Unification of Criteria for Distinguishing Morphotypes of Cheek Teeth in Lemmings (Lemmini, Arvicolinae, Rodentia)

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Abstract—This paper summarizes the data on morphotype dental patterns in recent lemmings (Lemmini) and their earliest presumed ancestors based on analysis of both the existing literature and zoological collections. The criteria for distinguishing the morphotypes are unified, and four metrics are proposed for assessment: (1) the occlusal surface complexity, (2) the regularity of enamel cutting edges, (3) the asymmetry of the lingual and buccal prisms, and (4) the degree of cement deposition in reentrant angles. A catalogue of basic, reserve, and rare morphotypes has been created for *Lemmus sibiricus* and *Myopus schisticolor*. The approach developed here is recommended for further research into the spatial, temporal, and ontogenetic variation in Lemmini, based on their dental characters.

INTRODUCTION

In studies on geographic and temporal variation of the wide-ranging animal species, selection of the features and approaches to effectively detect spatiotemporal trends and, at the same time, to efficiently generalize multiple data sets is one of the main stages. One possible way to approach range-wide data synthesis for widespread species is to take the features and approaches that allow direct comparison of the results of studies performed by different authors. For rodents of the Arvicolinae subfamily, an example of such an approach is the morphotype analysis of the occlusal surface of cheek teeth based on the qualitative characteristics (e.g., Bolshakov et al., 1980), sometimes supplemented by linear or angular measurements (Kochev, 1983; Smirnov et al., 1986). Although the morphotypic method is insufficient to consider fully the continuity of variation of the dental features due to the formally introduced discretization, this method is efficient for comparison of the results obtained from different studies and for generalization of large data sets. While useful in neontological studies, the morphotypic approach becomes critically important when the entire ranges of variation in recent species are compared with their extinct ancestors because the rates of structural changes in the cheek tooth patterns were very high in most phyletic lineages during the wide adaptive radiation of Arvicolinae (e.g., Chaline et al., 1993).

True, wood, and bog lemmings constitute a distinct taxonomic group in the subfamily Arvicolinae, which is different from other arvicolines in the genetic, phenotypic, and ecological features. Being specialized bryophages, true, wood, and bog lemmings play a significant role in the ecosystems of the Northern Hemisphere as first-order consumers. Their modern ranges are very broad. True lemmings are spread in the ecosystems of the tundra, forest tundra, and sparse taiga of Eurasia and North America. The range of wood lemmings covers the taiga zone of northern Eurasia, and the bog lemmings are spread across temperate and boreal forests of North America.

The results of phylogenetic reconstructions based on molecular genetic data indicate a monophyletic origin of the true, wood, and bog lemmings (Buzan et al., 2008; Abramson et al., 2009; Yannic et al., 2011). The divergence of their common ancestor occurred at the first (basal) radiation wave of Arvicolinae rodents, in the Late Miocene, approximately 7.2 ± 1.1 million years ago (Abramson et al., 2009). According to paleontological data (Fejfar et al., 2011), the divergence of the true (Lemmini) and bog (Synaptomyini) lemmings occurred in the Early Pliocene. This is supported by the discovery of teeth of two potential ancestors of these groups, the root-toothed Lemmini gen. n., sp. n. and *Tobienia kretzoii* gen. n., sp. n. in sediments of the Late Ruscinian, MN15b biozone

(Fejfar and Repenning, 1998). It is assumed that both of these forms descended from early *Promimomys* and could have originated two branches, Lemini and Synaptomyini, respectively (Fejfar et al., 2011).

In the literature data, there is no consensus on the taxonomic categories and supraspecific relationships among true, wood, and bog lemmings. For example, one tribe Lemmini Gray 1825, including three genera, *Lemmus*, *Myopus*, *Synaptomys*, is distinguished (Gromov and Polyakov, 1977; Musser and Carleton, 2005; Abramson and Lissovsky, 2012); or bog lemmings are considered to be a tribe Synaptomyini Von Königswald et Martin 1984 independent of Lemmini (Martin et al., 2003). In the latter representation, bog lemmings are considered to belong to different genera, *Synaptomys* and *Mictomys*, which differs from the traditional assumptions, according to which recent bog lemmings belong to one genus, *Synaptomys*.

Despite the divergent views on the supraspecific and supergeneric relationships, the independence of true, wood, and bog lemmings from other species of the subfamily is not disputed. This independence is confirmed by both molecular genetic data and the results of fossil record studies. By appealing to the ample material on recent and extinct species, the evolutionary trends in the dentition of true, wood, and bog lemmings (Königswald and Martin, 1984; Abramson, 1993; Abramson and Nadachowski, 2001; Martin et al., 2003), which appear amid the preservation of the similarity in phenotypically expressed trophic adaptations (Abramson, 1989), are established. Throughout their evolutionary story, true, wood, and bog lemmings preserved common ecological specializations and, in particular, the ability to use terrestrial mosses as a primary source of food (Rogers and Lewis, 1986; Eskelinen, 2004; Soininen et al., 2013).

Common trophic specialization (bryophagy) determines the extreme similarity in the dental structure, which is most pronounced in Palearctic *Lemmus* and *Myopus* species. The lack of species-specific dental traits leads to the necessity of using multivariate statistical methods, which, however, do not provide 100% accuracy of the diagnosis, or cannot be applied to isolated molars (Chaline et al., 1989; Smirnov et al., 1997; Borodin, 2009). As a result, in studies of the temporal variability, researchers have to rely on assumptions about how many species of lemmings are represented in one or another fossil assemblage (see Ponomarev et al., 2015). When investigating modern species, there may be challenges in identifying certain representatives of the *Lemmus* genus to overcome that requires the use of molecular genetic techniques (e.g., Abramson and Petrova, 2016).

The geographic and temporal variation in dentition within the the time span of the existence of modern taxa has been studied fragmentary and mainly within the context of searching for between-species differences. Almost every study suggests different schemes for identification of tooth morphotypes to describe the range of dental variation (Nadachowski, 1982; Abramson, 1986; Smirnov et al., 1986; Cheprakov, 1993, 2016; Abramson, 1993; Abramson and Nadachowski, 2001; Martin et al., 2003; Takken Beijersbergen, 2006; Ponomarev et al., 2015).

Our previous studies (Markova, 2014; Markova et al., 2017) have demonstrated that the descriptive schemes of Arvicolinae cheek tooth morphotypes may be transformed into research schemes by introducing formal criteria based on the data on tooth morphogenesis and evolutionary trends within the subfamily. Unlike the descriptive schemes, research schemes take into account the fact that the features distinguishing morphotypes are only formally discrete and reflect continuous patterns of evolutionary changes characteristic for one or another lineage. Ranked schemes of morphotypes elaborated for research purposes are widely used in studies of temporal variation of grey voles of the Arvicolini tribe, steppe lemmings of the Lagurini tribe, and collared lemmings of the Dicrostonychini tribe (Bolshakov et al., 1980; Smirnov et al., 1986; Krukover, 1992; Khenzykhenova, 2003; etc.). However, no morphotype ranking has been elaborated for Lemmini.

