Assessment of Tooth Complexity in Arvicolines (Rodentia): A Morphotype Ranking Approach

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Abstract—A unified ranking scheme to assess variation of teeth according to their complexity was developed for arvicolines based on an analysis of the existing descriptive classifications of molar morphotypes and comparison of dental variability in species of the subfamily Arvicolinae, which are widespread in northern Eurasia. The scheme relies on counting the number of additional prisms of the crown and the corresponding number of dentine elements of the occlusal surface in *m1, m2, m3, M1, M2,* and *M3*. This approach allows us to consider the dental complexity as an interval scale quantitative variable; it can be implemented when comparing the arvicoline taxa separated by various phylogenetic distances or when studying temporal or spatial patterns of intraspecific variation. Based on analyzing the frequencies of the ranked complexity estimates in different species, a model to describe the morphological shift toward increased tooth complexity in arvicolines is proposed.

Keywords: variability, morphotype, occlusal surface, molar, Arvicolinae

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INTRODUCTION

Arvicolines (Rodentia) are a rodent subfamily specializing in feeding on vegetative plant parts, which serves as the basis for common morphological characteristics of their dentition. The cheek teeth of arvicolines are considered to be prismatic, which developed in the course of evolution from the bunodont teeth of their hamster-like ancestors. The transition to a diet of low-calorie vegetative plant parts with enhanced abrasive properties and to grinding (in the anterior–posterior direction) chewing movements led to the formation of a hypsodont tooth of the arvicoline type with a crown divided by deep re-entrant angles into prisms and with a flat chewing surface. Complication of molars by adding new prisms to the crown is a general trend in the evolution of the arvicoline subfamily, which reflects the degree of efficiency of grinding cellulose food (Guthrie, 1971; Gromov and Polyakov, 1977; Agadjanian, 1996; Borodin, 2009). In most phyletic lineages of arvicolines, trends can be traced toward complication of molars from Pleistocene forms to modern taxa, although the pace and nature of evolutionary transformations of teeth can vary significantly even in the representatives of the same genus (Smirnov and Bol'shakov, 1985; Nadachowski and Zagorodnyuk, 1996, etc.). At the same time, the complexity of cheek teeth is subject to intraspecific variation. Examples of geographic trends associated with change in the proportion of simplified or complicated

variations are known (Guthrie, 1971; Markova et al., 2010). The factors influencing the rate and direction of evolutionary transformation of teeth in arvicolines are widely discussed (Guthrie, 1971; Chaline et al., 1993; Jernvall et al., 2000), as well as the genetic (Stohl, 1984) and ontogenetic components of the complexity of molars (Kourova, 1986; Cheprakov, 2010). Despite the numerous works on the factors that determine the complexity of teeth in arvicolines, the results of investigations conducted on different model species are often not comparable with each other directly. This is due primarily to the fact that there is no universal scheme for estimation of the complexity of the dental system for arvicolines. Even for one species, different studies usually develop different plans of morphological analysis (a set of morphotypes, schemes of linear and angular measurements, and landmark layouts in geometric morphometrics). The most known examples are the widespread species such as the common vole (*Microtus arvalis* sensu lato) (Rörig and Börner, 1905; Eremina, 1974; Schimmelpfennig, 1991; Rekovets, 1994; Uhlíková, 2008; Markova et al., 2010), narrow-skulled vole (*Microtus gregalis*) (Bol'shakov et al., 1980; Maleeva and Shuvalova, 1980; Nadachowski, 1982; Smirnov et al., 1986; Rekovets, 1994), bank vole (*Clethrionomys glareolus*) (Nadachowski, 1982; Niethammer, 1984; Rekovets, 1994; Ledevin et al., 2010), and others. As a result of using different approaches to the analysis of

variability, it is often impossible to verify whether the tendencies to complication or simplification of molars identified in certain regions or populations are characteristic of the entire species. The absence of uniform methods of morphological analysis also causes difficulties in matching the results obtained on modern material with paleontological data.

Among the various morphological methods of evaluation of the complexity of the chewing surface in arvicolines, the simplest one is morphotypic analysis. It involves distinguishing conditionally discrete variations in the structure of the chewing surface, i.e., morphotypes, and evaluation of the frequency of their occurrence in modern natural populations and fossil samples. Schemes of morphotypical variability were developed for the majority of modern species (Rörig and Börner, 1905; Angermann, 1973; Eremina, 1974; Bol'shakov et al., 1980; Niethammer, 1984; Kaneko, 1996; Pozdnyakov, 1993, 2005; etc.) and fossil arvicolines (Maleeva, 1976; Maleeva and Shuvalova, 1980; Rabeder, 1981; Nadachowski, 1982; Smirnov et al., 1986; Rekovets, 1994; Abramson and Nadachowski, 2001; Fadeeva and Smirnov, 2008; etc.). In all these schemes, the following characteristics are taken into account: the number, shape, position (opposition−alternation), and degree of confluence or separation of elements of the chewing surface. This allows researchers to develop schemes that fully describe the range of variability of species, which is crucial for the evaluation of the reliability of taxonomic diagnostics (Borodin, 2009) and enables development of multidimensional schemes for comparison of complete spectra of morphotypical variability in different species (Schimmelpfennig, 1991; Pozdnyakov, 2005). Using the schemes of morphotypical analysis that take into account the most complete set of parameters (number, shape, degree of fusion of prisms, etc.) is essential for understanding the patterns of variability of the species, but these schemes are not always suitable for studying the factors that regulate the complication of teeth in arvicolines. As has been illustrated for the voles of the genera *Microtus* and *Alticola*, the degree of complexity of a tooth estimated by the number of elements on the chewing surface and by the confluence patterns between its elements does not correspond, i.e., the features that characterize the number of elements of the chewing surface and their fusion may occur independently of each other (Bol'shakov et al., 1980).

