Keys to Identify Modern and Pleistocene Arvicolines (Arvicolinae, Rodentia) from the Urals and Western Siberia Based on Odontological Characteristics

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Abstract—Taxonomic identification of arvicolines (Arvicolinae, Rodentia) based on dental characteristics without taking into account cranial, external, or other nondental features is an important task in neontology when studying the diets of carnivorous mammals and birds of prey and in Quaternary paleontology, biostratigraphy, and paleoecology. The morphological criteria for the taxonomic identification of arvicoline molars are formalized in this paper. Dichotomous keys to identification of modern and Pleistocene arvicoline taxa of the Urals and Western Siberia based on the structural and histlogical characteristics and the occlusal configuration of the first lower molar are proposed.

INTRODUCTION

Arvicoline rodents (Arvicolinae, Cricetidae, Rodentia) are a subfamily whose broad adaptive radiation occurred against the background of formation of modern ecosystems in the Northern Hemisphere during the Quaternary period. Owing to their rapid evolution, abundant fossil record, and broad geographical distribution, arvicolines are a traditional object of biostratigraphic and biochronological research (Agadzhanyan, 1979; 2009; Zazhigin, 1980; Vangengeim et al., 2001; Tesakov, 2004; Maul and Markova, 2007; and others). The presence of species with a clear ecological specificity allows us to use members of the subfamily as paleoenvironmental and paleoecological markers, which carry information at different levels: from the main types of vegetation at the regional and continental levels to the local biotopic characteristics (Smirnov, 1994; *Evolyutsiya ekosistem...*, 2008). At the same time, the diversity and abundance of arvicolines in modern ecosystems determine the importance of this group as a food resource for birds of prey (Dinesman, 1979; Shepel', 1992) and their wide use as model objects in neontological studies, in particular, for the purposes of environmental monitoring (Vasiliev et al., 1996; Gileva, 1997; Lukyanova and Lukyanov, 1998; Gileva and Yalkovskaya, 2009).

For taxonomic identification of both modern and fossil arvicolines, diagnostic tables based on the characteristics of the dental system (e.g., Rörig and Börner, 1905; Hinton, 1926) have long been used, but works on creating diagnostic keys based solely on the charac-teristics of the dental system without involving cranial and exterior parameters are rare (e.g., Semken and Wallace, 2002). Revision of previously established taxonomic keys is associated with changes in the systematic position of some taxa, and new information on the resolution capacity of individual characteristics, ranges, and factors of their variability. From these positions, it appears urgent to systematize the diagnostic characteristics of the arvicoline dental system both for the subfamily as a whole and for the faunas of separate major regions.

The Urals and Western Siberia are vast regions in the central part of Northern Eurasia, representing biogeographic crossroads where the ranges of species of the European and Asian sectors of the Palearctic overlap. Currently, 16 species of arvicolines inhabit the Urals and Western Siberia: *Ellobius talpinus* (Pall. 1770), *Clethrionomys rufocanus* (Sundev. 1846), *C. glareolus* (Schreb. 1780), *C. rutilus* (Pall. 1779), *Lagurus lagurus* (Pall. 1773), *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).

For all these species (except the muskrats introduced in the 20th century), ancestral forms are known within the studied region since at least the turn of the Pliocene–Pleistocene. Currently, about 40 Pleis-

tocene forms of species rank are known in the Urals and the Western Siberian plain (Borodin, 2012).

The most ancient genera, representatives of which are known from the Pliocene and have survived to our day, are *Ellobius* and *Clethrionomys*. The early stages of evolution of the Lemmini family are not understood well; however, remnants of the true lemmings of the genus *Lemmus* are known for the territory in question since the *Eopleistocene*, whereas representatives of *Myopus* were registered in the Late Pleistocene and Holocene localities of the Urals (Smirnov et al., 1990, 1997; Fadeeva and Smirnov, 2008; Borodin, 2012).

The Arctic lemmings in the region are represented by the evolutionary stages from late †*Praedicrostonyx* to the modern Arctic lemming: †*Praedicrostonyx meredionalis*, †*D. renidens*, †*D. simplicior*, †*D. henseli*, and *D. torquatus* (Smirnov et al., 1986, Borodin, 2012).

The tribe Lagurini is represented in fossil fauna of the region by four genera: †*Borsodia*, †*Prolagurus*, *Lagurus*, and *Eolagurus*. In the late Pleistocene and Holocene faunas, both *Lagurus* and *Eolagurus* genera are found, whereas in the modern fauna, only one species *L. lagurus* is found, which is a terminal taxon of the lineage †*Borsodia prolaguroides*–†*Prolagurus ternopolitanus*–†*P. pannonicus*–†*P. posterius*–†*Lagurus transiens*–*L. lagurus* (Borodin, 2012).

Among the members of the tribe Arvicolini in the study area, water voles of the lineage †*Mimomys*–†*Arvicola mosbachensis*–†*A. chosaricus-kalmankensis*–*A. terrestris* are widespread, as well as gray voles of the lineages †*Allophaiomys deucalion*–†*A. pliocaenicus*–*Microtus*. The genus *Microtus* is currently represented by 6 species, among which the history of the lineage *Stenocranius* is characterized the most fully: †*M.* (*S.*) *hintoni*–†*M.* (*S.*) *gregaloides*–*M.* (*S.*) *gregalis* (Borodin, 2012).

The problem of criteria for taxonomic identification of arvicolines using odontological characteristics was covered by the authors in a series of publications (Borodin, 1988; 2009; Borodin and Ivakina (Pogodina), 2000; Markova et al., 2003, 2012; Borodin et al., 2005; Markova and Borodin, 2005). In particular, an interactive identification guide to modern representatives of Arvicolinae, which have inhabited the studied region since the Late Pleistocene, was proposed (Borodin, 2009). It did not include extinct taxa of the Pleistocene fauna of the region.