According to the established opinion, the members of the tribe are not characterized by variability in the complexity of occlusal surface (Abramson, 1993). The exception is the third upper tooth, which was hypothesized to have become more complex throughout the Pleistocene in lemmings identified as *Lemmus* cf. *sibiricus* (Smirnov et al., 1986).

We have previously (Markova, 2014) assumed that the principle of distinguishing the complexity ranks for cheek teeth common for arvicolines may also be applied to Lemmini. However, the question of how the variation trend towards complication of cheek teeth common for arvicolines corresponds to the specific adaptations to bryophagy determined for the tribe remains open.

The present study focuses on unification of the criteria for determination of the cheek tooth morphotypes in Lemmini in order to develop ranked schemes for quantification of the features that reflect the main trends in evolution of cheek teeth in the subfamily (the complexity of cheek teeth), tribe (pairwise fusion of the dental crown prisms along with the increase in the relative width of the occlusal surface), and particular genera (increasing asymmetry of the buccal and lingual tooth elements).

MATERIALS AND METHODS

Collections (Table 1) of the following three modern species, *Synaptomys cooperi* (Baird 1858), *Myopus schisticolor* (Lill. 1844), and *Lemmus sibiricus* (Kerr 1792), and materials on the variability of modern and fossil forms of Lemmini (Nadachowski, 1982;

Table 1. The materials from the modern populations of lemmings of the Lemmini tribe

Species	Region and locality	Storage location	N, animals
S. cooperi	North America	ZIN RAS	5
M. schisticolor	The North Ural region, PINR	PINR	474
	North Ural, Kytlym	The museum of IPAE RAS	8
	Western Siberia, Little Sosva	The museum of IPAE RAS	3
	Western Siberia, Sibirskie Uvaly	Surgut University	28
	Western Siberia, Sorum Reserve	Surgut University	22
L. sibiricus	The Polar Ural region, Vorkuta	The museum of IPAE RAS	64
	The Yamal Peninsula, Seyakha River	The museum of IPAE RAS	30
	The Yamal Peninsula, Harasaway River	The museum of IPAE RAS	71 m1, 80 m3, 132 M3*

* The material consists of osteological remains from pellets of predatory birds.

Smirnov et al., 1986; Krukover, 1992; Abramson, 1993; Abramson and Nadachowski, 2001; Khenzykhenova, 2003; Martin et al., 2003; Takken Beijersbergen, 2006; Cheprakov, 2010, 2016; Ponomarev et al., 2015) were used in this study. The modern taxonomy is presented according to the classification of Abramson and Lissovsky (2012).

Both right and left cheek teeth were analyzed. The morphotypic characteristics were taken into account for animals at the postjuvenile stage of ontogenesis in which the occlusal surface of all cheek teeth is entirely formed. The age of the animals was assessed according to the method of Larina and Lapshov (1974), which allows determination of the degree of skull maturity in a percentage form.

Terminology and Abbreviations

In this study, we used the nomenclature of the occlusal surface of teeth of arvicolines according to Van der Meulen (Van der Meulen, 1973). The list of abbreviations is as follows: m1, m2, and m3 are the lower cheek teeth and M1, M2, and M3 are the upper cheek teeth with the order number; AL is the anterior lobe, AC is the anterior unpaired cap of m1, PL is the posterior unpaired lobe, T1–Tn are the paired elements of the crown and corresponding elements of the occlusal surface, RA is the reentrant angle, SA is the salient angle, L is the lingual, and B is the buccal side of a molar. The numeration of all elements corresponds to the traditional scheme and is presented in Fig. 1.

Abbreviated names of organizations: IPAE, the Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences; PINR, the Pechora-Ilych Nature Reserve; ZIN, Zoological Institute, Russian Academy of Sciences.

Approaches to Morphotype Identification

The descriptive morphotypical schemes of tooth variability in modern species and fossil forms of true,

wood, and bog lemmings were analyzed (Nadachowski, 1982; Königswald and Martin, 1984; Smirnov et al., 1986; Cheprakov, 2010, 2016; Abramson, 1989; Krukover, 1992; Abramson, 1993; Abramson and Nadachowski, 2001; Martin et al., 2003; Takken Beijersbergen, 2006; Borodin et al., 2009; Ponomarev et al., 2015).

To reduce the descriptive schemes of morphotypes, the meristic characteristics that describe the main evolutionary trends determined for the subfamily as a whole, i.e., crown complexity (Guthrie, 1971; Chaline et al., 1993; Boroding, 2009), and also for the clade, i.e., changes in the regularity of cutting edge alterations due to paired fusion of the prisms of the crown, and for particular genera, i.e., the increasing asymmetry of buccal and lingual crown elements (Königswald and Martin, 1984; Abramson, 1993) were selected. In this study we do not consider the traits characterizing the shape of certain enamel loops since, in most cases, these features are determined by the degree of the development of reentrant and salient angles (and, therefore, may be assessed in accordance with the criteria used for the determination of the degree of crown complexity and regularity of the cutting edges).

Deposition of cement in the reentrant angles is considered separately. The inclusion of this characteristic for the identification of tooth morphotypes in Arvicolines has been proposed relatively recently (Ponomarev et al., 2015; Cheprakov, 2016).

The crown complexity, regularity of the cutting edges, the degree of cement deposition in the reentrant tooth angles, and the asymmetry were assessed for each animal in accordance with the schemes presented in Fig. 2.

