

Arvicolines (Arvicolinae, Rodentia) as Paleoenvironmental Proxies: Classification of Species Inhabiting the Central Part of Northern Eurasia Based on Environmental Preferences of Their Modern Representatives

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Abstract—In order to identify uniform criteria for the classification of arvicoline species as paleoenvironmental proxies in studies of the environmental dynamics in the Late Pleistocene and Holocene, published data on the distribution and environmental preferences of modern Arvicolinae species inhabiting the central part of northern Eurasia have been compiled. For each of the 17 Arvicolinae species, the following characteristics were examined: (1) thermal neutral zone parameters and temperature preferences of adult individuals; (2) biotopical associations (i.e., the range of abiotic and biotic features of habitats used for breeding, feeding, expansion, and survival in unfavorable conditions), and (3) trophic preferences. It is shown for each of the study species that their most sustainable and conservative environmental preferences within their modern ranges relate to the requirements on the soil and vegetation properties of their breeding and/or survival habitats, as well as trophic specialization. Taking the factors limiting the modern distribution and abundance of the study species, a classification of the arvicolines inhabiting the central part of northern Eurasia based on their environmental preferences has been proposed. The classification specifies the parameters that can be reconstructed based on the species composition of arvicolines, as paleoenvironmental proxies, in micromammalian subfossil assemblages dating back to the Late Pleistocene and Holocene. It also contributes to a better understanding of the position of this taxonomic group within the entire complex of paleoecological proxies. This approach to the identification of environmental groups, based on the trophic specialization and characteristics of breeding and/or survival habitats, is universal for all representatives of the subfamily and may be used as a classification template for Arvicolinae species in any region of the Northern Hemisphere.

Keywords: paleoecology, arvicolines, environmental preferences, habitat preferences

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INTRODUCTION

Arvicolines (Arvicolinae, Cricetidae, Rodentia) are a subfamily of rodents the adaptive radiation of which has been developing throughout the Quaternary period amid the formation of modern ecosystems in the Northern Hemisphere. Because of their fast evolution, rich fossil chronicles, and broad geographic distribution range, arvicolines are traditionally used in biostratigraphic and biochronological studies (Agadjanian, 1979; Vangengeim et al., 2001; Tesakov, 2004; Maul and Markova, 2007). The existence of species with a certain environmental specificity makes it possible to use the subfamily representatives as paleoenvironmental proxies containing information of various levels: from main vegetation types at the regional and continental level to local biotopical parameters (Gromov and Polyakov, 1977; Agadjanian, 1979; Maleeva, 1989; Smirnov, 1990, 2001; Borodin, 1992, 2012;

Kolfschoten, 1995; *Evolyutsiya ekosistem...*, 2008). However, despite the, by now, traditional use of arvicolines in paleoenvironmental reconstruction studies, there are still no universal classification criteria for the modern fauna based on the environmental preferences of the species. The results of studies of modern faunal assemblages show that the same species may be elements of communities of different types (Gromov and Polyakov, 1977). At the same time, the biotopical association of a species may change in different natural zones in accordance with the habitat change principle (Maleeva, 1983). Within the same population, the range of habitats used by this species is variable as well and may change with cyclical changes in the population abundance and density (Sokolova et al., 2014) and depending on the weather conditions in different years or seasons (Litvinov and Panov, 1998). The difficulty of identification of the most significant environmental

parameters determining the presence and abundance of a species at a certain geographic point is the need for a critical approach to the formalization of the environmental preferences of a species. This becomes especially important when environmental preferences of modern species are extrapolated to their extinct conspecifics.

Modern Arvicolinae taxa can be used in paleoenvironmental studies encompassing the period from the Late Pleistocene to the present (i.e., the last 126000 years). Virtually all the modern species were present in the world fauna of the subfamily in the Late Pleistocene and Holocene. The reconstruction of environmental conditions in the period of formation of modern ecosystems is an objective of historical ecology (Savinetskii et al., 2005; Smirnov, 2006).

The purpose of this study was to identify environmental characteristics steadily featured throughout the entire ranges of modern species and classify the species by the most sustainable environmental preferences through the example of arvicolines of the modern fauna of the central part of northern Eurasia, including the species inhabiting this area in the Late Pleistocene and Holocene.