The aim of this paper is to formalize the comparative morphological criteria for the diagnosis of modern and Pleistocene arvicoline taxa from the Urals and Western Siberia (in the time interval from the early Pleistocene to the present) and to offer dichotomous key sequences to be used in practice.

MATERIALS AND METHODS

In the development of identification keys, reference collections from the Zoological Museum of the Institute of Plant and Animal Ecology, Russian Academy of Sciences, were used, as well as classic general works on the variability of contemporary forms (Rörig and Börner, 1905; Ognev, 1950; Gromov et al., 1963; Angermann, 1973; Gromov and Poliakov, 1977; Kochev, 1986, Gromov and Erbaeva, 1995; Meyer et al., 1996) and universal laws of evolutionary transformation of the dental system in the subfamily Arvicolinae (Guthrie, 1971; Shevyreva, 1976; Bolshakov et al., 1980; Markova, 1982; Nadachowski, 1982; Agadzhanyan and Erbaeva, 1983; Smirnov et al., 1986; Chaline and Graf, 1988; Rekovets, 1994; Chaline et al., 1999; *Evolyutsiya ekosistem*..., 2008; Agadzhanyan, 2009).

The systematics and nomenclature of arvicolines is reviewed according to Pavlinov, 2003, with some modifications. Thus, we use *Clethrionomys* Tilesius 1850 as a valid name for the forest voles (instead *Myodes* Pallas 1811), according to the latest taxonomic interpretations of Tesakov and coauthors (Tesakov et al., 2010). It should also be noted that the supraspecific classification of arvicolines is currently the subject of much discussion owing to the accumulation of molecular and genetic data (e.g., Pavlinov and Lisovskii, 2012). Given the lack of consensus on the systematics of the group of genera *Microtus*, as well as the generic or subgeneric status of red-backed (*Clethrionomys*) and gray red-backed (*Craseomys*) voles, we used traditional notions about the systematics of these groups in developing the keys.

The Discrimination Capacity of the Keys and Approaches to Defining the Taxonomic Identification of Arvicolines

The designed diagnostic keys apply to all modern species and allow us to define up to the genus all Pleistocene arvicoline taxa in the studied region, as well as some genera of the Pliocene—Pleistocene age.

The keys were compiled based on the traditional criteria used for comparative and morphological analysis of the dental system characteristics. Complicated cases of diagnostics of arvicoline species by odontological characteristics require the use of special techniques, such as discriminant analysis of metric traits (e.g., Chaline et al., 1989; Smirnov et al., 1997; Markova and Borodin, 2005), shape parameters (e.g., Wallace, 2006; McGuire, 2011), or histological studies (Koenigswald, 1980). As a rule, such approaches are not universal; that is, they are designed to identify a limited number of species, taking into account their characteristics.

The keys are designed to identify specimens at postjuvenile ontogenetic stages, i.e., for molars with a fully formed crown and occlusal surface.

The determination (substantiation that specimens belong to the established taxa) is considered to be complete in those cases when it is carried out to the species. However, in practice, it is not always possible to establish the species of all specimens in the sample. This may be due to poor preservation of the identified specimens (for example, when studying fossil material or food residues of predators), or the need to draw additional criteria for the diagnosis of morphologically poorly differentiated species.

In the cases when species identification is impossible or complicated, it is expedient to use the open classification, which is widely used in paleontology (e.g., Barskov et al., 2004). If the sample is so badly preserved that the identification of its genus and species is almost impossible, it is possible to identify it up to a subfamily or family. Thus, broken teeth and fragments of prisms of molars can be attributed to Arvicolinae gen. et sp. indet. (Arvicolinae, genus and species indeterminable). In some cases, due to lack of diagnostic criteria, the identification is only possible to the tribe (e.g., Lemmini gen.—tribe Lemmini, genus is not identified). If the genus is established, but the condition of the specimen precludes further definition completely, the abbreviation sp. indet. is used. Thus, broken teeth can often be identified to the genus by the structural and histological elements when it is impossible to establish the species (e.g., *Microtus* sp. indet.). If the genus is identified and the possibility exists for more precise definition, but the sample preservation and/or discrimination ability of the diagnostic methods do not allow it, the abbreviation sp. is used. For example, due to lack of developed criteria for the determination of species, isolated M1, M2, m2, and m3 of meadow voles are currently defined as *Microtus* sp. (with the exception of M2 and M1 of *M. agrestis*, with species-specific additional loops); red-backed voles determined by these teeth are also often referred to as *Clethrionomys* sp. (except for *C. rufocanus*, which differs in size). If features are observed in the identified specimen that are common to a number of species, but no characteristics are found that would allow one to identify any of these species accurately, the identification to a group is designated as ex gr. or ex grege, which, translated from Latin, means "out of the flock" (e.g., *Clethrionomys* ex gr. *rutilus-glareolus*, *Microtus* ex gr. *arvalis-agrestis*). The abbreviation cf., from the Latin conformis—"similar"—is used in those cases when, in terms of preservation or other characteristics of the material, the determined forms are closest to the mentioned known species, but this cannot be stated with certainty (not all features that are characteristic of this species are present in the determined forms). Identification to a complex of sibling species can be designated by the Latin term sensu lato ("in a broad sense"), which is used in conjunction with the name in reference to the nominal taxon in its broad sense (*International Code...*, 2004). Thus, it is permissible to use the names *Microtus arvalis* sensu lato to indicate sibling species of the group "arvalis."

The Morphology of the Dental System of Arvicolines

The rodents of the subfamily Arvicolinae Gray 1821 = Microtinae Cope in 1891 are, on the whole, characterized by the following features of the dental system (Fig. 1):

—Incisor (two upper and two lower incisors, one in each branch of the jaw), three molars in the upper and lower jaws on each side: I = 1, C = 0, Pm = O, M = 3/ i = 1, c = 0, pm = 0, and m = 3 (Fig. 1);

—Diastema (in arvicolines, a break in the dentition associated with the reduction of teeth between the incisor and molars), incisors in all members of the subfamily, as in all rodents with constant growth;

—Prismatic molars (with a flat occlusal surface of the crown, formed by dentine prisms and the surrounding enamel, which forms cutting edges on the occlusal surface), paired lingual and buccal prisms are displaced (to varying degrees) relative to each other (Fig. 1).

