The "developmental conduit" of the tribe Microtini (Rodentia, Arvicolinae): Systematic and evolutionary aspects

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ABSTRACT. According to the recent data on molecular genetics and comparative genomics of the grey voles of the tribe Microtini it is supposed, that their Nearctic and Palearctic groups had independently originated from different lineages of the extinct genus *Mimomys*. Nevertheless, that tribe is considered as a natural taxon. The American narrow-skulled voles are referred to a new taxon, *Vocalomys* **subgen. nov**.

KEY WORDS: homology, homoplasy, phylogeny, vole, Microtini, evolution, taxonomy.

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«Канал развития» полевок трибы Microtini (Rodentia, Arvicolinae): систематико-эволюционный аспект.

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РЕЗЮМЕ. В соответствии с последними данными молекулярной генетики и сравнительной геномики серых полевок трибы Microtini делается вывод о независимом происхождении неарктических и палеарктических групп от разных представителей вымершего рода *Mimomys*. Несмотря на это, данная триба считается естественным таксоном. Американские узкочерепные полевки выделяются в самостоятельный подрод *Vocalomys* **subgen. nov**.

КЛЮЧЕВЫЕ СЛОВА: гомология, гомоплазия, филогения, полевки, Microtini, эволюция, таксономия.

Introduction

The Holarctic subfamily Arvicolinae Gray, 1821 is known to comprise a number of transberingian vicariants together with a few Holarctic forms. Originally, the extent of their phylogenetic relationships was judged on their morphological similarity. Further, the data on comparative cytogenetics and postzygotic reproductive isolation made the taxonomists challenge the systematic position of some microtine forms that had been impossible only on the base of traditional morphology. However, it has not been possible to revise considerably either macroevolutionary scenario of formation of voles' recent diversity or ideas about systematic relationships between the transberingian vicariants without summarized results of different molecular-genetic analyses. The common or the grey voles of the genus *Microtus* Schrank, 1798 (sensu lato) were usually included together with *Arvicola* L., 1758 (and sometimes with *Ondatra* Link, 1795) in the broadly defined tribe Arvicolini (Pavlinov *et al*., 1995; Pavlinov, 2003). However, molecular data indicate that *Arvicola* and *Microtus* are not sister taxa (Conroy & Cook, 2000). So apart from *Arvicola* and *Ondatra* the species of the genus *Microtus* were lumped together in a tribe Microtini Miller, 1886 (Shenbrot & Krasnov, 2005) that includes a number of Palearctic forms and their Nearctic ecomorphological vicariants with rootless ever-growing molars and crown cement.

The history of the group in the light of the molecular data

The grey voles are usually altogether regarded as a first-hand descendant of the Early Pleistocene genus *Allophaiomys* Kormos, 1930, in which molars, like in common voles, had already become rootless. Their primitive dental pattern resembling that of such Central Asiatic living groups of the genus *Microtus* as subgenera *Phaiomys* Blyth, 1863, *Blanfordimys* Argyropulo, 1933, and *Neodon* Hodgson, 1849 (Gromov & Polyakov, 1977; Golenishchev & Sablina, 1991; Nadachowski & Zagorodnyuk, 1996). Martin & Tesakov (1998), considering that state of dental morphology as a symplesiomorphy, suggested to include *Allophaiomys* in *Microtus*. *Allophaiomys*, in its turn, is believed to have originated from the Late Pliocene-Early Pleistocene genus *Mimomys* Major, 1902, in which molars possessed roots, crown cement in inward angles, and negatively differentiated enamel. As far as the latter trait is concerned, among the recent species they are only *Microtus* (*Orthriomys*) *umbrosus* Merriam, 1898 and *M*. (*Herpethomys*) *guatemalensis* Merriam, 1898 which have such kind of dental morphology (Martin, 1998).

