



PANNONICOLA AND ISCHYMOMYS – WHAT MAKES THE DIFFERENCE? ABOUT TWO GENERA CLOSE TO THE BASE OF ARVICOLINAE (CRICETIDAE, RODENTIA)

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Abstract: *Pannonicola* and *Ischymomys* are two extinct genera of the family Cricetidae, and both of them were placed at the base of the evolutionary trunk of the subfamily Arvicolinae. Over the last 100 years, the latter has provided the most important fossils for the biostratigraphy of terrestrial Neogene and Quaternary deposits of the Holarctic. The type material of *Pannonicola* comprises only one m2 and one m3. The first finds of *Ischymomys* were initially rare, not figured, and their nomenclatural status was faced with various problems. Some authors finally assumed that *Ischymomys* was a junior synonym of *Pannonicola*. In this paper, we use new finds from the territory of Ukraine and previously published data to show that *Ischymomys* is an independent genus, and that the finds described as *Pannonicola* should probably be placed in the genus *Microtodon*.

Key words: basal arvicolines, microtoid cricetids, taxonomy, Late Miocene

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Introduction

Most rodent lineages that were widely distributed in the Northern Hemisphere during the Pliocene and Pleistocene first appeared in the Miocene (Mein 2003). Among them, voles (Arvicolinae), a subfamily of hamsters (Cricetidae), are one of the most taxonomically diverse and evolutionarily successful groups. This subfamily now includes far more than 150 extant and fossil species. Numerous remains of voles, represented by isolated teeth and jaws, are very common in Pliocene and Pleistocene terrestrial deposits of the Holarctic. Due to the rapid evolution and wide distribution of voles, and frequent occurrence of their remains, they often provide crucial information about the age, ecology, and palaeobiogeography of these finds themselves and

the associated fauna. Thus, the remains of arvicolines are among the best-studied mammalian fossils over more than 100 years. However, despite a long history of the study of voles, the early stages of their dispersal are still debatable.

In particular, the ancestry of the Arvicolinae is still controversial. A derivation from hamster-like rodents in the Late Miocene is clear, and has long been substantiated with morphological data (e.g., Stehlin and Schaub 1951, Kretzoi 1969, Gromov and Polyakov 1977, Rekovets and Kovalchuk 2017). In more recent years, this derivation has also been confirmed by several molecular studies (e.g., Steppan et al. 2004, Galewski et al. 2006, Robovský et al. 2008, Abramson et al. 2021).

The split between the Arvicolinae and Cricetinae lineages, based on results of the latest DNA studies, was estimated

to take place during the Late Miocene, ca. 11.31 (9.48–13.30) or 10.70 (8.42–13.31) Ma, respectively (Abramson et al. 2021). However, molecular biology can only provide information on the relative phylogenetic relationships between sister groups, and sometimes also infer consistent divergence times. Moreover, this only works with recent material, the so-called crown groups, and possibly also using the ancient DNA analysis of late Quaternary finds, but not with the relevant material of Late Miocene age. In addition, molecular biology cannot say anything about the dental morphology of the respective ancestral forms. Thus, the challenge remains to identify potential Late Miocene precursors at around 11 Ma, as predicted by the DNA phylogenies, from the proven, mostly long-extinct fossil forms that show morphological affinities to Arvicolinae. In addition to various taxa that belong to the group of the “microtoid (= arvicolid-like) Cricetidae” (Schaub 1934, Fejfar et al. 2011) and are excluded from the consideration as ancestors due to special morphological apomorphies (e.g., *Microtocricetus* FAHLBUSCH et MAYR, 1975, *Microscoptes* SCHAUB, 1934, *Trilophomys* DEPÉRET, 1892, etc.), the genera *Pannonicola* KRETZOI, 1965 and *Ischymomys* ZAZHIGIN, 1977 have been brought into discussion as potential ancestors of the subfamily Arvicolinae, or of certain groups within this subfamily.

However, the study of both genera was, at least initially, problematic, because either their finds are extremely rare (*Pannonicola*) or they have nomenclatural issues (e.g., these fossils were only briefly described or not figured at all and hardly accessible for studies, such as *Ischymomys* at the beginning). This led to the hypothesis being put forward 30 years ago (Kordos 1994) that *Pannonicola* and *Ischymomys* were so similar in dental morphology that the latter genus should be regarded as a junior synonym of *Pannonicola*. This view was also followed by other authors, most recently by Fejfar et al. (2011).

In the meantime, there have been significantly more finds of *Ischymomys*, especially those from the territory of Ukraine, which are available to the authors. As all stages of wear of the molars are available, their morphological range of variation is therefore much better detectable, and a comparison of the corresponding *Ischymomys* molars with those of *Pannonicola* can be performed in a well-founded manner.

The aim of this paper is to determine whether synonymisation of *Ischymomys* and *Pannonicola* is justified or not. However, the question of the exact phylogenetic position of the two taxa in the context of the subfamily Arvicolinae is not discussed in this article. We will comment on the latter point in a paper to be published shortly after the present work, which will deal with a detailed morphological analysis of the material of *Ischymomys*, which was recently found in Ukraine .

