

# A Comparative Morphotypic Analysis of the First Lower Molars of the Reed Vole *Alexandromys fortis* (Büchner, 1889) from Insular and Fossil Populations in the South of the Russian Far East (Primorskii Krai)

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**Abstract**—The morphotypic variability of the anteroconid shape of the first lower molar of fossil and modern (continental and insular) populations of the reed vole (*Alexandromys fortis*) from the territory of Primorye (the south of the Russian Far East) has been analyzed. The morphotypic variability is considered based on the study of variations in the structure of the labial and lingual sides of the anterior unpaired loop and structural features of the lingual reentrant angle 4. Thirty-six morphotypes of the structure of the unpaired anterior loop of anteroconid m1 have been revealed using the developed combinatory matrix. The most widespread morphotype on the continent is IIIc, which prevailed in the Late Pleistocene. The features of the morphotypic composition of m1 in the differentiated populations of the reed vole on the Durnovo, De-Livron, and Vera islands (Peter the Great Bay) are determined both by the phenotypic and genotypic characteristics of the founders of the insular populations. The original new habitat conditions must have initiated a high rate of evolution, released hidden diversity, and increased the number of rare morphotypes.

**Keywords:** anteroconid, morphotypes, islands, fossils, Primorye, *Alexandromys fortis*

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Although the use of geometric morphometry methods has shown a significant variability in the pattern of the chewing surface of the first lower molar in East Asian voles of the genus *Alexandromys* (Voyta et al., 2019), there is still no alternative to using the shape of this tooth in the identification of vole fossil remains. Fossil material is usually represented by separate teeth and the species identification of voles is usually determined by this most informative tooth (Semken and Wallace, 2002; Borodin and Markova, 2014; Golenishchev et al., 2018; Golenishchev et al., 2019). At the same time, there are no studies on the intraspecific variability of the pattern of the chewing surface of the first lower molar in East Asian vole species except *A. oeconomus* (Nadachowski, 1982; Kostenko and Allenova, 1989; Pozdnyakov and Litvinov, 1994; Fadeeva, 2003, 2005). Different researchers who previously studied the variability of this tooth in *A. fortis* identified three to ten morphotypes (Meyer, 1978; Alekseeva and Golenishchev, 1986; Pozdnyakov, 1993, 2010; Lisovskii et al., 2018; Kovaleva et al., 2021).

In our opinion, the most appropriate method for identifying morphotypes was proposed by Pozdnyakov

(1993). Based on this technique and the method of constructing a morphological classification table, which was previously used during the study of the chewing surface of the third lower premolars of northern pika (Gusev and Tiunov, 2021), the primary task of the study was to construct a similar table for *A. fortis*. It should be noted that it has been recently shown that it is possible to use the features of the morphotypic variability of teeth in the interpretation of paleochronological events in the history of Arvicolinae (Markova et al., 2020). The recent data on the morphological and genotypic variability in the insular populations of this species in the Far East (Sheremetyeva, 2003, 2020) and the fossil material available to us determined the following task: to study the morphotypic variability of the shape of anteroconid m1 in *A. fortis* in the insular populations of the Peter the Great Bay (Sea of Japan) and compare this variability with the secular variability of this tooth in fossil populations from the Late Pleistocene and Holocene deposits of the Medvezhyi Klyk (Bear Fang) cave (Primorskii krai).



**Fig. 1.** Sampling sites: (1) Vera Island; (2) Astafyev Bay; (3) De Livron and Durnovo islands; (4) Hildebrandt Island; (5) Falshivy Island; (6) Russky Island; (7) Bolshoy Pelis Island; (8) Rikord Island; (9) Putyatin Island; (10) village of Hasan; (11) Medvezhyi Klyk cave.

## MATERIALS AND METHODS

The variability of the structure of the chewing surface of the first lower molars of the reed vole was studied based on collection materials from the Laboratory of Theriology at the Federal Scientific Center for Biodiversity, Far East Branch, Russian Academy of Sciences. We studied 165 teeth from two localities of the continental part of the south of Primorsky krai (near the village of Khasan and on the coast of the Astafyev Bay), 341 teeth from specimens taken from the islands of the Peter the Great Bay (26 specimens from the Russky Island, 65 specimens from the Putyatin Island, and 10 specimens from the Rikord Island), 10 specimens from the Pelis Island, 116 specimens from the Vera Island, eight specimens from the Hildebrandt Island, and 106 specimens from the De-Livron and Durnovo islands), and 10 specimens from the Falshivy Island. Previously, the attribution of the insular populations to *A. fortis* was additionally confirmed by molecular genetic methods (Chelomina and

Sheremetyeva, 2007; Sheremetyeva, 2020). In addition, we also studied Late Pleistocene–Holocene fossil material (125 first lower molars) from the Medvezhyi Klyk cave on the Lozovyi Ridge, Partizansky district of Primorsky Krai (Fig. 1). Voyta et al. (2019), who analyzed this material, stated that all these teeth belong to “*A. fortis*, which is unambiguously determined by the characteristic shape of the anteroconid and large size...” (Voyta et al., 2019, p. 333).

The structure of the chewing surface of m1 was assessed using both the morphotypic approach and an analysis of dimensional features. The tooth was measured using six parameters (Fig. 2): L1 (the space between the tops of the lingual reentrant angle 4 and labial reentrant angle 3), L2 (the width of the anterior unpaired loop m1), L3 (the measurement result is achieved by the following sequential actions: (a) line A is drawn from the top of the lingual exiting angle 4 to the top of the lingual reentrant angle 4, (b) line B is drawn from the top of the labial reentrant angle 3 to

