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Morphotypic Variability of the Third Upper Cheek Tooth of the Chromosomal Races of *Alexandromys evoronensis* (Arvicolinae, Rodentia) from Natural and Laboratory Populations

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Abstract—The Evoron vole is a narrow-range species known from isolated populations of three mountain basins in the south of the Russian Far East. The species has a multiple chromosomal polymorphism, detected in two chromosomal races ("Evoron" and "Argy"). Morphotypic variability of the surface pattern of 357 third upper molars (M3) was analyzed in voles from six natural samples (Evoron-Chukchagir Lowland, 2; Verkhne-Bureinskaya Depression, 1; Verkhne-Zeya Basin, 2; and upper reaches of the Amgun River, 1), as well as three groups of laboratory breeding of chromosomal races. The traditional and complex methods were used to isolate the morphotypes. Using the complex method, 16 morphotypes were isolated, ten of which were not previously described for this species. Each sample was characterized by its own set of the main morphotypes. The number of reserve morphotypes in natural samples was lower (from 0 to 5) than in laboratory groups (from 5 to 10). In individuals of the chromosomal race "Evoron" (samples from the Evoron-Chukchagir Lowland), M3 morphotypes with fused first two prisms, as well as lower morphotypic variability as compared to the "Argy" chromosomal race (samples from the Verkhne-Bureinskaya Depression and Verkhne-Zeya Basin), were identified using the complex method. It was also demonstrated that the chromosomal races have differences in the number of morphotypes, asymmetry index, and frequency of their combinations. A comparison of M3 complexity coefficients in two groups of all samples taken at different times in the 1970s and 2000s from three intermountain basins allowed us to identify a chronographic trend of an increase in the portion of simple teeth in a forty-year study interval.

Keywords: Evoron vole, chromosome races, molars, morphotypes, geographic variability, M3

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INTRODUCTION

In recent years, it was demonstrated in numerous publications that karyotypic change accompanies the speciation (Murphy et al., 2005; Schubert, 2007; Zhdanova et al., 2007; Schubert and Vu, 2016; Sacerdot et al., 2018; Mudd et al., 2020; Damas et al., 2022; Nosil et al., 2023). A comparative analysis of the genome, including fluorescence in situ hybridization of chromosomes (FISH) of more than 40 different mammalian species, compilation of ordered gene maps of several representatives of different orders of mammals, as well as large-scale sequencing of the human and mouse genomes allowed us to create an idea about the rates and patterns of chromosomal evolution on a genome-wide scale, as well as about the factors that formed the genomes of existing mammalian species (Murphy et al., 2001). Chromosomal rearrangements were one of such factors. The number of chromosomal rearrangements is not the same in different groups of mammals. Record-high rates of karyotypic evolution (one rearrangement per million years) were detected in mouse-like rodents, canids, gibbons, and perissodactyls. However, each of these mammalian orders contains taxa with slow rates of chromosomal rearrangements (family Sciuridae among rodents, families Felidae and Phocidae among carnivores, great apes). Comparative cytogenetic data demonstrate that high rates of chromosomal rearrangements typical for Myomorpha were not accompanied by rapid evolution of morphological traits (Romanenko et al., 2007). The analysis of the ratio of cytogenetic variability (variability in the number of chromosomes as a result of their fusion) and morphological differentiation in mammals at an intraspecific level "did not provide grounds for considering the contribution of structural transformations of the karyotype to the evolutionary transformation of exophenotypic traits to be somewhat significant" (Gileva, 1990, p. 76). Thus, the study of morphotypic variabil-

ity of the masticatory surface of molars (M3, m3, and m1) (Yakimenko and Vorontsov, 1982) of mole voles of the superspecies *Ellobius talpinus* (living in the river valleys of Tajikistan) revealed no association of chromosomal rearrangements with morphotypic variability in chromosomal forms. There are no morphological studies of chromosomal forms by multiple tandem fusions. The discovery of two chromosomal races in the Evoron vole (Kartavtseva et al., 2021a), differing in five tandem and two Robertsonian fusions, makes the species a convenient object for studying microevolutionary processes in isolated natural populations at different levels (molecular, cellular, and organismal).