Data on the development of teeth in early ontogenesis (Jernvall et al., 2000) indicate that the setting of the lateral topography of a tooth (two-row position of the main elements and the establishment of the degree of their displacement relative to each other: opposition or alternation) is determined by the action of molecular prepatterns long before the formation of the prismatic structure of the crown, i.e., at the earliest stages of morphogenesis. Additional elements of the crown emerge later, against the background of the already formed lateral topography of the tooth. As the confluence of the elements of the chewing surface of the tooth of arvicolines is determined by the position of prisms and the degree of their separation, while the number of elements of the chewing surface is determined by the number of dentine prisms, it is evident that two-dimensional schemes of the morphotypes constructed taking into account the number of elements of the chewing surface and the degree of their fusion include features related to different stages of tooth morphogenesis. The contour of elements of the chewing surface attains its definitive form in postnatal ontogenesis, in the process of wearing of the crown; i.e., it belongs to a later ontogenetic stage.

The aim of this work is to develop a morphogenetically homogeneous one-dimensional scheme of assessment of morphotypical characteristics of the dental system of arvicolines, which would enable us to rank the morphotypes by the degree of complexity, and to evaluate the applicability of this scheme in studying the patterns of variability among various representatives of the subfamily Arvicolinae.

MATERIALS AND METHODS

Material

This work was carried out on mass and widespread arvicoline species of northern Eurasia, in particular, species whose distribution ranges include the Urals and adjacent plains. The material for this work came from the collections of the Zoological Museum of the Institute of Plant and Animal Ecology of the Russian Academy of Sciences, as well as published data on the variability of modern and fossil forms (Ognev, 1950; Bol'shakov et al., 1980; Nadachowski, 1982; Smirnov et al., 1986; Rekovets, 1994; Tesakov, 2004; Borodin, 2009; Rabeder, 1981; Markova et al., 2010, etc.). A quantitative assessment of the range of morphotypical variability of teeth was carried out for 1916 individuals of 16 species of modern fauna.

Terminology and Statistical Analysis

In this paper, we used the nomenclature of the chewing surface of teeth of arvicolines according to Van der Meulen (Van der Meulen, 1973). Letter designations: (*m1*, *m2*, and *m3*) lower and (*M1*, *M2*, and *M3*) upper molars with the order number; (*T1−Tn*) paired elements of the crown and corresponding elements of the occlusal surface, (*RA*) re-entrant angle, (*SA*) salient angle, (*L*) lingual, and (*B*) buccal angles. The numbering of all elements is according to the traditional scheme and is given in Fig. 1. Statistical analysis of the material was performed with the Statistica 6.0 program package. The Kolmogorov−Smirnov test was used to test for a normal distribution.
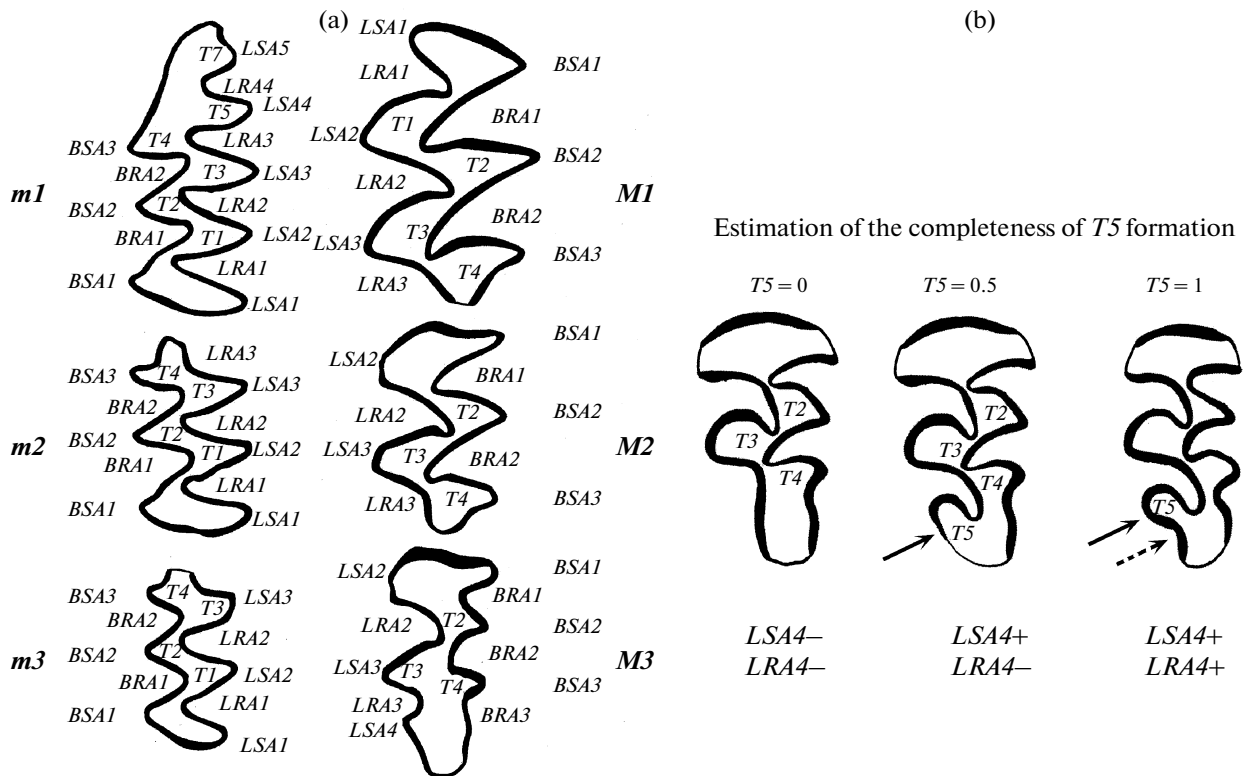
Fig. 1. (a) Designations of the elements of the occlusal surface of molars (Van Der Meulen, 1973; Tesakov, 2004) and (b) principle of determining the (+) presence or (−) absence of the additional prism of the crown illustrated by formation of the fifth prism *T5* on the third upper tooth of a meadow vole. The arrow indicates the position of the fourth lingual salient angle (*LSA4*), the dotted arrow indicates the fourth lingual reentrant angle (*LRA4*), which mark the degree of completeness of the formation of *T5*. See the text for abbreviations.

