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VASSEUROMYS BALATONICUS N. SP., A NEW LATE MIOCENE, TUROLIAN (MN 11) GLIRID FROM THE CSODABOGYÓS CAVE (KESZTHELY HILLS, WESTERN HUNGARY)

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Abstract: During study of the fossil rodent material from the Csodabogyós Cave, a rich *Vasseuromys* assemblage was elaborated. Some metrical and morphological characteristics of the finds differ from the Late Miocene (MN 11) *Vasseuromys pannonicus* from Eichkogel and Kohfidisch and also vary from *Vasseuromys tectus* described from Ukraine. In this publication a taxonomical description of the new species is presented with its palaeogeographical and paleoecological relationships.

Key words: Late Miocene, Carpathian Basin, Rodentia, Gliridae, taxonomy

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Introduction

The Csodabogyós Cave is located north of Lake Balaton, on the eastern periphery of the Keszthely Hills, near the village of Balatonederics at an altitude 393 m above sea level. In 2023, about 200 kg of sediment was collected from the cave from which a rich fossil assemblage of mainly small mammals was recovered. The Late Miocene (Turolian, MN 11) material, presented in this volume (Pazonyi et al. 2025), also yielded a new species of glirid. This paper aims to describe its taxonomy, evolutionary relationships and palaeoecology of the new species.

Material and methods

Measurements were taken using an MBS-10 stereomicroscope. Morphological terminology follows Freudentahl (2004) and Sinitsa and Nesin (2018). The micrographs of the rodent teeth were taken with a CMEX-5 digital microscope. Retouching was done by JH.

Systematic palaeontology

Genus *Vasseuromys* Baudelot et de Bonis, 1966

Type species. *Vasseuromys rugosus* Baudelot et de Bonis, 1966, Laugnac, France, Early Miocene, MN 2b.

Referred species. *Vasseuromys pannonicus* (Kretzoi, 1980), Kohfidisch, Austria, Late Miocene, MN 11; *Vasseuromys tectus* Sinitsa et Nesin, 2018, Palievo, Ukraine, Late Miocene, MN 11.

Vasseuromys balatonicus n. sp.

http://zoobank.org:act:773179A3-3574-4299-814F-72F6275E532C

Holotype. M1, PAL 2024.143.1 (Pl. 1, Fig. 7).

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Derivation nominis. After Lake Balaton, which is close to the type locality.

Type locality and stratum typicum. Unconsolidated silty clay sediment of the Csodabogyós Cave (close to the village Balatonederics). The whole fauna is referable to the Late Miocene MN 11 zone.

Diagnosis. This *V. balatonicus* has on average the largest molars among the representatives of the genus *Vasseuromys*. On P4 the anterior valley is closed in 45 % of specimens, and the prototrope is developed in 76 % of specimens. In M1 and M2 the posterior valley is always closed labially. Numerous additional ridges are present, the number of prototropes in M1 is 1–3, number of metatropes in M2 is 1–2, number of prototrope in M3 is 1, number of metatropes in M3 is 1–2. The length of m2 is always greater than the width.

Measurements of the holotype. L: 1.40 mm, W: 1.53 mm.

Measurements of the complete material. See Table 1.

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Table 1. Measurements of the *Vasseuromys balatonicus* n. sp. material from the Csodabogyós Cave. Abbreviations: SD – standard deviation, CV – coefficient of variation.

Tooth	Length					Width				
	n	min–max	mean	SD	CV	n	min–max	mean	SD	CV
D4	6	0.69–0.77	0.71	0.032	4.47	6	0.73–0.92	0.84	0.07	8.39
P4	33	0.70–0.92	0.84	0.049	5.76	33	0.87–1.15	1.05	0.066	6.25
M1	40	1.15–1.40	1.24	0.052	4.22	40	1.27–1.55	1.39	0.059	4.27
M2	40	1.12–1.41	1.25	0.066	5.30	40	1.16–1.55	1.40	0.076	5.43
M3	29	1.06–1.34	1.20	0.083	6.91	29	1.13–1.39	1.25	0.059	4.69
d4	1	–	0.94	–	–	–	–	0.71	–	–
p4	22	0.76–0.99	0.90	0.052	5.82	22	0.70–0.98	0.89	0.066	7.42
m1	43	1.22–1.43	1.33	0.055	4.17	43	1.08–1.30	1.20	0.049	4.10
m2	44	1.20–1.44	1.31	0.055	4.22	43	1.13–1.34	1.25	0.053	4.25
m3	25	1.13–1.32	1.21	0.059	4.84	25	1.06–1.20	1.13	0.039	3.47