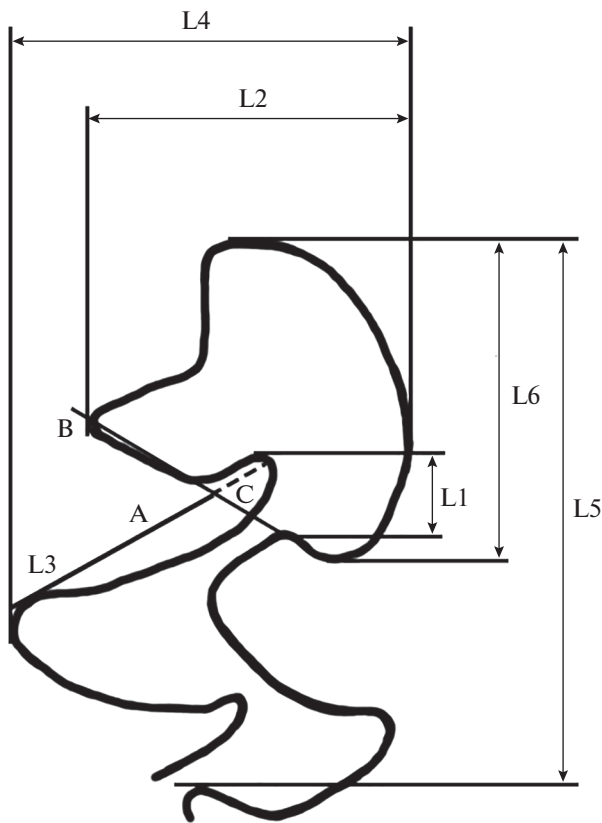


Fig. 2. The scheme of measurements of m1 of the reed vole. See the explanation in the text.

the top of the lingual exiting angle 5, which divides the line A into two segments, (c) the ratio of the segment length C to the total line length A), L4 (the width of the anteroconid), L5 (the length of the anteroconid), and L6 (the length of the anterior unpaired loop m1).

The dimensional characteristics of the teeth were calculated based on the standard stepwise discriminant analysis without including and excluding variables. Groups were classified by calculating the Mahalanobis distance and based on the matrix classification function using the jackknife method. Since the size of the studied specimen is  $n > 100$ , the significance of the Mahalanobis distances was calculated using the significance p-level of 0.01 (Nasledov, 2004). All calculations were made in Statistica 13 and SYSTAT 12.

All measurements were made using a Zeiss STEREO Discovery V.12 stereomicroscope. The resulting images of teeth were then processed on a microscope in the Photoshop CS6 software program to compile the morphological classification table.

The morphotypic variability was considered based on the study of variations in the structure of the labial and lingual sides of the anterior unpaired loop and

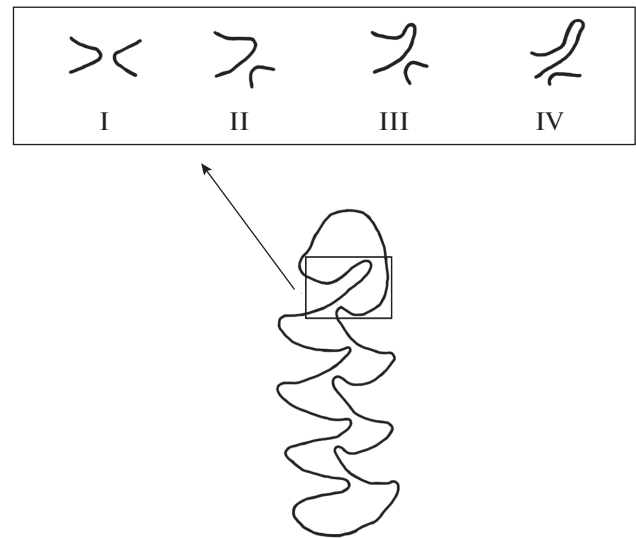


Fig. 3. Variants of the structure of lingual reentrant angle 4. See the explanation in the text.

structural features of the lingual reentrant angle 4, which was estimated based on the measurement of L3.

Four types of structure of lingual reentrant angle 4 were distinguished: I–II–III–V (Fig. 3).

**Type I.** The tops of lingual reentrant angle 4 and labial reentrant angle 3 are at the same level one opposite the other.  $L3 = 0$ .

**Types II, III, and IV** differ in the depth of lingual reentrant angle 4.

**Type II** included teeth with L3 values from 0.06 to 0.20 mm.

**Type III** included teeth with L3 values from 0.21 to 0.38 mm.

**Type IV** included teeth with L3 values from 0.39 mm and higher.

The shapes of the lingual and labial sides were divided into several types (Fig. 4).

The shape of the lingual side

**Type A.** The lingual side without a concavity.

**Type B.** The lingual side has a concavity with a straight inner edge.

**Type C.** The lingual side has a concavity at a right or obtuse angle.

**Type D.** The lingual side has a concavity at an angle of less than  $90^\circ$  or a reentrant angle.

**Type E.** The lingual side has two concavities.

Shape of the labial side

**Type a.** Labial side without a concavity.

**Type b.** The labial side has a small concavity in the lower part.

**Type c.** The labial side has a wide concavity covering the entire median part or a concavity in the upper part.

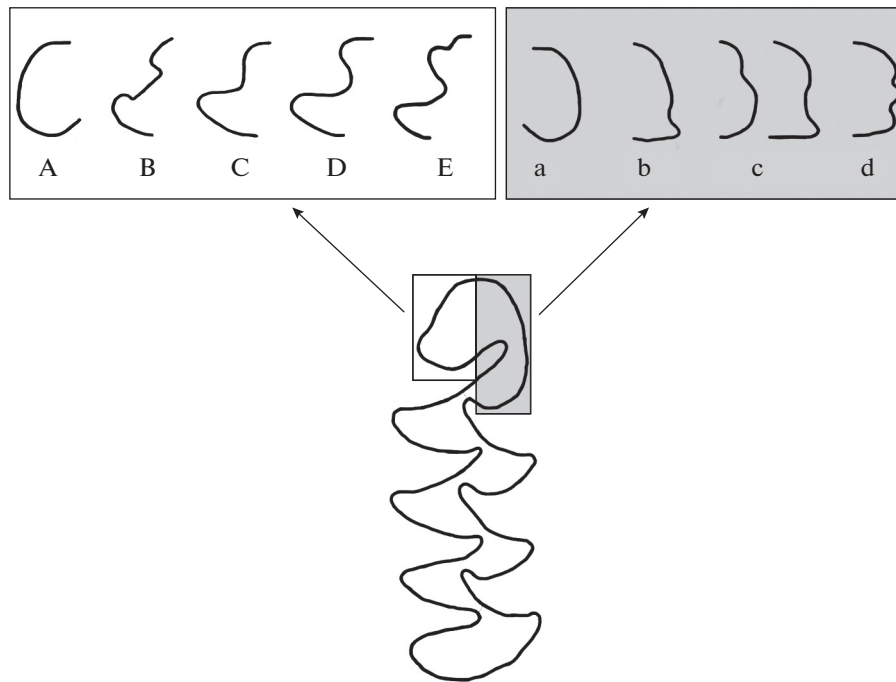


Fig. 4. The shape of the lingual (left) and labial (right) sides of the anteroconid head. See the explanations in the text.