The Evoron vole (*Alexandromys evoronensis* (Koval'skaya et Sokolov, 1980)) is an endemic species of Northeast Asia, south of the Russian Far East, is represented by three isolated populations and two chromosomal races: "Evoron" ($2n$ = 38–41) and "Argy" ($2n$ = 34–37) (Kartavtseva et al., 2021a). The species karyotype is characterized by multiple chromosomal structural rearrangements: centric and tandem fusions. While centric fusions are mainly not harmful and are common in mammalian populations, tandem fusions are usually lethal (Dobigny et al., 1917). The Evoron vole is a unique species by the presence of intra- and interpopulation polymorphism for tandem fusions. Eleven chromosomes are involved in these fusions, four of which are also involved in acrocentric fusions. A total of 20 karyotype variants were described (Kartavtseva et al., 2021a).

According to differential staining and FISH of the chromosomes, the formation of many vole species of the genus *Microtus* was accompanied by both centromeric and tandem rearrangements (Modi, 1987; Lemskaya et al., 2010); however, polymorphism associated with multiple tandem fusions is known only for the Evoron vole (Kartavtseva et al., 2021a, b). This species is a convenient object for studying the role of tandem fusions in the morphotypic variability of molars in voles of the subfamily Arvicolinae. The diversity of vole molars without the analysis of their genetic variability is relatively well studied (Ognev, 1950; Angerman, 1973; Maleeva, 1976; Bol'shakov et al., 1980; Pozdnyakov, 1993; Koenigswald, 1980; Rabeder, 1986; Kawamura, 1988; Chaline et al., 1999; Borodin, 2009; Fejfar et al., 2011; Voyta et al., 2013; Markova and Smirnov, 2018; Markova et al., 2019; Vinokurova et al., 2022; Moroldoev et al., 2024; etc.). Morphotypic variability of molars was studied for a single population of the Evoron vole (Meyer et al., 1996; Pozdnyakov, 1993).

The species was described from the Evoron Lake valley in the Evoron-Chukchagir Lowland of Khabarovsk krai (Koval'skaya and Sokolov, 1980). Previously, individuals from the western shore of Lake Evoron were attributed to Maximowicz's vole (*A. maximowiczii* Shrenck, 1858) (Ognev, 1950; Geptner and Shvetsov, 1960; Kuzikov et al., 1979). As a result of the study of the fauna and abundance of small mammals in the Amur-Bureya interfluve in the south of the Russian Far East, zoologists from the Research Institute of Epidemiology and Microbiology of the USSR Academy of Medical Sciences captured a vole, subsequently identified as Maximowicz's vole. Five points of four sections of the Baikal-Amur Railway (BAM) under construction, located between the city of Komsomolsk-on-Amur and the village of Chegdomyn (1975–1977), were studied: Evoron, Verkhne-Amgunsky, Dusse-Alinsky, and Chegdomynsky (Kuzikov et al., 1979). Researchers from the same group reported that two other species previously noted here (*A. fortis* (Büchner, 1889) and *A. oeconomus* (Pallas, 1776)) were not found in this part of the BAM under construction (Kuzikov et al., 1979). E.I. Korenberg drew the attention of V.E. Sokolov, head of the Severtsov Institute of Evolutionary Morphology and Animal Ecology of the USSR Academy of Sciences (Moscow), to the need to clarify the species affiliation of the grey voles from the shore of Lake Baikal. In the work (Koval'skaya and Sokolov, 1980, p. 1409), devoted to the study of the chromosomes of these voles, it was indicated: "In 1976–1978, employees of the Laboratory of Medical Zoology of the Institute of Epidemiology of the USSR Academy of Medical Sciences collected a series of grey voles from the shore of Lake Evoron (Khabarovsk krai, Solnechny district). Voles from Khabarovsk krai, given to us in 1976 for the determination by some peculiarities of the cranium, were closely related to Maximowicz's vole, but differed from the latter by larger body and cranium sizes. A comparison of karyotypes of the voles from Lake Evoron and Maximowicz's vole, as well as hybridization of these forms, indicate the species independence of the voles caught in the north of Khabarovsk krai." In this work, a new species (Evoron vole) was described based on the chromosome analysis data and the results of experimental hybridization of the Evoron vole with the Muya vole and Maximowicz's vole (sterile first-generation hybrids were obtained). Later, similar results were obtained by other researchers (Meyer et al., 1996; Bikchurina et al., 2023). By chromosome sets, the Evoron vole differed from a closely related species (Maximowicz's vole). At the moment of the species description, the karyotype of *A. evoronensis* had numerical characteristics of $2n$ = 38–40, NF = 52–58, while that of *A. maximowiczii* was 2n = 38–44, NF = 54–62 (Koval'skaya and Sokolov, 1980). In the study of the ecology of the Evoron vole in the Evoron section of the Baikal-Amur Mainline (BAM) (Kovalevskii et al., 1980, pp. 206–207), it was noted that "in the publication (Kuzikov et al., 1979), *M. evoronensis* appears under the name "Maximowicz's vole." On the eastern part of the BAM route, this animal is distributed up to the upper reaches of the Amgun River, but is most common on the plains of the Chukchagir-Evoron Depression. It reaches the largest abundance in large lakeside basins occupying hundreds of square