A criterion for evaluation of the complexity was the degree of prism development determined based on the presence of the reentrant angles and the corresponding enamel walls as presented in Fig. 1 by the example of ranks 0 and 1 of the third upper and first lower teeth (Fig. 1b). If there were neither reentrant angle BRA3 nor buccal enamel wall of the prism T4, the rank of the
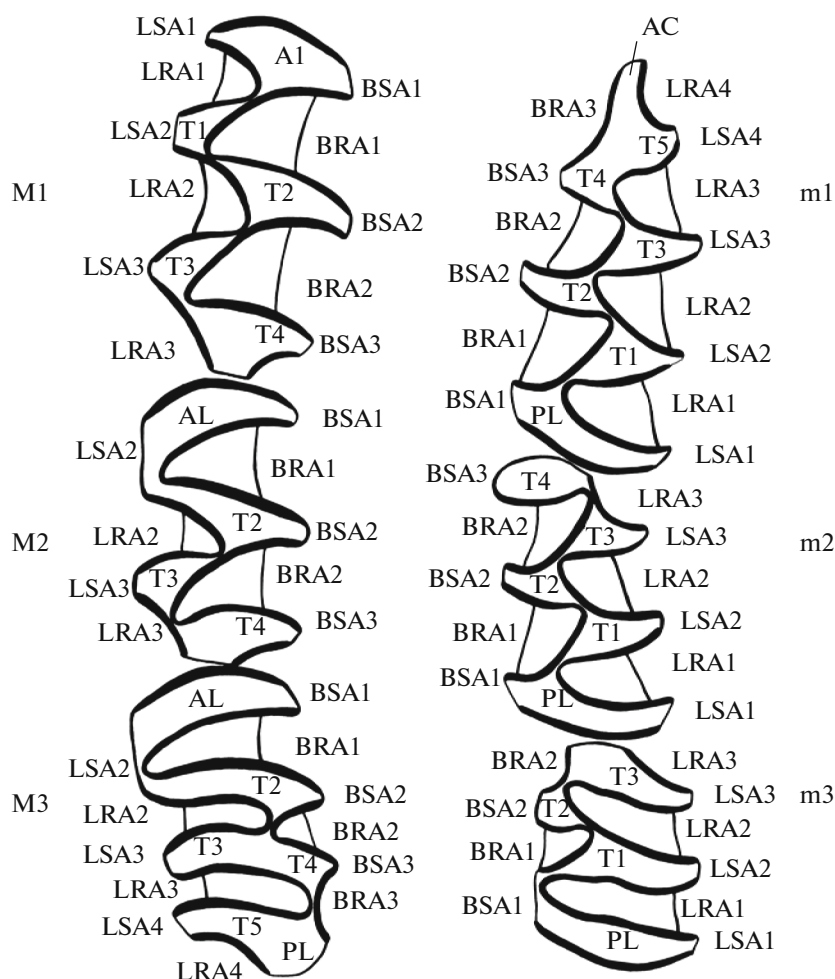
Fig. 1. Nomenclature of the occlusal surface of cheek teeth in Lemmini.

complexity was taken equal to 0. If there was no BRA3, but buccal enamel wall of T4 was found, this pattern was considered intermediate between 0 and 1, i.e., numerically equal to 0.5. If BRA3 was fully formed by the respective enamel wall, the rank was taken equal to 1. The presence of a fold on the antero-buccal enamel edge of the anterior cap of m1 or a minor additional enamel wall was not regarded as a feature of complication of the m1 occlusal surface, since no continuity of variation was observed at population level (considered as rare morphs without transitional forms). Juvenile traits, such as enamel islets or marks identified in fossil lemmings (see Smirnov et al., 1986, Fig. 25, *9*) were also not regarded as the increase in complexity since their occurrence might be associated with the recapitulation of a transitional stage to the secondary simplification of m1 at the early stages of tribe evolution that, to date, have not been sufficiently studied (Borodin, 2009).

A ridge in the posterior part of M3 (Figs. 3a; 4b, M3_e, M3_g, M3_n) is found in several populations. Moreover, several transitional forms between weak and strong intensities of the feature within the same

population were observed. This continuity of variation allowed the assumption that the ridge on the postero-lingual surface of M3 is an element of increasing complexity, which may be designated as LSA5 and included in the scheme for ranking the morphotype complexity (Fig. 3a).

Ranking of m3 morphotypes according to their complexity was performed based on the prisms T2 and T3. If the anterior enamel walls on T2 and T3 were found and the reentrant angles BRA2 and LRA3 were expressed sufficiently to measure their depth, the rank was taken equal to −1. If the anterior enamel walls of prisms T2−T3 were identified, but there were not one or two reentrant angles (BRA2 and/or LRA3), the rank was equal to −1.5. If the anterior enamel wall and the corresponding reentrant angle were observed on one of the prisms (T2 or T3), but on the other prism neither enamel nor reentrant angle were found, then the rank was equal to −2. If the enamel was absent on the frontal walls of both T2 and T3, the rank was set to −3.

The regularity of cutting edges on the occlusal surface was assessed based on the degree of paired fusion
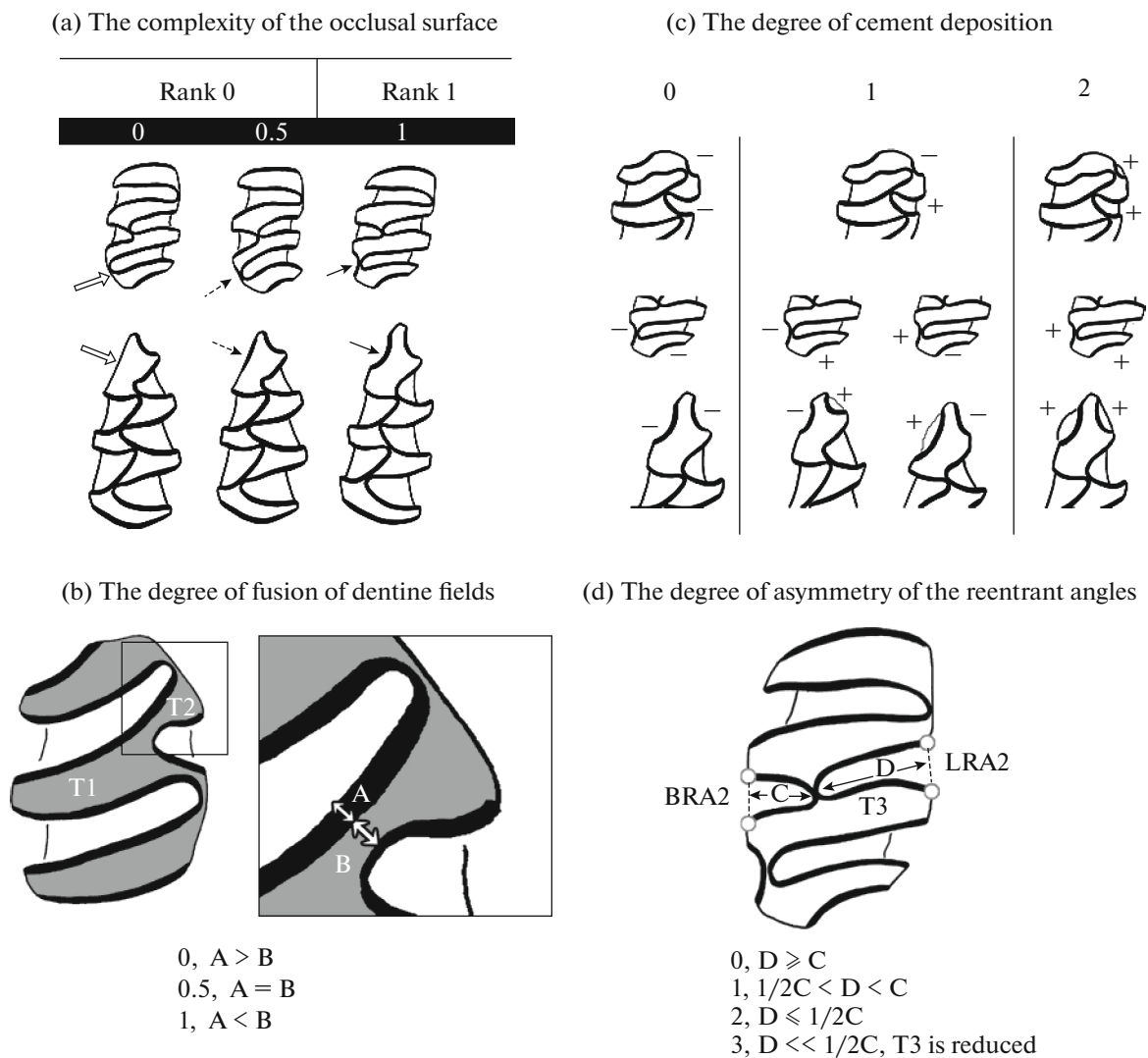
(a) The complexity of the occlusal surface