MATERIALS AND METHODS

This study was conducted with representatives of the Arvicolinae family inhabiting the central part of northern Eurasia, including the Urals. This region is a biogeographical intersection where species originating from the European and Asian sectors of the Palearctic realm encounter each other (Borodin et al., 2013). The following species were used in the analysis: *Ellobius talpinus* (Pall. 1770), *Clethrionomys rufocanus* (Sundev. 1846), *Clethrionomys glareolus* (Schreb. 1780), *Clethrionomys rutilus* (Pall. 1779), *Lagurus lagurus* (Pall. 1773), *Eolagurus luteus* (Eversmann 1840), *Myopus schisticolor* (Lill. 1844), *Lemmus sibiricus* (Kerr 1792), *Dicrostonyx torquatus* (Pall. 1778), *Ondatra zibethicus* (L. 1766), *Arvicola terrestris* (L. 1758), *Microtus oeconomus* (Pall. 1776), *M. middendorffi* (Poljak. 1881), *M. gregalis* (Pall. 1779), *M. agrestis* (L. 1761), *M. arvalis* (Pall. 1778), and *M. rossiaemeridionalis* (Ognev 1924). Except for the muskrat introduced in the 20th century and the East European vole the presence of which in the Late Quaternary fauna currently requires clarification, these species have been present in the fauna of the central part of northern Eurasia since at least the Late Pleistocene (Borodin, 2012). It is necessary to include the muskrat into the classification of environmental preferences of arvicolines due to the possibility to find subfossil remnants of this introduced species in the uppermost layers of Quaternary micromammal-bearing sites.

This study presents a critical synthesis of approaches to the classification of environmental characteristics of arvicolines used in paleoecology and

historical ecology (Jánossy and Kordos, 1976; Gromov and Polyakov, 1977; Galkina, 1980; Semken, 1980; Maleeva, 1983, 1989; Smirnov, 1990; Borodin, 1992, 2012; Kolfschoten, 1995; Dupal, 2005; etc.). For each of the species studied, out of the numerous formulations of environmental requirements used in paleoenvironmental studies, only those consistent with the requirements steadily featured throughout the maximum possible diversity of habitat conditions through the whole of the modern species habitat areas have been selected. For species with questionable positions in the existing classifications, formulations of environmental requirements based exclusively on neontological data have been proposed.

To characterize the temperature preferences of the modern species, the parameters of the thermal neutral zone and critical high temperature values for adult individuals (Bashenina, 1960, 1977; Aalto et al., 1993; McDevitt and Speakman, 1994; Peterson and Wunder, 1997; Wang, D.-H. and Wang, Z.-W., 2000; Safronov, 2009; etc.), as well as preferred temperature ranges (Kalabukhov, 1970), were used. Due to the lack of temperature preferences data for some species, data on the closest representatives of the same genus were used (Table 1).

The biotopical characteristics and trophic preferences were examined based on the published data (Krivoshchev, 1963; Ismagilov and Bekenov, 1969; Kalabukhov, 1970; Faber and Ma, 1986; Batzli and Lesieutre, 1991; Eskelinen, 2004; Panteleev, 2001; Sokolova, 2004; Tsvetkova et al., 2005; etc.). The diversity and biotopical association of feeding, breeding, expansion, and survival habitats within the modern ranges were taken into consideration. For widespread polyzonal species, the inclusion of habitat features into the classification was considered justified if the links with a certain type of soil and vegetation conditions could be tracked not only locally, but throughout the entire distribution range encompassing different natural zones. The inclusion of trophic features of a species into the classification was considered justified if, according to the literature data, a certain group of plants was not only its main food source, but also a factor determining the species distribution and/or its survival during a certain season. The association of habitats with local relief features was taken into consideration if, according to the literature data, such links were a mandatory precondition for the long-term existence of the species in a certain area or a mandatory precondition for burrowing. The traditional terminology was used for the classification of relief forms by height (*Geologicheskii slovar'*, 1978).

The modern habitat areas of voles were examined based on the literature data (Shenbrot and Krasnov, 2005).

The traditional concepts of the subfamily taxonomy (Pavlinov, 2003) were used in the study with slight changes. For instance, we use *Clethrionomys* Tilesius

