Vestnik zoologii, **51**(2): 99–110, 2017
DOI 10.1515/vzoo-2017-0015

DE GRUYTER
OPEN

UDC 575.83:569.323.4

PHENOMENON IN THE EVOLUTION OF VOLES (MAMMALIA, RODENTIA, ARVICOLIDAE)

L. I. Rekovets[1], O. M. Kovalchuk[2]

[1]*Wrocław University of Environmental and Life Sciences,*
Chełmońskiego st., 38C Wrocław, 50-630 Poland
E-mail: leonid.rekovets@up.wroc.pl
[2]*National Museum of Natural History NAS of Ukraine,*
B. Khmelnitskogo st., 15, Kyiv, 01030 Ukraine
E-mail: Biologiest@ukr.net

Phenomenon in the Evolution of Voles (Mammalia, Rodentia, Arvicolidae). Rekovets, L. I., Kovalchuk, O. M. — This paper presents analytical results of the study of adaptatiogenesis within the family Arvicolidae (Mammalia, Rodentia) based of morphological changes of the most functional characters of their masticatory apparatus — dental system — through time. The main directions of the morphological differentiation in parallel evolution of the arvicolid tooth type within the Cricetidae and Arvicolidae during late Miocene and Pliocene were identified and substantiated. It is shown that such unique morphological structure as the arvicolid tooth type has provided a relatively high rate of evolution of voles and a wide range of their adaptive radiation, as well as has determined their taxonomic and ecological diversity. The optimality of the current state of this group and evaluation of evolutionary prospects of Arvicolidae were presented and substantiated here as a phenomenon in their evolution.
Key words: Arvicolidae, Cricetidae, teeth, morphology, evolution, adaptation.

Introduction

Voles (family Arvicolidae) seem to be one of the most studied taxa within Holarctic rodents. However, this is the most difficult group in taxonomic, systematic and phylogenetic contexts. The need to use the methods of morphological and functional analysis of individual characters for addressing the issues of adaptatiogenesis, micro- and macroevolution, phylogeny of arvicolids was proved and substantiated earlier (Mehely, 1914; Hinton, 1926; Chaline, 1972; Gromov, Polyakov, 1977; Rabeder, 1981; Tesakov, 2004; Agadzhanian, 2009). The results of synthetic analysis of scrutiny of individual species of the family (including molecular data) are presented by Zagorodniuk (1990), Conroy & Cook (2000), Jaarola et al. (2003), Galewski et al. (2006), Robovsky et al. (2008), Piras et al. (2012), and others.

A wide range of the variability of structural and functional characters and their transformation in time and space is recently known for the members of the family Arvicolidae. Most of these characters are related to teeth and associated with a variety of conditions for existence (Maleeva, 1976; Nadachowski, 1992; Rekovets, 1994; Tesakov, 2004; Fejfar et al., 2011). It is reflected in morphological parallelisms that continually manifested in the transformation of masticatory apparatus and teeth during relatively short evolutionary history of the family, i. e. from late Miocene, MN 9 (Repenning, 1968; Shevyreva, 1976; Agadzhanian, Kowalski, 1978; Nesin, Topachevsky, 1991; Nesin, 1996; Nesin, Nadachowski, 2001; Agadzhanian, 2009). However, the issues of the comparative analysis of such data remain relevant, especially in the study of the early stages of formation of the arvicolid tooth type, and the parallelisms with their subsequent fixation in certain phylogenetic lineages (Rekovets, 2003).

Thus, the main purpose of this study is an attempt to find the features of adaptatiogenesis in the dental system as a phenomenal process in the evolution of masticatory apparatus in voles, especially at the early developmental stages of this group (late Miocene, MN 9–12). Here we present the analysis of data concerning the possible ways of morphogenesis of their teeth, forming of the arvicolid tooth type, and manifestation of the morphological parallelisms during the evolution of voles.

State of the problem and analytical results

At the heart of the evolution of adaptations lays the variability of characters (ontogenetic, spatial, and temporal), parallelisms and morphological correlation. Together they characterize the ability of organisms to respond on environmental changes, which ultimately reflect their level of adaptatiogenesis. The latter, using morpho-evolutionary rather than cladistic approach refers to the most important functional characters for the family Arvicolidae, such as the structure of masticatory apparatus. It is the most reliable criterion for taxonomic differentiation of voles. This structure reflects the level of their evolutionary advancement, taxonomic rank and systematic position. It is also a basis for biostratigraphic conclusions.

There were attempts of similar studies with the definition of trends in the evolution of voles (e. g., Kretzoi, 1969; Topachevsky, 1973; Maleeva, 1976; Shevyreva, 1976). This issue was reflected in the International symposia on the evolution and phylogeny in Arvicolidae (International…, 1990), as well as in a series of publications (Nadachowski, 1991; Nesin, Topachevsky, 1991; Abramson, 1993; Chaline et al., 1993; Rekovets, 1993; Nesin, Nadachowski, 2006; Fejfar et al., 2011).

Theoretical bases have been developed for the analysis of possible directions of transformation and adaptatiogenesis of molars in Arvicolidae. Based on these results, it is possible to characterize more soundly "advantages" of voles (both extinct and recent) as compared with other rodents:

1) great taxonomic diversity and significant amount of fossil remains throughout the Holarctic (arvicolids are the dominant group in the Neogene and Quaternary fauna);

2) members of this family have the most significant value in faunal analysis and reconstruction of temporal consistency of single faunal associations;

3) arvicolids reflect most clearly and convincingly morphological and evolutionary changes (adaptatiogenesis) of characters in separate lineages;

4) high variability and functional features of characters as structures transforming in time (apomorphies) define the individual morphological trends of voles — the basis for allocation of numerous phyletic lineages;

5) family Arvicolidae is characterized by the presence of well-defined parallelisms in the development and correlation of characters — a manifestation of the law of homologous series in genetic variability;

6) voles are the evolutionary model for creating the phylogenetic schemes based on morphological approach and DNA data analysis;

7) well-studied relations in the system "ancestor–descendant", and, therefore, relatively well-known the initial groups for extant species;

8) it is possible to trace the path of species migration in more detail and soundly, and to understand the history of consistent formation of their ranges;

9) species within the family Arvicolidae are dynamic components of faunal communities reflecting the successional processes in ecosystems;

10) voles are the most important group for analyzing palaeoecological conditions, as well as for palaeogeographic reconstructions.