**Type d.** The labial side has a small projection in the median part.

Based on the description of the chewing surface, we get a combination of three character states, e.g., the **IIIBa morphotype**.

Further analysis of the variability was based on a combinative method (Vasil'eva, 1978; Bol'shakov et al., 1980; Krukover, 1989; Pozdnyakov, 1993).

Based on the derived morphotypes (Table 1), we built a data matrix (Table 2), which was analyzed in PAST-Palaeontological Statistics (version 4.05) (Hammer, 2021) using the unweighted pair group method with arithmetic mean (UPGMA), Pearson's correlation coefficient, and bootstrap analysis in 1000 replicates.

## RESULTS

The discreteness of the combinations of separate characters made it possible to build a combinative morphological classification table and carry out a multidimensional classification of separate teeth by certain morphotypes (Table 1). The classification table is a rectangular grid with the indication of types of structure of lingual reentrant angle 4 in the center. Accordingly, all the morphotypes in the upper left corner of the table have structure **type I** of this angle, all the morphotypes in the upper right corner have **type II**, morphotypes in the lower right corner have **type III**, and morphotypes in the lower left corner have **type IV**. The vertical column in the middle of the table

shows variants of the structure of the lingual side of the anteroconid head. The horizontal line in the middle of the table shows variants of the structure of the labial side. All the variants of the structure are arranged in order of increasing complexity: from I to IV, from A to E, and from a to d. Graphic diagrams of the pattern of the anterior unpaired loop of m1 were placed in the cells that were formed from the intersection of the columns and lines. The actual number of morphotypes is lower than their theoretically expected number; therefore, not all cells are filled. It is possible that some of the cells will be filled in the future and some will remain unfilled due to the effect of natural factors limiting the variability.

The combination of the selected characters gives 36 morphotypes of the structure of the unpaired anterior loop of the anteroconid, each of which has an alphanumeric designation. The discriminant analysis confirmed the correctness of the differentiation of the four types of structure of lingual reentrant angle 4 (the percentage of correct classification by the jackknife method was 97% (Table 3, Fig. 5)). To assess the usefulness of the canonical discriminant functions, we calculated the main statistical parameters (Table 4). The data in the table show good discrimination of the groups. The first two discriminant functions are statistically significant. The high value of the canonical correlation ( $R = 0.94$ ) of the first discriminant function indicates its better separation capacity. In turn, the statistical significance of the third discriminant function exceeds the threshold value ( $p = 0.27$ ); therefore,

**Table 1.** The morphological classification table

-	-	-	-	E		-	-		-
-	-			D					-
-		-		C					-
-	-	-		B		-	-	-	-
-	-	-	-	A		-	-	-	-
d	c	b	a	I	II	a	b	c	d
-	-	-		A				-	-
-	-	-		B				-	-
-				C					
				D					-
-	-	-		E					-

See the explanations in the text.

**Table 2.** The morphological characteristics of samples of m1 of the reed vole from Primorye

@Морфо типы	@Выборки													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
IBa	0	0	0	0	0	0	0	0	0.94	0	0	0	0	0
ICa	7.69	0	0	0	0	0	0	0	2.83	0	0	0	0	0
ICc	0	0	0	0	0	0	0	0	0	0	0	10	0	0
IDa	2.56	0	0	0	0	0	0	0	7.55	25	0	0	0	0
IDb	2.56	0	0	0	0	0	0	0	1.89	0	0	0	0	0
II Ca	18	7.41	22.2	14.8	2.56	6.25	0	2.59	25.5	25	0	10	3.85	3.08
II Cb	5.13	11.1	7.41	7.41	0	0	0	0.86	2.83	0	0	10	0	3.08
II Cc	0	3.7	3.7	0	0	4.17	0	0	1.89	25	0	0	7.69	4.61
II Da	2.56	3.7	0	3.7	0.85	0	0	0	2.83	0	0	0	0	3.08
II Db	0	7.41	0	3.7	0	0	0	0	0	0	0	20	0	3.08
II Dc	0	0	0	0	0.85	0	0	0	0	0	0	10	0	1.54
II Ec	2.56	0	0	0	0	0	0	0	0	0	0	10	0	0
III Aa	0	0	0	0	0	0	0	1.72	1.89	0	0	0	0	0
III Ab	0	0	0	0	0	0	0	0.86	0	0	0	0	0	0
III Ba	2.56	0	0	0	0	0	0	0	0.94	0	0	0	0	0
III Bb	0	0	0	0	0	0	0	0	0	0	0	0	3.84	0
III Ca	23.1	22.2	22.2	14.8	38.5	35.4	70	34.5	10.4	13	50	30	34.6	33.85
III Cb	15.4	11.1	29.6	14.8	14.5	6.25	10	2.59	0	0	10	0	0	7.69
III Cc	0	7.41	0	3.7	12	14.6	10	0	0.94	0	0	0	0	1.54
III Cd	0	0	0	3.7	0	0	0	0	0	0	0	0	0	3.08
III Da	10.3	11.1	0	0	12	10.4	10	5.17	3.77	13	0	0	30.8	23.07
III Db	5.13	7.41	3.7	25.9	5.98	2.08	0	0.86	0	0	10	0	3.85	6.15
III Dc	0	3.7	3.7	0	2.56	0	0	0.86	0	0	20	0	7.69	1.54
III Ea	0	0	3.7	0	0	2.08	0	1.72	0	0	0	0	0	1.54
III Eb	0	0	3.7	0	0	0	0	0	0	0	0	0	0	1.54
III Ec	0	0	0	0	0	4.17	0	0	0	0	0	0	3.85	0
IV Aa	0	0	0	0	0	0	0	3.45	9.43	0	0	0	0	0
IV Ba	0	0	0	0	0	0	0	1.72	4.72	0	0	0	0	0
IV Ca	0	0	0	0	6.84	4.17	0	17.2	10.4	0	0	0	3.85	0
IV Cb	0	0	0	3.7	0	0	0	0	0.94	0	0	0	0	0
IV Cc	0	0	0	0	1.71	0	0	0	0	0	0	0	0	0
IV Da	0	0	0	0	1.71	4.17	0	23.3	8.49	0	10	0	0	0
IV Db	2.56	0	0	0	0	2.08	0	0.86	1.89	0	0	0	0	1.54
IV Dc	0	0	0	3.7	0	4.17	0	0	0	0	0	0	0	0
IV Dd	0	0	0	0	0	0	0	0.86	0	0	0	0	0	0
IV Ea	0	3.7	0	0	0	0	0	0.86	0	0	0	0	0	0