Description of the holotype. Juvenile, unworn M1. Rectangular outline, the anterior width is slightly shorter than the posterior width. The occlusal surface is concave. The anteroloph has a continuous transversal ridge on the mesial margin. The antero-lingual corner is curved and the anteroloph is connected to the endoloph (= longitudinal protoloph in Sinitsa and Nesin 2018), without interruption. There is a narrow sulcus between the labial end of the anteroloph and the anterior surface of the paracone. The anterotrope is a long ridge. It occupies 90 % of the length of the anterior valley. The protoloph is a slightly curved, continuous ridge between the endoloph (= longitudinal protoloph in Sinitsa and Nesin 2018) and the paracone. There are 3 prototropes. In anteroposterior order, the 1st prototrope is short, labially positioned and connected to the paracone. The 2nd one is long and its lingual end is close to the lingual end of the protoloph, the labial end is connected to the paracone. The 3rd prototrope is the shortest and labially positioned without connections. The anterior centroloph is long. Its lingual end is close to the endololoph (= longitudinal protoloph in Sinitsa and Nesin 2018). There is a narrow sulcus between the labial end of the anterior centroloph and the paracone. There are two centrotropes. The anterior one is medium developed, and the posterior one is short and positioned on the labial margin of the central valley. There is a strong sulcus between the anterior centrotrope and the metacone. The posterior centroloph is shorter than the anterior one. The metatrope is medium developed and labially positioned. The metaloph and the posteroloph are continuous transversal ridges between the endoloph (= longitudinal protoloph in Sinitsa and Nesin 2018) and the metacone closing off the posterior valley. The labial end of the posterior valley is closed. There is a long posterotrope in the posterior valley. The anteroloph, endoloph (= longitudinal protoloph in Sinitsa and Nesin 2018) and posteroloph form a continuous rim on the mesial, lingual and posterior margin. Three roots.

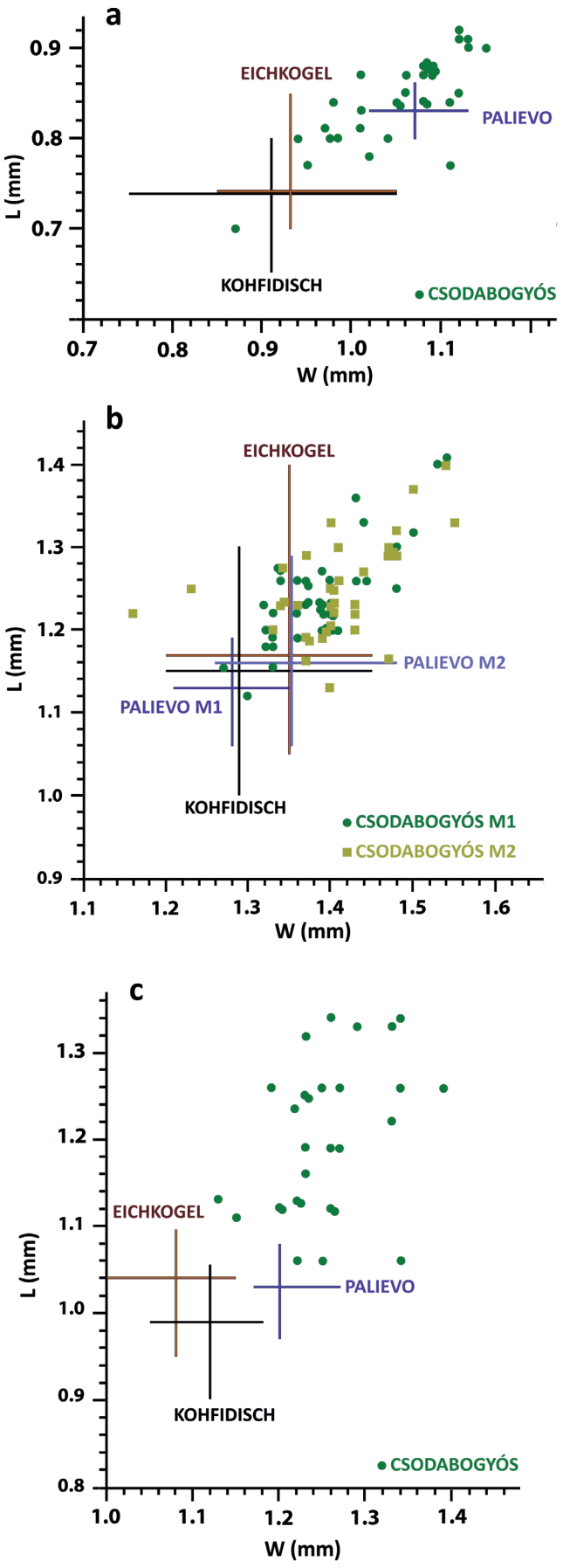
Description of the complete material. **General features of the upper molars**. Concave occlusal surface. The main transversal ridges, anteroloph, protoloph, anterior centroloph, posterior centroloph, metaloph, and posteroloph are all present. The protoloph, metaloph and posteroloph ridges are lingually connected to the endoloph (= longitudinal protoloph in Sinitsa and Nesin 2018). Labial connections from the main ridges: protoloph-anterior centroloph in the paracone, posterior centroloph, metaloph and posteroloph in the metacone. The connections from the anteroloph are variable. There are numerous additional ridges. Disintegration, undulation and irregular connections are possible in cases with numerous additional ridges.

D4 (Pl. 1, Fig 1). 6 teeth were suitable for morphological study. Triangular outline. Four main ridges: anteroloph, protoloph, metaloph, posteroloph are present. The anteroloph has a labial connection to the paracone. Its lingual end is free. The protoloph is long and oblique, whereas the metaloph and posteroloph are transversal and parallel.