Although the characteristics of incisors can be used for taxonomic diagnostics (Hinton, 1926; Gromov and Polyakov, 1977; Borodin, 2009), most often, it is the characteristics of molars that are used. In this paper, we used the nomenclature of the occlusal surface of the teeth of voles according to Van der Meulen (van der Meulen, 1973) (Fig. 2).

Taxonomic Identification and Intraspecific Variation

The search for diagnostic characteristics, i.e., characteristics that are applicable to all specimens in the isolated group and are unique for this group, involves determining the limits of intraspecific variation. Special attention must be paid to the possibility of overlapping of the variation ranges across the species. The overlapping of the ranges of variation of characteristics that reflect the configuration of the occlusal surface of teeth in arvicolines is due to the mechanism of complication of the crown in ontogenesis and phylogenesis with unequal rates of this complication, which is common to most members of the subfamily (e.g., Chaline et al., 1999). In general, the characteristics that describe the uniqueness of the morphology of the occlusal surface of the teeth allow us not only to determine the species, but also to assess intraspecific differentiation and conduct interpopulation comparisons.

Sometimes one feature of the occlusal surface allows us (in conjunction with knowledge of the morphological and histological characteristics of the molars) to identify the species clearly. For example, among the species occuring in the studied region, the presence of a fully formed additional element on the occlusal surface of the M2 and/or M1 (no roots, cementum is present) is characteristic only of
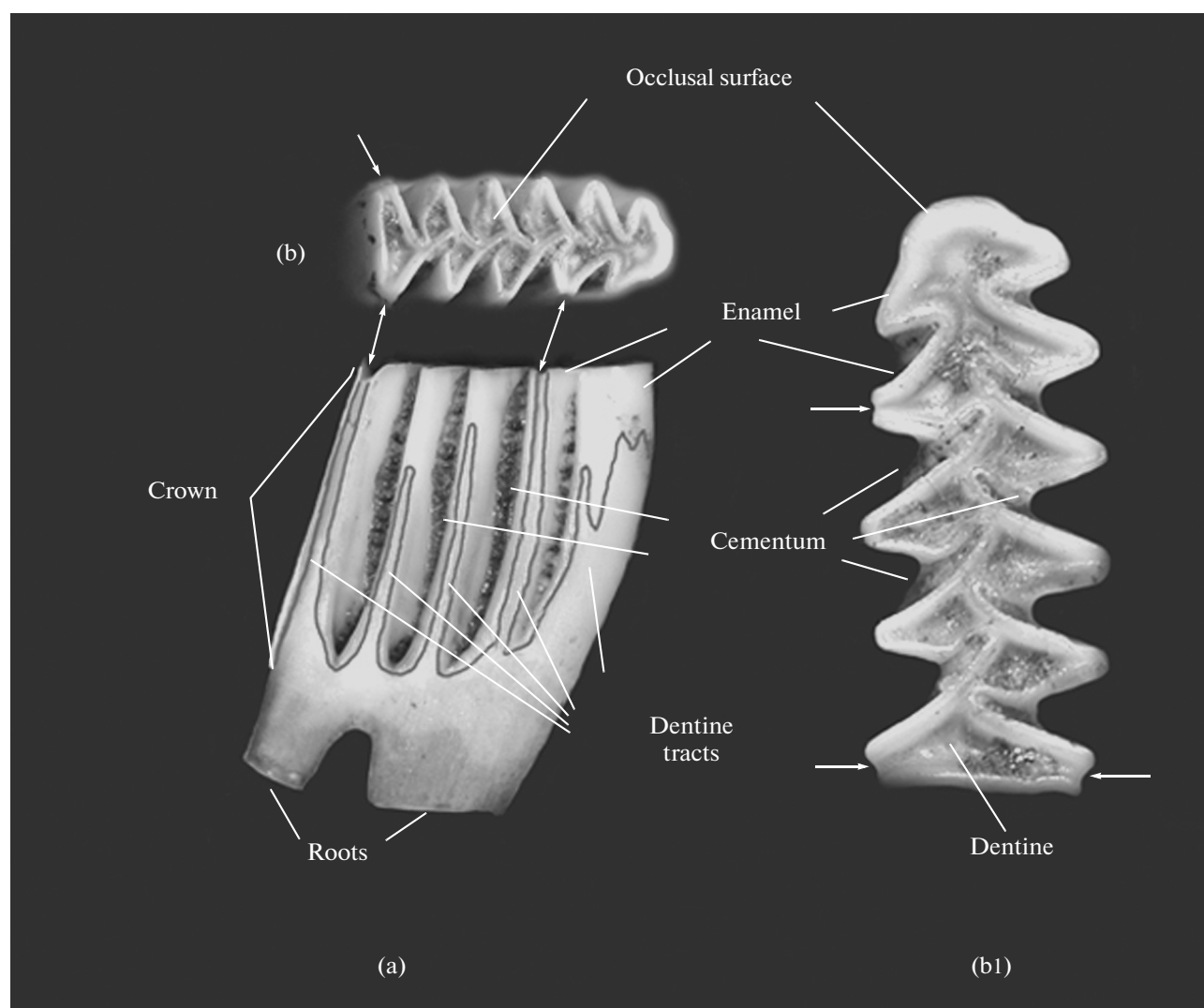
Fig. 1. The main structural and histological elements of a molar of vole from the example of the first lower tooth (m1) of *Ondatra zibethicus*: (a) view from the buccal (cheek) side; (b and b1) types of occlusal surfaces; arrows indicate enamel breaks (dentine tracts) on the apexes of the salient prism angles.