(1) Late Pleistocene sample 1; (2) Late Pleistocene sample 2; (3) Middle Holocene sample; (4) Late Holocene sample; (5) environs of the village of Khasan, (6) Astafyev Bay coast, (7) Falshiv Island, (8) Vera Island, (9) Durnovo and De Livron islands, (10) Hildebrandt Island, (11) Pelis Island, (12) Rikord Island, (13) Russky Island, (14) Putyatn Island.

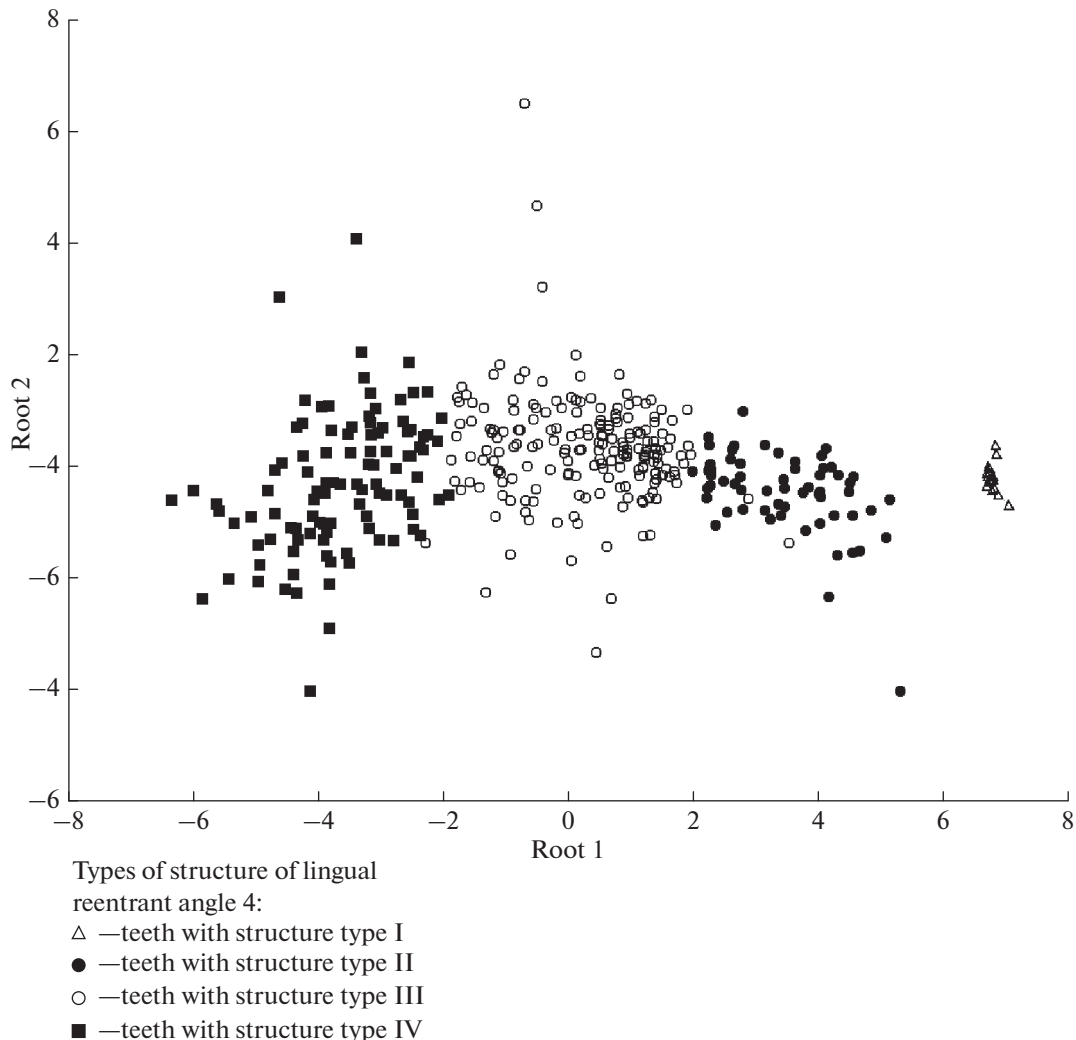
the difference between the types in this function cannot be subject to meaningful interpretation. The greatest contribution to the classification of morphotypes was made by L1, L3, and L5 measurements. Among them, the measurement of L3, which is responsible for the measurement of lingual reentrant angle 4, proved to be most significant and valuable (Wilk's Lambda = 0.21, Partial Lambda = 0.47). It should be noted that the classification table was constructed based on the modern material. M1 morphotypes in fossil voles were identified based on the previously constructed table. We did not find any new morphotypes not included in the previous table.