Approaches to Identification of Morphotypes

The morphotypical schemes of tooth variability in modern species and fossil forms of arvicolines were analyzed (Rörig and Börner, 1905; Hinton, 1926; Angermann, 1973; Eremina, 1974; Maleeva, 1976; Bol'shakov et al., 1980; Rabeder, 1981; Nadachowski, 1982; Niethammer, 1984; Smirnov et al., 1986; Schimmelpfennig, 1991; Pozdnyakov, 1993; Rekovets, 1994; Fadeeva and Smirnov, 2008; Borodin, 2009; etc.).

To reduce the descriptive schemes of morphotypes, only meristic characteristics were selected: the number of salient and re-entrant angles on the lingual and buccal sides of molars, as well as the presence of the respective fields on the occlusal surface. To distinguish the ranks of complexity of morphotypes, only the prisms of the crown were taken into account (main and additional), whereas the Mimomys-ridges and enamel islets (Gromov and Polyakov, 1977) were not considered, as these elements of the occlusal surface are eliminated in the course of evolution of most arvicoline lines. The confluence of the elements of the occlusal surface and their lateral displacement were not taken into account on the basis of data on tooth

morphogenesis in arvicolines, according to which the formation of lateral topography and additional elements of the crown occurs at different morphogenetic stages (Jernvall et al., 2000).

Morphotypical characteristics were taken into account for individuals at the post-juvenile stages of ontogenesis; i.e., the occlusal surface was fully formed on all molars. Both right and left molars were included in the analysis.

Ranking of Morphotypes by Complexity

The complexity of teeth was analyzed using a traditional morphotypical approach (e.g., Bol'shakov et al., 1980) when morphotypes are regarded as conventionally discrete variants of the structure of the occlusal surface, while the frequencies of morphotypes carry information about the share of individuals with a specific phenotype in the population. However, to take into account the evolutionary tendency toward complication of the contour of the occlusal surface, which is common for arvicolines, the morphotypes were sorted and ranged by complexity. The complexity rank was determined by the number of dentine prisms

and the respective elements of the occlusal surface (Fig. 1). Both fully formed and emerging (additional) prisms, which correspond to triangular loops of the occlusal surface, were taken into account; the enamel ridges and islets were not considered. The complete formation of one additional element—the dentine prism and the corresponding salient angle—tends to raise the rank of complexity of the morphotype by 1. This suggests that the ranked variations are separated by formally equal distances: they differ by one additional element of the occlusal surfaces. Such ranking allows us to consider the tooth complexity as a quantitative variable measured by an interval scale. The complexity of the morphotype can thus be evaluated at the individual level (for example, for individual specimens) for any molar.

The criterion by which the presence of an additional prism of the crown was registered consisted in the presence of the re-entrant angle as shown in Fig. 1 for the third upper tooth in meadow voles (Fig. 1b). If prism $T5$ is absent and angles $LSA4$ and $LRA4$ are not registered, the rank of complexity equals 0. If prism $T5$ is formed completely (i.e., $LSA4$ and $LRA4$ are present), the rank of complexity is 1. If $T5$ is forming (the salient angle $LSA4$ is present, but the reentrant angle $LRA4$ is not developed sufficiently for its depth to be measured), this variant of the structure is estimated as intermediate between 0 and 1; i.e., numerically it is equal to 0.5.

Distinguishing the Main and Reserve Morphotypes

The main and reserve morphotypes were distinguished on the basis of estimation of the frequency of variations with a certain rank of complexity in modern species. This approach is based on the classification proposed by A.G. Maleeva for studying variability of teeth of arvicolines in space and time. According to this classification, the morphotypes that constitute 36% of a sample or more are considered as superdominant, those from 12 to 35.9% are dominant and subdominant, and less than 12% are reserve; the group of the main morphotypes includes variations, the proportion of which exceeds 12% (Bol'shakov et al., 1980).

RESULTS

Ranking Morphotypes by Complexity and Evaluation of the Universality of the Approach within a Subfamily

A comparison of morphotypical schemes of modern and fossil arvicoline forms showed that a series of morphotypes ranked by the presence of the main and additional prisms of the crown can be built for any species of the subfamily. This allows us to suggest a principle for identifying the rank of complexity of any molar in arvicolines (Table 1). The distinguished ranks

of complexity characterize certain stages of evolutionary changes in each molar.

Unlike traditional classifications, the proposed scheme (Table 1) implies not only ranging morphotypes but also sets the interval between them. Each of the complexity ranks reflects the stage of completion of formation of one sequentially adding element—the dental prism—from its full formation to the start of formation of the following pair of prisms on its basis. An increase in the complexity of rank by 1 occurs when one of the following prisms (lingual or buccal) is fully formed, and by 2, when both the buccal and lingual prisms are fully formed.

The intervals between the ranks of complexity of morphotypes in the proposed scheme are morphological distances. The rate and nature of realization of the tendency to adding of crown prisms in different species, genera, and phylogenetic lineages differ significantly (on an evolutionary time scale). Therefore, two variants of the scale can be suggested for differentiating the intervals: integral and fractional. The integral scale (Table 1) can be used for comparing the evolutionary trends at the interspecies level and for representatives of different phylogenetic lineages. To investigate the variability at the intraspecific level and for phylogenetically closely related species, it is possible to divide the suggested intervals and to introduce a fractional scale (for example, in increments of 0.5). It is expedient to use the fractional scale in the cases when variation within the same rank of complexity is rather high (for example, for collared lemmings and voles of the genus *Microtus*) (Figs. 2, 3).

The proposed scheme (Table 1) is universal for each molar (*m1, m2, m3, M1, M2*, and *M3*) and can be applied to any arvicoline taxon. An analysis of the occurrence of complexity ranks in modern arvicolines (Tables 2, 3) showed that the prevailing morphotype complexity ranks and relatively rare variations can be distinguished for any taxon; the main morphotypes for a species are the closest in terms of the rank of complexity.