Qualitative characteristics of the family Arvicolidae listed above determine their significance as a leading group in the field of general evolution, detailed biostratigraphy and faunistic correlations. Here we discuss the issues of morpho-functional analysis and adaptatiogenesis of the arvicolid tooth type (position 3 in the text), the direction of the morphological transformations at the initial stages of their evolution (position 4), and parallelisms in separate lineages (position 5).

Discussion

Morphogenetic processes within the family Arvicolidae reflect the morphology of their osteological characters, especially on teeth and jaws. These elements of the skeleton are most frequently encountered in fossil state in arvicolid taxa and other small mammals. Differences in diagnostic characters may be considered as the morphological chronoclines closely related to environmental conditions and stratigraphic levels. These trends characterize the evolutionarily stable morphology of this group and usually regarded as adaptations directed by the natural selection.

Adaptatiogenesis (fixing of adaptations in time under the influence of selection) of voles has a distinct focus on the statement of arvicolid type of the teeth and composed of differently directed, but morphologically limited adaptations (Maleeva, 1976; Rabeder, 1981; Rekovets, 1993). The limits of these adaptations are defined by the morphology at the actual evolutionary level; i. e. teeth can change depending on the environment only within their current morphology. It means that the development of arvicolid teeth is not a chaotic process, but limited to their morphology, which, together with the natural selection, is a guide mechanism for the evolution of this group. This is clearly visible in morphology of late Miocene rodents (Chaline, 1987; Chaline, Graf, 1988; Fejfar et al., 2011), and justified for molars in the evolutionary lineage *Allophaiomys–Microtus* or *Mimomys–Arvicola* (Rabeder, 1981; Heinrich, 1990; Rekovets, 1990, 1994; Maul et al., 2000).

For the above-mentioned genera and for the tribe Lagurini, tooth morphology can vary in time only (sic!) in limited possible directions, which form the developmental basis for separate lineages or monophyletic clades. An example may be the differentiation within the genus *Microtus* (subgenera *Terricola*, *Stenocranius*, *Pallasiinus*, *Microtus*), *Chionomys*, *Dicrostonyx*, *Lemmus*, as well as groups *Prolagurus–Villanyia–Lagurodon*, *Jordanomys–Kalymnomys*, *Promimomys–Mimomys–Arvicola*, *Pliomys–Clethrionomys*, etc.) (see Terzea, 1989; Topachevsky, Nesin, 1989; Nadachowski, 1992, 1992; Abramson, 1993; Rekovets, Nadachowski, 1995; Zazhigin, 2003; Abramson et al., 2009; Agadzhanian, 2009 for details).

The criterion of morphological differentiation is constantly manifested in the evolution of Arvicolidae and simultaneously reflects processes of adaptation and transformation of characters. It is characterized by correlations and parallelisms, reflects the breadth of adaptive radiation and the levels of evolutionary advancement. The action of natural selection in this case was focused on mechanics and morphology of occlusal surface of their teeth. Such strategy is a reflection of general aridification during the Pliocene (Shevyreva, 1976; Abramson, 1993).

A functional characteristics of the teeth of extinct Arvicolidae allows us to formulate their morpho-adaptive features as a rule of steadiness of the adaptatiogenesis: *adaptatiogenesis of a single taxon is determined by the variability of characters, manifested by the actual state of its morphology (metabolism for extant forms) under the influence of natural selection and is consistent with its evolutionary level.* The close relationship between morphological features of the taxa (in this case — Arvicolidae), their ability to adaptations (pre-adaptations), evolutionary advancement and correlation with certain stratigraphic level should be perceived in this definition. Morphological character may respond in a particular way to environmental conditions, which are guiding factors for the adaptatiogenesis and qualitative criterion through the action of natural selection.

Against this background of morpho-adaptive changes, the arvicolid tooth type has been occurred in parallel within the Cricetidae (*Baranomys*, *Germanomys*, *Stachomys*, *Betfiomys*, *Trilophomys*, *Microtoscoptes*) and was fixed in the first Arvicolidae, e. g. *Microtodon–*

Baranarviomys–Promimomys (fig. 1). This scheme does not reflect the phylogenetic relationship between the mentioned groups. It is just a schematic diagram of the possible morphological transformations of molars within the Cricetidae and Arvicolidae in time, since the second half of Miocene.

Morphological changes from the primitive Cricetidae with the bumps on teeth (e. g., in *Nanomys* and related genera) were possible in two main directions — the preservation of these dental bumps (*Cricetus*), or the fixation of morphology in the teeth erasure. Potential directions of the possible merger of dental bumps are diverse: *Collimys*, *Meriones*, *Rattus*, *Microtocricetus*, *Cricetodon*, *Baranarviomys* (Arvicolidae). Each of these directions yielded a number of intermediate (transitional) stages; all of them are connected with the respective stratigraphic level. However, our scheme is not tied to geological time as those