Though the diversity of living and extinct Arvicolinae shows that quite often different lineages achieve some similar characters independently of each other (Gromov, 1972; Angerman, 1973; Gromov & Polyak-

ov, 1977), the overall common voles' state of morphology is still supposed to have been inherited directly from their hypothetical common ancestor. Most of the taxonomists consider the common voles as Holarctic genus *Microtus* (Hinton, 1926; Ellerman, 1941; Ellerman & Morrison-Scott, 1951; Gromov & Polyakov, 1977; Corbet, 1978; Musser & Carleton, 2005) that is of a Palearctic origin. According to those authors it is comprised of about 63 species (including 19 Nearctic ones), of 17 subgenera (among which six are New World's endemics, and three are Holarctic ones). In spite of the clear evidence that the striking environmental resemblance between those continents had to cause a strong tendency towards parallel formation, there are some Palearctic microtines, each of them was quite often referred to the same subgenus or even to the same species with its Nearctic morphoecological analogue. Those vicariants (Tab. 1) together with some former ideas about their systematic relationships were listed previously (Golenishchev & Malikov, 2004).

As regards extinct forms, according to the cladistic analysis Nearctic *Microtus pliocaenicus* Kormos, 1933 and *M. meadensis* Hibbard, 1944 were placed in the subgenera *Phaiomys* and *Terricola* subsequently (Martin, 1995), as well as *Pedomys* Baird, 1858 was synonimized under *Pitymys* s. lato (Martin, 1987), and all advanced voles with T4–5 confluent were lumped in the tribe Pitymyini (Repenning, 1983; Repenning *et al.*, 1990). Then Martin (1995), according to the results of cladistic evaluation of dental morphology, separated

Pedomys from *Pitymys* and *Orthriomys* from *Phaiomys*, having doubts about the natural unity of voles with the pitymyan rhombus. Indeed, neither living nor fossil representatives of any Palearctic taxa with the pitymyan rhombus have ever been known from Asiatic part of Beringia or adjacent regions of North-East Siberia. Nevertheless, Repenning (2001) supposed that some ancient representatives of the subgenus *Terricola* could have immigrated to North America via Beringia about 800 000 years ago.

It has been considered that all the American microtines originated from some Asiatic forms of the genus *Microtus*, which immigrated to North America via Beringia as three subsequent waves. That supposition seemed to be quite reasoned because of a large amount of data on repeated Pleistocene glaciations that caused sinking of the sea-level and emerging of the Bering Bridge. According to that point of view the first wave reached Laurentia after Blancan V Glaciation about 2.1 Mya (Hoffman & Koeppl, 1985; Repenning, 2001). In particular Repenning *et al.* (1990), and initially Martin (1998) supposed that it was Early Pleistocene *Allophaiomys deucalion* Kretzoi, 1969 (sensu lato), which had a very widespread geographic range throughout Europe and into Siberia, and, thus, could have dispersed to North America where it might have given an origin to *M. californicus* Peale, 1848, *M. umbrosus* and *M. guatemalensis* which are the most archaic extant Nearctic common voles. The immigrants of the second wave were thought to have crossed the Bridge in the Middle

Table 1. The Palearctic and Nearctic species of the common voles, which were believed as closely related.

Palearctic species	Nearctic species
Semi-aquatic forms	
genus *Arvicola* Lacepede, 1799 *Arvicola terrestris* L., 1758	subgenus *Aulacomys* Rhoads, 1894 *Microtus* (*Aulacomys*) *richardsoni* De Kay, 1842
Inhabitants of meadows	
subgenus *Microtus* Schrank, 1798 *M.* (*Microtus*) *agrestis* L., 1761	subgenus *Microtus* *M.* (*Microtus*) *pennsylvanicus* Ord, 1815 *M.* (*Microtus*) *chrotorrhinus* Miller, 1894
Petrophilous forms	
genus *Chionomys* Miller, 1908	subgenus *Microtus* *M. longicaudatus* Merriam, 1888
The voles of forbs	
subgenus *Sumeriomys* Argyropulo, 1933	subgenus *Chilotus* Baird, 1857 *M.* (*Chilotus*) *oregoni* Bachman, 1839
Semi-subterranean forms	
subgenus *Terricola* Fatio, 1867	subgenus *Pitymys* McMurtria, 1831 *M.* (*Pitymys*) *pinetorum* Le Conte, 1830 *M.* (*Pitymys*) *quasiater* Coues, 1874
Narrow-skulled voles of tundra-steppe	
subgenus *Stenocranius* Kastschenko, 1901 *M.* (*St.*) *gregalis* Pallas, 1778	subgenus *Stenocranius* *M.* (*St.*) *miurus* Osgood, 1901 *M.* (*St.*) *abbreviatus* Miller, 1899