kilometers." Thus, according to the results of long-term zoological and parasitological studies (Kuzikov et al., 1979; Kovalevskii et al., 1980), *A. evoronensis* inhabits two intermountain basins: the Evoron-Chukchagir Lowland (Evoron region) and Verkhne-Bureinskaya Depression (Chegdomynsky region). Despite these data, individuals from the vicinity of the village of Polina Osipenko (Evoron-Chukchagir Lowland) were classified as the reed vole (*A. fortis*) (Tagirova, 1998). The voles from the Urgal River basin (Verkhne-Bureinskaya Depression) continued to be considered as Maximowicz's vole (Kostenko, 2000; Shenbrot and Krasnov, 2005).

Later, the belonging of voles from the Urgal River valley to the Evoron vole was genetically confirmed (Sheremetyeva et al., 2016), and this species was discovered in the Upper Zeya Plain of Amur oblast (Sheremetyeva et al., 2017). Since this species is reliably identified only by genetic methods, it is not surprising that the voles from the intermountain basins were classified as a morphologically similar species (Maximowicz's vole).

Studying karyotypes of the voles from three isolated populations in the south of the Russian Far East allowed us to describe two chromosomal races that differ in structural rearrangements (Robertsonian and tandem chromosome fusions). Thus, voles from the Evoron-Chukchagir Lowland in Khabarovsk krai were assigned to the chromosomal race "Evoron" with $2n = 38–41$, NF = 54–59 (Kartavtseva et al., 2021b), while individuals from the Upper Zeya Plain in Amur oblast and Verkhne-Bureinskaya Depression in Khabarovsk krai were assigned to the chromosomal race "Argy" with $2n = 34, 36, 37$, NF = 51–56 (Kartavtseva et al., 2021a). Initially, we questioned whether two chromosomal races belonged to the same species, since the races had large karyotypic differences. The production of fertile offspring from hybrids when crossing the "Evoron" and "Argy" chromosomal races allowed us to consider them as a single species (Kartavtseva et al., 2021a). By morphometric characteristics of the bodies, individuals from three populations were almost indistinguishable (Kartavtseva et al., 2022). The study of meiosis of first-generation hybrids between individuals from three isolated populations of two chromosomal races (Bikchurina et al., 2023) demonstrated that chromosomal rearrangements do not lead to chromosome-pairing failure and a decrease in recombination frequency. These data confirmed the belonging of voles of two races to the same species. The detected meiotic abnormalities in hybrids (F1) between the Evoron vole and Muya vole, as well as between the Evoron vole and Maximowicz's vole, confirmed the validity of three species of the "maximowiczii" group (*A. evoronenesis*, *A. maximowiczii*, and *A. mujanensis*) and significant role of chromosomal rearrangements in the speciation. According to molecular genetic data, the voles in the subfamily Arvicolinae are young (Abramson and Lisovskii, 2012). Namely for these species, multiple chromosomal polymorphism was detected. This meant that the karyotype in each of these species is still not stabilized.