The main and most common morphotype in the two studied samples from the mainland is the **IIICa** morphotype. It is characterized by a medium depth of the lingual reentrant angle 4 (L3 measurement from 0.16 to 0.38), a wide shallow concavity on the lingual side of the anterior unpaired loop, and the absence of

**Table 3.** Assessment of the correctness of the classification using the jackknife method

Group	1	2	3	4	Classification accuracy, %
1	17	0	0	0	100
2	1	61	0	0	98
3	0	3	184	6	95
4	0	0	0	104	100
Total	18	64	184	110	97

a concavity on the labial side. The sample from the environs of the village of Khasan had 38% of its teeth with this morphotype and the sample from the coast of the Astafyev Bay has 35%. Among the other 11 morphotypes, the **IIICb**, **IIICc**, and **IIIDa** morphotypes were relatively common in the Khasan sample (14, 12,



**Fig. 5.** The distribution of the studied first lower molars of the reed vole in the space of the first (Root 1) and second (Root 2) discriminant functions according to the results of m1 measurements.

**Table 4.** Statistical results for discriminant canonical functions

Discriminant function	Eigenvalues	Canonical <i>R</i> correlation	Wilk's lambda	$\chi^2$	Significance level
1	7.801516	0.942	0.1009	848.78	$p < 0.0001$
2	0.110835	0.316	0.8878	44.06	$p = 0.000003$
3	0.014066	0.118	0.9861	5.17	$p = 0.2705$

and 12%, respectively). In addition to the **IIICa** morphotype, **IIIC** and **IIIDa** can also be considered as the prevailing morphotypes (about 15 and 10%, respectively) in the Astafyev sample of 13 morphotypes. One of the eight rare or reserve (Maleeva, 1976) morphotypes was found only in the Khasan sample, while the others are more widespread. In the Astafyev sample, one of the rare morphotypes was also found in the Late Holocene sample, another one on the Russky Island, and the other eight rare morphotypes are more widespread (Table 2). It should be noted that the mainland samples have no morphotypes from the upper left corner of Table 1, i.e., morphotypes with structure type I.

The available fossil material from the deposits of the Medvezhyi Klyk cave can be divided into four samples. Late Pleistocene sample 1 represents material from layers 12 and 11 (the age of deposits is about 40000–35000 years) (Panasenko and Tiunov, 2010; Omelko et al., 2020). Late Pleistocene sample 2 represents material from inclined layers 6–9 (the age is about 14000–11000 years). The Middle Holocene sample represents material from layer 5 (the age is about 6000 years). The Late Holocene sample is material from layers 3 and 4 (the age is about 3000–4000 years). The most widespread morphotypes are morphotype **IIICa** in both Late Pleistocene samples, morphotype **IIICa** in the Middle Holocene sample, and morphotype **IIIDb** in the Late Holocene sample. An occurrence of over 10% was also recorded for morphotypes **IIICa**, **IIICb**, and **IIIDa** in Late Pleistocene sample 1, **IIICb**, **IIICb**, and **IIIDa** in Late Pleistocene sample 2, **IIICa** and **IIICa** in the Middle Holocene sample, and **IIICa**, **IIICa**, and **IIICb** in the Late Holocene sample (Fig. 6). There are no strong fluctuations in the number of morphotypes in the fossil samples. Thirteen morphotypes were recorded in Late Pleistocene sample 1, 12 morphotypes in Late Pleistocene sample 2, nine morphotypes in the Middle Holocene sample, and 11 morphotypes in the Late Holocene sample.

The highest occurrence is also characteristic of morphotype **IIICa** in most of the samples from the isolated island populations of the Peter the Great Bay, except samples from the populations of the Durnovo and De Livron islands. On the Durnovo and De Livron islands, the most widespread morphotype is morphotype **IIICa** (~26%). The second most widespread

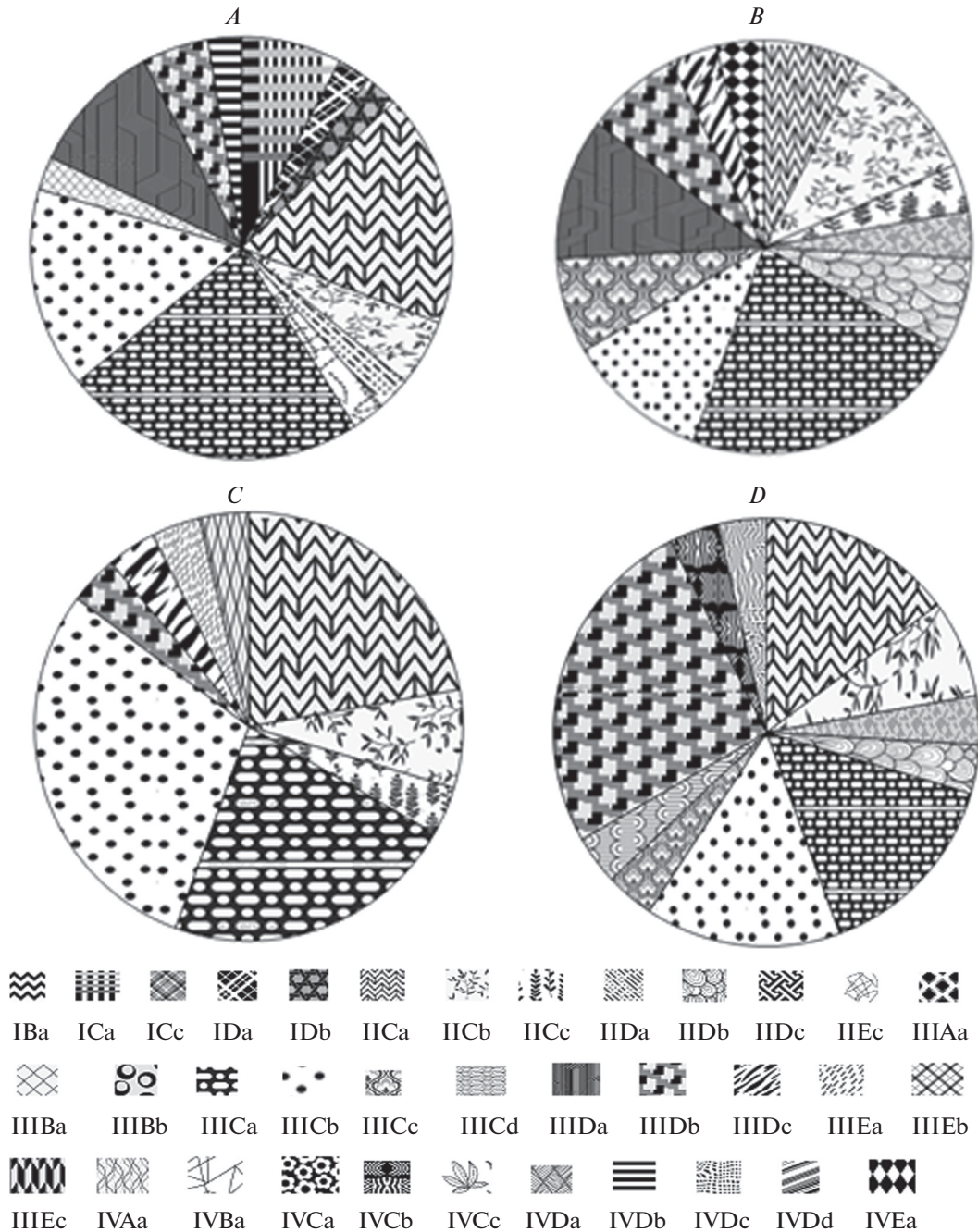
morphotype on these islands is morphotype **IIICa** (~10%), followed by morphotype **IVCa** (Fig. 7, Table 1). Nineteen morphotypes were found on these islands. This is the largest number among all the studied samples. Two of the 16 morphotypes that rarely occur here were recorded only on these islands. Two morphotypes were encountered not only on these islands but also on the Vera Island, three morphotypes were recorded in Late Pleistocene sample 1, and one morphotype in the Late Holocene sample.

