MN9). The simplified dental pattern, size increase and hypsodonty are general evolutionary trends in *Anomalomys* (Bolliger 1996, 1999). In addition, the Pezinok teeth are clearly larger than *A. rudabanyensis* from Rudabánya and comparable with *A. gaillardi* from Montredon.

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Family Gliridae Muirhead, 1819
Subfamily Dryomyinae de Bruijn, 1967
Genus *Graphiurops* Bachmayer & Wilson, 1980
Graphiurops austriaticus Bachmayer & Wilson, 1980
(Figs. 3.1 – 3.8)

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Type species: *Graphiurops austriaticus* Bachmayer & Wilson, 1980
Type locality: Kohfidisch (Austria), Late Miocene (MN10).
Material: Pezinok A: 8 isolated molars: 1 P4 (PK040401 0.80x0.93), 2 M1/2 (PK040402 0.90x1.05, PK040403 0.82x0.97), 1 M3 (PK040404 0.71x0.80), 2 m1 (PK040408 0.89x0.80, PK040406 0.92x0.82), 1 m2 (PK040405 0.92x0.89), 1m3 (PK040407 0.73x0.76).

Description: P4 – the occlusal surface outline is trapezoidal and narrower in its anterior portion. It has a simple dental pattern, with the paracone, metacone and hypocone forming distinctive cusps. While the anteroloph is separated from the endoloph and paracone, the protoloph is connected to both. The metaloph is long but not connected to the endoloph, and the posteroloph is oblique and arched posteriorly.

M1/2 – the occlusal surface outline is sub-trapezoidal, and although the dental pattern is similar to P4, the ridges are more complete. The anteroloph is connected to the paracone and endoloph; forming a closed anterior basin. Specimen PK040402 has a short anterior centroloph connected to the paracone. The posterior portion of the occlusal surface is formed by the posteroloph which is connected to the metaloph in the metacone. The metaloph is straight and ends freely in the centre of the tooth (PK040403) or is longer and connected to the endoloph (PK040402). The root patterns here cannot be determined.

M3 – the P4 occlusal surface outline is sub-trapezoidal and rounded in the posterior portion. The dental pattern is simple. The protocone, anteroloph, paracone and protoloph are connected forming a large anterior valley. The protoloph is curved anteriorly in its central part. The posteroloph is strong and connected to the metacone and metaloph forming a small symmetrical circular structure in the posterolabial part of the tooth. The roots are not preserved.

m1– the occlusal surface is sub-rectangular and posteriorly rounded. The tooth is more slender anteriorly than posteriorly and specimen PK040408 is more rounded; resembling p4 shape. The continuous rim around the tooth connecting the main distinguishable cusps is a typical character. The metalophid(?) is transverse, forming a wide basin in the posterior part of the tooth. There is a small transversal crest, between the anterolophid and metalophid(?) which reaches the central part of the anterior basin. The root pattern here cannot be determined.

m2 – the tooth morphology is very similar to m1; but the occlusal surface is more posteriorly rounded and the posterior portion is not as wide.

m3 – the single specimen is reduced posteriorly, and also has the main typical characteristic of a continuous rim around the entire tooth surface. The protoconid, hypoconid and metaconid are distinguishable as higher cusps on the rim. In addition to the anterolophid and posterolophid, two transverse lophids are also developed: metalophid(?) and mesolophid(?). The mesolophid(?) is slightly interrupted. The roots are not preserved.