Practical Application of the Ranked Approach in Studying the Variability of Arvicolines in Space and Time

The ranked approach to analyzing the complexity of molar in arvicolines can be used for various research tasks. At the level of distinct species, it was used in studying intraspecific variation. In comparing geographically remote populations, it was shown for the common vole that a change in the main and reserve morphotypes may be observed and the variety of complexity ranks in one population may vary from reduced (one rank is super-dominant) to increased, when the main morphotypes belong to three consecutive ranks of complexity (Markova et al., 2010). The possibility exists of using the ranged morphotypical approach for
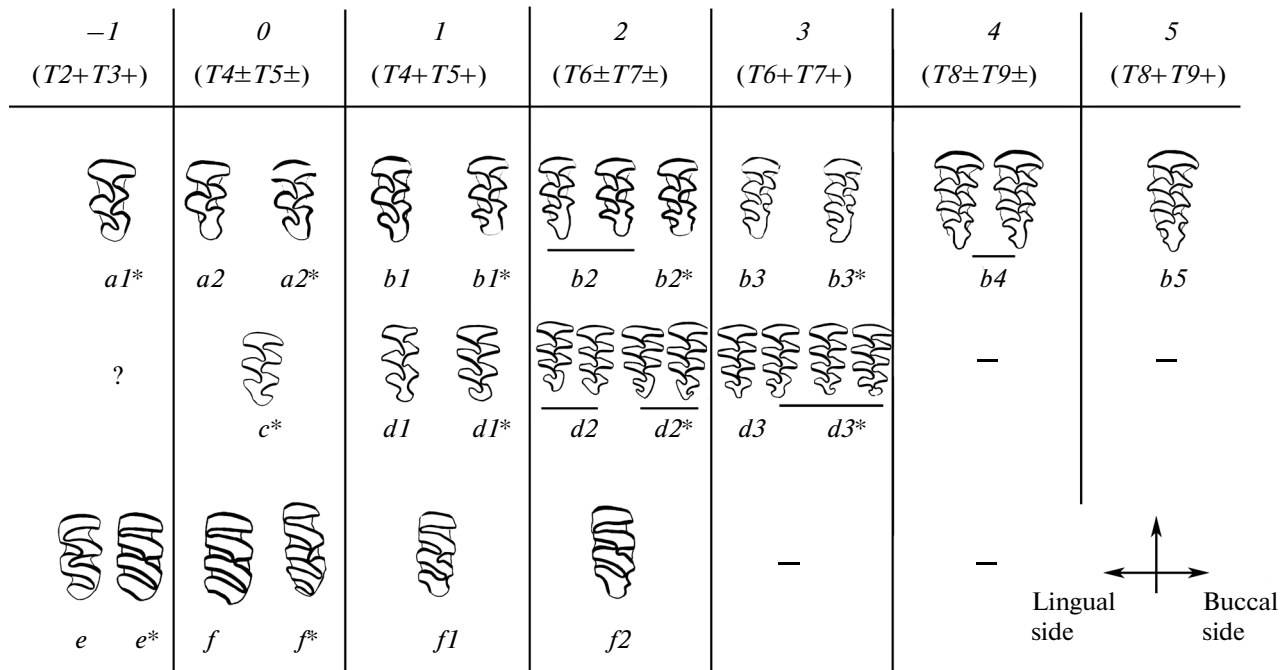
Fig. 2. Ranking scheme of molar morphotypes for the third upper tooth in representatives of the phyletic lineages *Allophaiomys–Microtus* (*a–b*), *Praedicrostonyx–Dicrostonyx* (*c–d*), and the tribe Lemmini (*e–f*). (From −1 to 5) Complexity ranks of morphotypes on an integral interval scale (ranking principle, see Table 1); morphotypes *M3*: (*a1*–*a3**) genus *Allophaiomys*† (Rekovets, 1994; Borodin and Ivakina, 2000; Tesakov 2004); (*b1–b5*) genus *Microtus* (Rörig and Börner, 1905; Angermann, 1973); (*c**) *Dicrostonyx simplicior*† (Borodin et al., 1998), (*d1*) genus *Praedicrostonyx*†, (*d1*–*d3**) genus *Dicrostonyx* (Smirnov et al, 1986); (*e–f2*) Lemmini (Smirnov et al., 1986; Abramson and Nadachowski, 2001). An asterisk denotes a variation for which using a fractional scale in increments of 0.5 is possible (see explanation in text).

researching age variability in hypsodont arvicolines, whose teeth grow throughout their entire life: for the tundra (Kropacheva et al., 2012) and narrow-skulled (Markova et al., 2013) voles. By making a series of tooth-prints of *m1* in their lifetime, it was established that, in the course of wearing of the crown at the post-juvenile stages in the same individual, the values of the complexity index can vary within one or, more rarely, two ranks, but these changes are not systematic (both a slight increase and a decrease in the rank of complexity can be observed). In the course of analysis of variance (Markova et al., 2013), it was shown that age variation in the complexity index can be considered negligibly small compared with the variability among individuals. A comparison of the range of variability of the forms with rooted teeth, for example, in the genera *Ellobius* and *Clethrionomys* (Tables 2, 3), showed that the variation of complexity indices in the species of these genera is higher than in the forms with rootless teeth due to later ontogenetic stages. With the gradual wearing of crown prisms in old individuals, the number of elements of the occlusal surface decreases, which is manifested in reduced rank of complexity (Tables 2, 3). Therefore, the ranked morphotypical approach for the forms with rooted teeth should be used with the obligatory reference to the stage of wearing of the crown.

Application of the ranged morphotypical approach in comparing the range of variability in time within one phyletic lineage can be demonstrated for *M. arvalis obscurus* and the forms that are ancestral to it: *M. arvalinus* (early Pleistocene), *Allophaiomys pliocaenicus* (Late Eopleistocene–start of Early Pleistocene), and *A. deucalion* (Early Eopleistocene).