Oldřich Fejfar made extraordinary contributions in many areas of mammal palaeontology. However, he was always particularly interested in fossil remains of voles and was recognised by all his colleagues as the undisputed specialist with the best overview of this group. We dedicate this article to Oldřich’s memory.

Brief overview of the genera *Pannonicola* and *Ischymomys*

Pannonicola

Kretzoi (1965) erected a new genus and species, *Pannonicola brevidens* KRETZOI, 1965, based on one m2 and one m3, each from the site of Jászladány in Hungary, a fossiliferous segment of a drill core of a deep borehole in ocean sediments of Miocene age. These molars were morphologically more primitive and older than all arvicoline remains found up to that time. In Kretzoi’s (1965: 137, translated from German by LM) opinion, “*Pannonicola* ... can be regarded as the first – already known – true arvicolid... Its clear arvicolid molar construction plan excludes all types of arvicolid tooth construction that have so far been regarded as direct ancestors of the arvicolids, which were able to produce molar construction plans from more recent deposits that, despite their «microtoid» tendency, ultimately represent lateral specialisations of the «buissonant» (= bush-like) cricetid family tree.” The age of the site was given as upper Pannonian, determined from the index fossil *Congeria triangularis* found in surrounding sediments (Kretzoi 1965: 132). In his later synthesis of the vole phylogeny, Kretzoi (1969: 163, 169) also placed *Pannonicola* at the base of the Arvicolinae evolutionary lineage because, despite its unusual for Arvicolinae brachyodonty, it displays a clearly prismatic bauplan, with pointed triangular prisms in the occlusal pattern. However, a big obstacle to systematically positioning the new Hungarian form and comparing it with other taxa was the absence of the first lower molar (m1), which is so decisive for the diagnosis of Arvicolinae. *Pannonicola brevidens* remained the only species of the genus. In later years, further single teeth of *Pannonicola* were reported from Hungary, in particular from Sümegprága, and Nyarad (Kretzoi 1976, Kordos 1994, Bernor et al. 1999).

Ischymomys

The name of the genus *Ischymomys* was first published in Gromov (1972: 16) as a mentioned information from a letter of the year preceding the publication date (“*Ischymomys* ZAZHIGIN, 1971 (in litt.)”), with morphological notes (Gromov 1972: 19), but without illustration of the molars. The so-called *Hipparion* fauna of the Pri-Irtysh was indicated as the stratigraphic age of the find horizon (Gromov 1972: 19). In later literature, the date of the genus was cited either as 1972 (according to Gromov’s article), as for example in Savinov (1982, 1988), or as 1971 (according to Zazhigin’s letter), as for example in Kordos (1994) or McKenna and Bell (1997: 150).

However, neither date is correct, because the first mention of the name *Ischymomys* in Gromov (1972) does not follow the rules of ICZN (International Code of Zoological Nomenclature), and is therefore a nomen nudum. This naming did not conform because it lacks a diagnosis and is not based on a type species (cf. Articles 13.3 and 42.3). Regarding genus-group names, it says: “The application of each genus-group name is determined by reference to the type species of the nominal taxon that it denotes.” According

to Articles 13.3.1–3 and 42.3.2 of the ICZN (1999), the only exceptions from this rule are nominal taxa of the genus group established before 1931, which is not the case here.

The species *Ischimomys kalbica*, has been established one year later by Mos'kina (1973) from the Makovka locality in Kazakhstan in unpublished thesis, and therefore it also must be regarded as *nomen nudum* (for the usage of the genus name *Ischimomys* instead of *Ischymomys*, see comment below).

In 1977, *Ischymomys*, the former *nomen nudum*, was used again in the context of a description of the corresponding finds. In the description and diagnosis (Zazhigin in Gromov and Polyakov 1977), the explicit designations *Ischymomys* gen. nov. and *I. quadriradicatus* sp. nov. were applied. This is a legitimate procedure, permitted by the ICZN rules, which leads to valid genus and species names: “A *nomen nudum* is not an available name, and therefore the same name may be made available later for the same or a different concept; in such a case it would take authorship and date from that act of establishment, not from any earlier publication as a *nomen nudum*” (ICZN 1999).

Therefore, in Gromov and Polyakov's (1977) monograph on Microtinae (= Arvicolinae), this new genus *Ischymomys* was first described with the type species *I. quadriradicatus* (designated by monotypy) from Petropavlovsk (now Petropavl) from the Upper Miocene deposits of the Ishim Formation. Holotype is the right m1, No. 952/51 in collection of Geological Institute, Russian Academy of Sciences. It was diagnosed as follows (Gromov and Polyakov 1977: 210; translation from the English version Gromov and Polyakov 1992): “Voles with cementless molars. M1 with three roots and M2, M3 with four ones. Posterior “island” may be present on all upper molars, rapidly disappears on anterior molars, but always present on M3. Anterior “island” absent on M3. Paraconid section of m1 with an “island” that forms during closure of first medial fold and disappears before roots reach half-crown height. True prismatic fold absent; false (juvenile) fold often observed instead. Enamel equally thick throughout periphery of tooth. Position of roots of posterior lower molars relative to incisor not known.” However, no illustrations were provided in this publication either.