Comments: Bachmayer & Wilson (1980) described unusual glirid teeth from Kohfidish (Austria) as; "Size of cf. *Myomimus dehmi* Bachmayer & Wilson, 1978. Protoconid and hypoconid cusps of M1 and M2 are well separated. Metalophid(?) crest well developed; other basin structures variable and vestigial". These authors determined the genus *Graphiurops*, and compared them to recent *Graphiurus murinus* Smuts, 1832 material from Congo. They subsequently considered the relationship with *Graphiurus* is not so close; and hence *Graphiurops* origin and relationships remain unclear. Bachmayer & Wilson (1980) suggest that the Graphiurinae from Africa are an isolated branch of the Gliridae which extended to Europe in the Vallesian or early

Fig. 3. 1–8. *Graphiurops austriacus*: **1. P1** (PK040401), **2. M1/2** (PK040402), **3. M1/2** (PK040403), **4. M3** (PK040404), **5. m1** (PK040408), **6. m1** (PK040406), **7. m2** (PK040405), **8. m3** (PK040407); **9.** *Paraglirulus* **sp., M3** (PK040501); **10-15.** *Eomyops catalaunicus*: **10. P4** (PK040601), **11. M1/2** (PK150301), **12. M1/2** (PK040603), **13. m1/2** (PK150302), **14. m1/2** (PK040604), **15. m3** (PK040605); **16.** *Keramidomys* **sp., m3** (PK040608); **17.** *Spermophilinus* **sp., M1/2** (PK040701); **18-19.** *Albanensia* **sp.: 18. ?M1/2** (PK150602), **19. ?M1/2** (PK150603). **Underlined numbers indicate reversed specimens.**

Turolian. Other findings of this peculiar dormouse are from Austria (Daxner–Höck & Höck 2009, 2015) Richardhof–Golfplatz (MN9), Richardhof–Wald (MN10), Schernham (MN10) and Eichkogel (MN11); from France Dionay (MN11) (Mein 1984), Ambérieu 1, 2A, 2C (MN10) (Mein, 1999), Ambérieu 3 (MN11) (Mein, 1999), Bernardiére (MN11) (Mein, 1999) and from Czech Republic locality Suchomasty (MN10) (Fejfar, 1989). In addition to our Pezinok *G. austriacus*, this glirid appear also in the newly discovered localities Krásno and Šalgovce in Slovakia; both most likely MN11 (Joniak, unpublished data). The stratigraphic range of *G. austriacus* appears limited only to the Late Miocene of Europe (MN9–MN11). The size of this species from Pezinok is comparable to other known occurrences. The dental pattern of Pezinok material is more complex than type material, especially in the lower teeth, where one complete transverse ridge is developed in all specimens. However, this configuration is known from both Ambérieu 3 (MN11) and Suchomasty (MN10). *G. austriacus* is recognized by great intraspecific variability in its simple dental pattern.

<div align="center">

Subfamily Dryomyinae de Bruijn, 1967
Genus *Paraglirulus* Engesser, 1972
Paraglirulus sp.
(Fig. 3.9)

</div>

Type species: *Paraglirulus werenfelsi* Engesser, 1972
Type locality: Anwil (Switzerland), Middle Miocene (MN7/8).
Material: Pezinok A: 1 M3 (PK040501 0.93x0.96) and fragment of M3? (PK040502 –x–)

Description: M3 – one worn tooth without roots and a labial fragment of a heavily worn specimen are available. The posterior portion of the molar outline is rounded and the occlusal surface is slightly concave. The anteroloph, protoloph, anterior centroloph, metaloph and posteroloph are all connected to the endoloph. There are 4 extra ridges between the main ridges: between anteroloph and protoloph, between the protoloph and anterior and posterior centrolophs and one short ridge between the metaloph and posteroloph. Although none of the extra ridges are connected to the endoloph, the extent of tooth-wear ensures that they form shallow connections to the labial elements on the occlusal surface.

Comments: The difference between *Glirulus* and *Paraglirulus* has been extensively discussed by many authors; including Mayr (1979); Daxner-Höck & de Bruijn (1981); van der Meulen & de Bruijn (1982) and Daxner–Höck & Höck (2009, 2015). Repetition here is therefore unnecessary. Determination of material as *Paraglirulus* is mainly based on the size and configuration of the anterior centroloph. Although the Pezinok specimen is morphologically close to *Paraglirulus werenfelsi* from Nebelbergweg (Kälin & Engesser, 2001), further determination to species level is hazardous; if not impossible.