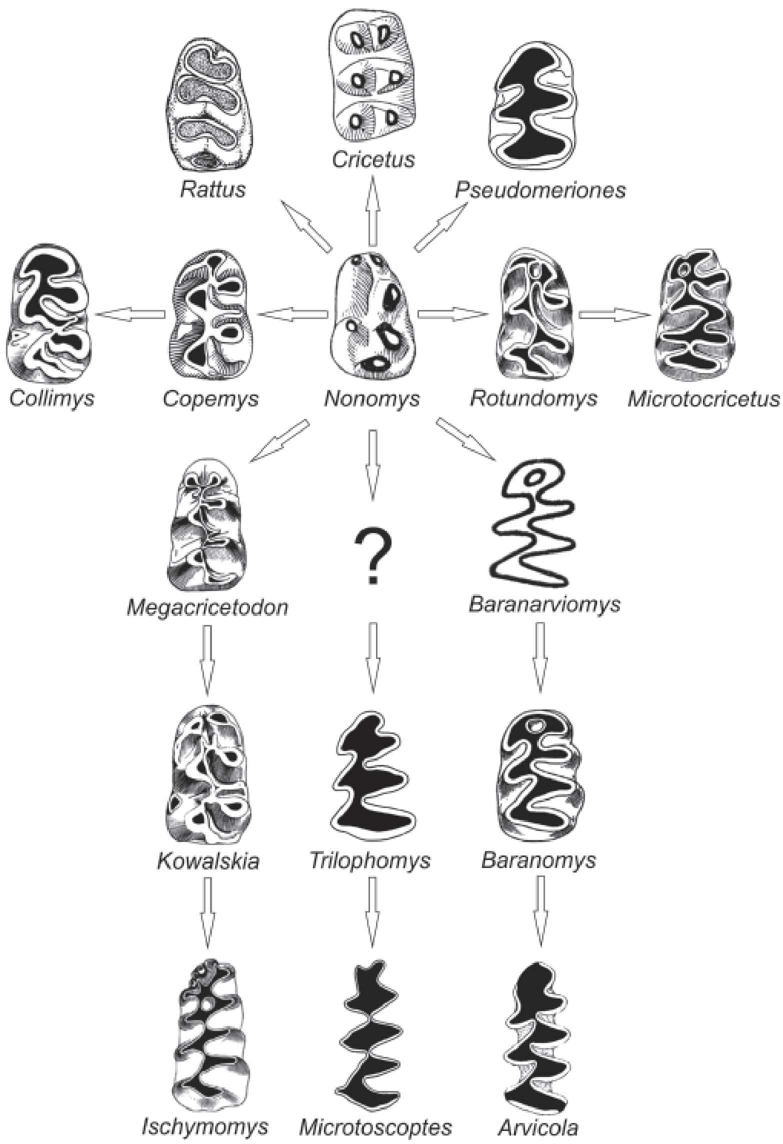

Fig. 1. Possible ways of the morphological differentiation of molar teeth within the Cricetidae and Arvicolidae. Images of single teeth were taken from special publications (Shevyreva, 1976; Nesin, 1996; Fejfar et al., 1998, 2011). Original material from the localities of Ukraine was also taken into consideration.

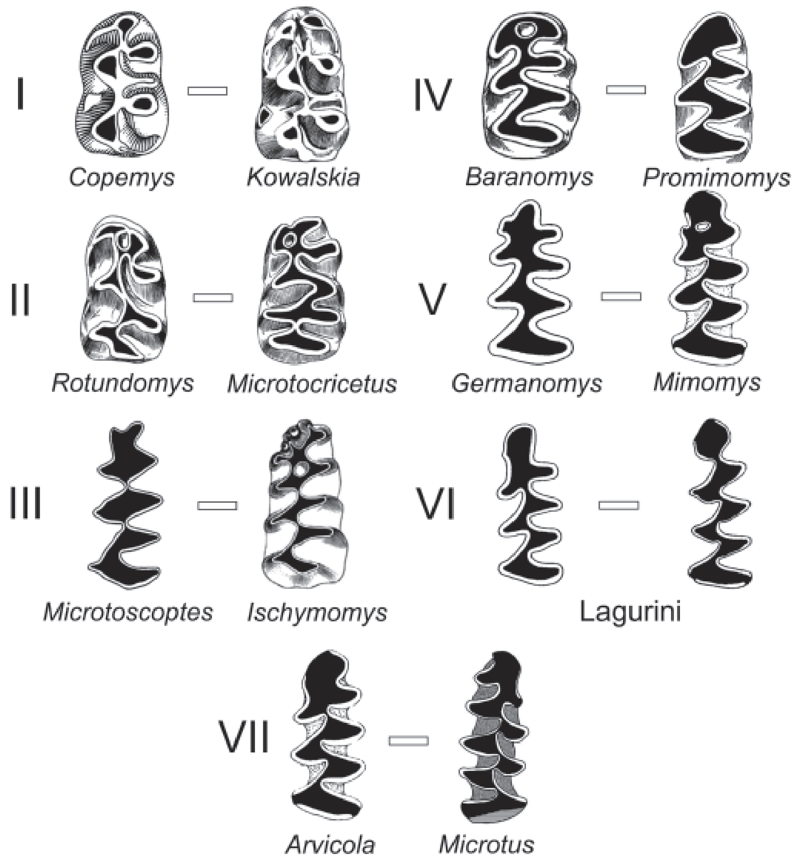

Fig. 2. Stages of complication of the m1 morphology (forming of the arvicolid tooth type) within the Cricetidae and Arvicolidae. Explanation — in the text.

presented by Maleeva (1976). The directions mentioned above include a number of morphological parallelisms. They are traced in detail for the arvicolid line of transformation. This primitive morphological structure can persist even in extant forms, such as *Ellobius*, *Prometheomys*, *Phajomys* (*Neodon*) and others.

Arvicolid tooth type and parallelisms of its manifestation is a phenomenon of the adaptation of voles, which allowed them to fill numerous ecological niches in modern coenoses, i. e. be able to biological progress, which undoubtedly was also typical for this group in geological past. Since the late Miocene, adaptatiogenesis within the Cricetidae and Arvicolidae proceeded through a series of successive phases of morphological changes of their teeth. The morphological phasing in complexity of their teeth in time is manifested as shown on the fig. 2[1].

Morphological parallelisms have been manifested especially at the initial developmental stages of arvicolid tooth type and were characteristic for late Miocene Cricetidae (fig. 2, I–III). They have been arranged as alternatively located dental prisms (*Trilophomys*, *Pseudomeriones*, partially *Microtoscoptes*) or relatively shifted to each other (*Ischymomys*). The anteroconid portion in advanced forms (*Paramicrotoscoptes*, *Ischymomys*) was complicated by folds and the mark.