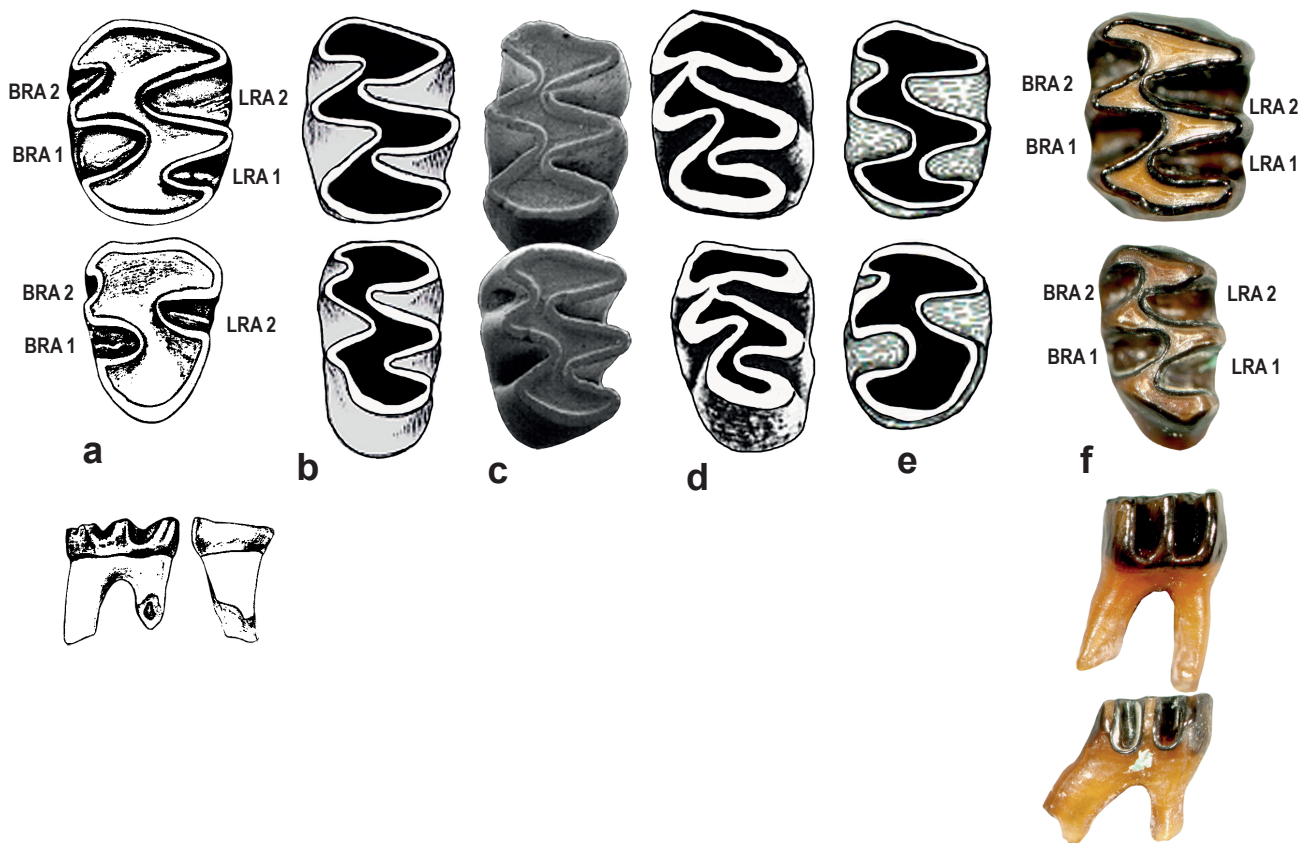
Over the years, literature has sometimes inconsistently used the name *Ischymomys* or *Ischimomys*. Although the river on the bank of which the site is located is called Ишим (in Cyrillic) and would be letter by letter transliterated as Ishim, the genus was given the name *Ischymomys*. A. Tesakov (reviewer of this paper) provides the following explanation: “Ishim in Russian is pronounced using the sonant of the middle row transliterated [actually transcribed into English as «y»].” The spelling *Ischymomys* is the case in both the first (invalid) mention by Zazhigin cited in Gromov (1972), and the second (valid) description and diagnosis of Zazhigin in Gromov and Polyakov (1977), i.e., correct original spelling. This is also quoted in Gromov and Baranova (1981): *Ischymomys quadriradicatus* ZAZHIGIN, 1977. On the other hand, Savinov (1982, 1988) named the genus *Ischimomys* ZAZHIGIN, 1972. This spelling was also used by Kordos (1994), although he noted in a footnote “P.S.: The name of *Ischimomys* and *Ischymomys* are mixed in different publications.” Interestingly, even Zazhigin himself once wrote in Zazhigin et al. (2002) the genus name as *Ischimomys*.