<div align="center">

Family Eomyidae Winge, 1887
Genus *Eomyops* Engesser, 1979
Eomyops catalaunicus (Hartenberger, 1966)
(Figs. 3.10 – 3.15)

</div>

Type species: *Eomyops catalaunicus* (Hartenberger, 1966)
Type locality: Can Llobateres (Spain), Late Miocene (MN9).
Material: Pezinok A: 2 P4 (PK040601 0.87x0.96; PK040602 0.80x0.93), 1 M1/2 (PK040603 0.77x0.90), 1 m1/2 (PK040604 1.02x0.90), 1 m3 (PK040605 0.73x0.75). Pezinok B: 1 M1/2 (PK150301 0.90x0.98), 1 m1/2 (PK150302 0.95x0.92).

Description: P4 – the occlusal surface is sub-trapezoidal with four main cusps. The tooth is wider anteriorly than posteriorly, and the anterior border of the occlusal surface is slightly oblique. The labial branch of the anteroloph is strongly reduced and the lingual branch is absent. The protoloph and metaloph are parallel and directed anteriorly. The mesoloph is short or medium in length and the posteroloph is massive and slightly curved towards the metacone. The PK040601 specimen has a mesostyle. The roots are not preserved.

M1/2 – the occlusal surface is sub-rectangular with well–developed main cusps; and all cusps are equally high. The anteroloph has longer labial and shorter lingual branches. The second syncline is longer than the third one. The mesoloph is short, directed anterolabially and the lingual syncline is wide and lies transverse or is slightly curved anteriorly. The posteroloph is long and curved towards the base of metacone. The roots are not preserved.

m1/2 – the anterolophid of Pezinok B specimen PK150301 has two branches with approximately the same length, but the labial one is low and descend towards the base of the protoconid. A specimen PK040604 has its anterolophid developed as an isolated crest without connection to the longitudinal crest. The metalophid and hypolophid diverge labially. The mesolophid is short (PK040604) or medium (PK150302). The posterolophid descending to the base of the entoconid is long, oblique or L shaped. The roots are not preserved.

m3 – the occlusal surface is reduced in the posterior portion. While all cusps are developed, the entoconid is strongly reduced and incorporated in the posterolophid. The protoconid, metaconid and hypoconid have approximately equal size. The lingual branch of the anterolophid is longer than the labial, and the medium-sized mesolophid is directed posteriorly. The hypolophulid is absent, and the labial syncline is slightly curved posteriorly. The roots are not preserved.

Comments: The *Eomyops catalaunicus* material from Pezinok A and B has similar size to type material from Can Llobateres (Spain), and also agrees with material published from Austria (Daxner–Höck & Höck, 2009, 2015). Size differences in *E. catalaunicus* and *E. oppligeri* Engesser, 1990, however, are subtle and overlap. The teeth from Pezinok A and B are almost identical with those of *E. catalaunicus* from Richardhof–Golfplatz (MN9) and Richardhof–Wald (MN10). The only morphological differences are the presence of an isolated anterolophid without connection to the longitudinal crest and the L-shaped posterolophid in Pezinok A specimen PK040604. These features appear in *E. oppligeri* (Engesser, 1990; Prieto, 2012) and are also reported in Austrian *E. catalaunicus* populations (Daxner–Höck & Höck, 2009, 2015). In contrast, this tooth (PK040604) is larger than its equivalent in *E. oppligeri* populations (Prieto, 2012: fig. 3).

Therefore, this molar is attributed to *E. catalaunicus*, and I consider the population of *Eomyops* from Pezinok as homogenous.

Genus *Keramidomys* Hartenberger, 1966
Keramidomys sp.
(Fig. 3.16)

Type species: *Keramidomys pertesunatoi* Hartenberger, 1966
Type locality: Can Llobateres (Spain), Late Miocene (MN9).
Material: Pezinok A: 1 m3 (PK040608 0.70x0.69).