Table 1. Temperature preferences of voles

Species	Environmental temperature values, °C	Source
<i>Ellobius talpinus</i>	TN 26	Moshkin et al., 2001
<i>Eolagurus luteus</i>	TN 23–27, P 17.9–37, on average, 24–26	Kalabukhov, 1970
<i>Lagurus lagurus</i>	CH 27–35, on average, 30; TN 20–30 (1); P 22.9–30.8, on average, 27.2–28.0 (2); P 14.6–42.5, on average, 27.0–28.9 (3)	(1) Bashenina, 1960; (2) Livchak, 1960; (3) Kalabukhov, 1970
<i>Microtus gregalis</i>	P 15.2–38.1, on average, 23.6–26.0 (1); P 24–27 (2)	(1) Livchak, 1960; (2) Safronov, 2009
<i>Microtus arvalis</i> s. l.	TN 20–30, CH 27–33 (on average, 30)	Bashenina, 1960
<i>Microtus agrestis</i>	CH 32 (1); TN up to 25 (2)–30.9 (3)	(1) Gebczynski, 1989; (2) McDevitt and Speakman, 1994; (3) Slonim, 1961
<i>Microtus middendorffi</i>	P 12.2–22.6, on average, 16.6	Livchak, 1960
<i>Arvicola terrestris</i>	TN up to 28–30 (1); P 26–28.1 (2)	(1) Vincent, 1974; (2) Panteleev, 2001
<i>Microtus oeconomus</i>	TN in Sakha (Yakutia) Republic: 20–24 in May and 17–20 in December (1), in Tibet: 28–32.5 (2)	(1) Safronov, 2009; (2) Wang, D.-H. and Wang, Z.-W., 2000
Genus <i>Dicrostonyx</i> (<i>D. groenlandicus</i>)	TN 15–20 (1), 21–23 (2)	(1) Peterson and Wunder, 1997; (2) Powell et al., 2002
<i>Lemmus sibiricus</i>	P for <i>L. sibiricus</i> 12.9–19.0 (1); CH for <i>L. lemmus</i> 28 (2)	(1) Livchak, 1960; (2) Hissa, 1970
<i>Myopus schisticolor</i>	TN 20–24	Saarela and Hissa, 1993
<i>Clethrionomys glareolus</i>	P 18–23 (2); TN up to 32.3 (2), 25–30 (1)	(1) Aalto, 1993; (2) Slonim, 1961
<i>Clethrionomys rufocanus</i>	TN 15–25 (1); P 22–23 (2)	(1) Safronov, 2009; (2) Kusumoto and Saitoh, 2007
<i>Clethrionomys rutilus</i>	TN 15–25	Safronov, 2009

Thermal neutral (TN), preferred (P), and critically high (CH) values of the environmental temperature for adult individuals are provided. For the values obtained from several sources, source numbers are provided in brackets.

1850 as a valid name for red-backed voles (instead of *Myodes* Pallas 1811) in accordance with the taxonomic interpretations of Tesakov et al. (2010). We consider the North Siberian vole (*M. hyperboreus*) conspecific to *M. middendorffi*. Due to their significant ecological similarity, for the purposes of this study, twin species from the “arvalis” group were examined together and defined as *M. arvalis* s. l.

The taxonomy of voles is currently broadly discussed due to the significant amount of accrued molecular genetic data and assignment of the generic status to some subspecies (Pavlinov and Lisovskii, 2012). However, taking the lack of a universally established view on the taxonomy of some subfamily members, we consider it appropriate to use the traditional nomenclature in this study.

RESULTS

Voles as Temperature Indicators

The idea to reconstruct the temperature conditions of the past based on the species composition of subfossil vole complexes was suggested by Hungarian researchers (Kretzoi, 1957; Jánossy and Kordos, 1976;

Kordos, 1977). The so-called “vole thermometer method” employed the use of optimal temperatures of modern model vole species for the reconstruction of optimal temperatures of the warmest month within the habitat areas of the same species in the Late Pleistocene and Holocene. The “optimal” temperatures were considered the averaged temperature values within the habitat areas of the most widespread Eurasian voles (Jánossy and Kordos, 1976). However, in reality, temperature reconstruction data based on the vole species composition may contradict data obtained for the same area through similar reconstruction studies based on different biotic markers, for instance, mollusks and vegetation (Magyari, 2002). In our opinion, such inconsistencies may originate not only from taphonomic features and local biotopical differences (Magyari, 2002), but also from insufficient justifiability of the temperature preference assessments for the species studied.

The analysis of data on the thermal neutral zone of voles inhabiting the central part of northern Eurasia (Table 1) indicates a discrepancy between the temperature preferences used in the framework of the “vole thermometer method” and empirical data obtained through heat exchange experiments. The

interspecies differences are manifested not so much by the absolute values of thermal neutral temperatures as by their amplitude. For instance, for adult individuals of the majority of the study species, the upper threshold of the thermal neutral zone does not exceed 27–30°C. Even the species currently associated with the southern latitudes, for example, *L. lagurus*, demonstrate changes in heat exchange parameters at such temperatures with a possible lethal outcome (Bashenina, 1960).

At the same time, the thermal neutral zone parameters feature geographic and seasonal variability. For instance, temperatures in the range of 28–32°C are considered optimal for *M. oeconomus* in Tibet (Wang and Wang, 2000), while in the Sakha Republic, these values are lower: 20–24°C in May and 17–20°C in December (Safronov, 2009). Therefore, taking the variability of the thermal neutral zone borders (both the seasonal variability and that within the species' ranges), the thermal neutral zone parameters cannot be used as species-specific markers of the environmental temperature.