[1] Here we present only the directions of possible morphological changes in time; these directions are not a real reflection of phylogenetic relationships between the representatives of Cricetidae and Arvicolidae.

The main elements of the arvicolid tooth type have appeared in primitive Arvicolidae (fig. 2, IV): posterior loop, anterior loop — anteroconid with (or without) the mark; protoconid, metaconid, entoconid (*Baranarviomys*, *Baranomys*, *Prosomys*, *Promimomys*). Pliocene forms (fig. 2, V), as late Miocene Cricetidae, have acquired the complicated anteroconid at the expense of the forming of additional fold (*Germanomys*, *Stachomys*, *Ungaromys*, partially *Pliomys*) and the mark (*Mimomys*, *Borsodia*). Then there was a reduction of the mark and folds of the anteroconid (*Prolagurus*, *Allophaiomys*, *Arvicola*). A complication of occlusal surface was due to the formation of additional dental prisms at the base of anteroconid. The cement was absent (fig. 2, VI) or gradually appeared (fig. 2, VII).

It has been occurred in parallel, almost independently, in different lineages of Cricetidae (Rekovets, 2003; Shevyreva, 1976; Fejfar et al., 2011). Such type of the teeth have appeared earlier in Cricetinae and was even more morphologically progressive than those in Arvicolidae. An example can be the species group of *Microtoscoptes–Ischymomys* from early late Miocene (MN 9), which have had more complicated teeth (mark, mimomys fold, corrugation of anteroconid) and recently regarded as the side specialized branch in the evolution of Cricetidae (Topachevsky, Nesin, 1992). Formation of the arvicolid tooth type in *Ischymomys* revealed a rather complex morphological structure for Cricetidae. It was too specialized for providing more progressive changes of their teeth during the Pliocene (Topachevsky et al., 1978; Topachevsky, Nesin, 1992). This specialization was based on relatively primitive morphological basis — the presence of roots, mark, mimomys fold, etc. Transient Pliocene forms of Cricetidae–Arvicolidae (*Baranomys*, *Baranarviomys*) were morphologically more primitive and regarded as initial forms for the Arvicolidae.

In terms of morphology and function, it is important to know why and how the arvicolid tooth type initially formed within the Arvicolidae as a parallel morphological structure in different phyletic lineages of the family. The evolution of such tooth type in Pliocene voles went not the way of complication of existing corrugated unpaired loop on the anteroconid (AC-1), but on the forming of additional elements at the base of anteroconid. The enamel mark and prism fold (*Ischymomys*) have appeared for the first time (during late Miocene) within the Cricetidae as progressive characters. However, later (in Pliocene) such characters became inadaptive for the Arvicolidae and underwent a reduction (*Promimomys*, *Pliomys*, species group of *Villanyia–Borsodia*, *Mimomys*). The evolution of teeth in voles during Pliocene followed the way of formation of additional elements and extension of the teeth (*Allophaiomys*, *Microtus*, tribe Lagurini). This direction has been supported by the natural selection, because it morphologically provides a functionality in food consumption which was more effective than those for Cricetidae or optimal for Arvicolidae (Topachevsky, Skorik, 1992). Natural selection has gained an inertia action in all lineages of Arvicolidae, as manifested through the complication of the occlusal surface of their teeth due to appearance of additional enamel prisms on M3 as well as T4, 5 on m1 at the base of paraconid (Markova, 2014; Borodin, Markova, 2015). The adaptatiogenesis of *Dicrostonyx* is the peak of this process.

Such parallelisms, which are inherent to closely related groups, have manifested in separate phyletic lineages of the Arvicolidae such as *Pliomys–Clethrionomys*, *Borsodia–Prolagurus–Lagurus*, *Mimomys–Allophaiomys–Microtus*, *Mimomys–Arvicola*. They clearly traced in separate lineages at the generic level (e. g., *Mimomys*, *Borsodia*, *Allophaiomys–Microtus*) many of which are regarded as side evolutionary branches. Such conclusions about the evolution of voles are based not only on the literature data, but they were also proved on the fossil material from Miocene and Pliocene localities in Ukraine.

Adaptive parallelism was particularly evident during the Pliocene, when the divergent evolution of Arvicolidae was the most intense. The above-mentioned morphological changes in all phyletic lineages of Arvicolidae have had different speed and were aimed at lengthening the teeth, especially the m1 (A/L ratio — the relative elongation of anteroconid) and M3, reduction of the mark and fold, as well as the loss of roots. The rate of such changes is different in individual lineages and in application to various teeth. The most evolutionary mobile and progressive were m1 and M3. The latter bears an ancient appearance. Other molars also changed, but they have not acquired such characters. Probably, it can be explained by their less significant functionality. The most revealing are *Mimomys*, *Borsodia*, *Pliomys*, whose molars have changed rapidly over time and reached the maximum of morphological diversity. Other forms, e. g. *Prometheomys* and *Ellobius*, appeared to be more conservative depending of numerous factors. Some species, e. g. *Microtus agrestis* and *M. socialis*, as well as *Dicrostonyx* and *Stenocranius*, represent a special group of morpho-ecological adaptations within Arvicolidae. In the latter case, narrow skull and all connected structures in representatives of the subgenus *Stenocranius* can be seen (along with other explanations) as a macromutation at the level of *Allophaiomys hintoni*; this mutation was supported by the natural selection, which, however, requires additional evidence. Numerous teeth of this species were found in the Karaj-Dubina locality (Ukraine, early Tiraspolian faunistic complex). It would be helpful to find the palatinum of this species, which could clarify the initial stages of formation of the narrow-skulled voles (subgenus *Stenocranius*).

Morphological adaptations of the extant species (narrow and elongated skull) yet do not fit into the usual scheme of explanation the evolution of Arvicolidae. Some Nearctic and Palearctic groups of the tribe Microtini are of independent origin from the genus *Mimomys*. The American narrow-skulled vole *Mynomes* was allocated to a separate subgenus *Vocalomys* (Golenishchev, Malikov, 2004, 2006). The parallel development of characters in paragenetically related groups of the Old and New World Arvicolidae is obvious.