The correct designation is therefore *Ischymomys quadriradicatus* ZAZHIGIN, 1977. Finally, it should be mentioned that MEIN (2003: 414) incorrectly stated the year of the first description as *Ischymomys* ZAZHIGIN, 1992, which is obviously based on the translated version of the book of Gromov and Polyakov from 1977 into English in 1992 (Gromov and Polyakov 1992).

It always helps the reader when illustrations of the dentition of a newly described species are published as well. However, according to ICZN (1999), illustrations of the species are only recommended for species described after 1999 (cf. Article 16. Names published after 1999: Recommendation 16F. “... to add information about the type specimens and illustrate holotype or syntypes”). However, the first illustrations of *Ischymomys* were not provided for the type species *I. quadriradicatus*, but for the species *I. ponticus* TOPACHEVSKIY, SKORIK et REKOVETS, 1978, which was discovered at the Ukrainian site Frunzivka (now Frunzivka) 2, and described in 1978 with clear drawings of these specimens. The new species was diagnosed (Topachevskiy et al. 1978: 39; translated from Russian with some terms slightly modified according to the current usage): “The middle pair of salient angles (paracone and hypocone) of M3 are almost completely separated: the width of the connection between the dentine fields is smaller or approximately similar to the thickness of the enamel. The linea sinuosa and, apparently, the enamel islet on M1, are more strongly developed than in the type species *I. quadriradicatus* ZAZHIGIN.”

Only Savinov (1982) provided descriptions with illustrations and measurements of the type species *Ischymomys quadriradicatus* from the type locality Petropavlovsk, but based on different material than that of Zazhigin. The illustrations show some examples of all molar positions in occlusal and lateral view. However, some of the figures are small drawings in which the features (confluence, shape of re-entrant and salient angles) are not particularly easy to recognise. Better illustrations of this material can be found in a later work by Savinov (1988) (for m2s and m3s, see Text-figs 4 and 5 of this paper).

Over the years, the number of originally rare finds of the genus *Ischymomys* has increased significantly, and now includes (1) the material from the type locality of *I. quadriradicatus* Petropavlovsk, for which Zazhigin (in Gromov and Polyakov 1977) reported more than 60 isolated molars, and Savinov (1982) nearly 300 isolated molars of all tooth positions and 10 mandible fragments; (2) the finds from Makovka in Kazakhstan (Mos'kina 1973, Savinov 1988, Zazhigin et al. 2002); (3) the finds from Frunzivka 2 (Topachevskiy et al. 1978, Nesin and Topachevskiy 1991, Topachevskiy and Nesin 1992) and other Ukrainian localities (Rekovets and Pashkov 2009, Nesin 2013, Rekovets et al. 2014, Kovalchuk 2017, Nesin and Kovalchuk 2017) such as (4) Popove 3 (formerly Popovo), (5) Lysa Gora 2, (6) Mykhailivka-on-Bug 1, (7) Mykhailivka-on-Bug 2 (formerly Mikhailovka 1 and 2), and (8) Verkhnya Krynytsia; (9) Kohfidisch (mandible with m2, originally determined as *Promimomys (Prosomys)* sp.) in Austria (Bachmayer and Wilson 1978, but as *Ischymomys* sp. in Daxner-Höck and Höck 2015); (10) Shala in Chia (a single m1 fragment) (Qiu and Li 2016); and (11) Leordoia in Moldova (1 M1)



Text-fig. 1. Lower m2 and m3 (both in occlusal view). a: *Pannonicola brevidens* (below: m2 in lingual and mesial view) from Jászladány (Hungary) (after Kretzoi 1965). b: *Promimomys moldavicus* from La Gloria 4 (Spain) (after Fejfar et al. 1990). c: *Aratomys bilikensis* from Bilike (China) (after Qiu and Storch 2000). d: *Baranomys loczyi* from Węże (Poland) (after Sulimski 1964). e: *Microtodon atavus* from Ertemte (China) (after Fahlbusch and Moser 2004). f: *Ischymomys ponticus* from Popove 3 (Ukraine) (below: lingual view of different wear stages). Figures taken from literature sources are slightly modified. All figures scaled to same size.