The material for comparison consisted of data on the variability of *m1* in *M. arvalis obscurus* (sampling from the city of Yoshkar-Ola; Markova et al., 2010) and images of *m1* in *M. arvalinus*, *Allophaiomys pliocaenicus*, and *A. deucalion* from the localities in southern Eastern Europe (Rekovets, 1994). The distribution of values of the complexity of *m1* using the ranked approach are shown in Fig. 4. At the super-domination of rank 1 in *A. deucalion* and *A. pliocaenicus*, the latter is characterized by a high proportion of complicated teeth. In *M. arvalinus* and *M. arvalis obscurus*, the super-dominant rank is rank 3. The increase in the share of complex morphotypes in *M. arvalis obscurus* compared to *M. arvalinus* is comparable to the differences between *A. deucalion* and *A. pliocaenicus*.
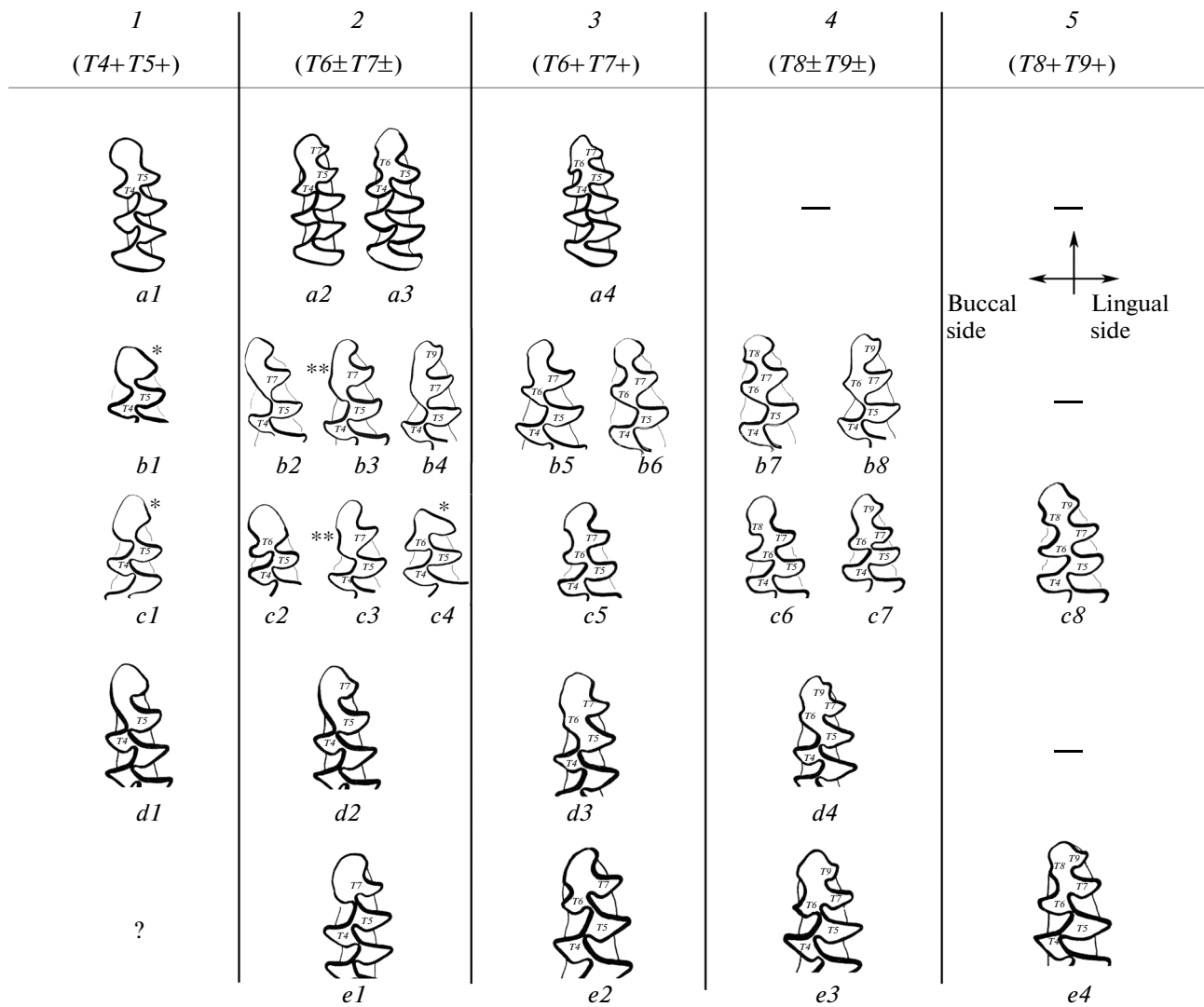
Fig. 3. Scheme of ranking of morphotypes of *m1* by complexity in meadow voles from the central part of northern Eurasia. (*1−5*) Complexity ranks on an integral scale from Table 1; morphotypes: (*a1−a4*) genus *Allophaiomys*† (Rekovets, 1994; Borodin and Ivakina, 2000; Tesakov, 2004), (*b1*) *Microtus* ex gr. *hintoni-gregaloides*† (Rekovets, 1994), (*b2−b8*) *M. gregalis* (Maleeva and Shuvalova, 1980; Markova et al., 2013), (*c1*) *M.* ex gr. *arvalis*, (*c2−c8*) *M. arvalis* sensu lato (Markova et al., 2010), (*d1−d4*) *M. oeconomus* (Smirnov et al., 1986, and original data), and (*e1−e4*) *M. middendorffi* (Smirnov et al., 1986). An asterisk denotes a variation with incomplete formation of the prism *T7* and two asterisks designate incomplete formation of prism *T6*.

Apart from the graphic representation of the studied tendencies, the methods of parameteric or non-parametric statistics can be used in the analysis of complexity estimates. At the individual level, the rank of complexity is considered as the individual estimate of complexity, whereas at the population level, it is the average values of complexity (in the case of normal distribution of complexity ranks) or modal values of complexity if the distribution of complexity ranks is different from normal.

An analysis of the frequency distribution of ranked estimates of tooth complexity in the arvicolines from the Ural Mountains and adjacent plains showed that for many species, the distribution of complexity ranks in *m1* and *M3* are characterized by a positive excess kurtosis and skewness (e.g., the distribution of complexity ranks of *m1* in *M. arvalis obscurus*) and can also have an unskewed distribution and negative excess kurtosis (e.g., the distribution of complexity ranks of *M3* in *Dicrostonyx torquatus*).