Somewhat different than those for *Stenocranius*, was morpho-adaptive evolution of the collared lemming *Dicrostonyx*. It is characterized by the complication of m1. The M3 and other molars have additional enamel loops with their subsequent conversion into prisms (van der Meulen, 1973; Rabeder, 1981; Rekovets, 1994; Tesakov, 2004; Agadzhanian, 2009). Morphological changes of the teeth aimed at increasing complexity of their occlusal surface have affected the entire dental system within the *Praedicrostonyx*–*Dicrostonyx* (Agadzhanian, 1976; Zazhigin, 1976, 2003; Rekovets, 1983; Nadachowski, 1992; Rekovets, Maul, 2011). This group yielded a number of transitional forms with uncertain systematic position (Alexandrova, 1982; Rekovets, 2004). Appearance of additional prisms on all molars happened (and is happening) simultaneously based on their functional correlations.

Changes of characters in *Microtus agrestis* and *M. socialis* are slightly different. Additional small dental prism is developed only on M2 — a constant diagnostic character for *Microtus agrestis* and partially for *M. socialis*.

The appearance of cement on molars is characteristic in the evolution of most representatives of the family Arvicolidae unlike Cricetidae. This character is adaptive and can be regarded as apomorphy in relation to cricetids. Cement as a structural tooth element undoubtedly strengthens it, especially when the hard food is chewing. However, *Lagurus* and *Dicrostonyx* did not acquire this character. The evolutionary history of voles has many examples of the parallel occurrence of cement in *Promimomys*–*Mimomys*–*Arvicola*, *Promimomys*–*Mimomys*–*Allophaiomys*–*Microtus*, *Pliomys*–*Clethrionomys*, *Dolomys*. The important characteristics of this process are the initial stages of the cement appearance and its fixation in evolution, e. g. in *Dolomys* (Topachevsky, Nesin, 1989).

Representatives of the tribe Lagurini do not have the cement on molars, though they feed on rough-textured food in xerophilous conditions. This is somewhat inconsistent with the concept of adaptive traits in the Arvicolidae and requires further explanation. Probably, representatives of this tribe were not pre-adapted to that. The absence of cement on teeth of extant *Lagurus* towards its ancestors (*Promimomys–Cseria–Borsodia–Prolagurus*) can be evaluated as a plesiomorphy. The same we can say about the presence of roots on molars in Pliocene cricetids and arvicolids. However, roots gradually disappeared at the expense of pedomorphosis at the initial stages of the Plio-Pleistocene evolution of voles with subsequent fixation of teeth with constant growth (Rekovets, 1994). This transitional process in Arvicolidae was relatively fast (at the Plio-Pleistocene boundary), however, *Prolagurus* and *Lagurodon* have lost the roots on their molars slightly earlier than *Allophaiomys* (Topachevsky, 1973; Rekovets, Nadachowski, 1995).This pedomorphic process within Arvicolidae continues recently (*Clethrionomys*, *Prometheomys*, *Ellobius*). There are also other viewpoints on these characteristics (Tesakov, 2004).

An important character for the taxonomy and systematics of voles is a developmental stage of dentine tracts, which defines the edge of enamel coating on the inferior part of the tooth (Rabeder, 1981). This character is correlatively associated with the presence of roots and the hypsodont teeth (Nesin, 1988; Tesakov, 2004). Recently, it is still difficult to assess the adaptive value of this character, but it is believed that such dentine tracts (linea sinuosa) speeds the erasure process, and thus contributes to its more intensive growth. It can be argued that this character is highly variable in time and is characterized by the unidirectional development (elongation of tracts), as well as the parallelism in its manifestation in different taxonomic groups. The lowest tracts, resembling slightly wavy line, are in Cricetidae (*Microtodon*, *Ischymomys*, *Trilophomys*) and ancient Arvicolidae (*Baranomys*, *Baranarviomys*, *Polonomys*, *Promimomys*). Voles of the first half of Pliocene (*Mimomys*, *Borsodia*, *Pliomys*, *Dolomys*) are characterized by the higher (extended) dentine tracts. Later, in the second half of the Pliocene, many above-mentioned groups have had the most extended dentine tracts (linea sinuosa) reaching the occlusal surface.

In recent years, characters of the tooth enamel ultrastructure were included into the practice of taxonomy of the family Arvicolidae (Koenigswald, 1980, 1997). The functionality and adaptability of these characters is well known. It is shown the difference of the enamel structure in different taxa, levels of their evolutionary advancement (primitive and progressive enamel), as well as the enamel functionality in different parts of the tooth. The enamel has a similar structure (radial, tangential and lamellar), typical for the most of Arvicolidae. However, *Mimomys*, *Arvicola*, *Allophaiomys*, *Microtus* have all three major enamel layers; representatives of the tribe Lagurini have lost the tangential enamel; *Lemmus* has a specific “lemming” enamel layer, etc. The enamel structure is also susceptible to variability (especially in ontogeny), correlations (with hypsodonty) and, of course, to adaptatiogenesis, especially in different parts of the tooth (Koenigswald, Sander, 1997).

Contrasting climatic conditions during Pleistocene caused another rapid adaptatiogenesis within the Arvicolidae. It was manifested in a wide divergence of *Microtus* in the Holarctic during the early Pleistocene (van der Meulen, 1973). This genus is represented as a very dynamic structure having substantial variability both in time and in range, often with the status of uncertain taxonomic units (transitional forms, subspecies, semispecies, superspecies). Recently this genus is represented by hundreds of species occupying different ecological niches (Jaarola et al., 2003).

Morpho-physiological progress of the family Arvicolidae is manifested through a number of adaptations for digging, aqueous conditions, etc. These were characterized for the extinct Pliocene forms, whose adaptations were similar in similar habitat as evidenced by the morphology of their teeth. During the Plio-Pleistocene, voles have had a high genetic diversity, physiological adaptations and morphological variability (Gromov, Polyakov, 1977).

Conclusions

We can distinguish the patterns associated with a particularly inertial type of manifestation of the natural selection and evolution of Arvicolidae as a whole.