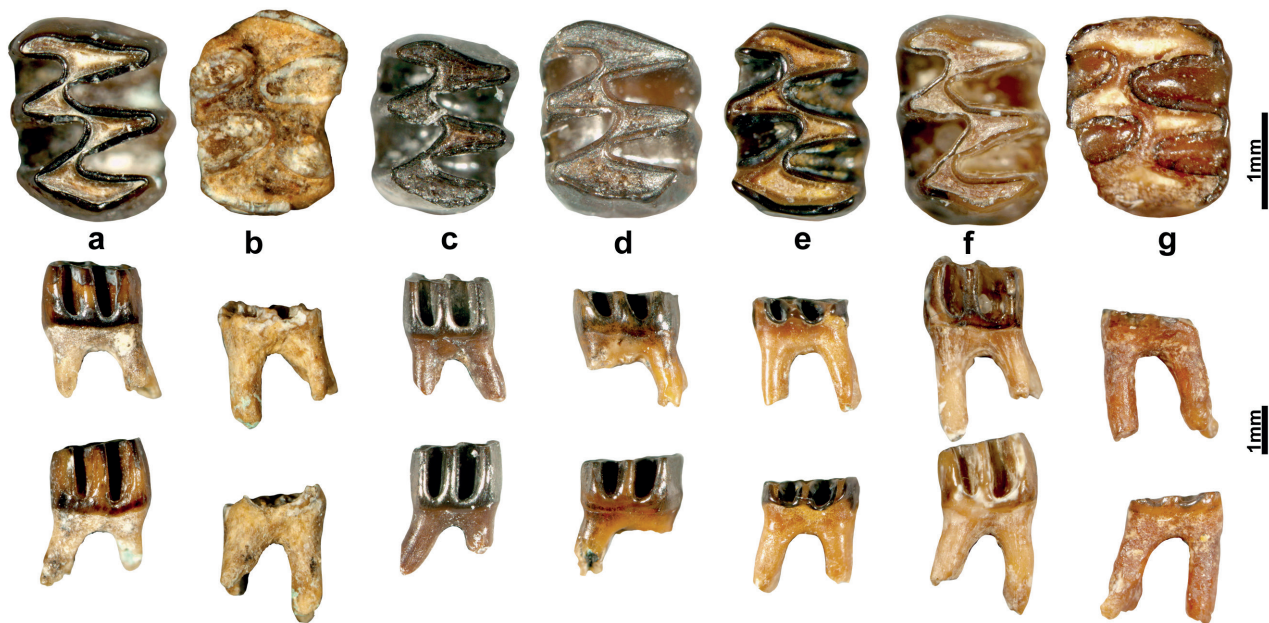
(Nicoara and Lungu 2008, Nicoara 2013: pl. IX, fig. 2). It also seems very likely that the finds from (12) Nyarad (1 M1) (Kretzoi 1976, Kordos 1994, Fejfar et al. 2011: 11) and (13) Sümegprága (2 m1, 1 m3) (Kordos 1994, Fejfar et al. 2011: 11) are actually not *Pannonicola*, but *Ischymomys* remains (see below).

Morphological comparisons of m2 and m3 of relevant taxa

As can be seen in Text-fig. 1, in *Pannonicola* from Jászladány BRA 2 (Buccal Re-entrant Angle 2) and LRA 1 (Lingual Re-entrant Angle 1) (nomenclature after van der Meulen 1973: fig. 10) on the m2 are only about half as deep as BRA 1 on the buccal side and LRA 2 on the lingual side. The posterior lobe and T1 as well as T2 and T3 are broadly confluent. At m3, BRA 2 is even shallower (about 1/3 of the depth of BRA 1), and LRA 1 is completely absent. Kretzoi (1965: 134) had already pointed this out: “On the lower m2, however, the anterior outer and the posterior inner folds are still weakly developed, on the m3 the former, ‘in an advanced stage of wear only hinted’ the latter has disappeared, which leads to the fusion of the hypo- and endolophid prisms into a uniform field.” According to Kretzoi (1965), only the m3 is heavily worn, the m2 is considered to be very brachyodont, but not extremely chewed off. Fejfar et al. (2011), on the other hand, judged both molars to be extremely worn.

The comparison with other early forms of the Arvicolinae and other Arvicolinae-like (“microtoid cricetids”) taxa (*Promimomys* KRETZOI, 1955, *Aratomys* ZAZHIGIN, 1977, *Baranomys* KORMOS, 1933, *Microtodon* MILLER, 1927, and *Ischymomys*) shows similarities at m2, in that BRA 2 is less deeply incised than BRA 1 in all taxa, but the difference between the two re-entrants is strongest in *Pannonicola* and *Microtodon*. The same applies to the depth of LRA 1. At m3, BRA 2 is much more shallowly incised in all forms compared to that of *Ischymomys*. LRA 1 is relatively deep in *Promimomys*, *Aratomys* and *Baranomys*, but not as deep as in *Ischymomys*. In *Pannonicola*, this re-entrant angle is completely absent, which is similarly the case in *Microtodon*, but only in heavily worn stages. In less worn molars of *Microtodon*, the re-entrant is still present in a shallow degree (see series of different wear stages in *Microtodon*, figured in Fahlbusch and Moser (2004).

Ischymomys finds from Frunzivka 2 show almost completely separated, non-confluent dentin fields on both m2 and m3. In addition, BRA 2 is relatively much larger on the m2, and the depth corresponds to about 2/3 of the depth of BRA 1. LRA 1 is almost as deep as LRA 2. The differences of the m3 are even more obvious: in contrast to *Pannonicola*, where BRA 2 is widely reduced, this structure is quite deeply incised in *Ischymomys*. LRA 1 is clearly developed in *Ischymomys* but absent in *Pannonicola*. Overall, the m3 of *Ischymomys* is significantly narrower than that of *Pannonicola*.