M. agrestis (Figs. 3, *7*; 3, *9*); such an element on a cementumless tooth is characteristic of *D. torquatus*, which is characterized by complexity of all molars (Fig. 2). The presence of a prismatic fold (in this case, reinforcementum rib) on the inner side of T2 of the upper teeth M1 and M2 in the representatives of the modern fauna is characteristic only of *L. lagurus* (Figs. 3, *10*; 3, *11*) and *E. luteus*, which, in turn, differ from each other in size (the yellow steppe lemming is larger than the steppe lemming). The primitive structure of M3 of the Northern mole vole, even without considering other odontological characteristics, will make it impossible to confuse it with any other species (Fig. 3, *12*). The peculiar structure of the dental system of wood lemmings and true lemmings appears in the characteristics of almost all the teeth; the traits that

distinguish these taxa from other Arvicolinae include a very deep reentrant BRA1 angle on the occlusal surface of M3 and M2, which reaches to the lingual apex of the anterior unpaired lobe (Figs. 3, *13*; 3, *14*), and a very deep lingual reentrant LRA1 on the occlusal surface of m3 (Fig. 3, *15*), which reaches to the buccal apex of the posterior unpaired loop. For fossil forms, such a trait as an enamel islet is characteristic of Eopleistocene species †*Mimomys* (teeth with deposits of cementum) (Figs. 3, *1*; 3, *3*) and early forms of †*Borsodia* (cementumless).

However, the construction of key sequences on the basis of these morphological features (islets, folds, depth, and shape of the re-entrant angles, etc.), which are characteristic of some taxa, can often be complicated by manifestations of intraspecific variation: age-
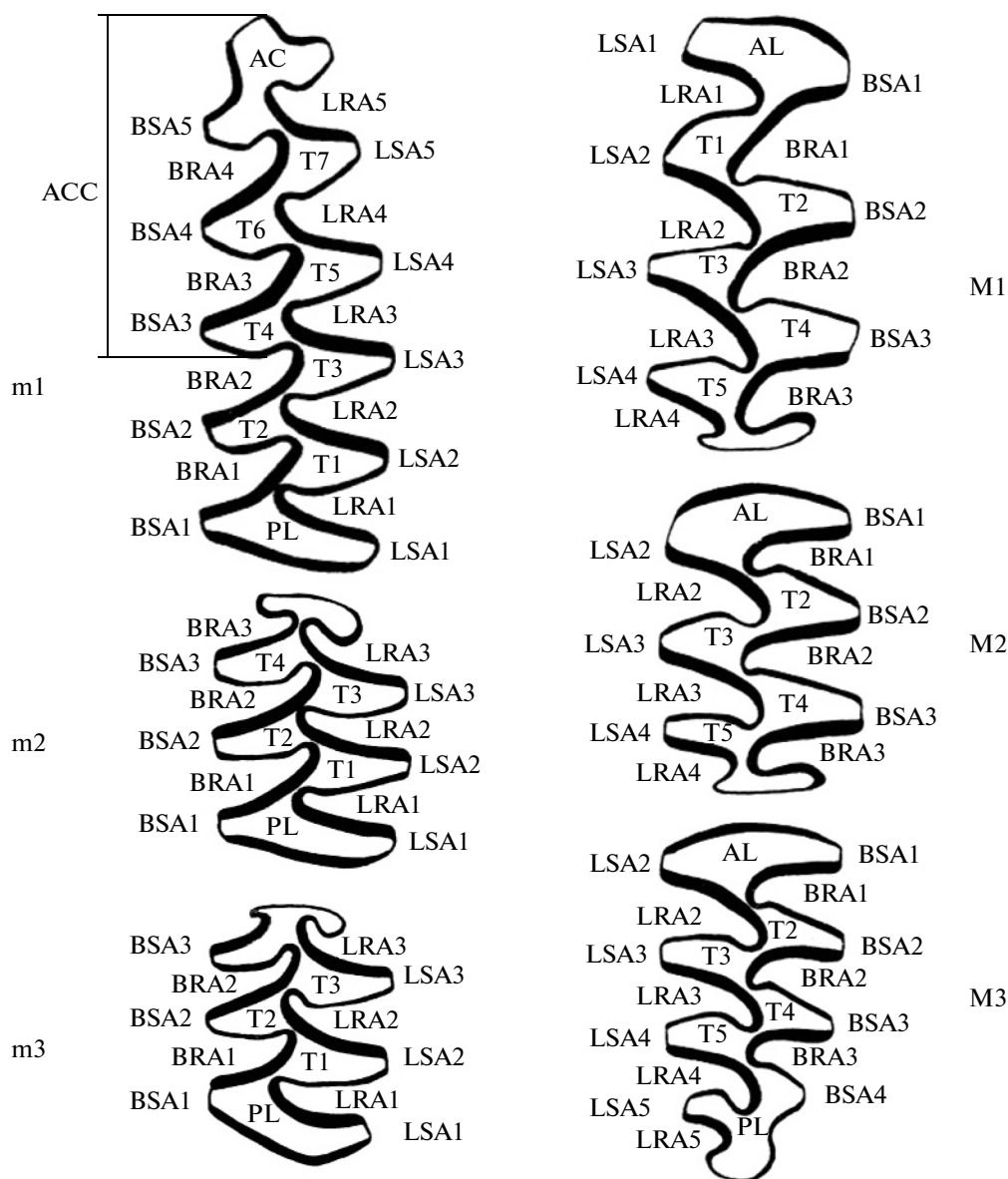
Fig. 2. Designations of elements of the occlusal surface of teeth of arvicolines using the example of *Dicrostonyx torquatus*: (M1–M3) upper molars, (m1–m3) lower molars in accordance with the ordinal number. Terminology according to van der Meulen, 1973: (T1, T2, etc.) triangular loops (dentine fields) of the occlusal surface, (PL) posterior unpaired loop of the lower teeth, (AL) anterior unpaired loop of the upper teeth, (AC) anterior unpaired loop of m1, (ACC) anteroconid complex, (BRA) buccal (outer, cheek) reentrant angle, (BSA) buccal salient angle, (LRA) lingual (inner) reentrant angle, and (LSA) lingual salient angle.