Seventeen morphotypes of the structure of the unpaired anterior loop of anteroconid m1 were recorded on the Vera Island. The most common morphotype is **IIICa** (~34%), followed by the **IVDa** (~23%) and **IVCa** morphotypes (~17%). Among rare morphotypes, two morphotypes were found only on the Vera Island and two morphotypes on the Vera Island and in Late Pleistocene sample 1.

In the other studied samples from the isolated island populations, the most common morphotype is **IIICa**. The **IIICb**, **IIICc**, **IIIDa**, and **IIIDb** morphotypes also frequently occur in these samples. Rare morphotypes that occur only in one of the studied samples were found on the Rikord and Russky islands (one morphotype per each island).

## DISCUSSION

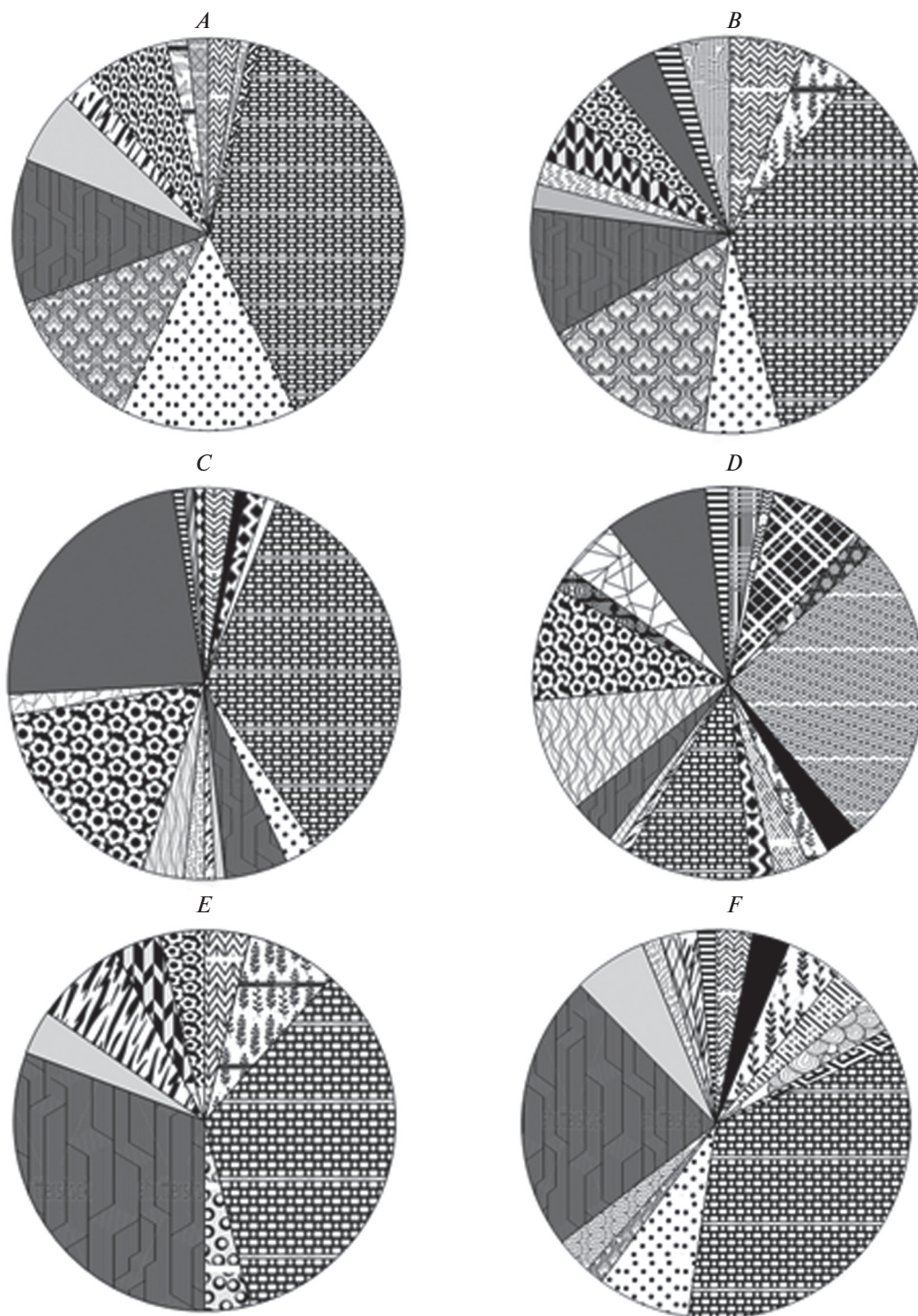
If we do not take into account samples in which the number of examined teeth is clearly insufficient for analysis (eight specimens from the Hildebrandt Island, ten specimens from the Falshivy Island, ten specimens from the Pelis Island, and ten specimens from the Rikord Island), small groups from two to four morphotypes occur most often (55–77%) in all fossil, modern mainland, and insular m1 samples of the reed vole, as shown by our studies. The predominance of the small group of morphotypes in samples was also recorded for many other vole species (Maleeva, 1976; Bol'shakov et al., 1980). The replacement of the dominant morphotype with respect to its occurrence was recorded only in Middle Holocene and Late Holocene samples and samples from the Durnovo and De Livron islands. The **IIICa** morphotype, which prevails in the Late Pleistocene with respect to occurrence, was replaced by the **IIICb** morphotype with a more complex labial side having a concavity in the lower part. It should be noted that whereas one of the main mor-