(c) The degree of cement deposition

(b) The degree of fusion of dentine fields

0, A > B
0.5, A = B
1, A < B

(d) The degree of asymmetry of the reentrant angles

0, D $\geqslant$ C
1, 1/2C < D < C
2, D $\leqslant$ 1/2C
3, D << 1/2C, T3 is reduced

Fig. 2. The criteria for ranking the morphotypes of cheek teeth in lemmings based on the complexity (a), the degree of confluence of the occlusal surface fields (b), the presence of cement (c), and the degree of asymmetry of the reentrant angles (d). (a) The arrow designates the location of the angle BRA3, which marks the degree of structural completeness of the prism T4: the light arrow indicates the absence of the external enamel wall on T4 (rank 0); the dashed arrow indicates the presence of the enamel wall without BRA3 (rank 0.5); the dark arrow indicates the presence of both the external enamel wall on T4 and BRA3 (rank 1). (b) A is the width of the thickest enamel ridge; B is the distance between the enamel ridges of the opposite reentrant angles; 0, 0.5, and 1 are the degrees of fusion of the elements of occlusal surface from total separation (0) to partial separation (0.5) and total fusion (1). (c) Variants of m3, M3, and m1 without cement deposition in two reentrant angles (0), with cement deposition found in one of the reentrant angles (1), and with cement deposition found in both reentrant angles (2); + and − mark cement depositions in those of the reentrant angles in which the variability of this characteristic should be observed. (d) The evaluation of the degree of asymmetry of the reentrant angles as exemplified by M3: 0, a lack of asymmetry, T3 is present; 1, weak asymmetry, T3 is present; 2, strong asymmetry, T3 is present; 3, complete asymmetry, prism T3 is reduced. C is the depth of the angle BRA2; D is the depth of the angle LRA2.

of the crown prisms and the corresponding dentine fields (Fig. 2b).

The degree of fusion of the dentine fields was taken equal to 0 if the distance between the enamel ridges of the opposite angles, B was less than the maximum thickness of the enamel ridge, A (Fig. 2b). If the distance B exceeded the maximum thickness of the enamel ridge A, the degree of fusion of the dentine fields was taken equal to 1. If A = B, the degree of fusion was set to 0.5. In the case of the complete fusion of dentine fields (B > A), the relative positions of the summits of the reentrant angles was not taken into account since it was impossible to formalize accurately the criteria for the evaluation of this feature.

The degree of cement deposition was evaluated for those teeth for which the variability of this feature was characteristic (Fig. 2c). Only the presence (+) or absence (−) of cement in the reentrant angles was con-
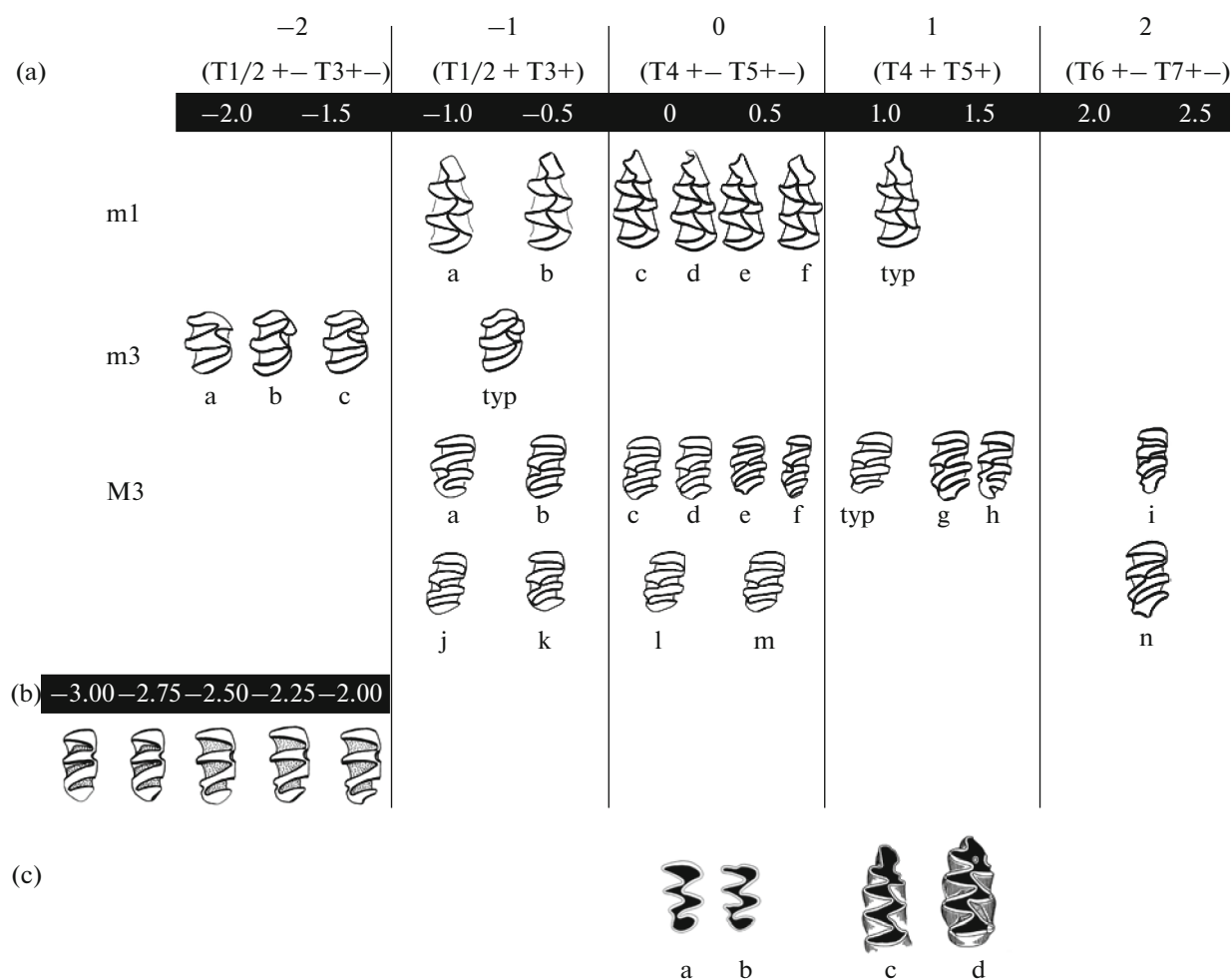
Fig. 3. Ranking of the morphotypes of cheek teeth in Lemmini according to their complexity and based on the presence (+) or absence (−) of dentine prisms T1−T7 detailed for the *Lemmus* and *Myopus* genera (a), and also an example of ranking of the morphotypes of M3 of the *Synaptomys* genus (b) and presumed ancestral forms of modern lemmings (c). (a) *Lemmus* and *Myopus* morphotypes: a−n, reserve and rare morphs; typ, typical morphs. (b) *Synaptomys* morphotypes of M3: M3_rank-2.00—*S. borealis* (Fejfar and Repenning, 1998); M3_rank-2.25, M3_rank-2.75—*S. cooperi* (according to Martin et al., 2003); M3_rank-2.50—*S. cooperi* (the collection of ZI RAS), M3_rank-3.00 − hypothesized for the genus. (c) Illustrations of the presumed ancestral forms of the modern lemmings: a−c, *Tobienia kretzoii*; d, Lemmini gen. n., sp. n. (Fejfar et al., 2011), arranged in accordance with the complexity ranks of M3 and m1.