A comparison of the temperature preferences calculated on the basis of the modern distribution ranges (Jánossy and Kordos, 1976) with heat exchange data (Table 1) makes it possible to conclude that for the species inhabiting the modern tundra, the preferable temperature values are significantly underestimated if such temperatures are calculated based on the averaged temperature values within the modern distribution range. Thermal neutral zone parameters for the Arctic lemming are comparable with those for wood voles belonging to the genus *Clethrionomys* and inhabiting the temperate zone (Table 1). This is because the biology of these subfamily representatives provides a relative independence from the macroclimate due to their ability to exist in specific microclimatic conditions. In addition, even species such as the Arctic lemming, defined by the "vole thermometer method" as a species with low optimal temperatures, features an increase in the population in the modern tundra with an increase in the average monthly temperatures of July and August (Shelford, 1943 quoted from Chernyavskii and Tkachev, 1982). This confirms that temperatures lower than 15°C are not preferable for the Arctic lemming, as well as for other species inhabiting the modern tundra.

Therefore, the thermal neutral zone parameters for all voles inhabiting the central part of northern Eurasia overlap in the range of 19–26°C. The species studied feature a high potential to change their thermal neutral zone parameters depending on the external conditions; this makes it impossible to reconstruct the temperature characteristics of the environment based on the vole species composition or the ratio between the vole species.

Voles as Indicators of the Moisture Regime

The reconstruction of moisture parameters of the environment on the basis of the species composition and structure of the vole fauna is traditionally based on estimation of the share of species associated with humid intrazonal habitats (*A. terrestris*, *O. zibethicus*, and *M. oeconomus*) or with arid conditions close to modern steppe conditions (*E. luteis*, *L. lagurus*, and *E. talpinus*) (Jánossy and Kordos, 1976; Gromov and Polyakov, 1977).

Based on the literature data on biotopical associations, vole species inhabiting the central part of northern Eurasia are traditionally divided into three groups: hygrophilous, mesophilous, and xerophilous species. The borders between hygro- and mesophilous species, as well as between xero- and mesophilous ones, are conditional. However, the differences between hygrophilous and xerophilous species are very clear. It is known that for mesophilous species, like *M. arvalis* s. l., the combination of temperature and moisture parameters is a key factor determining the spatial distribution of habitats: from upland dry ones in the north to lowland humid ones in the south (Bashenina, 1962). Various degrees of links with the habitat humidity in different seasons or in different regions are also typical for the water vole (Pantelev, 2001).

The link with the moisture characteristics of habitats is more distinct for arvicolines than the link with temperature conditions of the environment; however, this is not a direct link. It is determined by certain soil and vegetation conditions formed at the relevant moisture level. Therefore, it is more correct to speak about voles not as hygro-, meso-, and xerophilous species, but as species inhabiting the respective hygrophytic, mesophytic, and xerophytic plant communities.

The chemical composition of soils, including the acid–alkaline balance determining the phytocoenosis features, is also linked with the moisture regime. We do not possess data on the effect of the chemical composition of the soil horizon on voles; however, it is possible to identify for some species the degree of their tolerance to changes in the acid–alkaline balance of soils based on their ability to survive in solonchak conditions or in oxylophilous swamp phytocoenoses. For instance, the tundra vole can be considered, from the perspective of the acid–alkaline balance of phytocoenoses used by it, an eurybiotic species inhabiting salt marshes of southern Slovakia (Turček, 1976) and oxylophilous swamp communities of northern Eurasia. In both cases, the species distribution is determined by the sufficient humidity of the habitats and forage consumed.

The important role of mugworts, representatives of glycohalophytic flora resistant to elevated soil salinity, has been noted in the diet of the modern yellow steppe lemming in addition to the ability of this species to live on solonets soils in mugwort–saltwort biotopes (Ismagilov and Bekenov, 1969).

Voles as Indicators of Landscape and Biotopical Characteristics of the Environment

Environmental rodent groups are traditionally divided in paleotheriology by their affiliation with faunal assemblages taking into consideration the biotopical associations of the modern species and zonal location of their habitat areas (Gromov and Polyakov, 1977; Agadjanian, 1979; Maleeva, 1983, 1989). In particular, three groups are identified by the type of their preferred biotopes: inhabitants of open spaces, riverside (intrazonal) biotopes, and forest habitats subdivided into biotopical and subzonal groupings (see the review and classification by Maleeva (1983)). Various researchers define the composition of a group of species inhabiting riverside (intrazonal) biotopes more or less definitively: it includes species with clearly manifested fidelity to wet and waterside biotopes of freshwater bodies (*O. zibethicus*, *A. terrestris*, and *M. oeconomus*) (Gromov and Polyakov, 1977). However, with regards to the group identified based on the landscape and zonal characteristics, the existing classification systems demonstrate significant inconsistencies. One of the reasons behind such inconsistencies is underestimation of the habitat change principle when the same species occupies different biotope types in different landscape zones (for more detail, see Maleeva, 1989).