Description: m3 – is a complete but worn specimen, with a flat sub-triangular occlusal surface. The protoconid and lingual anterolophid form the anterior border of the tooth. The anterolophid is parallel with the metalophid and connects to the metaconid, forming a prolonged transversely oriented islet. A further three islets are formed by the forked mesolophid connection with the metalophid and with the posterolophid. This latter is long, it forms the posterolingual border of the tooth and is connected to the metaconid. The hypoconid and protoconid are equal in size. The roots are not preserved.

Comments: Only one relatively worn m3 from Pezinok A is available. It clearly differs from the *Eomyops* m3 in occlusal surface shape, lophodonty, narrower lophids and in the overall configuration of the surface elements. Morphologically, it resembles *Keramidomys ermannorum* Daxner-Höck & Höck, 2009 in having labially and lingually connected lophids, a flat occlusal surface and the same dimensions. This single m3 is insufficient to assign the specimen to species level.

Family Sciuridae Fischer de Waldheim, 1817
Subfamily Sciurinae Fischer de Waldheim, 1817
Genus *Spermophilinus* de Bruijn & Mein, 1968
Spermophilinus sp.
(Fig. 3.17)

Type species: *Spermophilinus bredai* (von Meyer, 1848)
Type locality: Oeningen (Switzerland), Middle Miocene (MN7/8).
Material: 2 fragments of M1/2 (PK040701 –x– , PK040702 –x–).

Description: M1/2 – only the following two fragments of isolated teeth are available from Pezinok A: a slightly damaged right M1/2 and an anterior fragment most likely coming from the left M1/2. The protoloph and the metaloph converge toward the protocone which forms the highest and largest part of the tooth crown. The metaloph is almost constricted near the protocone and the hypocone is reduced. The anteroloph is long and lacks the parastyl. The paracone and metacone are damaged and missing.

Comments: De Bruijn & Bosma (2012) discussed the validity of *Spermophilinus* and *Csakvaromys* genera names and concluded that they both are valid, because their definitions meet requirements of the International Code of Zoological Nomenclature. Although *Csakvaromys* has priority they argued that maintaining *Spermophilinus* is in the interest of nomenclature stability. I agree with this interpretation, and therefore I use the generic name *Spermophilinus* here.

The protoloph and the metaloph converging towards the protocone, the strong protocone and almost constricted metaloph near the protocone assign these ground squirrel teeth to genus *Spermophilinus*. Only molar size differentiates species allocation within this genus. De Bruijn (1995) demonstrated a clear size-increase trend from the oldest representative *S. besanus* Cuenca Bescós, 1988 (MN4), through *S. bredai* (MN6–12) and *S. turolensis* de Bruijn & Mein, 1968 (MN9–13) to the largest *S. giganteus* de Bruijn, Dawson & Mein, 1970 (MN14). The fragmentary material from Pezinok A cannot be measured, but when compared directly with both *S. bredai* and *S. turolensis* material from varied localities, it clearly approximated *S. turolensis* in size. Despite this favourable comparison, the Pezinok A material remains insufficient to be described other than under the heading of *Spermophilinus* sp.

Subfamily Pteromyinae Brandt, 1855
Genus *Albanensia* Daxner-Höck & Mein, 1975
Albanensia sp.
(Figs. 3.18, 3.19)

Type species: *Albanensia albanensis* (Forsyth Major, 1893)
Type locality: La Grive–Saint–Alban M (France), Middle Miocene (MN7/8).
Material: Pezinok A: 1 fragment of crenulated enamel of lower (?) molar (PK040703 –x–). Pezinok B: 2 fragments of M1/2? (PK150602, PK150603).

Description: PK150602 and PK150603 are almost identical fragments. Both are most likely postero–labial parts of M1 or M2 with preserved metacone and slightly lower metaconulus. Specimen PK150602 has a crest extending posteriorly from the metacone and specimen PK150603 has a short crest extending from the metaconulus. These crests are directed posteriorly; crossing the postero–labial valley and reaching the posteroloph. The specimen PK040703 represents only part of crenulated enamel.