The distribution boundaries of the Evoron vole in the south of the Russian Far East are expanding with each new discovery. According to the latest findings (Sheremetyeva et al., 2016, 2017), a presumptive range (Fig. 1b) of the Evoron vole was outlined (Kryštufek and Shenbrot, 2022), which still requires clarification. Thus, two new findings are absent in the map in this work: on the left bank of the Bureya River (Fig. 1a), at the confluence of the Urgal River (51°05′ N and 132°31′ E) (Sheremetyeva et al., 2023), and 120 km south of the previous point (50°01′ N and 132°03′ E) (Kartavtseva et al., 2023), but this locality is outside the boundaries of the presented range.

The first study of the molar surface pattern in the Evoron vole (Koval'skaya and Sokolov, 1980) allowed one to reveal a difference from the Maximowicz's vole in the frequency of the predominant morphotype of the third upper tooth (M3). To determine the predominant morphotype, a traditional approach was used (according to Rörig and Börner, 1905), the number of incoming and outgoing angles of the tooth on the lingual and labial sides was taken into account. Vole individuals from terra typica (the shore of Lake Evoron, source of the Devyatka River) (from Koval'skaya and Sokolov, 1980) had two predominant morphotypes by the frequency (4/3 (0.32) and 4/4 (0.23)). In this work, it was noted that the morphotype 4/3 of the studied individuals has a low frequency relative to that of Maximowicz's vole (the frequency of this morphotype was never less than 0.45). According to other authors (Meyer et al., 1996) (the shore of Lake Evoron, mouth of the Odan River), the morphotypes 4/4 (0.30) and 5/4 (0.30) were predominant. The morphotype 4/3 in the Evoron vole in this study was found with an even lower frequency (about 0.18), while the frequency of this morphotype for Maximowicz's vole (about 0.6) was high.

For M3, six morphotypes were identified; for the first lower tooth (m1), one morphotype, similar to the morphotype of Maximowicz's vole (Koval'skaya and Sokolov, 1980; Meyer et al., 1996). Meyer et al. (1996) did not compare the frequencies of M3 morphotypes they obtained with previously published data by Koval'skaya and Sokolov (1980). In the work of Meyer et al. (1996), only a high similarity of M3 with identical teeth of the Muya vole was noted. In the table for the species identification, it was stated for the Evoron and Muya voles that: "the number of protruding angles on the third upper molar (M3) on the inner side is 5; on the outer side, 4 or 5" (Meyer et al., 1996, p. 288). Thus, the authors attached a great importance to M3 morphotypes for the species diagnostics, despite the fact that differences are frequency-based, not discrete.