After the generalization of approaches to the classification of environmental characteristics of voles (Gromov and Polyakov, 1977; Semken, 1980; Borodin, 1992, 2012; Kolfshoten, 1995; Smirnov, 2001) and data on the ecology of modern forms, we have suggested distinguishing groups on the basis of the soil and vegetation characteristics of their habitats. Out of all the diversity of the species habitats, the most conservative throughout the habitat areas are the parameters of the breeding and survival habitats. These habitats become the locations of a high concentration of the animals during the phases of their low abundance and determine the species survivability under unfavorable conditions. A lack of certain biotope types is mentioned as a limiting factor for the so-called intrazonal species group (muskrat, water vole, and tundra vole) traditionally considered species of wetland biotopes with hydrophytic and hygrophytic vegetation (Vincent, 1974; Panteleev, 2001). Xerophytic dwarf shrub biotopes are named the factor determining the summer expansion of Arctic lemmings (Rodgers and Lewis, 1986); Xerophytic mugwort or mugwort—saltwort biotopes are a limiting factor for yellow steppe lemmings (Ismagilov and Bekenov, 1969), and mesophytic forest and shrub biotopes determine the expansion of voles belonging to the genus *Clethrionomys* (Borodin, 1992). The limiting factor for the species *Clethrionomys* is believed to be not the lack of trees and shrubs, but the lack of natural refuges (*Evropeiskaya ryzhaya polevka*, 1981); however, the genus population

is largely linked with the fruit and seed harvest of trees and shrubs.

Another important environmental characteristic determining the spatial and biotopical distribution of voles is the relief type. Meso- and microrelief elements (elevation differences up to 100 and 10 m, respectively) determine the spatial distribution of suitable habitats, while the nanorelief (elevation differences up to 1 m) determines their protective properties (mounds, holes, stony placers, etc.).

Almost all vole species in different seasons or under different weather conditions may change their habitat locations based on microrelief elements (spring habitats are located on slopes with exposure to the south, while winter habitats are located on lowlands or elevated areas). For the majority of the species, the link with microrelief features is noted as an adaptation to local conditions, but it cannot be considered an environmental preference. For three species (water vole (Panteleev, 2001), Middendorff's vole (Krivosheev, 1963), and yellow steppe lemming (Ismagilov and Bekenov, 1969)), the mosaic landscape structure with the formation of various moisture conditions on meso- and microrelief elements is named an essential condition for the long-term existence of the population within the same area, at least, throughout a major part of the habitat area.

The species' link with the degree of nanorelief manifestation may be demonstrated in relation to the nesting. Some Arvicolinae representatives steadily demonstrate this link in various parts of their habitat areas. Based on their burrowing requirements, all the vole species studied may be divided into three groups: (1) species creating complex holes directly in the soil; the spatial distribution pattern of the holes is indirectly linked to the micro- and mesorelief features (*E. talpinus*; *M. arvalis* s. l., *M. gregalis*, *L. lagurus*, and *E. luteus*); (2) species creating simple holes and nests in natural shelters—nanorelief elements, including those formed by tree roots (all the wood voles), located between stones (gray red-backed vole and wood lemming), and mostly in grass sod or ground cover (field vole); and (3) species creating various holes and nests, from underground to surface ones, depending on the season or local conditions (*O. zibethicus*, *A. terrestris*, *M. oeconomus*, *M. middendorffi*, *Dicrostonyx*, and *Lemmus*).

For the first group, the factors determining the possibility to create holes include the availability of open habitats well-drained in summer and not freezing through in winter. The softness of the ground is a mandatory condition only for summer habitats of the common vole and its twin species the southern vole. For the species of the second group, the possibility to create holes is determined by the availability of natural surface nanorelief (wood voles) or by the specific soil and vegetation conditions: the availability of grass sod (field vole) or moss (wood lemming). The species of

the third group are most labile with regards to nesting and do not have clear burrowing preferences.

Trophic Specialization

Voles are highly specialized phytophagous animals adapted to consuming fiber forage (Gromov and Polyakov, 1977; Agadjanian, 1996); a high, normally predominant, share of graminoids and forbs in the ration is typical for virtually all of them. However, there are vole species with clearly defined trophic features that can be used for reconstruction of the respective environmental parameters.