**Fig. 6.** The ratio (%) of m1 morphotypes in *A. fortis* in the Pleistocene–Holocene: (A) Late Pleistocene sample 1, (B) Late Pleistocene sample 2, (C) Middle Holocene sample, (D) Late Holocene sample. Shading shows the variants of morphotypes.

photypes was replaced by another one in the Middle Holocene sample, the **IIIDb** morphotype is the dominant morphotype in the Late Holocene sample, while it was previously among rare or reserve morphotypes. Currently, the **IIICa** morphotype prevails again in mainland samples. Although climate cooling reached the maximum level in the time interval between Late Pleistocene samples 1 and 2 at the turn of 18 000–20 000 years, the leading morphotype was not replaced during this period.

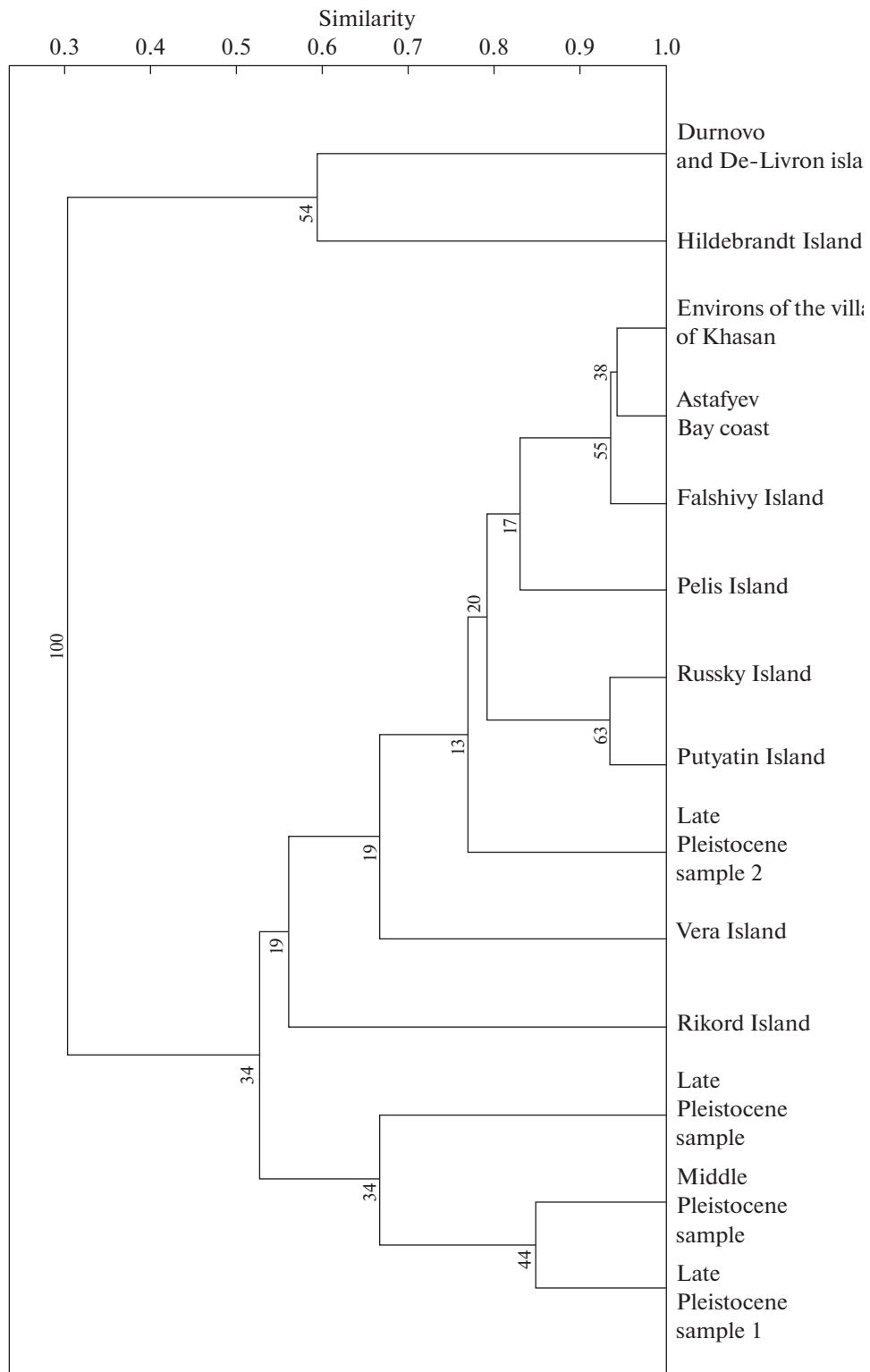
It is interesting that, judging from the six drawings of the chewing surface of the first lower molars of *Alexandromys fortis* from Late Pleistocene cave deposits on the Miyako Island (Japan) (Kaneko and Hasegawa, 1995), the following morphotypes were found on the island at that time: **ICa** (one tooth), **IICa** (four teeth), and **IICc** (one tooth). Morphotype **ICa** is a rare morphotype recorded in Late Pleistocene sample 1 and in sampling from the Durnovo and De Livron islands. Morphotype **IICa** occurs in all fossil samples,



**Fig. 7.** The ratio (%) of m1 morphotypes in *A. fortis* in modern samples: (A) environs of the village of Hasan; (B) Astafyev Bay coast; (C) Vera Island; (D) De Livron and Durnovo islands; (E) Russky Island; (F) Putyatın Island. See the designations of morphotypes in Fig. 6.

on the mainland and islands and is one of the main morphotypes in Late Pleistocene sample 1 and occurs most often among all other morphotypes on the Durnovo and De Livron islands. The widespread rare

morphotype **IICc** was recorded in Late Pleistocene sample 2 and the Middle Holocene sample on the mainland and islands. It is believed that the reed vole migrated from the continent to the Miyako Island in



**Fig. 8.** A similarity dendrogram of m1 samples of the reed vole based on cluster analysis.

the Middle Pleistocene. This species does not occur in the modern fauna of the island (Kaneko and Hasegawa, 1995; Kawamura, 2014).