Based on the analysis of the distributions of complexity ranks, a model describing the shift of the morphotypical structure of molars in arvicolines toward higher complexity of the occlusal surface can be proposed.
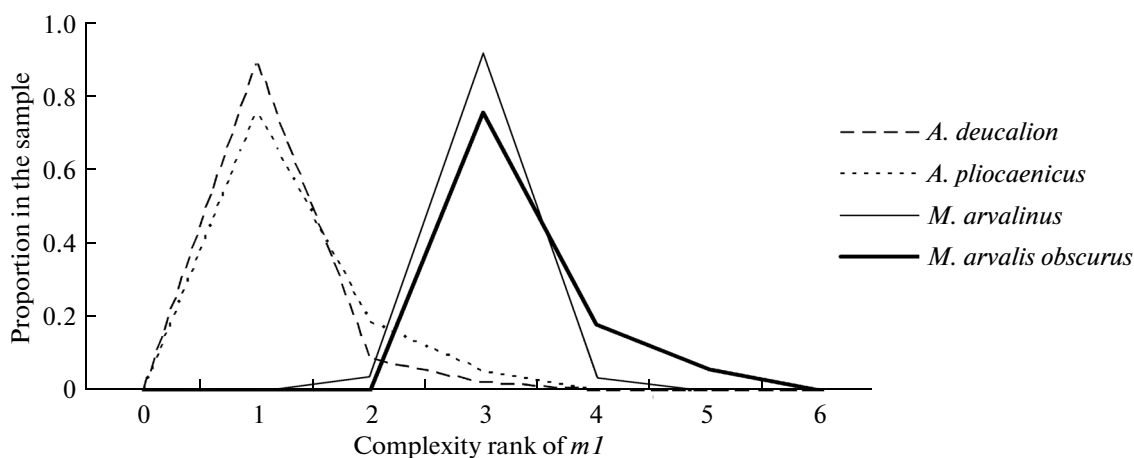
Fig. 4. Comparison of morphotypical characteristics of *m1* of the modern species *M. arvalis obscurus* from the Eastern Europe (Marii El; Markova et al., 2010, $N = 88$) and its ancestral forms (south of Eastern Europe; Rekovets, 1994): *M. arvalinus*† (Early Pleistocene, $N = 102$), *Allophaiomys pliocaenicus*† (start of Early Pleistocene−Late Pleistocene, $N = 56$), and *A. deucalion*† (Early Pleistocene, $N = 48$).

Model of Shift of the Morphotypical Structure Toward Increased Complexity of the Occlusal Surface

Combinations of the basic morphotypes in the populations of modern species or in fossil samples may be presented in the form of a graph (Fig. 5, the combinations are marked with arcs) describing the gradual transition from a relatively simple to a more complex type of morphotypical structure of molars in arvicolines. Points *1* and *2* represent the state of the populations at the transition from a simple (*1*) to a more complex (*2*) structure of molars. Each of these states can be realized with different levels of diversity, from a lowered one (when superdominance of one complexity rank (*1*, *2*) is observed in the population) to balanced (*1a*, *2a*), and to high (*1b*, *2b*) (Fig. 5). Accordingly, complexity rank *2* may constitute a reserve progressive variant within the framework of the morphotypical structure *1−1a−1b*, and at the same time, it gives rise to the subsequent more complex type of dental system *2−2a−2b*. The easiest transition from state *1* to state *2* is possible from states *1a* and *1b* as a result of the gradual decline in the proportion of super-dominant simple morphotypes (rank 1) up to their complete transition to the category of reserve and latent in the gene pool of the population.

DISCUSSION AND CONCLUSIONS

An analysis of the existing morphotypical schemes showed that despite more than a century-long period of development of approaches to classification of the variability of arvicoline teeth, common criteria for distinguishing morphotypes have been absent until recently. Depending on the objectives of creating the schemes and criteria for identifying the morphotypes,

all known classifications can be conditionally divided into descriptive and research types. In the first case, the aim consists in describing completely the range of variability on the basis of one characteristic (e.g., Niethammer, 1984) or by a combination of characteristics (e.g., Bol'shakov et al., 1980; Pozdnyakov, 1993). As the criteria for distinguishing morphotypes in descriptive schemes, almost any characteristics amenable to formalization can be used (most frequently, it is the degree of confluence between dentine fields and the number of salient angles). In schemes designed for hypothesis-driven research, when distinguishing morphotypes, it is taken into account that the characteristics by which morphotypes are distinguished are only conditionally discrete and reflect a tendency toward complication of the contour of the occlusal surface through the gradual formation of new elements of the crown, which is common to arvicolines. Such schemes are frequently used in researching the temporal variability only within individual phyletic lineages or genera of Arvicolinae (Bol'shakov et al., 1980; Smirnov et al., 1986), although the possibility of designing a common scheme of teeth morphotypes for the subfamily was mentioned more than forty years ago (Angermann, 1973).

A ranked sequence of morphotype dental patterns for any arvicoline species was designed by arranging morphotypes by the increase in the number of prismatic elements of the crown, which allows one to take into account the evolutionary tendency to complication of molars, which is common for arvicolines. The developed scheme dates back to the principle of distinction of morphotypes suggested by Rörig and Börner (1905) and is a logical continuation of the ideas of Angermann on homological rows of variability in arvicolines (1973), those of Maleeva on the changing
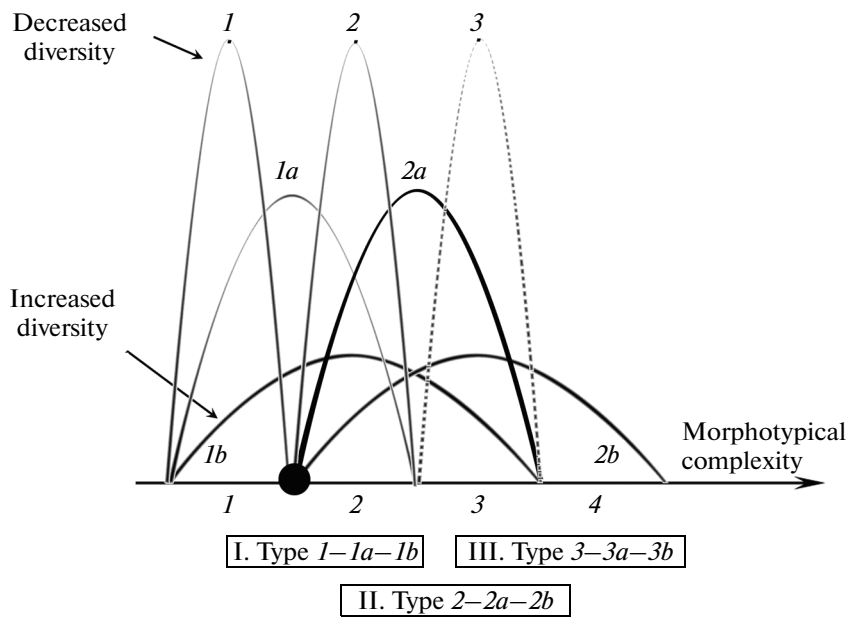
Fig. 5. Model explaining the morphological transition toward increased complexity of molars in arvicolines on the basis of changing combinations of the basic morphotypes. (*1–4*) Complexity ranks of morphotypes from Table 1 and their possible realization in the populations of species: (*1, 2,* and *3*) decreased diversity (the main group represents morphotypes of one rank of complexity), (*1a* and *2a*) balanced diversity (codomination of the morphotypes of two ranks of complexity), and (*1b* and *2b*) increased diversity (morphotypes of three ranks of complexity codominate). (I–III) Types of morphotypic structures corresponding to the dominant ranks of complexity. The black dot marks the change in the dominant morphotype: transition of the morphotype with complexity rank 1 from the main category to the reserve category.