sidered; the depth of the reentrant angle filling was not taken into account.

The degree of asymmetry of the reentrant angles was assessed based on the ratio between the depths of the buccal and lingual angles, BRA2 and LRA2, for M3 as demonstrated in Fig. 2d. The depth of the reentrant angle was defined as the distance from its vertex to the middle point of the segment connecting the edges of the enamel ridges that form this angle. The degree of asymmetry may be assessed for any pair of opposite reentrant angles using the same method.

Designations of the Morphotypes and Their Variations (Morphs)

In this study, the term morphotype was used to designate the formally discrete variations differing in the degree of crown complexity, the degree of fusion or separation of its elements or for the degree of cement deposition in the reentrant angles and the degree of tooth prism asymmetry. The criteria for distinguishing the morphotypes are illustrated in Figs. 2a−2d. Therefore, morphotypes are formal abstractions that allow quantitative evaluation of the four groups of characteristics. Each morphotype includes within itself the morphs, i.e., factual variations of the occlusal surface outline each of which, on one hand, matches the criteria for the corresponding morphotype, and, on the other hand, may be addressed as a discrete variation if the criteria for distinguishing this morph can be precisely formalized.

The morphotypes characterizing the degree of the development of prisms T1−Tn (the crown complexity) were designated in accordance with the ranks of com-

plexity from 2 to −3, for example, M3_rank2, M3_rank1, M3_rank0, M3_rank-1, M3_rank-2, M3_rank-3, m1_rank1, etc. The variations within each rank are designated with letters (Fig. 3).

The morphotypes describing the degree of separation-fusion of the dentine fields (the regularity of cutting edges) were designated according to the name of an isolated element of the occlusal surface (for example, m1_ T4 is an isolated prism T4 on m1, m1_AC is an isolated cap of the anterior unpaired loop of m1) or a pair of completely separated elements (M3_T3T4 is the third upper tooth with separated prisms T3 and T4 (A = B or A > B in Fig. 2b)).

The degree of cement deposition was designated in accordance with the Fig. 2c, for example, m1_cement0, m1_cement1, m1_cement2, etc.

The degree of asymmetry of the reentrant angles was defined according to the principle exemplified for morphypes M3_asym0−3 (Fig. 2d). The same principle may be used to assess asymmetry of LRA1-BRA1 on m1 and m3, or for any other pair of reentrant angles.

The morphotype classification based on the frequency was performed in accordance with the approach developed by A.G. Maleeva (Bolshakov et. al., 1980).

Statistical Analysis

Statistical data processing was performed using the Statistica 8.0 software.

To consider the degree of interdependence of the features that underlie the morphotypes of different groups, the Spearman correlation coefficient (R_S) was calculated.

To evaluate the statistical significance of the differences between the species, populations, and age groups based on the ranks of tooth complexity, the analysis of variance was used. The factorial model with the species and age group factors (fixed factors) and the hierarchical model with the species (fixed) and locality (random) factors were applied.

For the morphotypes characterizing the regularity of cutting edges and the presence of cement in the reentrant angles, the nonparametric Kruskall–Wallis test was used (H means the Kruskall–Wallis criterion) since the morphotype frequency distributions in these groups were characterized by a pronounced asymmetry.

RESULTS

During the development of ranked rows of the morphotypes reflecting the complexity of cheek teeth, both collection materials and published data on the variability of the modern Lemmini and their earliest presumed ancestors were used (Fig. 3). The modern lemmings of the Old World have preserved the initial rank of m1 complexity as the primary morphotype

(Fig. 3, m1_typ); however, they have lost the ridges and enamel islets on the frontal unpaired loop characteristic of their presumed ancestors (Fig. 3c) and also of various lineages of extinct Arvicolinae the origin of which is proposed to be associated with the genus *Promimomys* (Fejfar et al., 2011).

The frequencies of the complexity ranks were calculated for the representative samples (the number of teeth belonging to the same category ≥30) presented in Table 1. The cases of the Siberian and wood lemmings demonstrate that in modern natural populations of Lemmini the amounts of variability in tooth complexity ranks are comparable with those observed in other species of Arvicolinae (Table 2).

The analysis of the frequencies of the complexity ranks, and also the other groups of teeth morphotypes in wood and true lemmings demonstrate that, according to the traditional classification (Bolshakov et al., 1980), all established ranks of complexity may be classified as basic, reserve, or rare (Table 2). The set of morphotypes and the predominant complexity ranks are similar in both species, although, due to the increase in the proportion of the simplified variations of m1, m3, and M3, a higher diversity is characteristic for the wood lemming. The morphotypes of other groups (confluence of the occlusal surface elements, asymmetry, cement development) fall into two categories, basic and rare.

Between-species differences were statistically tested against the amounts of ontogenetic and geographic variation for a particular case of the Siberian and wood lemmings.

Five age classes with a skull maturity of 50 and 70−100% represented in the samples of both species were included in the analysis. The factorial model of the analysis of variance with fixed factors, such as species and age class, demonstrated that between-species differences in the ranks of complexity are statistically significant. m3 ($F = 28.5$, $p < 0.001$) and M3 ($F = 21.1$, $p < 0.001$), but do not reach the level of statistical significance in ranks m1 ($F = 3.5$, $p = 0.063$). Differences between the age classes according to the levels of complexity m1, m3, and M3 were not found ($F = 0.2–0.5$, $p = 0.741−0.963$).