related, individual, and sometimes interpopulation. Thus, the formation of islets, which is typical of m1 and M3 of the genera †*Mimomys* and †*Borsodia*, depends directly on the age-related changes of the crown, and is possible as aberrations in modern rhizodont forms. Thus, we have repeatedly registered cases of the formation of islets in modern muskrats and red-backed voles, not only in the final stages of the crown wear, but also on the molars of adult young individuals (Figs. 3, *2*; 3, *4*). Not all individuals in a population of steppe lemmings can have pronounced prismatic folds, which are characteristic for them. The development of additional elements on the hypselodont M2 with cementum can sometimes be found not only in *M. agrestis*, but also in *M. arvalis* sensu lato. Thus, the presence of intraspecific variation does not allow us to consider many characteristic features as diagnostic and to use them in the preparation of the classic keys. Owing to this, the development of interactive taxonomic keys and atlases (Borodin, 2009), as well as their online versions (http://lib.ipae.uran.ru/key_arvicolinae/), which include a large number of comparative illustrative material, appears to be promising.
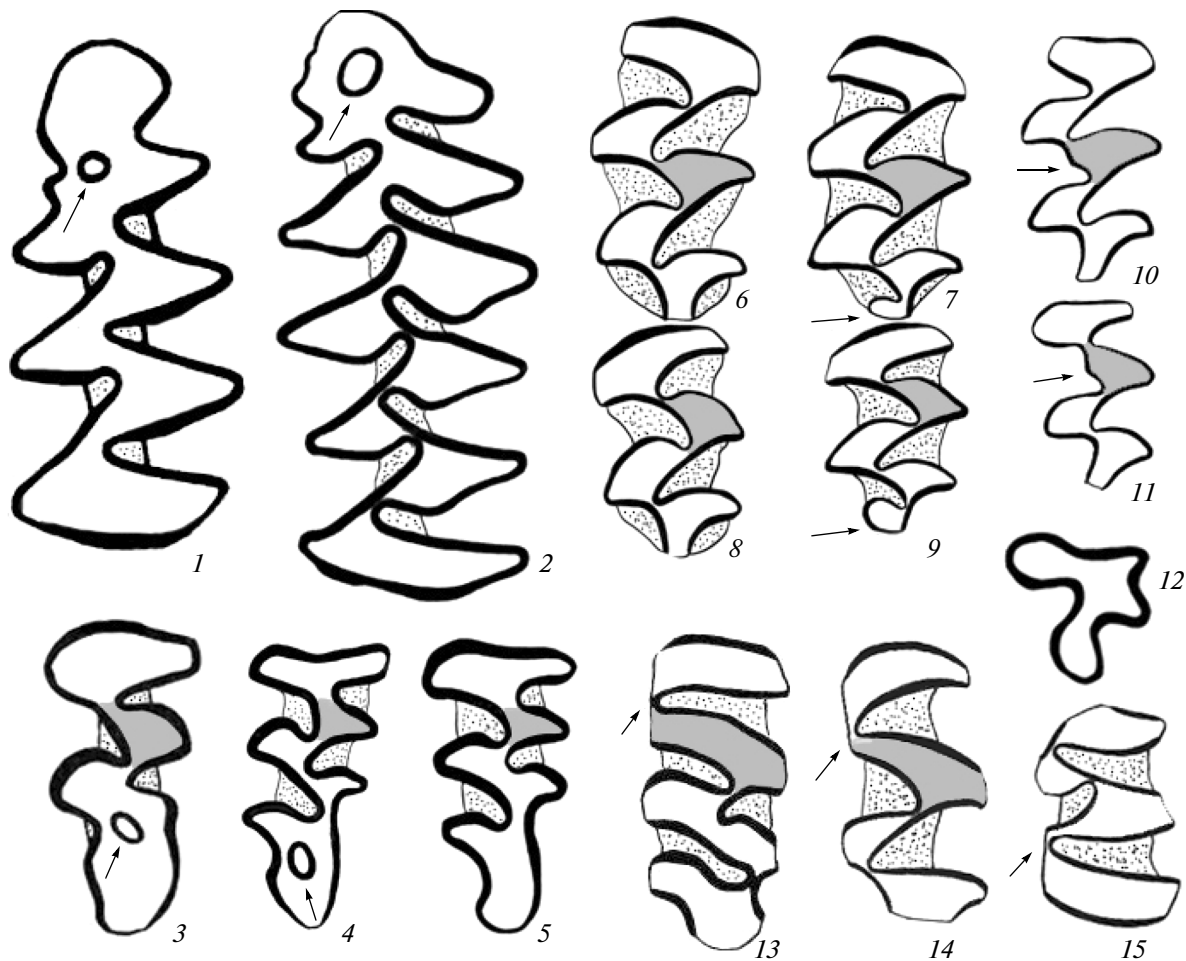
Fig. 3. Some morphological features of the fossil and modern molars of voles (the arrows show the position of the characteristic morphological features, and gray shading indicates the dentine field T2 of the upper molars). (*1*) Mark (islet of enamel) on anteroconid m1 of the genus †*Mimomys*; (*2*) mark on the anterior unpaired loop of anteroconid m1 of the genus *Ondatra*; (*3*) mark on the posterior unpaired loop M3 of the genus †*Mimomys*; (*4*) mark on the posterior unpaired loop M3 in the modern species *Clethrionomys glareolus*; (*5*) typical structure of the posterior unpaired loop M3 in *C. glareolus* (mark is absent); (*6*) M1 without additional prisms in the genus *Microtus*; (*7*) M1 with the additional prism, *Microtus agrestis*; (*8*) M2 without additional prisms, genus *Microtus* (except *M. agrestis*); (*9*) M2 with an additional prism, *M. agrestis*; (*10*) "lagurus" prismatic fold on M1; (*11*) "lagurus" prismatic fold on M2; (*12*) occlusal surface of M3 in *Ellobius talpinus*; (*13* and *14*) the buccal reentrant angle BRA1 on (*13*) M2 and (*14*) M3 in the genera *Lemmus* and *Myopus* reaches the lingual apex of the anterior unpaired loop; (*15*) lingual reentrant angle LRA1 of m3 in the genera *Lemmus* and *Myopus* reaches the apex of the posterior buccal unpaired loop.