1. The family Arvicolidae is phylogenetically related to Cricetidae. The transition from the "cricetid" to "arvicolid" type in structure of their teeth is based on the change of their function and characteristics of the whole masticatory apparatus and aimed at more effective mastication during the late Miocene.

2. Since that time, arvicolids have got an opportunity to evolve rapidly due to wide range of their teeth variability. It allowed to appear a wide adaptive radiation: stabilizing selection has replaced the driving form of natural selection.

3. The most important functional characters along with the natural selection caused a big taxonomic richness and diversity of voles during Pliocene and Pleistocene. Related groups of rodents have formed the separate phyletic lineages with a significant expression of parallelisms and in the molar teeth morphology.

4. Unidirectional trend of morphological transformations of the teeth was determined by the finding of the most optimally adaptive structure of occlusal surface (teeth with alternately located prisms, with constant growth (i. e. without roots), an extended paraconid, without the mark, parallel fold and corrugating unpaired lobe).

5. The level of evolutionary advancement of the Arvicolidae is determined by the degree of development of their dental system, whose complexity is explained by the gerontomorphosis — phylogenetic fixation of characters inherent to adult ontogenetic stages (*Mimomys*, *Villanyia* (*Borsodia*), *Pliomys*, *Dolomys*), or by the pedomorphosis — phylogenetic fixation of characters inherent to juvenile stages (*Lagurodon*, *Ellobius*, the loss of roots in Pliocene genera).

6. Voles are characterized by the inertia of natural selection which is determined by pre-adaptations (or genetic predisposition) to the development of characters which are not depended from the environment.

7. Rapid evolutionary rates of Arvicolidae during relatively short period of time (5 Ma) are well correlated with parallel morphological changes of their molars.

Phenomenon in the evolution of Arvicolidae is connected with a relatively fast process of changing of their teeth functionality (from the crushing to chafing or milling the food) and the unidirectional transition to teeth with constant growth. All these changes have provided a wide range of adaptive radiation for voles. The natural selection with genetic processes in palaeopopulations has determined the development of individual phyletic lineages within Arvicolidae and their high taxonomic diversity in ecosystems. The problem of the evolution of voles exactly lies in the above-mentioned phenomenon. In spite of numerous publications, this issue still remains difficult, especially after the use of molecular methods for solving the problems of taxonomy, systematic and phylogeny within the family Arvicolidae.

We are indebted to Alexey Tesakov (Geological Institute of the Russian Academy of Sciences, Moscow, Russia) and Igor Zagorodniuk (National Museum of Natural History NAS of Ukraine, Kyiv, Ukraine) for providing valuable comments and advice that significantly improved our article.

References

Abramson, N. I. 1993. Evolutionary trends in the dentition of true lemmings (Lemmini, Cricetidae, Rodentia): functional-adaptive analysis. *Journal of Zoology*, **230**, 687–699.

Abramson, N. I., Lebedev, V. S., Bannikova, A. A. & Tesakov, A. S. 2009. Radiation Events in the Subfamily Arvicolinae (Rodentia): Evidence from Nuclear Genes. *Doklady Biological Sciences*, **428**, 458–461.

Agadzhanian, A. K. 1976. Polevki (Microtinae, Rodentia) pliocenovogo mestonahozhdenija Uryv 1, Srednij Don. *Proceedings of the Zoological Institute AS U.S.S.R.*, **66**, 58–97 [In Russian].

Agadzhanian, A. K. 2009. *Melkie mlekopitajushchie pliocen-plejstocena Russkoj Ravniny*. Nauka, Moscow, 1–776 [in Russian].

Agadzanian, A. K. & Kowalski, K. 1978. *Prosomys insuliferus* (Kowalski, 1958) (Rodentia, Mammalia) from the Pliocene of Poland and of the European Part of the U.S.S.R. *Acta Zoologica Cracoviensia*, **23**(3), 29–53.

Alexandrova, L. P. 1982. Novyj vid kopytnogo lemminga (*Dicrostonyx okaensis* sp. nov.) i ego znachenie dlja opredelenija vozrasta otlozhenij okskogo oledenenija lihvinskogo stratotipicheskogo razreza. *In:* Nikiforova, K. V., ed. *Stratigraphia i palaeogeographia antropogena*. Nauka, Moscow, 15–21 [In Russian].

Borodin, A. V. & Markova, E. A. 2015. Keys to identify modern and Pleistocene arvicolines (Arvicolinae, Rodentia) from the Urals and Western Siberia based on odontological characteristics. *Biology Bulletin*, **42** (7), 1128–1139.

Chaline, J. 1972. *Les Rongeurs du Pleistocene moyen et superieur de la France*. Paris, 1–410.

Chaline, J. 1987. Arvicolid Date (Arvicolidae, Rodentia) and Evolutionary Concepts. *Evolutionary Biology*, **21**, 237–310.

Chaline, J. & Graf, J.-D. 1988. Phylogeny of the Arvicolidae (Rodentia); Biochemical and Paleontological evidence. *Journal of Mammalogy*, **69**(1), 22–32.

Chaline, J., Laurin, B., Brunet-Lecomte, P. & Viriot, L. 1993. Morphological trends and rates of evolution in arvicolids (Arvicolidae, Rodentia): towards a punctuated equilibria/disequilibria model. *Quaternary International*, **19**, 27–39.

Conroy, C. J. & Cook, J. A. 2000. Molecular systematics of a Holarctic rodent (*Microtus*: Muridae). *Journal of Mammalogy*, **81** (2), 344–359.

Fejfar, O., Heinrich, W.-D. & Lindsay, E. H. 1998. Updating the Neogene Rodent biochronology in Europe. *In:* Kolfschoten, Th. v., Gibbard, P. L., eds. *The Dawn of the Quaternary*: *Proceedings of the SEQS — European symposium (Kerkrade, 16–21 June 1996),* **60**, 533–554.