Pleistocene. They were considered as ancestral to *M. quasiater* Coues, 1874, *M. oaxacensis* Goodwin, 1966, *M. pinetorum*, and *M. ochrogaster*. Martin & Tesakov (1998) supposed those species to be descendants of *A. pliocaenicus* or its closest relatives, which evolved from early descendants of *A. deucalion*, which had already possessed the positive enamel differentiation. The third, Late Pleistocene portion of Palearctic forms, except *M. oeconomus* Pallas, 1776 (Lance & Cook, 1998) and the narrow-skulled forms united in the subgenus *Stenocranius*, which were considered as quite recent immigrants to the New World, was presumed to be ancestral to all the rest American living *Microtus*-like voles (Hoffman & Koeppl, 1985). According to all those versions, the *Microtus*-like state of the American common voles, as such, had already arisen in their Palearctic ancestors. Alternatively according to the data on protein electrophoresis (Graf, 1982), C-banding patterns (Modi, 1987), nuclear (Modi, 1996), or mitochondrial (Conroy & Cook, 2000; Jaarola *et al.*, 2004) DNA, and chromosomal localization of some repeated DNA sequences among species of *Microtus* (Modi *et al.*, 2003) all the Nearctic common voles seem likely to be closer to each other than to most of the Palearctic species. The exception is Iberian relict *M. cabrerae* Thomas, 1906, which, being of the most archaic dental morphology among the Palearctic forms (Gromov & Polyakov, 1977), is of a seemingly genomic nearness to the Nearctic species (Conroy & Cook, 2000; Modi *et al.*, 2003; Jaarola *et al.*, 2004), though without any reliable bootstrap support. The extremely archaic morphology of *M. cabrerae* in combination with its Mediterranean distribution and seeming genomic likeness to the Nearctic common voles shows that the American branch could have deviated from rather basic site of the common ancestral trunk which had been within the Palearctic range yet. As concerns the amount of "molecular-genetic divergence" between the representatives of different Eurasian superclades (Jaarola *et al.*, 2004), it seems likely to be even larger than that between their American ecomorphological vicariants. Anyway, the overall paleonthological and neonthological knowledge combining shows that the common voles' "phenomo-genomic" state is a level of evolutionary development. The latter had been independently achieved by the lineages, which were ancestral to the living species and their monophyletic groups. What were those ancestors like? That is the question. The chronology of fossil remains shows that on both of the continents the main ecomorphological types of the living *Microtus* had been formed by the middle of Pleistocene. In those times the alpine glaciers and the overall environment of North-Eastern Siberia, Alaska and Laurentia would have served as insuperable barriers on the way of the *Microtus*-like transcontinental migrants, except such highly dispersal or adopted to subarctic conditions species as *M. oeconomus* and, presumably, *M. miurus*. Therefore, the arvicolines, which were ancestral to the Nearctic *Microtus*-like species, could cross the Bridge only during some warmer time, no later than Late Pliocene-Early Pleis-

tocene. As concerns the notion about *Allophaiomys deucalion* as ancestral to American *M. umbrosus* and *M. guatemalensis* (Martin, 1998), which are the most archaic living voles with rootless molars, and *A. pliocenicus*, with the positively differentiated enamel, as ancestral to all the Palearctic and Nearctic advanced *Microtus*-like species (Martin & Tesakov, 1998; Chalin *et al.*, 1999; Repenning, 2001), there are two general objections to it as follows:

1) The *A. deucalion*-like form, with somewhat between slightly negative and neutral enamel differentiation does not seem likely to be ancestral to the living *M. umbrosus* with distinctly negative enamel differentiation. The point is that the idea about the reversion is not parsimonious in the frame of the commonly accepted evolutionary model of enamel's differentiation in microtines from negative via neutral to positive; that's why Martin (1998) finally supposed *M. umbrosus* and, with less probability, *M. guatemalensis* to have originated from some *Mimomys*-like ancestor with negatively differentiated enamel;

2) If *A. pliocenicus*, either as a single species, or a complex of closely related sibling species (Martin & Tesakov, 1998) had been ancestral to all advanced *Microtus*-like species with rootless molars and positively differentiated enamel, the data on the molecular genetic and comparative genomic would have shown the latter as two subdivided reliably monophyletic clades, the Palearctic and the Nearctic ones subsequently, which, in turn, would have been the branches of a monophyletic Holarctic superclade of a high bootstrap support. Our mode of thinking about the matter is based on a comparatively recent age of *A. pliocenicus* fossil remains (about 2 Mya) and supposingly few amount of divergence between its forms even if the latter had been distinct species. Nevertheless, judging by the data on molecular genetics and comparative genomic of the common voles, the phylogenetic relationships between most of the Palearctic, or the Nearctic, or the Palearctic and the Nearctic species groups, are still quite uncertain.

The facts and the arguments presented above, make us suppose that, though being undoubtedly related forms of the same evolutionary level, the hypothetical ancestors to the advanced living common voles were much more ancient or (and) might have initially possessed a larger amount of genomic divergence between each other, than the forms of the *A. pliocenicus* complex. Thus, on the one hand, the extent of "phenomo-genomic" homology between those ancestors was presumably enough to channel under the similar environmental conditions their homologous morphogenetic pathways to the *Microtus*-like level of organization. On the other hand, the terms and the rates of the "genomic divergence", as well as its amount, that had already been accumulated between the ancestral groups by the time of their "departure" for the *Microtus* level, could mould such uncertain pattern of "molecular" phylogeny, which was shown by the data on the cytochrome *b* gene in the living *Microtus*-like species. Having summarized all those speculations we proposed a new scenario of mi-