For instance, representatives of the genera *Lemmus* and *Myopus* may be used as indicators of the presence of moss cover (Hissa, 1970; Chernyavskii and Tkachev, 1982). Arctic lemmings specialize in dwarf shrubs: this is typical for all the species of the genus, including *D. torquatus*, *D. groenlandicus*, and *D. Hudsonius*, the ration of which consists mostly of willows and, taking the regional and local specificity, of mountain avens, birches, and Ericaceae (Chernyavskii and Tkachev, 1982; Rodgers and Lewis, 1986; Naughton, 2012). The importance of mugworts in the diet of *E. luteus* (Ismagilov and Bekenov, 1969; Dupal, 2005) makes it possible to link this species with xerophytic associations involving the genus *Artemisia*. The adaptation to consumption of underground plant parts is typical for *E. talpinus*, while the lack of underground phytomass of herbaceous plants may be considered a limiting factor. An increased diversity in the diet due to the consumption of protein-containing foods (primarily, fruits, seeds, and foods of animal origin) is typical for red-backed voles, while the abundance of species belonging to this genus is almost universally determined by the yield of trees and shrubs (Ognev, 1950; *Evropeiskaya ryzhaya polevka*, 1981). The trophic preferences of the muskrat, the water vole, and the tundra vole include inter alia juicy foods (a certain species composition of the plants consumed and predominance of nonchlorophyllous plant parts in the diet). The rest of the species are typical specialized herbivorous animals whose diet includes mostly forbs and graminoids.

Phenotypic Adaptations as an Indicator of the Environmental Preferences of Species

The formation of phenotypic species-specific adaptations to a certain way of life in mammals is normally a result of longtime evolution. This process develops over time intervals beyond the scope of the periods examined by historical ecology. However, the existence of ecologically determined phenotypic adaptations, regardless of the time of their appearance, may make it possible to identify the environmental preferences of the species and the degree of their evolutionary sustainability.

The adaptive radiation of Cricetidae, in general, and arvicolines, in particular, which has been developing from the Late Miocene—Early Pliocene, was linked with the exploitation of the ecosystem ground cover and highly productive grass communities. This is reflected in the structure of the body and limbs on the one hand and in the dentition and digestive tract morphology on the other hand.

Unlike other rodents (e.g., jerboas or dormice inhabiting desert landscapes and broad-leaved forests, respectively, since the Miocene (Agadjanian, 1979) and featuring clear adaptations in the structure of their body and limbs), voles are able to confine themselves to relatively small spaces of the ground layer. Belonging mostly to a single adaptive type (the aboveground terrestrial one), some species have acquired individual features of typical burrowing animals (e.g., the northern mole vole) or swimmers (e.g., the muskrat, water vole, and, to a lesser degree, the tundra vole (Gromov and Polyakov, 1977)). The specialization of the above vole species in the aquatic way of life is manifested mostly through the structure of their soft tissues, which are typically not preserved in the fossils. The features associated with the adaptation to the underground way of life are more distinct and can be tracked: for instance, by skull and incisor configuration features linked with the burrowing function.

An interesting adaptation of Arctic lemmings to the seasonal periodicity is the presence of winter claws enabling them to dig up the snow effectively. The genus includes island forms with unclear taxonomic status: *D. groenlandicus unalascensis* and *D. g. stevensoni* (MacDonald and Cook, 2009) living in the oceanic climate and having no such claws. It is possible to suppose therefore that this adaptation was formed relatively recently and that the ancestors of modern Arctic lemmings might not necessarily possess it.

The adaptation of the dentition system of the Arvicolinae to high-fiber forages is manifested most clearly through the structure of their cheek teeth. The study species can be divided into three groups: mesodont (with low crown and roots), hypsodont (with high crown and roots), and hypselodont (with continuously growing crown and no roots). The differences between feeding preferences of these groups are very significant and indicate the character and degree of their trophic specialization. On the other hand, if the trophic specialization commonality was inherited from the ancestral forms, then modern species and even genera may preserve a close similarity of odontological features. For instance, the dentition structure of true and wood lemmings reflects an adaptation to moss consumption (Abramson, 1989). The high similarity of teeth structures of *Lemmus* and *Myopus* can be considered indirect evidence of the closeness of their trophic preferences. Studies on the composition of fodder of modern lemmings confirm the importance of green mosses in the diet of modern representatives of the two genera

Table 2. Factors limiting the expansion and abundance of voles inhabiting the central part of northern Eurasia and characteristics of reconstructed biotope types with the purpose to use the study species as paleoenvironmental markers