The protoloph, metaloph, and posteroloph are lingually connected to the protocone. Labial connections: anteroloph-protoloph-anterior centroloph in the paracone. Posterior centroloph-mesoloph-posteroloph in the metacone. The metaloph and posteroloph have free labial ends in two cases (VER 2024.461.1, VER 2024.461.5). In the other four molars these ridges are connected in the metacone. A long labially positioned metatrope is regular. A vestigial anterotrope was found in two teeth (VER 2024.461.3, VER 2024.461.4). An incomplete posterotrope was found in 1 case (VER 2024.461.6).

P4 (Text-fig. 1a, Pl. 1, Figs 2, 3). 29 teeth were suitable for morphological study. The occlusal surface is oval. The anterior centroloph was usually longer than the posterior one (23). In 3 cases the posterior centroloph is longer. In 3 cases the centrolophs are of equal length. The lingual ends of the protoloph, metaloph, and posteroloph are merged in the protocone. The connections of the anteroloph are variable and in this case, the anterior valley was completely closed in 13 premolars, it was lingually open in 8 specimens, labially open in 6 teeth, and open on both sides in 2 premolars.

Among the additional ridges, the anterotrope is regular, it is developed in a vestigial form in 4 teeth. The prototrope



Text-fig. 1. Scatter plot of *Vasseuromys* upper teeth from Eichkogel, Kohfidisch, Palievo and Csodabogyós Cave. a: P4 teeth, b: M1–M2 teeth, c: M3 teeth. Data are after Daxner-Höck and Höck (2009) and Sinitsa and Nesin (2018).

is usually medium-developed (12), short, or vestigial (10). In 7 cases it is absent. The centrotrope is normal (28), or vestigial (1). The metatrope is normal (28), vestigial (1). Posterotrope: 27 normal, 2 vestigial.

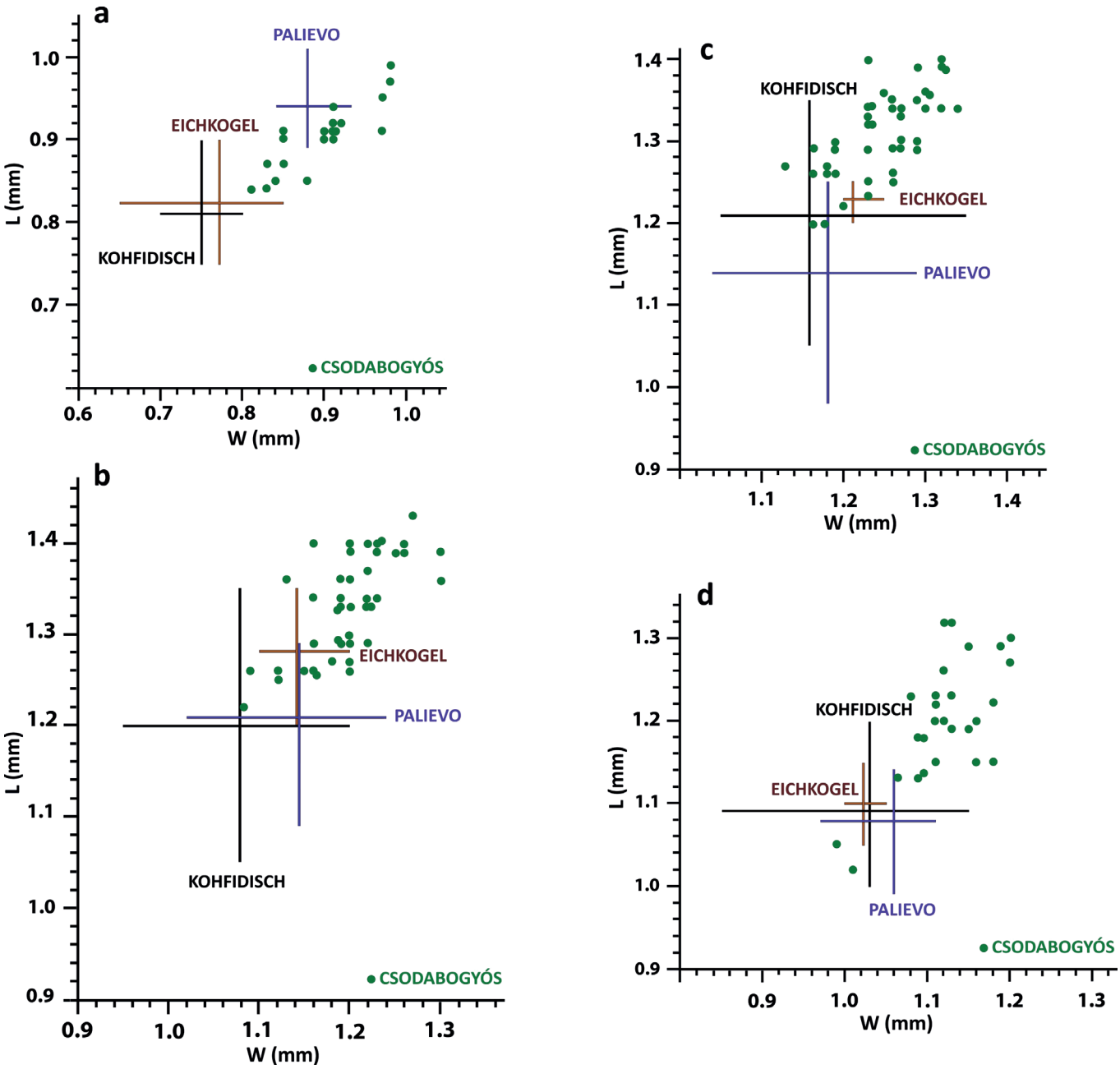
M1 (Text-fig. 1b, Pl. 1, Figs 4–7). 37 molars were suitable for morphological study. The outline is rectangular. The anterior width is slightly narrower than the posterior width. The connections of the lingual and labial ends of the anteroloph are variable. The two ends are equally connected and the anterior valley is closed in 20 molars; in 10 cases the lingual end of the anteroloph is connected to the endoloph (= longitudinal protoloph in Sinitsa and Nesin 2018) across a short narrow ridge. The lingual end of the anteroloph is free in 12 specimens. The labial end of the anteroloph is free in one case. The anteroloph is completely isolated (the two ends are free) and the anterior valley is open labially and lingually in 4 teeth. The anterotrope is mainly long and occupies nearly the complete length of the anterior valley (17). In 7 molars it is shorter and reaches the lingual part of the anterior valley extending to the middle of the tooth crown. In 11 cases it is short, or vestigial and lingually positioned. In 2 specimens it is absent. Among the centrolophs, the anterior one is the longer and reaches nearly to the endoloph (= longitudinal protoloph in Sinitsa and Nesin 2018) in 19 molars, both the anterior and the posterior centrolophs are equally long and reach nearly the endoloph (= longitudinal protoloph in Sinitsa and Nesin 2018) in 10 cases. The posterior centroloph is the longer in 8 specimens. Usually 3 prototropes are presented. In the anterior-posterior sequence the first one is usually short. The second one is the longest. The third one can be short, or vestigial (20). There are some molars with 2 prototropes (10) or with only one prototrope (7). In the labial margin, there is an incision between the two centrolophs (labial end of the central valley). In the central valley, there are 1 or 2 centrotropes, which are medium-developed or short. The metatrope is labially positioned and short. In one molar it is absent, in another one it is doubled. The posterotrope is regular and centrally positioned. It is vestigial in only 1 case.