crotines' evolution (Golenishchev & Malikov, 2004) according to which: 1) the ancestors to all the living Nearctic *Microtus*-like voles, dispersed to America from Eurasia before the Quaternary, being at the *Mimomys* evolutionary level; 2) the amount of divergence between the *Mimomys* ancestors to the main molecular-genetic *Microtus* clades was considerably larger than it is used to be between any sibling species; and 3) in both of the continents the *Mimomys* lineages had independently evolved into the clades of the living *Microtus*-like species via the *Allophaiomys* level of development. Our mode of thinking was influenced by a lump of quite old ideas, among which there were: E.R. Lankester's view, that "...under the term "homology" evolutionists have described and do describe two kinds of agreement - the one, now proposed to be called "homogeny", depending simply on the inheritance of a common part, the other, proposed to be called "homoplasy", depending on a common action of evoking causes or molding environment on such homogenous parts, or on parts which for other reasons offer a likeness of material to begin with" (Lankester, 1870: 42) (cited after Hall, 2003: 414); N.I. Vavilov's law of homologous series in variation (Vavilov, 1920); G.G. Simpson's comprehension of parallelism as "...the development of similar characters separately in two or more lineages of common ancestry and on the basis of, or channeled by, characteristics of that ancestry" (Simpson, 1961: 78) (cited after Hall, 2003: 420) and his approach to the relationships between homology, convergence, and parallelism, according to which "especially among more nearly related groups, the convergence is likely to involve homologous structures, as is also true of parallelism" (cited after Hall, 2003: 420); N.N. Vorontsov's idea, that a group, which has emerged in the result of the parallel evolution by means of natural selection of homologous mutations, should not be considered as a polyphyletic one, "because it is the parallel development on the base of the homologous mutating the descendants of some different lineages, which had quite considerably diverged from each other some when, have a tremendous capacity for, that was caused by similarity between the genotypes of the ancestors, and hence the common origination of the latter" (Vorontsov, 1966); B.K. Hall's notion about the convergent and at the same time parallel formation, according to which "Such overwhelmingly convergent evolution may reflect independent evolution when assessed at the level of the phenotypic character. At a deeper level of analysis, it yields insights into the evolution of the ancient genetic pathways and/or developmental processes that underlie character evolution, whether those characters are homologous or homoplastic" (Hall, 2003: 427). So, we accept synapomorphy not only as some unique state that is shared by all representatives of a monophyletic taxon with their common ancestor, in which such character had already been developed. It is also any morphogenetic "ambition" in common, which is based on the "phenomogenomic" homology the descending lineages share with each other, owing to their common origination. Such homologous evolutionary potency can be independently realized in different representatives of the group, especially if they pass through the same environmental history. In such case, the lineages of the same morphogenetic level, which have independently passed through the same "developmental conduit" (Martin & Tesakov, 1998), are to be lumped into a natural group, because that "conduit" was determined by the "phenomo-genomic state" of their common ancestor, no matter it was a species or a monophyletic group of a higher taxonomic rank. As concerns the Palearctic and Nearctic common voles, they manifest synapomorphy of such kind not only in the form of *Microtus*-like state of morphology, but in a homoplastic morpho-ecological radiation. Thus, we consider the voles of the tribe Microtini as a natural group, though their main subdivided lineages are thought to have independently got to the *Microtus*-like morphogenetic state from the presumably *Mimomys* evolutionary level of their hypothetical common ancestor.

In the light of the recent data on molecular genetics, the taxonomic structure of the tribe Microtini obviously needs changing. Each of the reliable "molecular" clades should have a definite taxonomic rank according to the hierarchy of their phylogenetic relations. However, as it was mentioned above, the problem is that the modern data on molecular genetics and comparative genomics of the common voles provide a lack of information about phylogenetic relations between the most of the reliably monophyletic groups. Nevertheless, we consider that some preliminary steps towards the taxonomic revision of the Microtini can be made even now. As far as the Palearctic clades of the grey voles, which were considered as subgenera of the genus *Microtus*, turned out to diverge from each other no less, than from the Nearctic branches, each of them seems likely to need a rank of a distinct genus. All the American forms can be conditionally lumped together into the genus *Mynomes* Rafinesque, 1817, where the forms, which have been regarded as the Nearctic representatives of the subgenus *Microtus* should be considered to comprise the nominative subgenus *Mynomes* of the same genus. The latter change, concerning the subgeneric name was already proposed by Pavlinov (2003). The American narrow-skulled voles *My.* (*St.*) *miurus* and *My.* (*St.*) *abbreviatus*, which are mentioned above as Nearctic vicariants of *M.* (*St.*) *greglis* can also be separated into a distinct subgenus.

Systematic interpretation

Order Rodentia Bowdich, 1821
Family Cricetidae Fischer, 1817
Subfamily Arvicolinae Gray, 1821
Tribe Microtini Miller, 1886
Genus *Mynomes* Rafinesque, 1817
Vocalomys Golenishchev & Malikov, **subgen. nov.**