The results of the hierarchical model of the analysis of variance with the species (fixed) and locality (random, nested in the species) factors indicate that the between-species differences in the ranks of complexity of m3 and M3 exceed the amount of variation among localities (m3: $F = 15.0$, $p = 0.016$; M3: $F = 43.1$, $p < 0.001$). No significant between-species differences in the ranks of m1 ($F = 3.5$, $p = 0.134$), were observed, although in the Siberian lemming the mean values were slightly higher (Fig. 5).

Therefore, using the ranked estimates of tooth complexity allows identification of differences between species: wood lemmings differ from Siberian

Table 2. The frequencies of the morphotypes and morphs of cheek teeth of wood and Siberian lemmings classified in accordance with the frequencies as basic (Basic), reserve (Res), and rare (R)

Morphotype	Myopus schisticolor			Lemmus sibiricus			The morphotype category
	PINR	Sorum	Siberian Uvaly	Vorkuta	Seyakha	Harasaway	
Ranks of the occlusal surface complexity							
m1_rank-1	0.001	0.068	0.019	0	0	0	R
m1_rank0	0.036	0.091	0.037	0.031	0	0	R
m1_rank1	0.963	0.841	0.944	0.969	1	1	Basic
m2_rank-0.5	1	1	1	1	1	1	Basic
m3_rank-3	0	0	0	0	0	0	R*
m3_rank-2	0.14	0.046	0.222	0	0	0.013	Res/R
m3_rank-1.5	0.14	0.136	0.278	0	0	0.013	Basic/R
m3_rank-1	0.72	0.818	0.500	1	1	0.974	Basic
M1_rank0	1	1	1	1	1	1	Basic
M2_rank0	1	1	1	1	1	1	Basic
M3_rank-1	0.012	0	0.018	0	0	0	R
M3_rank0	0.141	0.20	0.196	0	0	0.008	Basic/R
M3_rank1	0.832	0.75	0.786	0.976	0.966	0.962	Basic
M3_rank1.5	0.011	0	0	0.016	0.034	0.008	R
M3_rank2	0.004	0.05	0	0.008	0	0.022	R
Morphotypes with separation of dentine fields (the degree of confluence ≤0.5)							
m1_T4	0	0	0	0.023	0	0	R
m1_AC	0.002	0	0	0.008	0	0	R
m2_T3T4	0.999	1	1	1	1	1	Basic
m3_T1T2	0.997	1	0.963	0.933	0.933	1	Basic
M3_T3T4	0.007	0	0	0	0	0.023	R
M3_T4T5	0.003	0	0	0.033	0	0	R
Morphotypes distinguished according to the presence of cement in the reentrant angles							
m1_cement0	0.995	1	1	0.563	0.458	0.465	Basic
m1_cement1	0.005	0	0	0.437	0.542	0.521	R/Basic
m1_cement2	0	0	0	0	0	0.014	R
m3_cement0	0	0	0.019	0	0	0	R
m3_cement1	1	1	0.981	0.992	1	1	Basic
m3_cement2	0	0	0	0.008	0	0	R
M3_cement0	1	1	1	0.992	1	0.977	Basic
M3_cement1	0	0	0	0.008	0	0.023	R
M3_cement2	0	0	0	0	0	0	R*
Morphotypes distinguished according to the degree of asymmetry of the reentrant angles							
m1_asym0	1	1	1	1	1	1	Basic
M3_asym0	1	1	1	1	1	1	Basic
Morphs distinguished according to the presence of additional elements							
m1_g	0.002	0	0	0	0	0	R
m1_h	0.001	0	0	0	0	0	R
M3_e	0.001	0	0	0.031	0	0	R
M3_g	0.011	0.045	0	0.008	0.034	0	R
M3_n	0.004	0	0	0.008	0	0	R
M3_f	0	0	0	0	0	0	R*
M3_h	0	0	0	0	0	0	R*
M3_i	0	0	0	0.008	0	0.008	R

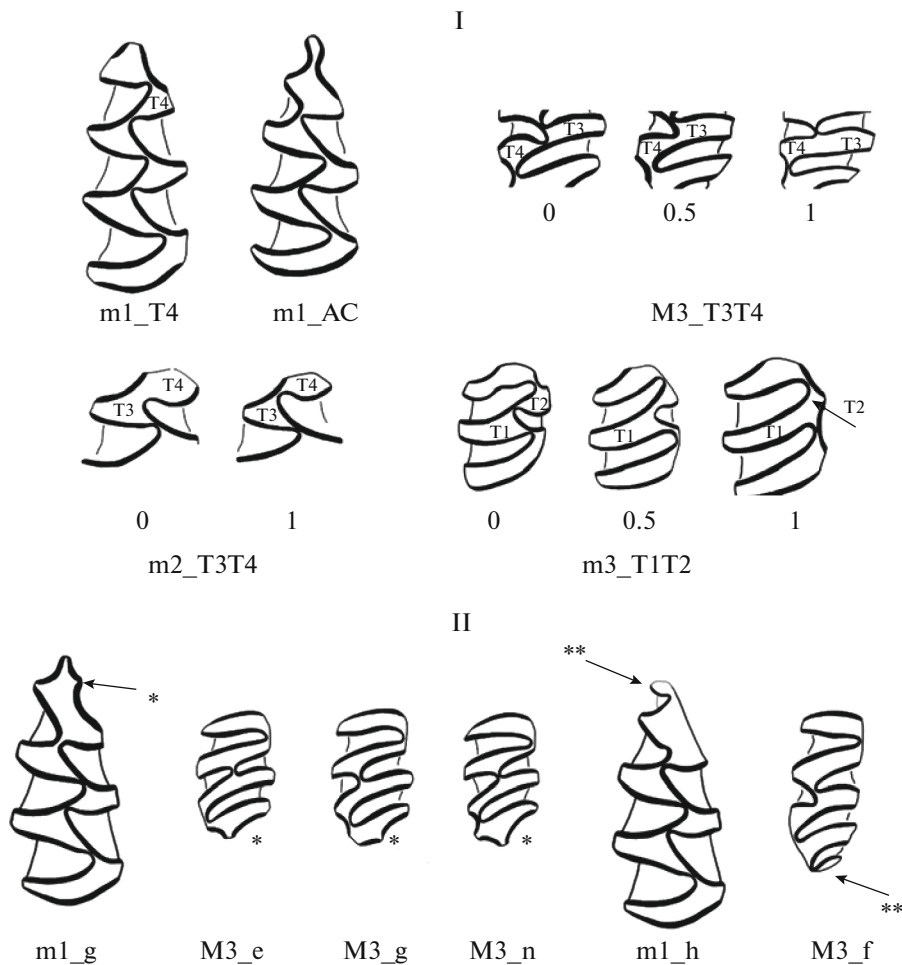* Morphotypes and morphs distinguished according to the published data.