RESULTS AND DISCUSSION

Taxonomic Identification of Arvicolines Based on Features of Structural and Histological Elements of Molars

To identify arvicoline molars to the genus (and sometimes up to the species level), the characteristics of the structural and histological elements of a tooth may be sufficient without the morphological characteristics of the occlusal surface. Thus, the presence of enamel breaks (dentine tracts) on the apex of all salient angles of the side prisms is characteristic only of the genera *Dicrostonyx*, *Lemmus, Myopus*, and *Synaptomys*, and the absence of cementum in the reentrant

angles suggests that the identified specimen belongs to the genus *Dicrostonyx* represented in the modern fauna of the region by one species, *D. torquatus*; cementumless teeth with roots in modern and Late Pleistocene fauna are unique to the genus *Ellobius*, also represented by only one species—*E. talpinus*; the cellular structure of the cementum in the reentrant angles of prisms is characteristic only of the muskrat, etc.

The identification of voles using structural and histological characteristics of the molars is especially useful in those cases when the material is presented as fragments of teeth. This is often observed when studying the remains of voles in the pellets of birds of prey or excrement of carnivores, but above all, it is important

for fossil material from localities of the alluvial type with a high degree of fragmentation of remains and in the cases where we are dealing with material of different ages (in the geological sense).

Diagnostic Key to Fossil and Recent Genera of Arvicolines from the Urals and Western Siberia Based on the Structural and Histological Characteristics of Teeth

1 (10). The cementum in the reentrant angles is not deposited.

2 (7). The roots of the molars are formed.

3 (4). The enamel is uniformly thick even in the reentrant angles: enamel breaks on SA are absent or (on worn down crowns) are not present on all SA .... Genus *Ellobius*.

4 (3). The enamel is not uniform.

5 (6). The enamel is differentiated by the mimomys type (is thicker on the convex side) .... †Genus *Promimomys* and †genus *Pliomys*.

6 (5). The enamel is poorly differentiated in thickness or undifferentiated on the anterior and posterior walls of the prisms, but is always thinner in reentrant angles; enamel breaks are formed on the anterior and posterior unpaired teeth loops; the roots are formed .... †Genus *Borsodia*.

7 (2). The roots are not formed.

8 (9). Enamel breaks are formed only on the anterior and posterior unpaired teeth loops; the enamel is thinner on convex prism walls .... †Genus *Prolagurus*, genus *Eolagurus*, and genus *Lagurus*.

9 (8). Enamel breaks are formed on all SA of teeth; the enamel on convex walls of prisms is thinner and can be barely noticeable .... †Genus *Praedicrostonyx* and genus *Dicrostonyx*.

10 (1). The cementum in reentrant angles is deposited.

11 (15). The roots are formed.

12 (13). The cementum is cellular .... Genus *Ondatra*.

13 (12). The cementum is dense.

14 (15). The enamel is differentiated by the mimomys type (thicker on the convex side) or weakly differentiated; the enamel breaks are formed on the anterior and posterior unpaired teeth loops .... †Genus *Mimomys* and genus *Clethrionomys*.

15 (11). The roots are not formed.

16 (19). Enamel breaks are formed only on the anterior and posterior unpaired teeth loops.

17 (18). The enamel is differentiated by the mimomys type (thicker on the convex side) or weakly differentiated; the enamel breaks are formed on the anterior and posterior unpaired teeth loops .... †Genus *Arvicola* (†*A. mosbachensis*), genus *Arvicola* (†*Arvicola* transitional form), and †genus *Allophaiomys* (†*A. deucalion*).

18 (17). The enamel is thinner on convex prism walls; enamel breaks are formed on the anterior and posterior unpaired teeth loops; the roots are not formed .... Genus *Arvicola* (*A. terrestris*), †genus *Allophaiomys* (†*A. pliocaenicus*), and genus *Microtus*.

19 (16). Enamel breaks are formed on all SA of teeth; the enamel on the anterior and posterior walls of prisms is poorly differentiated .... Genus *Lemmus* and genus *Myopus*.

Further identification is possible with the assistance of size and/or morphotypical odontological characteristics. Thus, the size of any molar among rhizodont cementum teeth can help identify genera *Arvicola* and †*Allophaiomys—Microtus. Lagurus* and *Eolagurus* differ considerably in size. In other cases, diagnosis is possible on the basis of analysis of the configuration and structure of the occlusal surface of molars (the number of dentine prisms, the degree of dentine fields merge on the occlusal surface, the presence of marks (enamel islets) and prismatic folds, and the degree of complexity of the ml anteroconid). Descriptions and differential diagnoses of modern and fossil arvicoline genera known in the literature can be used for this (Gromov and Polyakov, 1977; Smirnov et al., 1986; Rabeder, 1981; Markova, 1982; Rekovets, 1994; Tesakov, 2004; Agadzhanyan, 2009; etc.).

Classification by Configuration of the Occlusal Surface

In terms of the diagnostic value of the specific features of the occlusal surface configuration, the most informative tooth is m1, a tendency to complication of which is characteristic of many members of the subfamily. Complication manifests itself in the change in the number of elements of the occlusal surface—dentine prisms and their corresponding fields of the occlusal surface—as well as salient and reentrant angles.

Dichotomous key sequences can also be compiled for the remaining teeth (M1, M2, M3, m2, m3), but owing to the relative conservativeness of the number of elements of the occlusal surface in M1, M2, m2, and m3, and a significant overlap in the range of variation of M3 in meristic characteristics (the number of elements of the occlusal surface), it is mainly the structural and histological characteristics that can be considered diagnostically significant. Due to this, to determine voles by any tooth, a key sequence based on the structural and histological characteristics of molars can be used, and for m1, a key can be proposed based on the configuration of the occlusal surface (Fig. 4).