Fejfar, O., Heinrich, W.-D., Kordos, L. & Maul, L. C. 2011. Microtoid cricetids and the early history of arvicolids (Mammalia, Rodentia). *Palaeontologia Electronica*, **14**.3.27A, 1–38.

Galewski, T., Tilak, M., Sanchez, S., Chevret, P., Paradis, E. & Douzeri, E. 2006. The evolutionary radiation of Arvicolinae rodents (voles and lemmings): relative contribution of nuclear and mitochondrial DNA phylogenies. *BMC Evolutionary Biology*, **6**(80), 1–17.

Golenishchev, F. N. & Malikov, V. G. 2004. Palaearctic and Nearctic common voles (Rodentia, Arvicolini): evolution and outlook. *Proceedings of the Zoological Institute RAS*, **300**, 83–90.

Golenishchev, F. N. & Malikov, V. G. 2006. The "developmental conduit" of the tribe Microtini (Rodentia, Arvicolinae): Systematic and evolutionary aspects. *Russian Journal of Theriology*, **5** (1), 19–26.

Gromov, I. M. & Polyakov, I. Ya. 1977. *Fauna SSSR. Mlekopitajushchie. Vol. 3, is. 8. Polevki (Microtinae)*. Nauka, Leningrad, 1–504 [In Russian].

Heinrich, W.-D. 1990. Some aspects of the evolution and biostratigraphy of *Arvicola* (Mammalia, Rodentia) in the central European Pleistocene. *In:* Fejfar, O., Heinrich, W.-D., eds. *International Symposium on the Evolution, Phylogeny and Biostratigraphy of Arvicolids (Rodentia, Mammalia)*. Geological Survey, Prague, 165–182.

Hinton, M. 1926. *Monograph of the voles and lemmings*. Vol. 1. British Museum (Natural History), London, 1–488.

International Symposium Evolution, Phylogeny and Biostratigraphy of Arvicolids (Rodentia, Mammalia). Rohanov (Czechoslovakia) May 1987. Pfeil Verlag, München, 1990, 1–448.

Jaarola, M., Martinkova, N., Gunduz, I., Brunhoff, C. & Searle, J. 2003. Molecular phylogeny of the vole genus *Microtus* based on the cytochrome B gene. *4th European Congress of Mammalogy* (Brno, 27 July–1 August 2003), Brno, 123.

Koenigswald, W. v. 1980. Schmelzstrukture und Morphologie in den Molaren der Arvicolidae (Rodentia). *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft*, **539**, 1–129.

Koenigswald, W. v. 1997. Evolutionary trends in the differentiation of mammalian enamel ultrastructure. *In:* Koenigswald, W. v., Sander, P. M., eds. *Tooth Enamel Microstructure*. Balkema, Rotterdam, 203–235.

Koenigswald, W. v. & Sander, P. 1997. Glossary of terms used for enamel microstructures. *In:* Koenigswald, W v., Sander, P. M., eds. *Tooth Enamel Microstructure*. Balkema, Rotterdam, 267–297.

Kretzoi, M. 1969. Skizze einer Arvicoliden-Philogenie-Stand 1969. *Vertebrata Hungarica*, **11**(1/2), 155–193.

Maleeva, A. G. 1976. Ob izmenchivosti zubov u polevok (Microtinae). *Proceedings of the Zoological Institute AS U.S.S.R.*, **66**, 48–58 [In Russian].

Markova, E. A. 2014. Assessment of Tooth Complexity in Arvicolines (Rodentia): A Morphotype Ranking Approach. *Biology Bulletin*, **41** (7), 968–980.

Maul, L., Rekovets, L., Heinrich, W.-D., Keller, T. & Storch, G. 2000. *Arvicola mosbachensis* (Schmidtgen 1911) of Mosbach 2: basic sample for the early evoluvion of the genus and a reference for further biostratigraphical studies. *Senckenbergiana lethaea*, **80** (1), 129–147.

Mehely, L. 1914. Fibrine Hungariae. *Annales Historico-Naturales Musei Nationalis Hungarici*, **12**, 155–243.

Meulen, A. J. van der. 1973. Middle Pleistocene smaller mammals from the Monte Pegalia (Orvieto, Italy) with special reference to the phylogeny of *Microtus* (Arvicolidae, Rodentia). *Quaternaria*, **17**, 1–144.

Nadachowski, A. 1991. Systematics, geographic variation, and evolution of snow voles (*Chionomys*) based on dental characters. *Acta Theriologica*, **36** (1–2), 1–45.

Nadachowski, A. 1992. Early Pleistocene *Predicrostonyx* (Rodentia, Mammalia) from Poland. *Acta Zoologica Cracoviensia*, **35** (2), 203–216.

Nesin, V. A. 1988. Diagnostika korennyh zubov drevnih Microtinae. *Vestnik Zoologii*, 2, 84–87 [In Russian].

Nesin, V. A. 1996. Drevnejshaja iskopaemaja polevka (Rodentia, Cricetidae) iz nizhnego ponta juga Ukrainy. *Vestnik Zoologii*, **3**, 74–75 [In Russian].

Nesin, V. A. & Nadachowski, A. 2001. Late Miocene and Pliocene small mammal faunas (Insectivora, Lagomorpha, Rodentia) of Southeastern Europe. *Acta Zoologica Cracoviensia*, **44** (2), 107–135.

Nesin, V. A., & Topachevsky, V. A. 1991. Drevnie etapy evoljucii polevkovyh (Rodentia, Microtinae). *Vestnik Zoologii*, **6**, 41–46 [In Russian].

Piras, P., Marcolini, F., Claude, J., Ventura, J., Kotsakis, T. & Cubo, J. 2012. Ecological and functional correlates of molar shape variation in European populations of *Arvicola* (Arvicolinae, Rodentia). *Zoologischer Anzeiger*, **251** (4), 335–343.

Tesakov, A. S. 2004. *Biostratigrafija srednego pliocena–eoplejstocena Vostochnoj Evropy*. Nauka, Moscow, 1–247 [In Russian].

Rabeder, G. 1981. Die Arvicoliden (Rodentia, Mammalia) aus dem Pliozän und dem älteren Pleistozän von Niederösterreich. *Beiträge zur Paläontologie von Osterreich*, **8**, 1–373.