of the main and reserve morphotypes in the course of the phyletic evolution (Bol'shakov et al., 1980), and those by Borodin about the types of complications of teeth in arvicolines (Borodin, 2009). However, in contrast to the traditional morphotypical classifications, the proposed scheme implies not only arranging the morphotypes but also sets the spacing between them. The interval between the ranks of complexity reflects the morphological distances between the morphotypes: each of the distinguished ranks reflects the stage of completion of formation of one sequentially added additional element, i.e., the dentine prism. Another difference from the existing morphotypical schemes is the fact that morphotypes with a complication of either buccal or lingual side of the tooth can have the same rank in terms of complexity. Such merging is impractical from the point of view of the principles of construction of descriptive classifications; however, when morphotypes are ranked taking into account evolutionarily significant changes in the tooth structure, such a merging is justified as additional prisms are paired elements. No one-sided multiple complication of prismatic teeth of the arvicoline type is known for modern species, and it appears to be impossible from the perspective of morphogenetic mechanisms for iterative addition of paired elements (Jernvall et al., 2000). The complexity ranks thus represent not discrete variations but intervals containing the morphotypes, which might be dissimilar from one another in

shape or nature of confluence between dentine fields, but which have a formally identical degree of development of additional elements of the crown. These intervals may be set by the integral scale of values or the resolving capacity of the approach can be increased by introducing gradations within each interval. Introducing gradations within intervals is possible on the basis of quantitative criteria, for example, the grade measures of angles used for distinguishing molar morphotypes in collared lemmings, and narrow-skulled voles (Kochev, 1983; Smirnov et al., 1986).

The proposed approach can be used for any molar of any species of Arvicolinae and can take into consideration both the complication of the occlusal surface and the reduction of particular crown elements. It allows us to consider teeth complexity as a quantitative variable and to compare taxa with varying degrees of phylogenetic closeness within the subfamily Arvicolinae, and also to investigate the intraspecific variability in space (for example, to compare intraspecific forms and geographically divided populations of one species) and time (for instance, to compare the taxa of one phyletic lineage) by the complexity parameters of the dental system.

Thus, the ranked morphotypical scheme for intra- and interspecific comparisons in arvicolines satisfies the following conditions: (1) the one-dimensionality for an unambiguous ranking of morphotypes by com-

Table 1. Determining the rank of molar complexity in Arvicolinae by the presence or absence of additional prisms of the crown (the additional prisms are fixed by the presence of the respective salient angles (Fig. 1)) and an evolutionary and morphological characterization of the corresponding stages of complication of molars

Forming pair of prisms	Presence (+) or absence (−) of crown prisms and respective fields of the occlusal surface on molars								
	T1/2−T3−	T1/2+T3+	T1/2+T3+	T1/2+T3+	T1/2+T3+	T1/2+T3+	T1/2+T3+	T1/2+T3+	T1/2+T3+
T1/2T3	T1/2−T3−	T1/2+T3+	T1/2+T3+	T1/2+T3+	T1/2+T3+	T1/2+T3+	T1/2+T3+	T1/2+T3+	T1/2+T3+
T4T5	−	−	T4+T5−; T4−T5+; [T4+T5−{T6+T8+}; T4−T5+{T7+T9+}]	T4+T5+	T4+T5+	T4+T5+	T4+T5+	T4+T5+	T4+T5+
T6T7	−	−	−	−	T6+T7−; T6−T7+; [T6+T7−T8+{T10+}; T6−T7+T9+{T11+}]	T6+T7+	T6+T7+	T6+T7+	T6+T7+
T8T9	−	−	−	−	−	−	T8+T9−; T8−T9+; [T8+T9−T10+{T12}; T8−T9+T11+{T13+}]	T8+T9+	T8+T9+ [T10± T11±]
Complexity rank of the tooth	−2(−3)	−1	0	1	2	3	4	5	6
Characterization of the evolutionary and morphological stage	Reduction of crown prisms: only some prisms are traced as salient angles (−2). Or complete loss of the prismatic structure of the tooth (−3)**	T4 is not formed or reduced, T1/2 and T3 are present	The simplest type of structure: a pair of prisms T4T5 is incompletely formed (one of them is not formed completely)*	Completion of the formation of the pair T4T5 (there are no additional salient angles after T4T5)	Start of formation of the pair T6T7 (only one of these prisms is formed)	Completion of the formation of the pair T6T7 (there are no additional salient angles after T6T7)	Start of formation of the pair T8T9 (only one of these prisms is formed)	The pair T8T9 is formed (there are no additional elements after T8T9)	Start of formation of T10T11

The square brackets show the variants of nonuniform complication of the lingual and buccal sides of the tooth: the even additional elements (T2, T4, T6, T8, etc.) indicate the complication of the buccal side, and the odd ones (T1, T3, T5, T7, etc.) indicate the complication of the lingual side; curly brackets give hypothetical variants.