Comments: One fragment of a flying squirrel was found at Pezinok A during the 2004 excavation. On the basis of personal communication with Dr. Gudrun Daxner–Höck, I attributed this fragment to genus *Albanensia* (Joniak, 2005). The remaining two fragments were then discovered during the latest Pezinok B excavation in 2015. These fragments support my previous allocation of specimen PK040703 to *Albanensia*. However, assignment at species level is still impossible.

Family Castoridae Hemprich, 1820
Genus *Euroxenomys* Samson & Radulesco, 1973
Euroxenomys minutus (von Meyer, 1838)

Type species: *Chalicomys minutus* von Meyer, 1838
Type locality: Elgg (Switzerland), Middle Miocene (MN5).
Material: Pezinok A: 2 P4 (PK041001 –x4.50; PK041004 –x–), 2 M1/2 (PK041002 3.35x4.05, PK041003 3.60x3.95), 1 M3 (PK041005 3.60x3.85).

Description: P4 – both teeth are damaged; specimen PK041001 is heavily worn and its posterior portion is damaged and specimen PK041004 is damaged on its labial part. Hypoflexus is closed in the former and open in the latter. The cement is not developed. Paraflexus in the worn PK041001 is closed and forms a slightly curved parafossette. A slightly curved mesofossette extends from the labial to lingual margins of the occlusal surface. Specimen PK041004 has the mesofossette/mesoflexus in the same position, but labial end is missing due damage. The teeth have one main flattened anterior root and traces of a small root placed posteriorly.

M1/2 – these teeth are less worn than the premolars, and have a sub-rectangular occlusal surface. While the hypoflexus is open, the parafossette is closed and curved posteriorly. The enclosed mesoflexus and metafossete form two additional enamel islands on the posterior portion of the occlusal surface. These islands are elongated with a concave posterior part. There is one main anterior root and a small accessory root on the labial part. The teeth lack cement.

M3 – this tooth has the lowest crown of all permanent teeth and a sub-triangular occlusal surface which is elongated posteriorly. The hypoflexus is open and a small accessory enamel flexus is developed on the posterolingual portion of the tooth. The parafossette, enclosed mesoflexus and metafossette are all posteriorly concave. An additional enamel island is present in the posterior portion. The tooth has a main anterior root and recognizable posterior labial and lingual roots. This tooth also lacks cement.

Comments: There is great diversity of opinion on the generic and subgeneric status of this small beaver form; and taxonomic discussions are still on-going (for details see: Hugueney, 1999; Korth, 2001; Daxner–Höck & Bernor, 2009; Giersch et al., 2010; Stefen, 2011; Hugueney & Duranthon, 2012 and Prieto et al., 2014). The Pezinok material is too inadequate to provide new insight into the taxonomic position of small Miocene beavers; and also beyond the scope of this study. I follow the interpretation of Korth (2001) and Hugueney & Duranthon (2012) in assigning *Euroxenomys* to the genus level.

Beaver remains are relatively common in middle and late Miocene fossil assemblages. Five teeth, with different preservation and wear, were recovered from Pezinok A, and all share typical features of the genus *Euroxenomys*. These include: teeth with high crowns and roots, hypostria not reaching crown bases, m3 enlargement and the lack of cement. Morphologically, they are almost identical to *E. minutus* from Vallesian and Turolian localities throughout Europe. The subspecies *E. minutum rhenanum* Franzen & Storch, 1975 described from Dorn Dürkenheim (MN11) is typified by its significantly enlarged M3. The only available upper third molar from Pezinok A has identical prolongation and additional enamel folds. However, the Pezinok tooth is smaller than that from Dorn Dürkenheim but slightly larger than *E. minutus* from Atzelsdorf (MN9). Identification at subspecies level unfortunately remains open because of the paucity of available beaver teeth from Pezinok.