The increased morphotypic diversity on the Putyatin, Durnovo, De Livron, and Vera islands is also characteristic of many other island vole populations

and associated with the release of latent phenotypic variability due to inbreeding (Markova et al., 2020).

On the other hand, the constant passage through a “bottleneck” is the norm for the reed vole. Thus, the absolute abundance of voles on some islands during a depression period, which can last several years, is estimated at several dozen individuals (Katin, 1989).

Among the isolated island populations of the reed vole, the most interesting set of morphotypes is observed on the Durnovo, De Livron, and Vera islands. The most widespread IICa morphotype on the Durnovo and De Livron islands is among the main morphotypes in Late Pleistocene sample 1 and in the Middle Holocene and Late Holocene samples, while it is among rare morphotypes in other samples.

The Bolshoy Pelis, Hildebrandt, Durnovo, and De Livron islands are part of the Rimsky-Korsakov Archipelago. The islands of this archipelago separated from the mainland earlier than all the other islands of the Peter the Great Bay at the end of the Late Pleistocene and beginning of the Holocene (Velizhanin, 1976). It is quite possible that the features of the morphotypic structure of the vole population on the Durnovo and De Livron Islands are associated with the founder effect. One should also note the presence of a significant number of both “simple” and “complex” morphotypes in this sample. The presence of “simple” morphotypes is still typical only for Late Pleistocene sample 1. The number of “complex” morphotypes with a deep lingual reentrant angle 4 reaches 35.8% on the Durnovo and De Livron islands and 47.4% on Vera Island. These morphotypes rarely occur in other studied samples. The increased occurrence of individuals with a complex structure of the chewing surface of teeth in the vole population is explained by coarser food (Sorokina, 2011); in turn, the living conditions for the reed vole on the rocky soil of small sea islands (where there are few succulent plants) significantly differ from those on the mainland (Chugunov and Katin, 1984).

Whereas the Durnovo and De Livron islands have been isolated for not less than 10 000 years (or possibly even longer, taking the fact into account that they were hilltops isolated from each other and from the mainland by other landscapes during the retreat of the sea), Vera Island was separated much later from the mainland by a 480-m wide narrow shallow strait. The reed vole is the only rodent species that lives on the Durnovo, De Livron, and Hildebrandt islands. In addition to the reed vole, the Korean field mouse *Apodemus peninsulae* Thomas 1907 also occurs on Vera Island (Chugunov and Katin, 1984). However, these islands have common features that distinguish them from the other studied islands. The Durnovo, De Livron, and Vera islands are the smallest among the studied islands. Their last territorial connection with Primorye was the connection with its southernmost part (Khasan district). Individuals from Late Pleistocene

sample 1 existed during the climate optimum of the Middle Wurm period (43 000–33 000 years), a period that is similar to the Middle Holocene in terms of the intensity of temperature increase and humidity regime (Korotkii et al., 1996). During climate optima in the Middle Wurm and Middle Holocene, both vegetation and fauna zones significantly shifted to the north of their present location (Korotkii et al., 1988). This suggests that the southern forms of the reed vole that differed in haplotypes were also involved in the foundation of populations on these islands (Gao et al., 2017). Haplotypes similar to the southern forms common in China were found both among fossil voles from the deposits of the Medvezhiy Klyk cave and in vole populations from the islands of the Rimsky-Korsakov Archipelago (Haring et al., 2015; Sheremetyeva, 2020).

A certain role in the differentiation between the mainland and insular populations was probably also played by the difference in intrapopulation evolutionary processes in these areas (MacArthur and Wilson, 1967). It was previously shown that the rates of morphological evolution were much higher in insular mammal populations than in mainland mammal populations. The initial period of accelerated change (in a time interval from 21 years to 20 000 years) is followed by the slowing of the rate of evolution of insular species and becoming closer to the rates on the mainland (Millen, 2006). During this period, mammals develop more rapidly on smaller islands than on larger ones (Millen, 2011).

Samples from the large Russky and Putyatin Islands, which separated from the mainland about 8500–7000 years ago, are similar to each other and close to the mainland with respect to the composition of morphotypes (Fig. 8). The living conditions for the reed vole on these islands do not significantly differ from their living conditions on the mainland.

## CONCLUSIONS

As in most vole species (Maleeva, 1976), a small group of morphotypes (from two to four) predominates in all *Alexandromys fortis* samples.

A temporary complication of the prevailing type of chewing surface of m1 was recorded for the reed vole in the Holocene. At the present time, the morphotype that prevailed in the Late Pleistocene has become most widespread on the continent again. Changes in the frequency of occurrence of morphotypes in the Holocene may be associated with the renewed spread of the reed vole, merging of its isolated populations, and recovery of its abundance (Aleksieva and Golenishchev, 1986) after the reduction of its population during the period of maximum climate cooling.

The features of the morphotypic composition of m1 in the isolated populations of the reed vole on the Durnovo, De Livron, and Vera islands are determined

by both the phenotypic and genotypic characters of the founders of the island populations and by the peculiarity of new habitat conditions, which initiated a high rate of evolution, the release of latent diversity, and an increase in the number of rare morphotypes.

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#### CONFLICT OF INTERESTS

The authors declare that they have no conflict of interests.

#### COMPLIANCE WITH ETHICAL STANDARDS

This article does not contain any studies involving animals or human participants performed by any of the authors.

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SPELL: 1. OK