Type species: *Microtus miurus* Osgood, 1901
Diagnosis: Voles of medium size with thick fur; tail short, bicoloured; dark stripe on head and anterior back
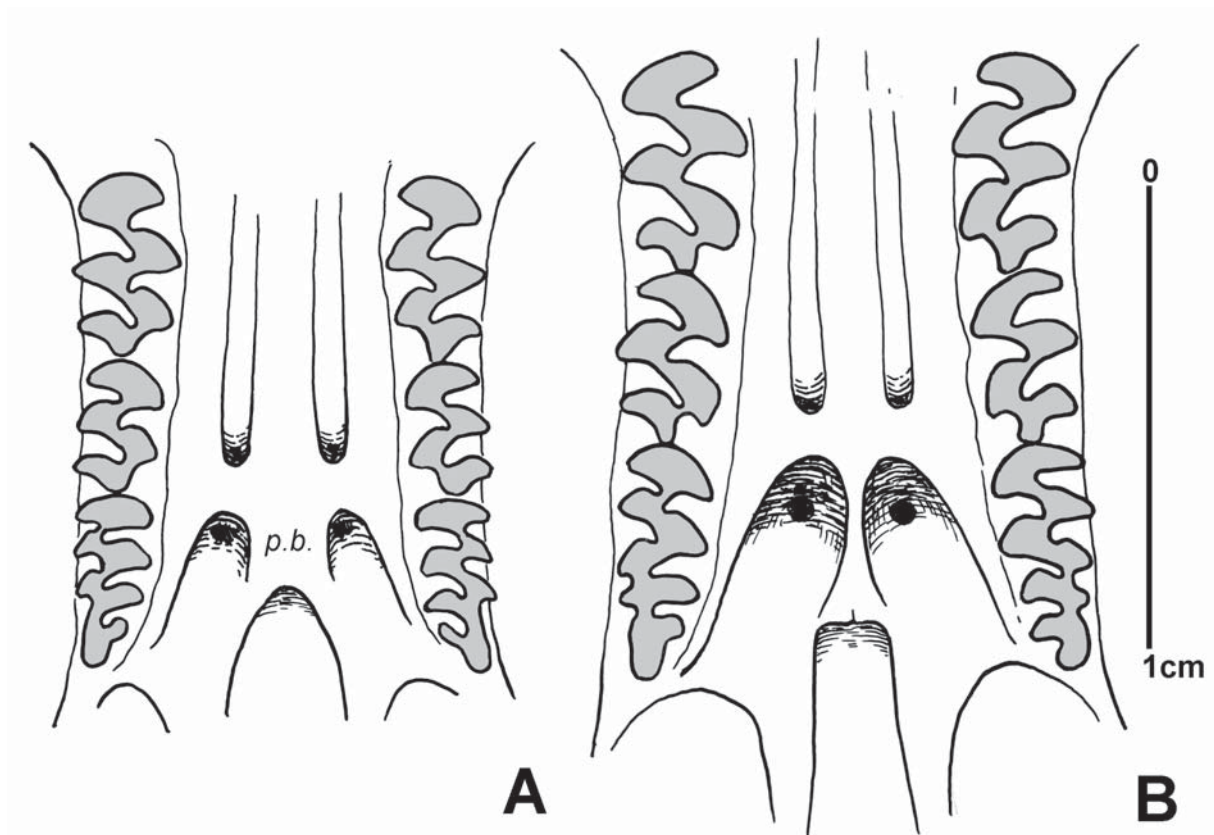
Figure 1. Palatal region of the skull in ventral view showing variation in the structure of the palatine bridge in *Mynomes* (*Vocalomys*) *miurus*, ZIN 40769 (A) and *Microtus* (*Stenocranius*) *gregalis*, ZIN 25399 (B). Abbreviation: *p.b.* — palatine bridge. Scale bar is 1 cm.

undeveloped; skull narrow with high braincase, narrow interorbital space, and well developed longitudinal crest. Skull shape similar to that of Palearctic *M.* (*St.*) *gregalis*; bony palate bridge broad and short; auditory bullae small, mastoids not enlarged. Paraconid section of m1 with second lobe complete and the lateral triangle completely isolated from anterior lobes; opposite triangles at base of paraconid isolated and have alternate position. Baculum large, the width of its base 30% of its total length and about 70% of the length of its column; the shoulders of the base either perpendicular to the column, or slanted; the lateral digital processes of the distal baculum either absent or not ossified for a long time as well as in the other *Mynomes*. Eight mammillae. 2n=54.