* For m1 this stage corresponds to the formation of the secondary-simplified tooth.

** This stage may be determined by (1) reduction of the crown prisms in the course of evolution (for instance, genus *Ellobius*), (2) wearing of the crown prism in arvicolines with rooted molars, or (3) morphogenetic abnormalities, natural or artificially induced (Jernvall et al., 2000).

Table 2. Frequency of occurrence of *m1* with various ranks of complexity (in fractions of 1) and the main morphotypes of *m1* in recent arvicolines in central northern Eurasia according to collection (numerical values) and literature data (marked with +)

Taxon	Rank of complexity of *m1*									N (teeth)
	−2 (−3)	−1	0	1	2	3	4	5	6	
Ellobius talpinus	c	c	**0.17**	**0.82**	+	—	—	—	—	122*
Lemmus sibiricus	—	—	+	**1**	—	—	—	—	—	76
Myopus schisticolor	—	—	—	++	—	—	—	—	—	Lit
Arvicola terrestris	—	—	—	**0.82**	**0.12**	0.06	—	—	—	34
Clethrionomys rutilus	c	c	c	**0.48**	**0.48**	0.04	—	—	—	44
C. glareolus	c	c	c	**0.39**	**0.55**	0.06	—	—	—	36
C. rufocanus	c	c	c	**0.48**	**0.36**	**0.16**	—	—	—	42
Microtus oeconomus	—	—	—	0.01	**0.56**	**0.43**	+	—	—	109
M. gregalis	—	—	—	—	**0.20**	**0.79**	0.01	—	—	363
Lagurus lagurus	—	—	—	—	0.09	**0.90**	0.01	—	—	82
M. middendorffi	—	—	—	—	**0.15**	**0.79**	0.06	+	—	80
M. arvalis arvalis	a	—	—	—	0.005	**0.94**	0.05	0.005	—	798
M. arvalis obscurus	—	—	—	—	+	**0.90**	0.08	0.02	—	536
M. rossiaemeridionalis	—	—	—	—	+	**0.67**	**0.22**	0.11	—	386
M. agrestis	a	—	—	—	—	**0.81**	**0.15**	0.04	—	244
Ondatra zibethicus	—	—	—	—	—	0.11	0.09	**0.80**	—	54
Dicrostonyx torquatus	—	—	—	—	—	0.05	**0.12**	**0.80**	0.03	153

The main morphotypes are in bold or indicated by two + characters. The letters refer to the rare variants of simplification of the occlusal surface: (c) wearing of the crown in senile individuals of the forms with rooted molars (possible stages of wearing range from *0* to −*3*); (a) anomalies of tooth morphogenesis with a complete (−*3*) or partial (−*2*) loss of the prismatic tooth structure.
* Collections of N.G. Evdokimov and N.V. Sineva, Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences.

Table 3. Frequency of occurrence of *M3* with various ranks of complexity (in fractions of 1) and the main morphotypes of *M3* in recent arvicolines in central northern Eurasia according to collection (numerical values) and literature data (marked with +)

Taxon	Rank of complexity of *M3*									N (teeth)
	−2 (−3)	−1	0	1/1.5	2	3	4	5	6	
Ellobius talpinus	**0.96** (0.04)	—	—	—	—	—	—	—	—	122*
Arvicola terrestris	—	—	+	**0.78**/0.06	**0.12**	0.06	—	—	—	38
Lagurus lagurus	—	—	**0.13**	0.01	**0.86**	—	—	—	—	84
Lemmus sibiricus	—	—	—	**0.92**/0.05	0.03	—	—	—	—	74
Myopus schisticolor	—	—	—	++	—	—	—	—	—	Lit
Ondatra zibethicus	c	c	0.10	**0.21**	0.69	—	—	—	—	58
Clethrionomys rufocanus	c	c	0.03	**0.50**/0.07	**0.34**	0.06	—	—	—	125
C. glareolus	c	c	c	**0.19**/**0.19**	**0.54**	0.08	—	—	—	34
Dicrostonyx torquatus	—	—	—	0/**0.41**	**0.39**	**0.20**	—	—	—	152
C. rutilus	c	c	c	0.018/0.05	**0.72**	**0.21**	0.002	—	—	533**
Microtus arvalis arvalis	a	—	—	0.08/**0.29**	**0.35**	**0.24**	0.04	—	—	792
M. arvalis obscurus	—	—	—	0.01/**0.29**	**0.41**	**0.27**	0.02	—	—	421
M. rossiaemeridionalis	—	—	—	0.07/**0.17**	**0.38**	**0.34**	0.04	—	—	323
M. gregalis	—	—	—	0/**0.17**	**0.39**	**0.39**	0.05	—	—	436
M. agrestis	a	—	—	0/**0.13**	**0.19**	**0.59**	0.09	—	—	261
M. oeconomus	—	—	—	0/0.02	0.11	**0.58**	**0.26**	0.03	—	229
M. middendorffi	—	—	—	—	0.02	**0.81**	**0.15**	0.02	—	151

The main morphotypes are in bold or indicated by two + characters. The letters refer to the rare variants of simplification of the occlusal surface: (c) wearing of the crown in senile individuals of the forms with rooted molars (possible stages of wearing range from *0* to −*3*); (a) anomalies of tooth morphogenesis with a complete (−*3*) or partial (−*2*) loss of the prismatic tooth structure.
 * Collections of N.G. Evdokimov and N.V. Sineva, Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences.
** Data by M.A. Fominykh.

plexity; (2) morphogenetic homogeneity (the scheme does not include features formed at different stages of morphogenesis); and (3) interpretability from the point of view of evolutionary trends in certain phyletic lineages in particular, and in the subfamily as a whole. The ranked morphotypical approach can be used as an independent method for estimating the complexity of the contour of the occlusal surfaces or in conjunction with linear measurements or geometric morphometrics. This approach allows us to obtain a biologically meaningful assessment of the degree of complexity and diversity parameters of odontological characteristics of representatives of the subfamily Arvicolinae.

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