Rekovets, L. I. 1983. Morfologicheskie osobennosti iskopaemyh kostnyh ostatkov gryzunov (Rodentia, Mammalia) iz pozdneplejstocenovyh mestonahozhdenij Pridneprovja Ukrainy. *In:* Manziy, S. F., ed. *Morfologicheskie osobennosti pozvonochnyh Ukrainy*. Naukova Dumka, Kiev, 53–56 [In Russian].

Rekovets, L. I. 1990. Principal developmental stages of the water vole genus *Arvicola* (Rodentia, Mammalia) from the Eastern European Pleistocene. *In:* Fejfar, O., Heinrich W.-D., eds. *International Symposium of Evolution and Biostratigraphy of Arvicolids* (Rohanov, May 1987). Prague, 369–385.

Rekovets, L. I. 1993. Osnovnye napravlenija morfologicheskih preobrazovanij korennyh zubov polevkovyh (Arvicolinae, Rodentia) vo vremeni. *In:* Topachevsky, V. A., ed. *Mlekopitajushchie Ukrainy*. Naukova Dumka, Kiev, 3–14 [In Russian].

Rekovets, L. I. 1994. *Melkie mlekopitajushhie antropogena juga Vostochnoj Evropy*. Naukova Dumka, Kiev, 1–370 [In Russian].

Rekovets, L. I. 2003. Morfologicheskie parallelizmy v evoljucii Arvicolidae (Rodentia, Mammalia). *In:* Abramson, N. I., Averianov, A. O., eds. *Taksonomija, filogenija i paleontologija melkih mlekopitajushchih*. Zoological Institute, St. Petersburg, 201–204 [In Russian].

Rekovets, L. I. 2004. Stratigraficheskie granicy i problema perehodnyh form v evoljucii gryzunov pozdnego neogena. *In:* Gozhyk, P. F., ed. *Problemy stratygrafii fanerozoju Ukrainy*. Institute of Geological Sciences NAS of Ukraine, Kiev, 191–194 [In Russian].

Rekovets, L. & Maul, L. 2011. The enigmatic *Ischymomys* — the same as or the sister of *Pannonicola*? New finds provide unexpected results. *In:* Horacek, I., Wagner, J., Cermak, S., eds. *Late Cenozoic Mammals: fossil record, biostratigraphy, palaeoecology. International Colloquim* (Praha, 16–19 May, 2011). Institute of Geology, Praha, 13.

Rekovets, L. & Nadachowski, A. 1995. Pleistocene voles (Arvicolidae) of the Ukraine. *Paleontologia i evolució*, **28–29**, 145–246.

Repenning, C. A. 1968. Mandibular musculature and the origin of the subfamily Arvicolinae (Rodentia). *Acta Zoologica Cracoviensia*, **13** (3), 29–72.

Robovski, J., Ricankova, V. & Zrzavy, J. 2008. Phylogeny of Arvicolinae (Mammalia: Cricetidae): utility of morphological and molecular data sets in a recently radiating clade. *Zoologica Scripta*, **37** (6), 571–590.

Shevyreva, N. S. 1976. O parallel'nom razvitii nekotoryh tipov zubnoj sistemy u gryzunov (Rodentia, Mammalia). *Proceedings of the Zoological Institute AS U.S.S.R.*, **66**, 4–47 [In Russian].

Terzea, E. 1989. Les Arvicolides (Rodentia, Mammalia) du Pleistocene moyen de Chiscau-1 (Depart. de Bohor, Roumanie). *Travaux de l'Institut de Spéléologie "Émile Racovitza"*, **28**, 57–72.

Topachevsky, V. A. 1973. *Gryzuny tamanskogo faunisticheskogo kompleksa Kryma*. Naukova Dumka, Kiev, 1–235 [In Russian].

Topachevsky, V. A. & Nesin, V. A. 1989. *Gryzuny moldavskogo i haprovskogo faunisticheskih kompleksov kotlovinskogo razreza*. Naukova Dumka, Kiev, 1–136 [In Russian].

Topachevsky, V. A. & Nesin, V. A. 1992. Novaja triba vymershih homjakoobraznyh Ishymomyini (Rodentia, Cricetidae). *Vestnik Zoologii*, 1, 28–32 [In Russian].

Topachevsky, V. A., Skorik, A. F. & Rekovets, L. I. 1978. Drevnejshie polevki triby Microtini (Rodentia, Microtidae) juga USSR. *Vestnik Zoologii*, 2, 35–44 [In Russian].

Topachevsky, V. A. & Skorik, A. F. 1992. *Neogenovye i plejstocenovye nizshie homjakoobraznye juga Evropejskoj chasti SSSR*. Naukova Dumka, Kiev, 1–244 [In Russian].

Zagorodniuk, I. V. 1990. Kariotipicheskaja izmenchivost' i sistematika seryh polevok (Rodentia, Arvicolini). Communication 1. Species composition and chromosome numbers. *Vestnik Zoologii*, 2, 26–37 [In Russian].

Zazhigin, V. S. 1976. Rannie etapy evoljucii kopytnyh lemmingov (Dicrostonychini, Microtinae, Rodentia) — harakternyh predstavitelej subarkticheskoj fauny Beringii. *In:* Kontrimavitchus, V. L., ed. *Beringija v kajnozoe*. AS U.S.S.R. Publishing House, Vladivostok, 280–288 [In Russian].

Zazhigin, V. S. 2003. O kopytnyh lemmingah (*Dicrostonyx*, Microtinae, Rodentia) Ojogos-Jara Vostochnoj Sibiri i o vidovom statuse sredneplejstocenovogo vida *roda Dicrostonyx*. *In:* Nikol'sky, P. A., Pitul'ko, V. V., eds. *Estestvennaja istorija rossijskoj vostochnoj Arktiki v plejstocene i golocene*. GEOS Publishing House, Moscow, 14–26 [In Russian].

Received 10 October 2016
Accepted 23 May 2017