Fig. 4. The morphotypes of cheek teeth of true and wood lemmings distinguished according to the degree of fusion of dentine prisms from 0 to 1 (a), and also several rare morphs with additional elements represented by enamel ridges (*) or small walls (**) in the anterior parts of the lower teeth and the posterior parts of the upper teeth (b). Morphotypes: m1_T4—*L. sibiricus*, Vorkuta; m1_AC, m2_T3T4, M3_T3T4, m1_g, m1_h, M3_e, M3_g, M3_n—*M. schisticolor*, Pechora-Ilych Nature Reserve; m3_T1T2—*M. schisticolor*, Sibirskie Uvaly, Western Siberia; M3_f—*Lemmus* cf. *sibiricus*, Middle Pleistocene (Smirnov et al., 1986).

lemmings in the higher percentage of the simplified cheek teeth.

Morphotypes that are characterized by the separation of dentine fields in m1 and M3 (the degree of fusion ≤0.5) and by the fusion of prisms in m2 and m3 (the degree of fusion >0.5) are found with a frequency of 0 to 6.7%; i.e., they belong to the "rare" category. Only in the morphotype M3_T3T4 do the interspecies differences reach the level of statistical significance (H (1, $N = 1378$) = 5.0, $p = 0.026$). In Siberian lemmings, the proportion of this morphotype was, on average, higher due to the increase in the frequency of M3 with complete separation of T3 and T4 in one of the samples, reaching up to 2.3% (Table 2).

Between-species differences in the degree of cement deposition are statistically significant in m1 (H (1, $N = 1317$) = 535.6, $p < 0.001$). In m3 and M3, the variability of the degree of cement deposition in the reentrant angles is extremely low. With age, the degree

of cement deposition, on average, increases. However, the differences between age classes do not reach the level of statistical significance in both species (Fig. 6).

The correlation between the characters used to establish morphotypes was assessed using the materials on wood and Siberian lemmings (Table 1). It has been demonstrated that the ranked estimates of complexity of upper and lower teeth positively correlate with each other ($R_S = 0.09-0.21$, $p < 0.01$) and with the degree of cement deposition in the reentrant angles of the anterior unpaired loop of m1 ($R_S = 0.09-0.15$, $p < 0.01$). The degree of fusion of dentine fields in M3 is not correlated with either the complexity ranks ($R_S = -0.05-0.2$, $p > 0.05$) or the degree of cement deposition in the reentrant angles of the anterior unpaired loop of m1 ($R_S = -0.07$, $p > 0.05$). A statistically significant correlation was observed between the degree of fusion of T1 and T2 on m3 and the lack of cement in both buccal reentrant angles ($R_S = -0.24$).
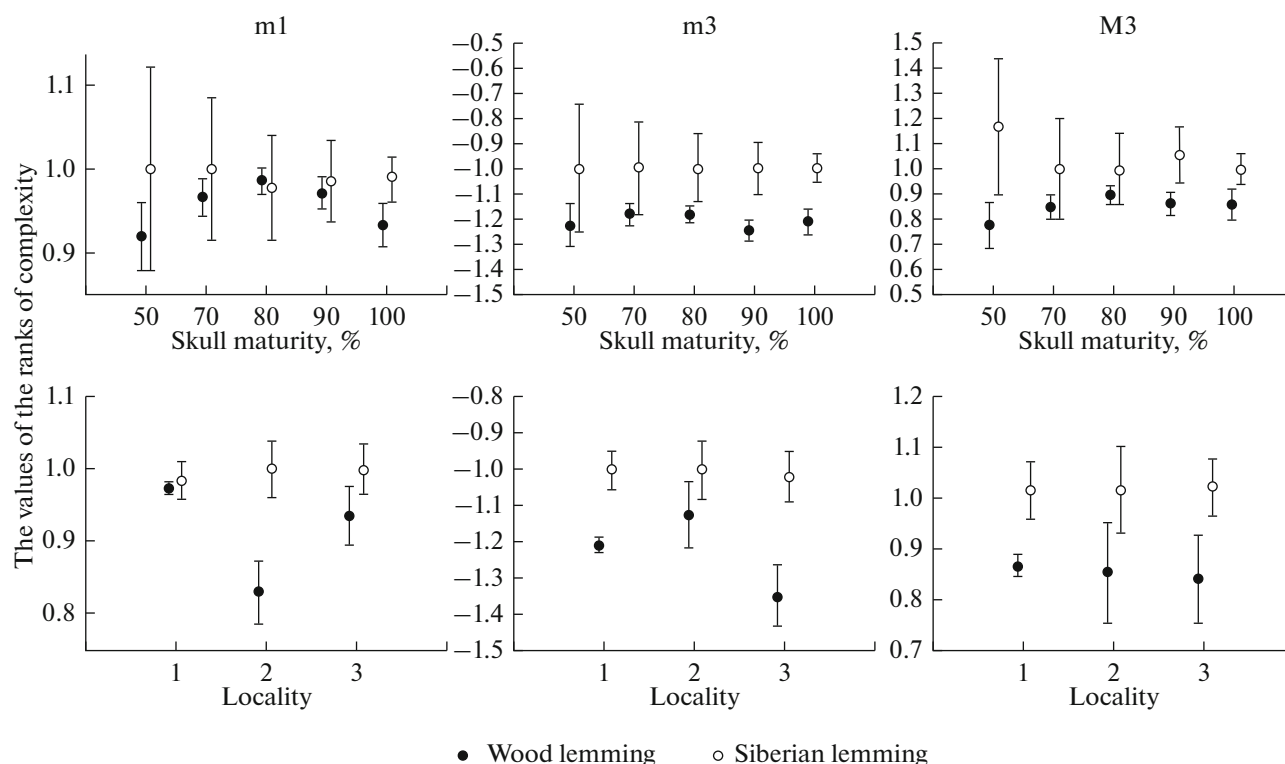
Fig. 5. The mean values and the 95% confidence interval of the complexity ranks m1, m3, M3 in wood and brown lemmings taking into account the age of the animals (the top row represents the age groups with the skull maturity of 50, 70, 80, 90, and 100% observed in samples of both species) and the locality (the bottom row represents the localities from which the representative samples of the wood (1, PINR; 2, Sorum; 3, Sibirskie Uvaly) and Siberian (1, Vorkuta; 2, Seyakha; 3, Harasaway) lemmings are obtained.