Key to Identification of Modern and Late Pleistocene Arvicolines of the Urals and Western Siberia by m1

1 (6). The anteroconid is not complicated. The occlusal surface consists of an unpaired posterior lobe, Tl, T2, T3, and a simple shamrock-shaped antero-
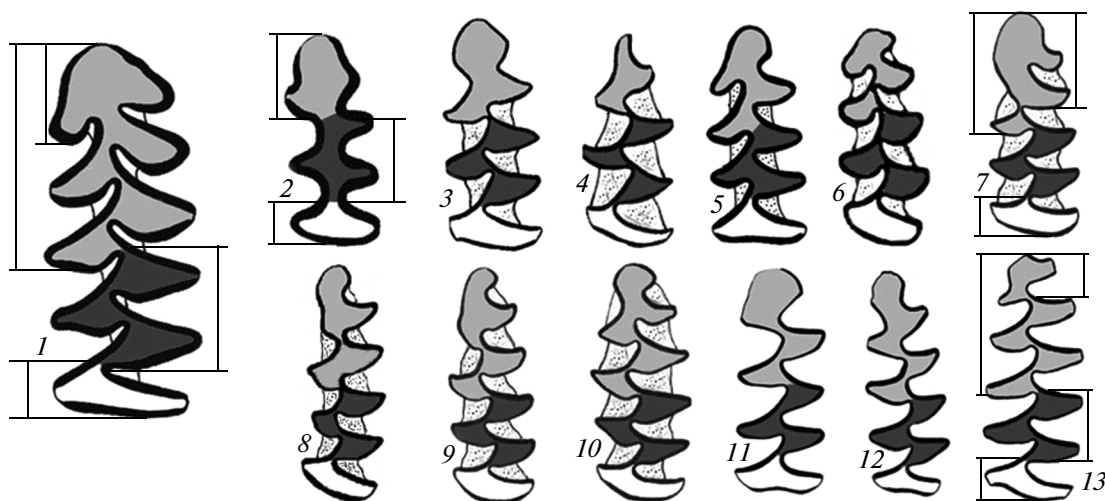
Fig. 4. The main variants of complication of anteroconid ml in modern and Late Pleistocene voles of the Urals and Western Siberia. Taxa: (*1*) genus *Ondatra*, (*2*) genus *Ellobius*, (*3*) genus *Arvicola*, (*4*) genus *Lemmus* or *Myopus*, (*5*) genus *Clethrionomys*, (*6*) *Cl. rufocanus*, (*7*) *Microtus oeconomus*, (*8*) genus *Microtus* ("pytymys" variant), (*9* and *10*) genus *Microtus*, (*11*) genus *Eolagurus*, (*12*) genus *Lagurus*, (*13*) genus *Dicrostonyx*. The light gray shading indicates the anteroconid, and dark gray shading designates the "basic triangles" (T1–T3); the bright field is the posterior unpaired lobe; oblique shading is the "pytymys merger" (merged dentine fields T4 and T5 are isolated from the anterior unpaired loop).

conid or without pronounced reentrant angles (Fig. 4, *2–4*).

2 (3). All dentine fields on the occlusal surface are always merged, the most extensive mergers are between T1–T2 and T3 (Fig. 4, *2*) ..... Genus *Ellobius*.

3 (2). The dentine fields of the basic triangles on the occlusal surface in adults and older individuals are divided by enamel loops (dentine mergers are no thicker than the enamel) (Fig. 4, *3*, *4*).

4 (5). The anterior part of the head of the anterior unpaired loop (in this case, anteroconid) is narrowed, the enamel breaks (dentine tracts) on all the apexs of the salient prism facets reach the occlusal surface (Fig. 4, *4*) .... Genus *Lemmus* and genus *Myopus*.

5 (4). The anterior part of the head of the anterior unpaired loop (in this case, anteroconid) is rounded, enamel breaks occur only on the salient angles of the unpaired loop and on the buccal side of the anteroconid head (Fig. 4, *3*) .... Genus *Arvicola*.

6 (1). The anteroconid is complicated (Fig. 4, *1*, *5–13*).

7 (8). The dentine field of the anteroconid is not completely divided by enamel loops of the reentrant angles, the width of mergers of anteroconid departments is significant (Fig. 4, *5*) ....
.... Genus *Clethrionomys*.

8 (7). The reentrant angles isolate at least one of the anteroconid sections.

9 (16). The anteroconid head is isolated, whereas the fields T4 and T5 are merged (Fig. 4, *8*) or the head of the anteroconid and T5 are merged, while the field T4 is isolated (Fig. 4, *6*, *7*).

10 (13). The dentine field T4 is isolated, the field T5 and the head of the anteroconid section are merged, the number of dentine fields is 6 (T5 is merged with the head of the anteroconid section)—the "oeconomus" variant (Fig. 4, *6*, *7*).

11 (12). The dentine field of T4 is isolated, while T5 can be merged with the dentine field of the anteroconid head, which, as a rule, is mushroom-shaped, skewed in the buccal direction. The enamel is thicker on the salient angles of the dentine prisms or almost identical in thickness on the anterior and posterior walls of the dentine prisms. In the reentrant angles, the enamel is thinner. Enamel breaks on slightly worn crowns reach the occlusal surface at the salient angles of the posterior unpaired lobe and on the head of the anteroconid department (Fig. 4, *6*). The cementum in the reentrant angles is dense. The roots are formed ......
.... *C. rufocanus*.

12 (11). The dentine field T5 is, as a rule, widely merged with the anterior part of the anteroconid forming a dentine field, the shape of which is similar to a "comma." On the lingual side of the anteroconid head, a salient angle is formed ("oeconomus nose"). The enamel is noticeably thinner on the convex walls, in the reentrant angles the enamel thins, and enamel breaks are observed only on the salient angles of the unpaired lobe and on the buccal side of the head of the anterior unpaired loop; the extending facets of the dentine prisms are sharpened (Fig. 4, *7*). The cementum in the reentrant angles is dense. The roots are not formed .... *M. oeconomus*.