4. DISCUSSION

4.1. Composition of assemblages

Fossil rodent remains were recovered from both A and B sites in the Pezinok new clay pit. Table 2 highlights the more diverse Pezinok A rodent assemblage and some taxa absent from Pezinok B. Their richness, however, is comparable because the same amount of sediment was processed from the sites and the same number of rodent specimens recovered; only insectivore numbers differed. Generally, the Pezinok B assemblage lacked mainly dormice *Graphiurops* and *Paraglirulus* and also murid third molars. The absence of small *Progonomys* third molars is peculiar because all other dental elements have almost equal presence; with 10 M1 and m1 specimens, 9 M2 and m2 but only one M3. However, it appears that the M3 small size is responsible for its relative absence from different rodent localities. Although dormouse exclusion from Pezinok B should support sampling bias, the A and B site samples were treated exactly the same and I alone picked the fossils from both samples. *Spermophilinus* is missing from Pezinok B, and is relatively rare in Pezinok A, and there was only one tiny *Keramidomys* tooth. While these absences are explained by their comparative rarity, the lack of *Euroxenomys* beaver specimens cannot be explained by either rarity or loss during sampling.

A likely explanation is natural assortment by stream power. This holds if both sampling sites actually come from the same layer or have the equivalent deposition time, and it is supported by the slightly better Pezinok A faunal preservation. This shows preservation of tooth dentine, root presence and it contains teeth most likely from the one animal, while site B teeth often consist only of enamel. It is also likely that tiny fragile teeth were unable to survive long stream transport. The significant disproportion in recovered taxa may alternatively be explained by different primary sources of the remains; in different preferences in birds of prey or slightly different local environments; however this does not explain the missing lower third molars of *Progonomys*.

4.2. Age of the assemblages

The rodent assemblages described above can be directly compared with Austrian upper Miocene faunas: Richardhof–Wald and Neusiedl am See. All these localities share co–occurrence of primitive *Progonomys hispanicus* and *Microtocricetus molassicus*. *M. molassicus* is relatively rare in upper Miocene faunas of southeastern, central and western Europe (Fejfar et al., 2011) and its stratigraphical range was restricted to the MN9 Biozone (Fejfar, 1999; Mein, 2003). Prieto et al. (2010) discussed earlier occurrence of *M. molassicus*, and concluded its possible appearance before onset of the Late Miocene. Last occurrence of *M. molassicus* is during the late Vallesian; it has been described at localities dated to MN10: Douvre (Mein, 1999), Priay II (Kälin, 1999), Neusiedl am See and Richardhof–Wald (Daxner–Höck & Höck, 2015). Its occurrence in the Vienna Basin indicates middle Vallesian – in association with *Albanensia grimmi* (Black, 1966) (during the middle to upper

Tab. 2. Composition of rodent assemblages from Pezinok A and B and stratigraphical ranges of taxa identified from Europe.

Pezinok A		Pezinok B		Taxa	MN Biozones						
N (%)	MNI	N (%)	MNI		6	7/8	9	10	11	12	13
9 (18)	2	39 (78)	6	*Progonomys hispanicus*				(species range 10–11)			
3 (6)	1	2 (4)	1	*Kowalskia* sp.			(genera range 9→13)				
4 (8)	1	2 (4)	1	*Microtocricetus molassicus*			(species range 9–10)				
12 (24)	2	4 (8)	1	*Anomalomys gaillardi*			(species range 9–11)				
8 (16)	1			*Graphiurops austriacus*			(species range 9–11)				
1 (2)	1			*Paraglirulus* sp.	(genera range ←6–10)						
5 (10)	1	2 (4)	1	*Eomyops catalaunicus*			(species range 9→13)				
1 (2)	1			*Keramidomys* sp.	(genera range ←6→13)						
2 (4)	1			*Spermophilinus* sp.	(genera range ←6→13)						
1 (2)	1	2 (4)	1	*Albanensia* sp.	(genera range ←6–10)						
5 (10)	2			*Euroxenomys minutum*	(species range ←6)						
Σ 51		Σ 51			— species range —				— genera range —		