Differential diagnosis: Differs from all the other Nearctic voles in that it has narrower skull with the most narrow interorbital space and a higher braincase. The most of the morphological characters are plesiomorphic to those of the Palearctic subgenus *Stenocranius*. The Nearctic genus differs from its Palearctic vicariant in: 1) more simplified palate structure: smaller posterior palatal fossae together with shorter and broader palatal bridge (Fig. 1); 2) presence of distinct apertures in pterygoid bones (Fig. 2); 3) more complex paraconid with two complete lobes instead of 1.5 ones in *Stenocranius*, and "smiling" unpaired anterior loop (Fig. 3); 4) wider base of the baculum, which in the American species is about 70% of the column's length, while in the Eurasiatic one is no more, than 50%.

Species included: Type species only (including *My.*(*V.*) *abbreviatus* Miller, 1899)..

Distribution: In Alaska up to the Mackenzie River, in the East and up to N 60° latitude in the South; the Hall and St. Matthew islands in the Bering Sea.

The biotops and the mode of life: Semi-subterranean forms, inhabitants of tundra and meadows in the mountains and in the plains. Those voles are known to store the green parts of herbs in small hays. Because of its characteristic chirp the American narrow-skulled vole is called "singing vole".

Etymology: From Latin *vocalis*, singing.

The narrow-skulled voles as a life form: the evolutionary integrity of adaptive shifts and their initially inadaptive consequences

Some authors consider the narrowness of the skull as a direct adaptation of that life form to permafrost, where there are a lot of narrow splits (Gromov & Polyakov, 1977). As it was mentioned above, from our point of view, such amazing similarity in morphology between those vicariants is the result of the parallel-convergent evolution under the similar environmental conditions at the base of their phenomo-genomic homology. At the same time, the idea about the natural
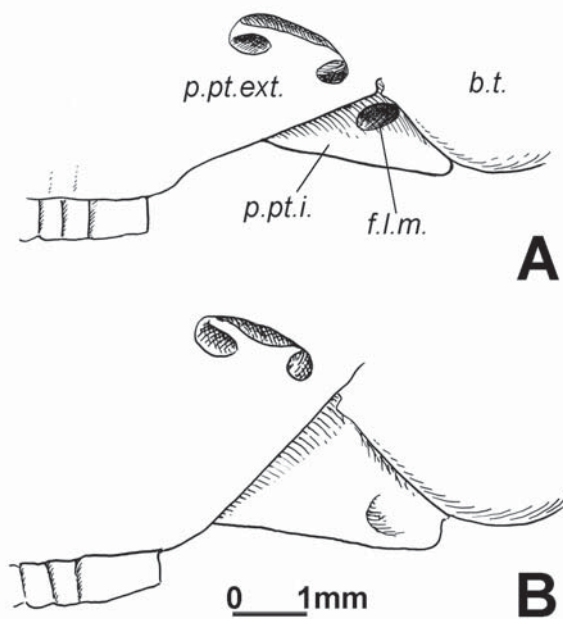
Figure 2. Lateral view of the skull showing structure of the processus pterigoideus internus of the basisphenoid in *Mynomes* (*Vocalomys*) *miurus*, ZIN 71075 (A) and *Microtus* (*Stenocranius*) *gregalis*, ZIN 25399 (B).
Abbreviations: *b.t.* — bulla tympanica; *f.l.m.* — foramen lacerum medialis; *p.pt.ext.* — processus pterigoideus externus; *p.pt.i.* — processus pterigoideus internus. Scale bar is 1 mm.
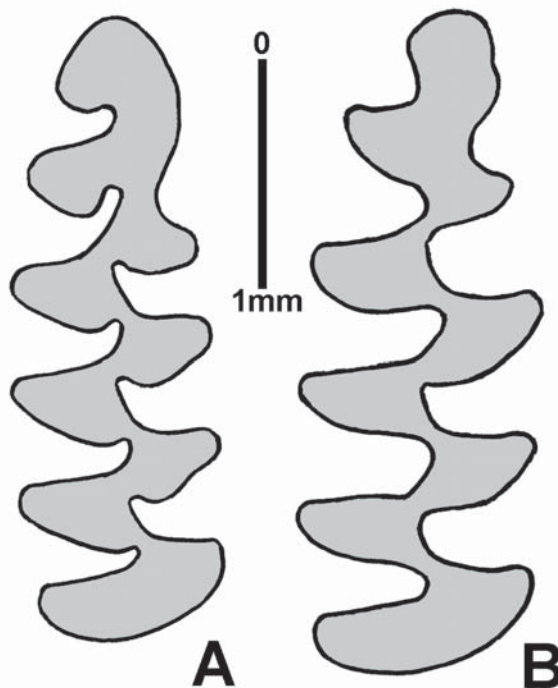