13 (10). T4–T5 represent a single field isolated from the main triangles and the head of the antero-conid—"pytimys" variant (Fig. 4, *8*).

14 (15). No cementum in the reentrant angles. The number of dentine fields is 6 (T4–T5 are merged—"pytimys merger"), and other fields can also be merged. The enamel is noticeably thinner on convex walls. There are enamel breaks on the salient angles of the unpaired lobe and on the buccal side of the head of the anterior unpaired loop, and they can also be present at the posterior facet of the anterior unpaired loop .... Genus *Lagurus* and genus *Eolagurus* (rare morphotypes).

15 (14). The cementum in the reentrant angles, 6 dentine fields (posterior unpaired lobe, Tl, T2, and T3, merged T4 and T5 ("pytimys merger"), and the anterior unpaired loop). The enamel is noticeably thinner on convex walls, enamel breaks are present only on the salient angles of the unpaired lobes and the buccal side of the head of the anterior unpaired loop ....Genus *Microtus* (rare morphotypes; the species is identified by the form of the anterior unpaired loop (see paragraph 24).

16 (9). Enamel loops of the anteroconid section isolate, at least, the dentine field T4 and T5 (Fig. 4, *1, 9–13*).

17 (18). The anteroconid department is divided by the reentrant angles into at least 5 dentine fields: T4, T5, T6, T7, and the head of the anteroconid department; no cementum is present, the enamel is sharply differentiated in thickness (very thin on the posterior walls of dentine prisms) (Fig. 4, *13*) .... Genus *Dicrostonyx*.

18 (17). As a rule, only T4 and T5 are isolated at the base of the anteroconid (Fig. 4, *1, 9–12*).

19 (20). The cementum in the reentrant angles is porous; the sizes are very large (min–max, mm): the length of m1 is 6.3–7.4 mm; the width of m1 is 2.7–3.5 mm .... Genus *Ondatra*.

20 (19). The cementum in the reentrant angles is dense or absent, and the sizes are significantly smaller than for the muskrat.

21 (22). The cementum is not deposited (Fig. 4, *11, 12*) .... Genus *Lagurus* and genus *Eolagurus*.

22 (21). The cementum in the reentrant angles is dense.

23 (24). The head of the anterior unpaired loop of the anteroconid section is flattened in a mushroomlike manner, and the enamel is thicker on convex posterior walls of the dentine prisms or nearly identical on the anterior and posterior walls .... Genus *Clethrionomys*.

24 (23). The enamel is always thinner on the convex posterior walls than on the anterior walls (Fig. 4, *9, 10*) .... Genus *Microtus*.

25 (26). The reentrant angle on the lingual side of the anteroconid head is, as a rule, substantially larger than on the buccal side. According to Kochev (1986), the reentrant angle on the buccal side (BRA3) is open, i.e., not limited at the anterior by the "overhanging" BSA4 (Fig. 4, *9*) .... *M. (Stenocranius) gregalis*.

26 (25). The anterior unpaired loop is similar in shape to a shamrock, the reentrant angle on the buccal side (BRA3) is, in the words of Kochev (1986), closed, i.e., limited in the anterior by the "overhanging" BSA4 (Fig. 4, *10*) .... *M. middendorffi, M. arvalis* s. l., and *M. agrestis*.

As can be seen from the structure of the keys, identification to a species is not possible for all members of the subfamily Arvicolinae in the region of study. This is due to the fact that the morphological differentiation of taxa to a species, and sometimes even to a genus, can be expressed relatively weakly. In the diagnosis of such morphologically similar species, discriminant analysis is often used based on linear measurements of molars or shape parameters within the framework of the method of geometric morphometrics. Thus, the diagnostics of the modern representatives of the genera *Lemmus* and *Myopus* is possible using the metric characteristics of M3 (Smirnov et al., 1997; Chaline et al., 1989). The diagnosis of *M. middendorffi*, *M. arvalis* s. l., and *M. agrestis* is possible using the classification functions including metric characteristics of m1 (Markova and Borodin, 2005). To determine the sibling species in the group "arvalis," discriminant analysis of a set of measurements of m1 can also be used (Markova et al., 2003). This approach was used for the identification of remains of *M. arvalis* sensu lato from Holocene sediments of the Middle Urals (Markova, 2003; Borodin et al., 2006). However, a study involving data on the mitochondrial DNA of Holocene forms showed that the discriminant functions developed on contemporary material may not prove to be sufficiently effective to identify fossil remains of the common and Eastern European voles due to the significant temporal variability of the morphological characteristics (Markova et al., 2012).

It should be noted that the discriminant ability of the morphological methods of diagnostics is generally well correlated with the the phylogenetic kinship of Arvicolinae species. For modern forms, taxonomic identification to the level of genus causes no difficulties and can be performed on any of the molars for all representatives of Arvicolinae in the studied region with the exception of the genera *Lemmus* and *Myopus* (see above). The identification of taxa at a species level requires, in most cases, a large amount of experience and comparative material. In the cases when species identification is difficult owing to the vagueness of species-specific traits or poor preservation of the material, it is advisable to use open nomenclature. In our opinion, when introducing the results of diagnosis into the scientific circulation, correct incomplete definition (to a taxon of supraspecific rank) is better than unreliable complete definition (to a species). This will allow us to avoid errors in the interpretation of species

lists both for the researchers themselves and for those quoting them.

Thus, as a result of formalization of the comparative morphological criteria of diagnosis of molars of arvicolines, dichotomous keys have been compiled based on structural and histological characteristics and configuration of the occlusal surface. The designed keys include modern and Pleistocene arvicoline taxa of the Urals and Western Siberia and can be used for taxonomic identification of arvicolines in the adjacent regions of the central part of Northern Eurasia.

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