MN9) or with *Progonomys hispanicus* (during the lower MN10) (Daxner–Höck & Höck, 2015). *M. molassicus* is associated with *Megacricetodon*, *Democricetodon* and *Eumyarion* at Borský Sv. Jur (MN9) in the Slovak part of the Vienna Basin (Sabol et al., 2004; Joniak, 2005), and the co–occurrence of *P. hispanicus* and *M. molassicus* in the Pezinok assemblage extends this association to the Danube Basin. *Progonomys hispanicus* from Pezinok is characterised by its following archaic morphology: slender upper molars, absence of anterocentral cusps in m1, t6–t9 connection and t1bis. These archaic features were also described by van Dam (1997) in the *P. hispanicus* population from Masia de la Roma in Spain (lower MN10, local biozone J1) which is the most primitive and oldest representative of the *P. hispanicus–Occitanomys sonaari* lineage. The type material of *P. hispanicus* from Masia del Barbo in Spain (Michaux, 1971; van de Weerd, 1976) is slightly younger (middle MN10, local biozone J2) and has more advanced characters; including wider upper molars, the more common occurrence of t1bis, t6–t9 connection and frequent presence of the anterocentral cusp in m1. The Pezinok *Progonomys hispanicus* is one of the oldest true murines in Central Europe, and its evolutionary characters are comparable to Masia de la Roma material. In addition, *P. hispanicus* populations from Richardhof–Wald and Neusiedl am See have almost identical characteristics (Daxner–Höck & Höck, 2015).

Further species from Pezinok A and B include *Kowalskia* sp. which is poorly represented but morphologically very close to *Kowalskia* sp. B from the lower MN10 in Austria (Daxner–Höck & Höck, 2015). The stratigraphical range of *Anomalomys gaillardi* is MN9–MN11, and the Pezinok species is slightly larger and evolutionary more advanced than *A. rudabanyensis* from Rudabánya (MN9). The dormouse *Graphiurops austriacus* has geographical range limited to the central part of Europe and stratigraphical range MN9-MN11. The last occurrence datum of *Paraglirulus* and *Albanensia* is in lower Late Miocene (MN10). The Eomyids, *Spermophilinus* and *Euroxenomys minutum* are all

considered to have minor stratigraphical importance because of their wide stratigraphic range.

The Pezinok A and B sites are biostratigraphically equal and their age is confidently correlated to the lower MN10 (middle Vallesian); and while these localities share identical faunal taxa, the Pezinok A assemblage has greater diversity.

The absolute ages of the Pezinok clay pit sediments (Ivánka Fm.) were recently calibrated by authigenic $^{10}Be/^{9}Be$ dating. The calculated age for sample Pez–1 from the lower part of the outcrop is 10.95 ± 0.6 Ma (Šujan et al. 2016, p. 41). The authors assume a low sedimentation rate lasting over 1 Ma for the sediments outcropping here, therefore the biostratigraphic correlation of the Pezinok faunas from the upper part of the outcrop to early MN10 ~ 9.6 – 9.7 Ma (Hilgen et al., 2012) is consistent with the obtained authigenic $^{10}Be/^{9}Be$ ages.

5. CONCLUSIONS

The rodent fauna from two fossiliferous sites at the Pezinok locality are described for the first time. The following eleven rodent species were recovered from the Pezinok A site: *Progonomys hispanicus*, *Kowalskia* sp., *Microtocricetus molassicus*, *Anomalomys gaillardi*, *Graphiurops austriacus*, *Paraglirulus* sp., *Eomyops catalaunicus*, *Keramidomys* sp., *Spermophilinus* sp., *Albanensia* sp. and *Euroxenomys minutum*. In contrast, the diversity is significantly lower at Pezinok B, because of absence of *Graphiurops austriacus*, *Paraglirulus* sp., *Keramidomys* sp., *Spermophilinus* sp. and beavers. The different diversity of the studied localities can be explained by different sedimentary conditions and/or different local environment.

The age of both assemblages is interpreted as middle Vallesian, lower MN10, and this is supported by isotopic dating. Finally, the assemblages are very similar to the Austrian assemblages of Richardhof–Wald and Neusiedl am See (both MN10) and can therefore be confidently correlated with them.

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