M2 (Text-fig. 1b, Pl. 1, Figs 8–9). 38 molars were suitable for morphological study. The outline is rectangular, anterior and posterior margins are the same length or the posterior margin may be a bit shorter. The anterior valley is most frequently closed (32), lingually open (5), or labially open (1). The anterotrope is usually long and occupies nearly the complete length of the anterior valley (20). In 11 molars it is medium developed. In 6 cases it is short, and in one molar it is vestigial. Among the centrolophs the anterior one is usually longer (21), and its lingual end is close to the endoloph. In 5 molars the posterior one is the longer and ends close to the endoloph. In 12 cases, the two centrolophs are the same length. Usually 3 prototropes are present (30). In an anteroposterior sequence, the first one is usually short and the second one is the longest. The third one can be long (1), medium developed (4), short (19), or vestigial (6). There are some molars with 2 prototropes (6) and others with only one prototrope (2). In the labial margin, there is a strong incision between the two centrolophs (labial end of the central valley). In the valley, there are 1 or 2 centrotropes which are medium-developed or short.

The metatrope is labially positioned. It can be long or medium-developed. In one molar it is doubled. The posterotrope is regular and centrally positioned. It is usually long or medium length.

M3 (Text-fig. 1c, Pl. 1, Figs 10–12). 29 molars were suitable for morphological study. The outline of the tooth crown is trapezoidal, the posterior margin is narrow, and the labial margin is oblique. The posterolabial corner is extended more posteriorly than the hypocone in 13 molars. The anterior valley is most frequently closed. The anterotrope is narrow, and of variable length: long (12), medium developed (7), short (5), vestigial (2), or absent (3). Usually, 1 prototrope is developed. It is usually long (5), medium developed (9), short (8), vestigial (6), or absent (1). There is most frequently one labially positioned metatrope. It is doubled in 3 cases. It can be medium developed (11), short (11), or vestigial (4). There are 1–5 centrotropes. Sometimes these are difficult to identify due to the irregular connections. The posterior valley is always closed. In comparison to the length of the posterior valley, the centrally positioned posterotrope is long (15), medium developed (4), short (8), or absent (2). There are two incisions in the labial margin. The anterior one is close to the anterior centroloph, but the exact position is variable: it can be situated in front of, behind, or in line with the anterior centroloph. The location of the posterior incision is similarly variable: it is found in front of, or behind the posterior centroloph, but a position between the centrotropes is also possible.

General features of the lower molars. Concave occlusal surface. The main transversal ridges are anterolophid, metalophid, centrolophid, mesolophid, and posterolophid. The labial ends of the metalophid, mesolophid, and posterolophid are anteriorly curved.



Text-fig. 2. Scatter plot of *Vasseuromys* lower teeth from Eichkogel, Kohfidisch, Palievo and Csodabogyós Cave. a: p4 teeth, b: m1 teeth, c: m2 teeth, d: m3 teeth. Data after Daxner-Höck and Höck (2009) and Sinitsa and Nesin (2018).