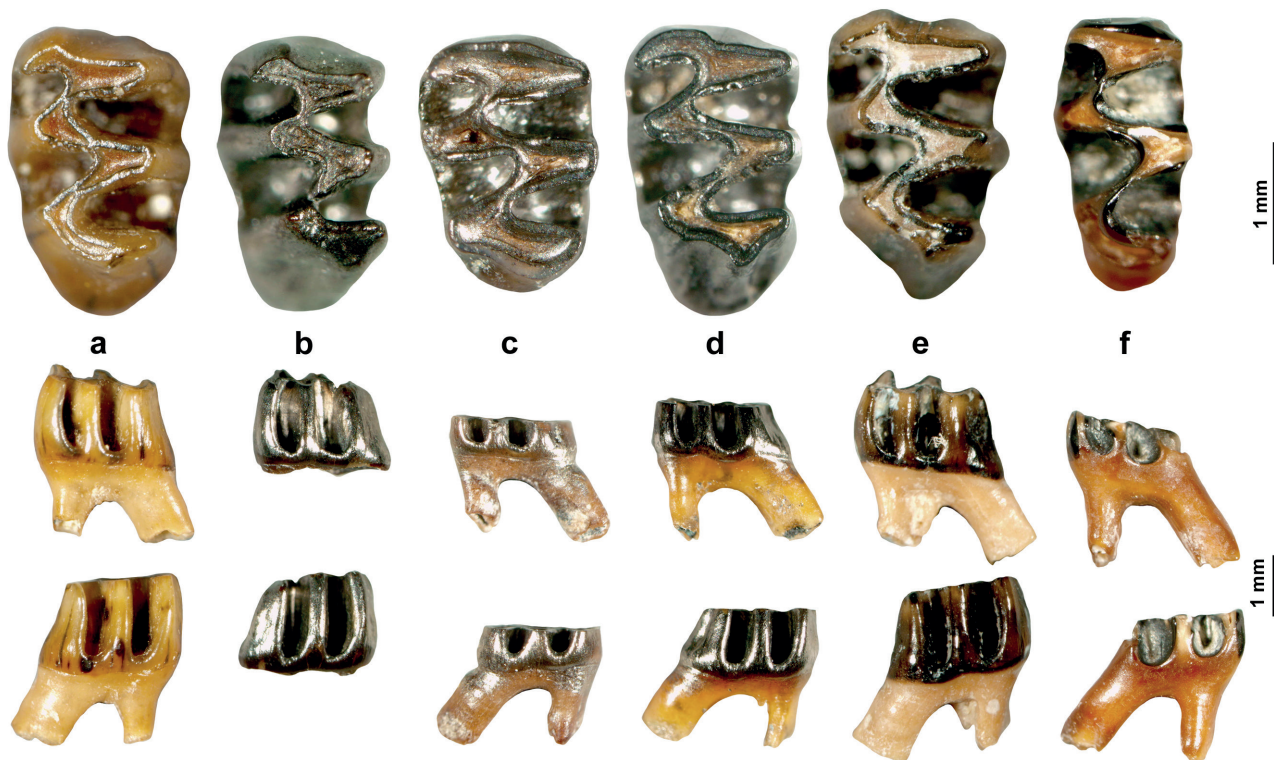


Text-fig. 2. Juvenile (little worn) and senile (heavily worn) m2 of *Ischymomys* from various Ukrainian localities, showing variability of dental elements. a, b: Frunzivka 2. c: Mykhailivka-on-Bug 1. d, e: Mykhailivka-on-Bug 2. f, g: Popove 3.

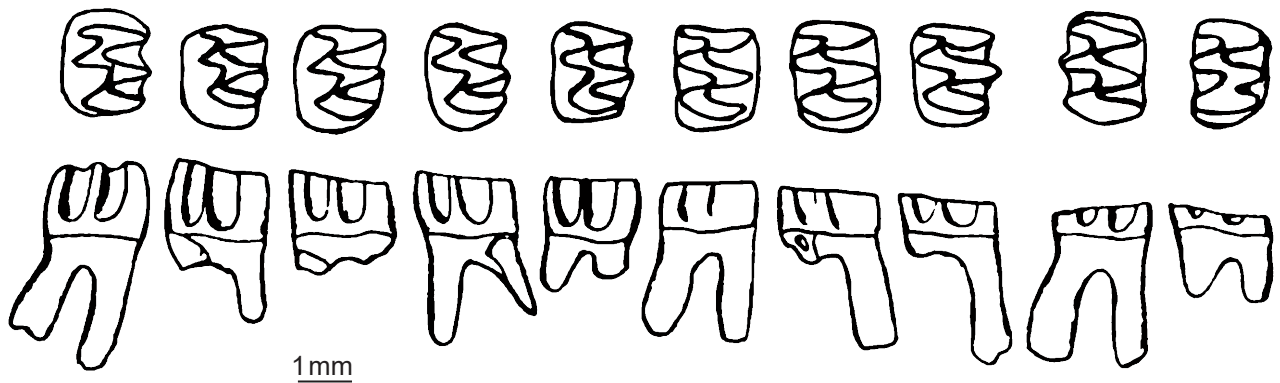
Concerning the potential problem to compare different ontogenetical stages, we summarise: If one compares *Ischymomys* with *Microtodon* (Fahlbusch and Moser 2004: 330–331), the LRA1 at m3 is clearly weaker in *Microtodon* in all ontogenetic/wear stages – even in the youngest – than in all (even the relatively strongly chewed) *Ischymomys*. In the ontogenetically oldest *Microtodon* this re-entrant angle is

missing. These conditions correspond exactly to the picture of *Pannonicola* m3. We therefore conclude that both type specimens (m2 and m3) of *Pannonicola* are morphologically much closer to *Microtodon* than to *Ischymomys*.