Figure 3. Occlusal view of m1 in *Mynomes* (*Vocalomys*) *miurus*, ZIN 40769 (A) and *Microtus* (*Stenocranius*) *gregalis*, ZIN 20097 (B). Scale bar is 1 mm.

selection that was initially directed towards the narrowness of skull seems us to be very naive, because it absolutely ignores the integrity of evolution. As early as in 1930-s it was already clear to D.N. Kashkarov, that most of the features, especially those ones, which are used in the identification keys, are of inadaptive nature, being a kind of stable "fellow-travelers" of the adaptive evolution as an integral process (Kashkarov, 1939). As in the result of the ontogenetic shifts, such inadaptive "coaches" are attached to the "locomotive" of the integral adaptive development, no wonder, that sooner or later they can emerge some serious problems for the evolutionary future of their owners (Chaikovsky, 2003). That's why evolution, as an integral process, is synergies between direct adaptations and adaptations to their stable inadaptive consequences (Malikov *et al*., 2006). As concerns the narrow-skulled voles as a life-form, their adaptive evolution under subarctic or alpine environmental conditions with extremely short periods of vegetation, low winter temperatures and a danger of summer droughts within the southern part of the Palearctic range, was directed to early sexual maturation that gives an opportunity to produce the maximum amount of offspring during the very short optimal season. For example in *M.* (*St*.) *gregalis* a pregnant female can be 12–13 days old (Chentsova, 1969).

The differences in the rates of growth and ontogenetic development are well known not only for distinct species (Golenishchev, 1982; Meyer *et al*., 1996) but for the geographical populations of the same species (Shvarts, 1980). For example, *M.* (*St*.) *gregalis major* Ognev, 1923 from Yamal Peninsula is characterized by considerably higher rate of growth, than the nominative subspecies from the southern part of the range (Pokrovsky & Bolshakov, 1979).

The comparison between the rate of growth of *M.* (*St*.) *gregalis* (Golenishchev & Petrovskaya, 2002) and that of *M. mujanensis* Orlov & Kovalskaja, 1975 (Meyer *et al*., 1996), which are of a quite similar size, showed that in the narrow-skulled vole the condylobasal length intensively enlarged up to the age of 1 month, while in the second species by the age of 3 months that process was almost finished. At the same time in *M.* (*St*.) *gregalis* the zygomatic width starts enlarging slowly by the age of 3 months, and in *M. mujanensis* it enlarges intensively up to the age of 5 months.

The sexual maturation is known to reduce the rate of growth. As far as *M.* (*St*.) *gregalis* is concerned, it was reported to stop growing and developing under unfavorable conditions, and then rapidly start those processes.

So we suppose that early sexual maturation of the narrow-skulled voles led to a very rapid longitudinal growth of the skull that is needed for achieving the optimal total size by the beginning of reproduction. At the same time, the high rates and early terms of the skull's longitudinal growth leave a lack of bioenergetics resources for increasing of the skull width. Further that initially inadaptive, though inevitable, shift in proportions might have become adopted to the narrow splits of the permafrost.

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