Lingual connections of the main ridges: anterolophid-centrolophid in the metaconid (lingual connection of the metalophid is variable), mesolophid-posterolophid in the entoconid.

There are numerous additional ridges. Disintegration, undulation and irregular connections are also possible.

d4. One tooth was suitable for morphological study. The outline is an anteroposteriorly elongated oval. The anterior width is slightly smaller than the posterior width. There are eight ridges. The anterolophid is semicircular and occupies the mesial margin of the tooth. The metalophid is short and isolated. The lingual and labial ends of the centrolophid are fused with the corresponding ends of the anterolophid. The centrotropid (?) is a long narrow ridge. Its lingual end is connected to the entoconid, the labial end reaches the labial margin. The lingual end of the mesolophid is close to the entoconid but does not reach it. There are two posterotropids with free ends: a longer anterior one and a shorter posterior one. The posterolophid is a semicircular ridge extending from the entoconid to the hypoconid on the posterior margin.

p4 (Text-fig. 2a, Pl. 2, Figs 1–3). 17 teeth were suitable for morphological study. The outline is triangular with rounded angles. In the anterior portion, there are the anterolophid, anterotropid, metalophid, and centrolophid ridges. The anterotropid is most usually vestigial (10), short (4) or absent (3). The centrotropid is frequently absent. The anterotropid and metalophid are usually isolated. On the lingual margin, there is an incision between the centrolophid and the mesolophid in 13 cases. In 4 premolars the endolophid is continuous. In the posterior portion, the posterotropid is situated within the mesolophid-posterolophid complex. The posterior valley is labially open in 4 cases. One posterotropid is clearly developed. In 13 premolars the ectolophid is continuous. There is one grooved root.

m1 (Text-fig. 2b, Pl. 2, Figs 4–6). 40 molars were suitable for morphological study. Their outline is rectangular, the anterior margin is narrower than the posterior one. The anterotropid is usually medium developed, the lingual and labial ends are free. In 9 cases it is doubled. A metatropid is always presented, but its length is variable. The metalophid is generally transversally oriented and has a free lingual end. In 4 of the molars this ridge is curved and the lingual end reaches the metaconid. The metatropid is long (8), medium developed (7), short (21) or absent (4). The metatropid is usually centrally positioned if it is long and medium-developed. The short metatropids are frequently located more lingually or labially oriented. In 5 molars the lingual end of the anterotropid-metalophid-metatropid ridges are merged in front of the metaconid. The centrolophid is usually long but labially ending just in front of the forward-extending labial part of the mesolophid (88 %). In the other 12 %, it undoubtedly reaches the labial end of the mesolophid. The centrotropid is absent in only 1 molar. It is most frequently narrow, and of variable length. In 4 cases the lingual end is anteriorly curved as is typical in the main ridges. In the lingual margin, an incision is developed between the centrolophid and the mesolophid (lingual end of the central valley). A complete endolophid is rare (2). In the labial margin, there are two incisions. The anterior incision is situated in front of the labial end of the mesolophid, the posterior one is found in front of the labial end of the posterolophid. An unambiguously entire ectolophid is found in 8 teeth. In the posterior valley 3 posterotropids are visible. The central one is the longest. There are three roots.

m2 (Text-fig. 2c, Pl. 2, Figs 7–9). 41 molars were suitable for morphological study. Their outline is rectangular. The width of the anterior and posterior margins are the same size. The length of the tooth crown is always slightly longer than the width. The anterotropid is regular, its two ends are free. In one molar it is doubled. The metalophid labial end is always connected to the anterolophid in the anteroconid. The lingual end is close to the metaconid but in most cases, it is not fused with it. Fusion is visible in 7 specimens. The metatropid is long or medium length, it is absent in only one molar. Its lingual end reaches the metaconid in 7 cases. In 5 teeth the lingual ends of the three ridges, anterolophid, metalophid, and metatropid, are merged in front of the metaconid. The centrolophid is long, the lingual part ends just in front of the forward-extending labial part of the mesolophid. The length of the centrotropid is variable, but in most cases, it is narrower than the other ridges. In the posterior valley, there are 3 or occassionally 4 posterotropids. In anteroposterior order, the second one is the longest. In the lingual margin, there is one prominent incision between the centrolophid and the mesolophid. A continuous endolophid was not found. In the labial margin, two narrow incisions were developed. The anterior one is situated in front of the labial end of the mesolophid and the posterior incision is in front of the labial end of the posterolophid. In 14 cases only the posterior incision is present. In 2 cases only the anterior one was present. A complete ectolophid (sensu Freudenthal 2004) is developed in 5 cases.

m3 (Text-fig. 2d, Pl. 2, Figs 10–12). 25 molars were suitable for morphological study. The outline is triangular with rounded angles. The anterotropid is regular, its two ends are free. In 17 molars it consists of 3 ridges (in antero-posterior sequence those are short, medium developed, short). The metalophid labial end is always connected to the anterolophid at the anteroconid. The lingual end is close to the metaconid but in 6 cases it is not fused with it. Fusion is visible in 19 specimens. The metatropid is short or vestigial, or absent in 3 molars. The centrotropid is reduced or frequently absent (13). In the posterior valley, there are 2 or 3 posterotropids. In the lingual margin, there is one prominent incision between the centrolophid and the mesolophid. A complete endolophid was not found. In the labial margin, two narrow incisions were developed. The anterior one is situated in front of the labial end of the mesolophid and the posterior one is in front of the labial end of the posterolophid. In 3 cases only the posterior incision was identified. In 7 cases only the anterior one was present. A complete ectolophid is developed in 3 cases.