Species	Factor			Reconstructed biotope type
	food resources*	protective conditions of the soil and vegetation cover for nesting*	humidity (acid–salt balance)**	
<i>Ellobius talpinus</i>	Underground phytomass of grass communities	Thick soil layer, at least 30 cm	X XM MX	Xerophytic and mesoxerophytic grass communities with sufficient underground biomass in areas with thick soil lawyer
<i>Eolagurus luteus</i>	Aboveground phytomass of mugwort and grass-forbs communities with mugwort	Soft ground and/or presence of nanorelief on a soil surface	X XM (H)	Xero- and xeromesophytic herbaceous communities with the involvement of mugworts; ability to exist in halophytic communities
<i>Lagurus lagurus</i>	Aboveground phytomass of mixed-grass and gramineous plant communities		X XM	Xero- and xeromesophytic grass communities with the involvement of graminoids
<i>Microtus gregalis</i>			XM MX M	Broad range of habitats: from xerophytic to mesophytic herbaceous communities, mostly forbs–gramineous ones
<i>M. arvalis</i> s.l.			M	Mesophytic herbaceous communities, including those formed at early stages of ecological succession
<i>M. agrestis</i>		Developed ground cover (undisturbed grass sod, wood debris, etc.)	M	Mesophytic plant communities: herbaceous coenoses with developed grass sod and/or forest coenoses with a sufficient area of open spaces
<i>M. middendorffi</i>	Aboveground phytomass of grass and grass–dwarf shrub communities without an obligatory link with the latter	Lability of requirements to protective conditions	M MH H (O)	Hygro-, mesohygro-, and mesophytic herbaceous communities, including oxylophytic ones
<i>Ondatra zibethicus</i>	Aboveground and underground phytomass of near-water grass communities	Not a limiting factor	Hd H HM	Hydro-, hygro-, and hygromesophytic herbaceous communities
<i>Arvicola terrestris</i>	Aboveground and underground phytomass of herbaceous and herbaceous-shrub communities	Lability of requirements for protective conditions	Hd H MH M	Hydro-, hygro-, and mesohygrophytic herbaceous communities; ability to expand to mesophytic communities with developed underground phytomass
<i>M. oeconomus</i>	Aboveground phytomass of herbaceous plant communities	Soft ground, soil horizon nanorelief, and/or ground cover protective properties	H HM (Ha, O)	Hygro and mesohygrophytic herbaceous communities; sufficient amounts of water in vegetation enabling the species to exist in both halophytic and oxylophytic habitats

Table 2. (Contd.)

Species	Factor			Reconstructed biotope type
	food resources*	protective conditions of the soil and vegetation cover for nesting*	humidity (acid–salt balance)**	
<i>Dicrostonyx torquatus</i>	Aboveground phytomass of herbaceous and dwarf shrub communities	Lability of requirements to protective conditions	X MX (O)	Xero- and mesoxerophytic grass–dwarf shrub communities, including oxylophytic
<i>Lemmus sibiricus</i> , <i>Myopus schisticolor</i>	Phytomass of green mosses		MH HM H	Habitats with developed moss cover: from mesohygrophytic to hygrophytic
<i>Clethrionomys glareolus</i>	Seeds and fruits of trees, shrubs, and dwarf shrubs	Nanorelief formed by tree and shrub roots, stony placers, etc.	M	Mesophytic coenoses with the involvement of fruit-bearing trees, shrubs, and dwarf shrubs and with defined nanorelief protection properties of biogenic or abiogenic origin
<i>C. rufocanus</i>			M MX	
<i>C. rutilus</i>			M MH	

Classification of breeding and/or survival habitats by the humidity and acid–salt balance: (X) xerophytes, (XM) xeromesophytes, (MX) mesoxerophytes, (M) mesophytes, (MH) mesohygrophytes, (HM) hygromesophytes, (H) hygrophytes, (Hd) hydrophytes, (O) oxylophytes, and (Ha) halophytes. * Factor deficiency is limiting. ** Upward or downward deviations from the preferable factor values are limiting.

(Rogers and Lewis, 1986; Eskelinen, 2004) and indicate the similarity of the taxonomic composition of the preferred mosses and predomination of *Dicranum* sp. and *Polytrichum* sp. in the diet of both wood and true lemmings (Rogers and Lewis, 1986; Eskelinen, 2004; Soininen et al., 2013). The similarity of the requirements of wood and true lemmings to temperature and moisture parameters of the environment, combined with the similarity of their trophic preferences, indicate the need to consolidate the *Lemmus* and *Myopus* genera into a group of species used as moss cover indicators without association with any specific forest or tundra biome.

Classification of Voles Inhabiting the Central Part of Northern Eurasia Based on Environmental Preferences of Their Modern Representatives

Based on the analysis of the environmental preferences steadily featured by the species studied throughout their modern ranges and taking into consideration the factors limiting their modern distribution and abundance, a classification of the arvicolines inhabiting the central part of northern Eurasia by their environmental preferences is proposed. Biotope types, the existence of which can be identified based on the discovery of certain species in the micromammalian subfossil assemblages, have been characterized (Table 2).