Another vole-like cricetid, *Baranarvionomys* NESIN, 1996, differs only slightly from *Microtodon*. According to Nesin's (1996) original description, the m3 of *Baranarvionomys* is



Text-fig. 3. Juvenile (little worn) and senile (heavily worn) m3 of *Ischymomys* from various Ukrainian localities, showing variability of dental elements. a: Frunzivka 2. b, c: Mykhailivka-on-Bug 1. d: Mykhailivka-on-Bug 2. e, f: Popove 3.



Text-fig. 4. *Ischymomys quadriradicatus*, Petropavlovsk/Petropavl (Kazakhstan) (modified from Savinov 1988; aligned where weak contours of original drawing were traced).

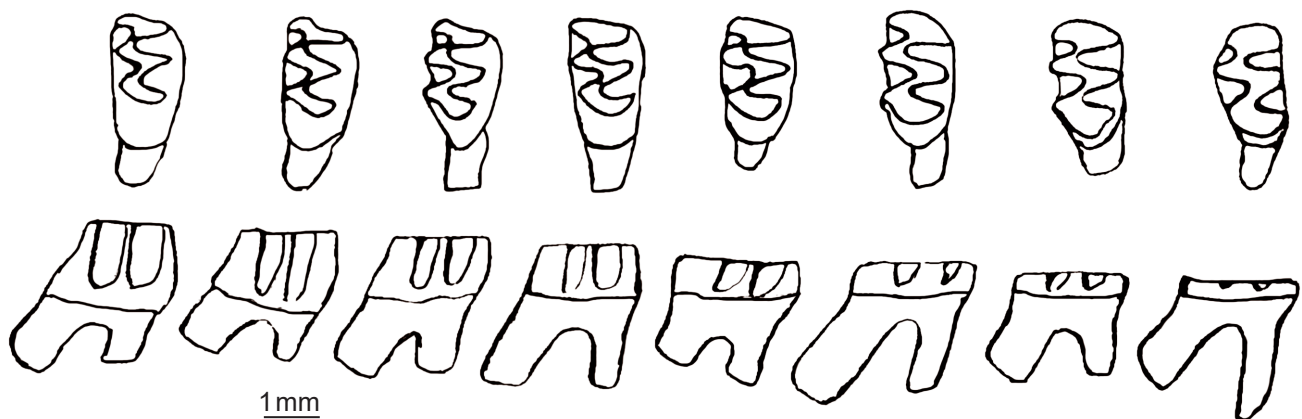
somewhat more complicated, but both the m3 and the m2 illustrated by Nesin are within the range of variation of the molars of *Microtodon* from Ertemte/China described by Fahlbusch and Moser (2004). Finally, according to Fejfar et al. (2011) *Baranarviomys* is a synonym of *Microtodon*.

Overall, there are great morphological differences in m2 and m3 between *Pannonicola* and *Ischymomys*, but great similarities between *Pannonicola* and *Microtodon*. In addition, the hypsodonty of *Ischymomys* is significantly larger than that of *Pannonicola*, as far as this can be judged from the present wear stages of the latter. Text-figs 2 and 3, in which m2 and m3 from different Ukrainian localities and different wear stages are illustrated, show that the above-mentioned traits occur consistently in all *Ischymomys* from the territory of Ukraine. The characters of *Ischymomys quadriradicatus* from Petropavlovsk appear to be the same, as Savinov's (1988) illustrations confirm (Text-figs 4 and 5 in the present paper). The photo of the m2 from Kohfidisch (Bachmayer and Wilson 1978: Taf. 4, fig. 17, Daxner-Höck and Höck 2015: pl. 55, figs 15, 16; Text-fig. 6a here) also suggests the characters of *Ischymomys*. The same applies to the finds from Nyarad (two typical *Ischymomys* m1, and one m2 corresponding to the above-mentioned conditions)

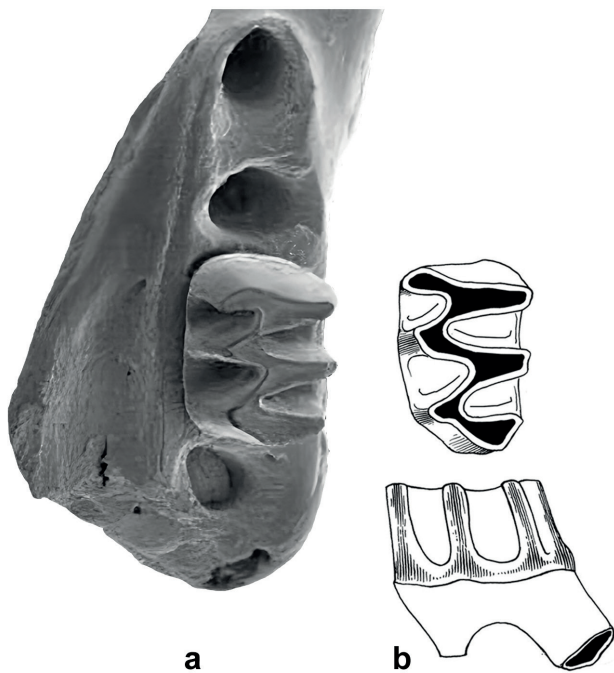
and Sümegpraga (one typical *Ischymomys* M1) illustrated in Fejfar et al. (2011: fig. 3/9–10).