Comparison

Sinitsa and Nesin (2018) provided a complex comprehensive phylogenetic analysis of the *Vasseuromys* genus that includes all the described species. In this work, the authors classified the *Vasseuromys* sensu stricto clade that includes *V. rugosus* (Baudelot and de Bonis 1966), *V. pannonicus* (Kretzoi 1980) and *V. tectus* (Sinitsa and

Table 2. A comparison of the morphological characters of Late Miocene *Vasseuromys* s. str. species.

Dental character	*Vasseuromys pannonicus*	*Vasseuromys balatonicus* Csodabogyós Cave	*Vasseuromys tectus*
P4 anterior valley	variable	45 % closed	closed
P4 anterotrope	absent	vestigial or absent	always distinct
P4 precentrolophe	usually longer than the postcentroloph	usually longer than the postcentroloh	much shorter than the postcentroloph
P4 centrotrope	absent	long in 24 %	long, frequent
P4 metatrope	rare	frequent	regular
P4 posterotrope	absent	frequent	regular
M1 anteroloph labial end	variable	3 % free	53 % free
M1 centrolophs	anterior CL is longer than posterior one	anterior one longer 54 %, posterior one longer 24 %, equal length 22 %	anterior CL is longer than posterior one
No. of M1 anterotropes	0–1	1 (or absent in 5 %)	1
No. of M1 prototropes	0–1	1–3	3
No. of M1 centrotropes	0–1	1–2	1–2
No. of M1 metatropes	0–1	1	1
No. of M1 posterotropes	0	1	1
M1 posterior valley	closed	100 % closed	37 % closed
No. of M2 anterotropes	0–1	1	1
No. of M2 prototropes	1–2	1–3	3
M2 centrolophs	anterior one is longer	anterior one is longer 56 %, posterior one is longer 13 %, equal length 31%	variable
No. of M2 centrotropes	1	1–2	1–2
No. of M2 metatropes	1	1–2	3 (1 medium + 2 short) in 70 % of the molars
No. of M2 posterotropes	0 – 1	1	1
M2 posterior valley	closed	100 % closed	30 % closed
M3 posterolabial	not extended	45 % extended	extended
angle	posteriorly	posteriorly	posteriorly
No. of M3 anterotrope	0–1	1	0–1
No. of M3 prototrope	0–3	1	1–3
No. of M3 centrotrope	0–1	1–5	1
No. of M3 metatrope	0–1	1–2	1
No. of M3 posterotrope	0–1	1	0–1
No. of p4 posterotropid	0–2	1	3 in 7/8
m1 anterotropid	1	doubled in 22.5 %	doubled in 37.5 %
m1 metalophid	?	transversal 90 %, lingual end is curved and joins to the metaconid 10 %	transversal 70 %, lingual end is curved and joins to the metaconid 30 %
m1 mesoconid	absent	absent	barely discernible
m1 mesolophid-posterolophid labial connection	?	17 %	60 %
m2 metalophid-metaconid fusion	?	17 %	54 %
m2 length/comparison	length is usually longer than width	length is always longer than width	width is always longer than length
m3 continuous ectolophid	?	12%	2/5

Nesin 2018) and forms the terminal monophyletic clade among the *Vasseuromys* s. l. Therefore it suggests that, the Early Miocene "*Vasseuromys*" species can be classified in a distinct genus (Sinitsa and Nesin 2018). Based on this statement, I consider a detailed comparative study of only these species is required. The comparison with *V. tectus* is based on the description given by Sinitsa and Nesin (2018). The comparison with *V. pannonicus* is based on the author's personal observation of specimens in the Naturhistorisches Museum, Wien in 1997 and the publications of Daxner-Höck and De Bruijn (1981), Daxner-Höck and Höck (2009, 2015). The comparison with *V. rugosus* is based on Baudelot and de Bonis (1966) and Álvarez-Sierra et al. (1990).

A morphological comparison of the species *V. pannonicus*, *V. balatonicus* and *V. tectus* is presented in Table 2.

V. balatonicus differs from *V. rugosus*: (1) in the longer and more developed anterotrope, in the regular connection (never unconnected) of the labial ends of the centrolophs to the paracone and the metacone, in the presence of 3 prototropes, and the regular connection of the posteroloph to the metacone in M1–2 and M3; (2) in the regular connection (never unattached) of the labial ends of the mesolophids to the entoconid in m1–2.