The classification of representatives of the subfamily Arvicolinae inhabiting central part of northern Eurasia includes the following:

1. Species of grass communities.

1.1. Species of xerophytic grass communities.

1.1.1. With well-developed underground phytomass and a sufficiently thick soil layer: *E. talpinus*.

1.1.2. With well-developed aboveground phytomass.

1.1.2.1. Grass communities with well-developed aboveground phytomass and with the involvement of mugworts: *E. luteus*.

1.1.2.2. Grass communities with well-developed aboveground phytomass and with a high share of graminoids: *L. lagurus*.

1.2. Species of xeromesophytic grass communities: *M. gregalis* (may act as a eurytopic species of unmoistened habitats subject to the availability of a broad range of habitats, from xero- to mesophytic ones).

1.3. Species of mesophytic grass communities.

1.3.1. Species of grass communities at early succession stages: *M. arvalis* and *M. rossiaemeridionalis*.

1.3.2. Species of grass communities at late succession stages with sufficient surface turfness or forest communities at early succession stages: *M. agrestis*.

1.4. Species of mesohygrophytic grass communities: *M. middendorffi* (may act as a eurytopic species subject to the availability of a broad range of habitats, from hygro- to mesophytic ones).

1.5. Species of moistened grass communities.

1.5.1. Stenotopic species of hydro- and hygrophytic grass communities close to water bodies: *O. zibethicus*.

1.5.2. Species able to change habitats from hydro- and hygrophytic to mesophytic ones: *A. terrestris*.

1.5.3. Eurytopic species of nonarid grass communities with a mandatory high share of wet foods: *M. oeconomus*.

2. Species of grass—dwarf shrub communities (xerophytic and xeromorphic oxylophytic ones): *D. torquatus*.

3. Plant communities with developed moss cover: *L. sibiricus* and *M. schisticolor*.

4. Plants communities with the involvement of trees and/or shrubs and with defined protective nanorelief features of biogenic or abiogenic origin.

4.1. Mesophytic communities: *C. glareolus*.

4.2. Mesophytic and mesoxerophytic communities: *C. rufocanus*.

4.3. Mesophytic and mesohygrophytic communities: *C. rutilus*.

CONCLUSIONS

The results obtained indicate that for voles inhabiting the central part of northern Eurasia, the values of thermal neutral temperatures overlap in the range of 19–26°C. The study species have a high enough potential to change the thermal neutral zone parameters depending on the external conditions; this makes it impossible to reconstruct, either directly or indirectly, the temperature characteristics of the environment based on the vole species composition or the ratio between the vole species in micromammalian subfossil assemblages and makes it impossible to compute the absolute values of the temperature parameters of the past environment. Out of the abiotic factors, the environmental moisture parameters can be reconstructed most reliably based on the phytocoenosis moisture regime. In particular, it is believed to be reasonable to distinguish groups of species associated with hygrophytic, mesohygrophytic, mesophytic, mesoxerophytic, and xerophytic habitats. Further studies are required to research the combined effect of the habitat humidity and acid–base balance of the soil horizon on the distribution of voles.

The analysis of factors limiting the expansion and abundance of voles has shown that representatives of the subfamily Arvicolinae, as an element of micromammalian theriocomplexes, can be used directly for reconstruction of soil and vegetation conditions of terrestrial ecosystems and the capacity of biotopes suitable for them in accordance with the above classification.

Based on the life forms of vascular plants and mosses determining the type of phytocoenosis used by voles (grasses, dwarf shrubs, trees and shrubs, and ground mosses), four environmental groups have been identified. Within each of these group, subgroups can be distinguished by the phytocoenosis moisture regime. We consider this approach to the identification of environmental groups universal for the subfamily; it can be used to extend the classification through the inclusion of species inhabiting adjacent regions

into it or for classification of regional faunas of geographically distant areas.

The differentiation of species within the subgroups is supplementary. The availability of literature data on sustainable environmental distinctions made it possible in a number of cases to use refining criteria for differentiation of environmental preferences of some species within a subgroup. Information on the succession stage of an ecosystem essential for a species was used as an additional refining criterion.

The narrowness of environmental preferences and the local biotopical level of effects from the factors limiting the abundance and expansion of the Arvicolinae indicate that the zonal principle cannot be used in the classification of voles by their environmental preferences. It is reasonable to use definitions such as “tundra,” “wood,” and “steppe” in paleoecology in relation to faunal assemblages (if their existence has been identified through an analysis of the complex of biotic markers). With regards to individual species, links with plant communities of a phytocoenosis or plant association level—but not with natural zones—may be considered justified.

Therefore, the proposed approach involves the identification of environmental groups of voles based on the soil and vegetation cover parameters of their breeding and survival habitats only, not the entire species habitat areas. In addition, we suggest to take into consideration the trophic specialization and burrowing requirements (when this is typical for a species). Such an approach makes it possible to define clearly the reconstructed environmental parameters and identify the place of representatives of the subfamily Arvicolinae in the general complex of paleoclimatic markers in the Late Quaternary period.

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