With our observation of the similarity of *Pannonicola* and *Microtodon*, we come to the same conclusion as Gromov and Baranova (1981: 148), who already placed the type material of *Pannonicola brevidens* in *Microtodon*, as they included it in the list of synonyms of this genus. However, *Microtodon atavus* SCHLOSSER, 1924 from the type locality Ertemte in China (Fahlbusch and Moser 2004) is significantly smaller (m2 length min 1.20 mm, mean 1.37 mm, max 1.57 mm; m3 length min 0.85 mm, mean 1.05 mm, max 1.23 mm; Fahlbusch and Moser 2004: 337) than the finds of *Pannonicola* (m2 length 1.70 mm, m3 length 1.60 mm; Kretzoi 1965: 134), but there are also other species that correspond metrically to the *Pannonicola* finds: *Microtodon komanensis* HORDIJK et DE BRUIJN, 2009 from Greece (Hordijk and de Bruijn 2009) and *Microtodon hoyensis* KELLY et MARTIN, 2023 from North America (Kelly and Martin 2023). The absence of the diagnostically important m1 of *Pannonicola* is the biggest obstacle for a clear determination of its finds.

Another argument to place *Pannonicola* apart from *Ischymomys* seems to be the geological age. Jászladány, the type locality of *Pannonicola*, yielded the marine mollusc



Text-fig. 5. *Ischymomys quadriradicatus*, Petropavlovsk/Petropavl (Kazakhstan) (modified from Savinov 1988; aligned where weak contours of original drawing were traced).



Text-fig. 6. Remains of *Ischymomys* from Central European localities. **a:** mandible with m2 from Kohfidisch (Austria) (from Daxner-Höck and Höck 2015: pl. 55, fig. 16). **b:** m3 from Sümegprága (Hungary) (from Fejfar et al. 2011: fig. 3/9–10).

key fossil *Congeria triangularis* layers (Kretzoi 1965: 132). According to Harzhauser and Mandic (2010), the zebra mussel *Congeria triangularis* (now *Mytilopsis triangularis* (PARTSCH, 1836)) is restricted to the period from the late late Pannonian to the late Pannonian/Pontian transition, which according to these authors (i.e., fig. 3, p. 19) corresponds to an age of ca. 8–6 Ma. This period correlates approximately with the duration of MN Zones 12–13 (Steininger 1999, Ezquerro et al. 2022). This dating fits the age of Ertemte and Harr Obo (MN 13) from where *Microtodon atavus* was described in detail by Fahlbusch and Moser (2004). The Greek sites Ptolemais and Komani (MN 14–15) (Hordijk and de Bruijn 2009) as well as the North American finds described by Kelly and Martin (2023) are both of early Pliocene age. In contrast, almost all Ukrainian *Ischymomys* finds originate from sites of MN 11 (Rekovets and Pashkov 2009, Nesin 2013, Rekovets et al. 2014, Kovalchuk 2017, Nesin and Kovalchuk 2017), the age of Petropavlovsk/Petropavl may be even older, MN 10 (Zazhigin et al. 2002). Only Leordoia in Moldova is slightly younger, probably from MN 12 (Nicoara and Lungu 2008, Nicoara 2013), but still older than Jászladány and all *Microtodon* finds.

Conclusions

The question of this paper was whether *Ischymomys* should be regarded as a synonym of *Pannonicola* or whether it is an independent taxon. The morphological arguments clearly support the latter. Moreover, the type material of *Pannonicola* shows great similarities with previous *Microtodon* finds. Finally, this assessment is also supported by the stratigraphic age of *Ischymomys*, which is higher than that of the type locality of *Pannonicola* and of all *Microtodon* records. These results

have consequences for the determination of the stratigraphic range of both taxa and their use as index fossils. The fact that there is still very little comparative material available from many sites, except for Petropavlovsk/Petropavl and the Ukrainian localities, naturally has a limiting effect. The work presented here will be continued by a detailed comparison of the relatively extensive material currently available from localities of Miocene age in the territory of Ukraine. These finds will be compared morphologically and morphometrically with each other and with other Late Miocene and Early Pliocene Arvicolinae and Arvicolinae-like taxa. This should also provide morphological/morphometric arguments as to the relationship of *Ischymomys* to the phylogenetic tree of the Arvicolinae, whether they are direct ancestors of all or only a part of this subfamily (Gromov 1972, Gromov and Polyakov 1977, Fejfar et al. 2011), or whether they are an independent side branch of evolved Cricetinae (Nesin and Topachevskiy 1991, Topachevskiy and Nesin 1992).

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