Discussion and remarks

Vasseuromys attained the most complicated dental structure of any glirids bearing a large number of crests, which, probably permitted a herbivorous diet not known in living forms (Van der Meulen and De Bruijn 1982). In general, the large number of ridges on the glirid molars is regarded as an adaptation to a more strictly vegetarian diet (Van der Meulen and De Bruijn 1982). Another essential morphological character of *Vasseuromys* molars is the concave occlusal surface. Hautier et al. (2009) regard the high occlusal concavity as an adaptation towards a more insectivorous diet. These two assumptions seem to contradict each other. A possible explanation could be a seasonal change in the preferred foods. Sinitsa and Nesin (2018) discussed the evolutionary relationship between *V. pannonicus* and *V. tectus*. They found that an ancestor-descendant relationship between *V. pannonicus* and *V. tectus* is possible. However one character conflicts with this hypothesis: in M1–2 from Kohfidisch and Eichkogel the posterior valley is closed whereas in *V. tectus* this valley remains open labially in about 70 % of cases. The difference might suggest a separate origin of *V. pannonicus* and *V. tectus*. In *V. balatonicus* the M1–2 posterior valley is also closed and the studied characters of P4 (Pl. 1, Figs, 2, 3) are more similar to those in *V. pannonicus*. We presume that an ancestor-descendant relationship between *V. pannonicus* and *V. balatonicus* is highly probable.

A close relationship between the species *V. pannonicus* and *V. tectus* with the population of Csodabogyós Cave is evident because of the geographical and biochronological proximity. Both species are known from Turolian localities.

The Late Miocene presence of *Vasseuromys* in Europe could be the result of a dispersal event from Asia (Sinitsa and Nesin 2018); this was the "*Progonomys* event" referred to by Koufos (2003). The easternmost occurrence of *V. pannonicus* is in Udabno, Georgia (Agustí et al. 2019). Regarding the geographical range of Late Miocene *Vasseuromys* species there are two interesting facts:

1. The Late Miocene *Vasseuromys* species did not populate the Mediterranean Region and Anatolia. The southernmost occurrences were in the Rhone Valley (Fortelius 2011) and Northern Greece, Lefkon, MN 10 (Koufos 2006).

2. The coexistence of the two glirid genera *Vasseuromys* and *Myomimus* Ognev, 1924 is most frequent in the MN 11 – MN 12 faunas of the Carpathian Basin, Moldova and SW Ukraine (Text-fig. 3). They are absent in the northernmost "*Hipparion* fauna" Dorn-Dürkheim (Franzen and Storch 1975).

Table 3. Late Miocene *Vasseuromys* occurrences in Europe.

Locality	MN zone	Reference
***Vasseuromys pannonicus* (Kretzoi, 1980)**		
Eichkogel, Austria	MN 11	Daxner-Höck and Höck 2009
Kohfidisch, Austria	MN 11	Daxner-Höck and Höck 2009
Széchenyi-hegy, Hungary	MN 12	Kretzoi 1980
Triblavina, Slovakia	MN 11	Joniak and Šujan 2020, Joniak et al. 2020
Krásno, Slovakia	MN 11	Sabol et al. 2021
Chobruchi, Moldova	MN 10 – MN 12	Delinschi 2013
Cucuron, France	MN 12	Fortelius 2011
Valreas, France	MN 11	Fortelius 2011
Dionay, France	MN 11	Fortelius 2011
Udabno, Georgia	MN 11	Agustí et al. 2019
***Vasseuromys* cf. *pannonicus* (Kretzoi, 1980)**		
Chimishliya, Moldova	MN 12	Delinischi 2013
***Vasseuromys tectus* Sinitsa et Nesin, 2018**		
Palievo, Ukraine	MN 11	Sinitsa and Nesin 2018
Otradovo, Ukraine	MN 11	Sinitsa and Nesin 2018
Cherevichnoye 3, Ukraine	MN 12	Sinitsa and Nesin 2018
Kubanka 2, Ukraine	MN 12	Sinitsa and Nesin 2018
Novoukrainka 2, Ukraine	MN 12	Sinitsa and Nesin 2018
Novoelizavetovka, Ukraine	MN 12	Sinitsa and Nesin 2018
Belka 2, Ukraine	MN 12	Sinitsa and Nesin 2018
Protopopovka 3, Ukraine	MN 12	Sinitsa and Nesin 2018
Egorovka 2, Ukraine	MN 12	Sinitsa and Nesin 2018

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Text-fig. 3. Geographical range of the *Vasseuromys* and *Myomimus* genera in the European MN 11 – MN 12 faunas. Circles: occurences of *Vasseuromys*, dots: occurences of *Myomimus*. Abbreviations of the Moldavian (M) and Ukrainian (U) localities: Pr – Protopopovka 3 (U), Ch – Cherevichnoe 3 (U), P – Palievo (U), Ku – Kubanka 2 (U), O – Otradovo (U), E – Egorovka 2 (U), Nu – Novoukrainka 2 (U), Be – Belka 2 (U), Ne – Novoelizavetovka 3 (U), Cho – Chobruchi (M), Chim – Chimisliya (M), Gr – Gradiste (M), Gu – Gura-Galbene (M), Ud – Udabno (Georgia).