The results of correlation analysis demonstrate that tooth complexity and regularity of alternation of enamel cutting edges vary independently. The degree of cement deposition is correlated with the depth of the corresponding reentrant angles; thus, it may be defined as a supplementary non-independent feature, when distinguishing the morphotypes of the occlusal surface.
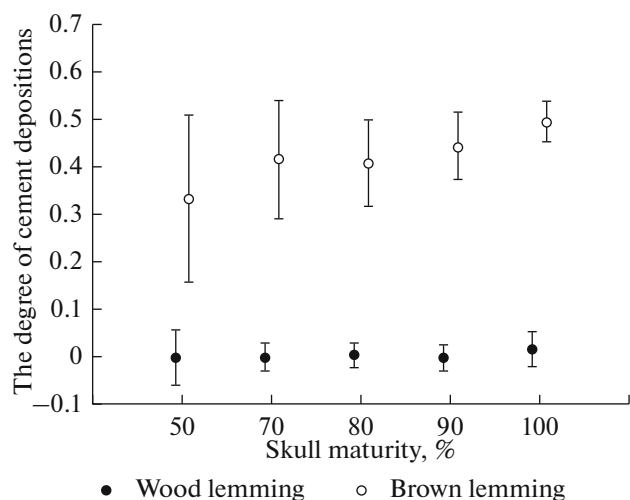
The lack of variability in the degree of asymmetry of reentrant angles in modern lemmings of the Old World does not allow any correlation analysis of the features of this group in the available dataset. However, it can be assumed that the negative associations may be observed between the degree of asymmetry and the degree of cement deposition in the corresponding reentrant angles, whereas positive correlations may be found between the degree of asymmetry and the degree of dentine field confluence. The first assumption is based on the fact that in the variants characterized by full asymmetry (for example, M3_asym3 found in all the *S. cooperi* specimens or m3_asym3 found in single specimens of the wood lemming (Fig. 4a, M3_T1T2, 1)), cement is not seen in the reentrant angles. The other assumption is based on the published data on the temporal variation of the extinct forms of Lemmini. According to these data, the increase in the degree of asymmetry of the reentrant angles occurs together with the fusion of the corresponding crown prisms (Königswald and Martin, 1984; Abramson, 1993).

Fig. 6. The mean values and the 95% confidence interval of the estimates of the degree of cement deposition in the reentrant angles of m1 in wood and Siberian lemmings depending on the skull maturity of the animal.

DISCUSSION

The results obtained demonstrate the variability of the cheek tooth complexity in modern populations of Lemmini. The species belonging to the *Lemmus* genus are least variable since the frequency of the atypical morphotypes in modern populations persists at a very low level. A high proportion of the simplified tooth variations, which are present as codominant or reserve morphotypes in the samples investigated, is characteristic for *Myopus*. The comparison of the ranked estimates of complexity of m1 and M3 in modern lemmings with the published data on their presumed root-toothed ancestors suggests that the features of the morphotypical structure of wood lemmings may be interpreted as a shift towards simplification in the anterior part of m1 and posterior part of M3. To address the question whether this shift is a feature of the modern *Myopus* genus or if the increased simplicity is inherited from ancestral rootless forms, further research is needed. With a given high proportion of the simplified variations, the complex M3s are also observed in the modern wood lemming populations as rare forms.

In the Siberian lemming, the most simple variations comparable to the complexity rank of −1 are found for m1 and M3 identified as *Lemmus* cf. *sibiricus* in the Early Pleistocene faunas of the Western Siberia (Smirnov et al., 1986). However, taxonomic identification of the fossil samples requires further clarification.

According to our data, morphotypes with the separation of dentine fields on m3 and M3 (the degree of fusion ≤0.5) are found in natural populations of wood and Siberian lemmings with a frequency of 0 to 6.7%; in other words, they fall into the "rare" category. The highest variability is characteristic for T3 and T4 of the third upper tooth, which has been previously demonstrated for Lemmini (Abramson, 1993; Khenzykhenova, 2003; Ponomarev et al., 2015; etc.). The analysis of the published data on the frequencies of morphotypes with complete and partial separation of T3 and T4 has demonstrated that in the continental populations of the Siberian lemming from the Bolshezemelskaya tundra, Taimyr, and the Magadan Region, the frequencies of morphotypes with separated T3–T4 are rare (Abramson, 1993; Khenzykenova, 2003). In the island populations of true lemmings, an increase in the frequencies of M3_T3T4(0) and M3_T3T4(0.5) may occur, and on the Wrangel Island, these morphotypes are frequent enough (Abramson, 1993) to enter the basic category of morphotypes. It suggests that the Siberian lemmings living in isolation for a long period of time may exhibit increasing proportions of rare dental features. Similar tendency has been also observed in other species of the subfamily living on islands (Markova et al., 2016).

The observed frequencies of morphotypes m1_cement2, m3_cement2, M3_ cement1, and M3_cement2 are consistent with the data published (Ponomarev et al., 2015; Cheprakov, 2016). This allows us to define these variations as rare for both the *Lemmus* and *Myopus* genera. The m1_cement1 morphotype is also extremely rare for the *Myopus* genus, whereas the frequency in the *Lemmus* genus is sufficiently high for this morphotype to fall into the basic category. According to our data, the frequency of m1 with cement in LRA4 in *Lemmus sibiricus* is 44−54%; in the samples from other natural populations, the frequency is 59−69% (Ponomarev et al., 2015). In the laboratory colonies of Siberian lemmings, the frequency of this feature is higher, 62−90% (Cheprakov, 2016). It should be noted that the laboratory colonies of other *Lemmini* species, compared to the naturally occurring conspecifics, are also characterized by increased frequencies of the morphotype m1_cement1, which, for example, in wood lemmings reaches 30%. A similar pattern was also observed in *Lemmus lemmus*, in which the frequency of this morphotype reaches 43−93% in natural populations and 81−95% in laboratory colonies (Cheprakov, 2016).

CONCLUSIONS

Therefore, based on consolidation of the data on zoological collections and the literature data on the variability of modern lemmings (Lemmini tribe) and their most ancient presumed ancestors, unification of the criteria for distinguishing the morphotypes of cheek teeth was conducted. The groups of morphotypes were identified based on the following characteristics: (1) the complexity of the occlusal surface; (2) the regularity of the enamel cutting edges and the degree of crown prism confluence; (3) the asymmetry of the buccal and lingual reentrant angles; (4) the degree of cement deposition in the reentrant angles. It has been demonstrated that the features of complexity of the occlusal surface and the degree of confluence of the crown prisms are independent. The degree of cement deposition in the reentrant angles depends on the degree of complexity and regularity of the enamel cutting edges.

Taking the example of the wood and Siberian lemmings, a catalogue of the basic, reserve, and rare cheek tooth variations is compiled. The catalogue may be recommended for studying geographic, temporal, ontogenetic, and other variations.

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COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interests. The authors declare that they have no conflict of interest.

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