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Explanations of the plates

PLATE 1

Occlusal surfaces of *Vasseuromys balatonicus* n. sp. upper teeth from the Csodabogyós Cave
1. D4, right, VER 2024.461.1, reversed.
2. P4, left, VER 2024.464.11.
3. P4, right, VER 2024.464.13, reversed.
4. M1, right, VER 2024.465.11, reversed.
5. M1, right, VER 2024.465.12, reversed.
6. M1, right, VER 2024.466.10, reversed.
7. M1, left, PAL 2024.143.1, Holotypus.
8. M2, left, VER 2024.466.9.
9. M2, left, VER 2024.466.4.
10. M3, left, VER 2024.467.2.
11. M3, left, VER 2024.467.1.
12. M3, left, VER 2024.467.16.

PLATE 2

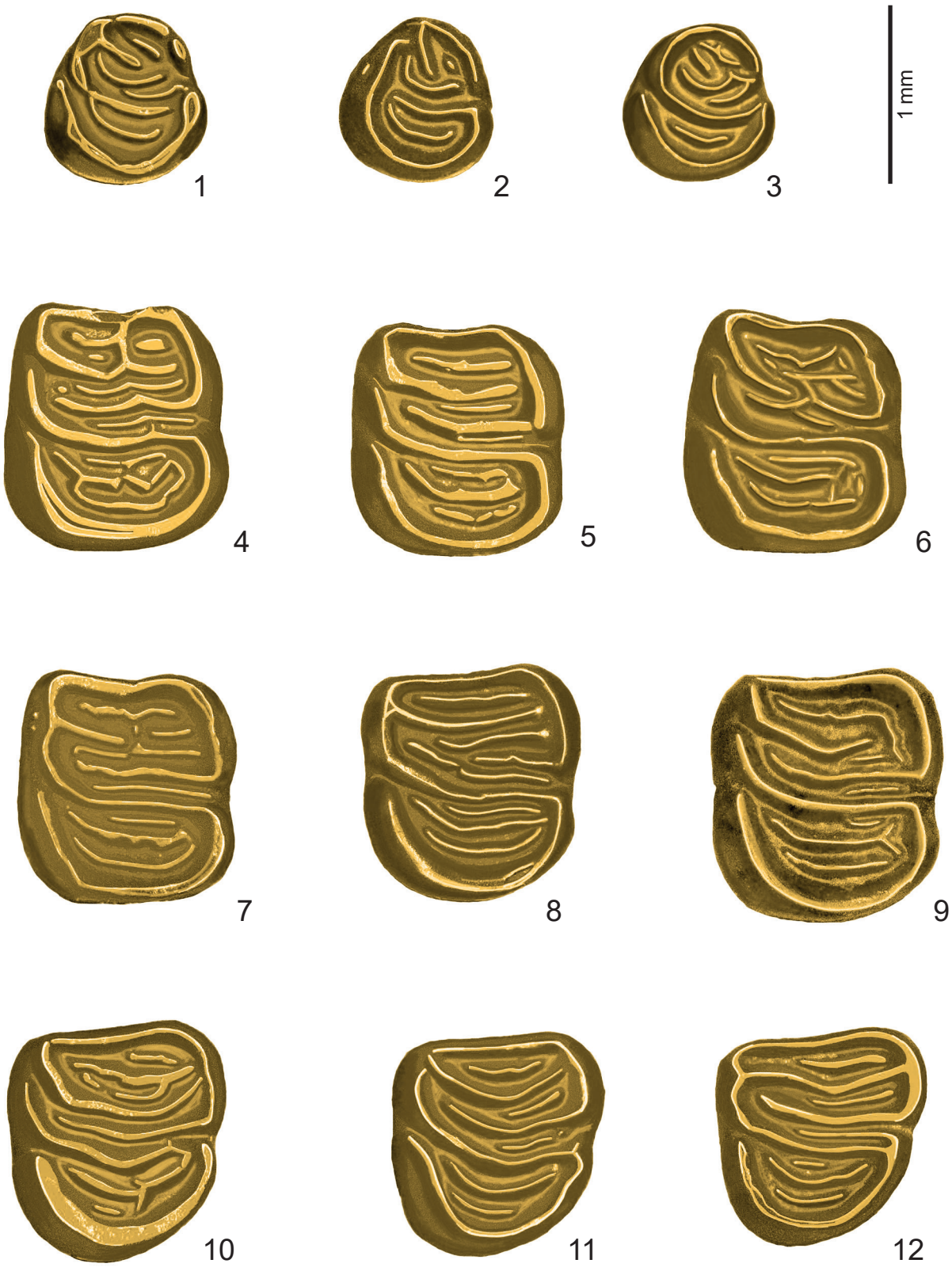
Occlusal surfaces of *Vasseuromys balatonicus* n. sp. lower teeth from the Csodabogyós Cave
1. p4, right, VER 2024.468.2, reversed.
2. p4, right, VER 2024.468.8, reversed.
3. p4, left, VER 2024.468.13.
4. m1, left, VER 2024.469.2.
5. m1, right, VER 2024.469.7, reversed.
6. m1, right, VER 2024.469.13, reversed.
7. m2, right, VER 2024.470.14, reversed.
8. m2, left, VER 2024.470.18.
9. m2, right, VER 2024.470.38, reversed.
10. m3, left, VER 2024.471.3.
11. m3, left, VER 2024.471.4.
12. m3, right, VER 2024.471.1, reversed.


1
2
3
1 mm


4
5
6


7
8
9


10
11
12


1
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