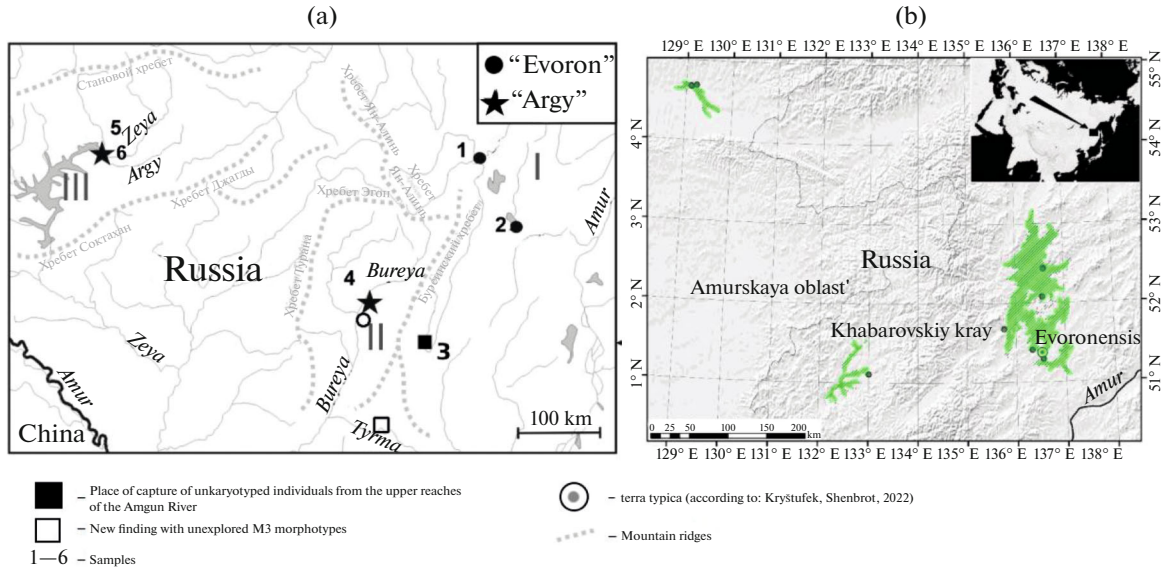

Fig. 1. (a) Collection sites of *Alexandromys evoronensis* material of two chromosomal races ("Evoron" and "Argy") from three intermountain basins in the south of the Far East: in Khabarovsk krai, Evoron-Chukchagir Lowland (I) and Verkhne-Bureinskaya Depression (II); in Amur oblast, Upper Zeya Basin (III), (b) reconstructed areal map (based on: Kryštufek and Shenbrot, 2022).

A method previously suggested by Bol'shakov et al. (1980) for grey voles was taken as a basis for using another method (Pozdnyakov, 1993, 2003, 2004) in the study of molar variability in the species of the genus *Alexandromys* (including the Evoron vole from the Lake Evoron valley). In this study, both the number of fused triangles (closed fields) and the peculiarities of the masticatory surface outline were taken into account for M3. This approach was called "complex". The prism fusion and number of angles of the entire tooth were considered separately, and a grid for distinguishing the morphotypes was constructed. The method used by A.A. Pozdnyakov is similar to the previously proposed one. A difference of the new approach was that there was no grid of the studied traits and that the numbers of tooth prisms were designated by letters. Instead of designating the angle numbers of the entire tooth, the angle numbers of the posterior unpaired loop (talon) were designated on each side. Essentially, this is the same complex approach.

At present, it is unclear which M3 morphotypes of the Evoron vole population from the shores of Lake Evoron (chromosomal race "Evoron"), previously identified using the classical method (Meyer et al., 1996), correspond to the morphotypes determined for the same population using the complex method (Pozdnyakov, 1993). It is also unclear how variability (according to two approaches) is traced in populations of the chromosomal race "Argy."

It is known that geographic isolation is an important factor in the speciation. Chromosomal rearrangements are more rapidly fixed in isolated (small) populations than in large populations and be one of the factors of speciation (King, 1995). The discovery of isolated chromosomally polymorphic populations (having not only different karyotypic characteristics (2*n* and NF), but also different pairs of chromosomes involved in rearrangements (mainly tandem fusions)) of voles from three intermountain basins in the south of the Russian Far East suggests that, along with chromosomal differences, morphotypic differences in M3 can be also detected. The study of morphotypic and genetic variability of the Evoron vole makes it a convenient model for studying microevolutionary processes at the initial stages of speciation. At present, there are very few studies on the relationship between chromosomal and morphotypic variability in mammals at the speciation stage (Heng and Heng, 2023).

The aim of the present study was to estimate the morphotypic diversity of the third upper molar of the Evoron vole (both natural and laboratory samples) in isolated populations of two chromosomal races from three geographic regions of the south of the Russian Far East (Evoron-Chukchagir Lowland, Verkhne-Bureinskaya Depression, and Verkhne-Zeya Plain) using two methods (traditional and complex). The obtained morphotypic results were compared with data on karyological and molecular genetic analyses.

MATERIALS AND METHODS

The morphotypic variability of the shape of M3 masticatory surface ($n = 157$) was studied in the Evoron vole from natural populations of three geographic regions of the south of the Russian Far East: the Evoron-Chukchagir Lowland, Verkhne-Bureinskaya

Table 1. Material for studying the shape of the masticatory surface of *Alexandromys evoronensis*

Samples		Localities (number of tooth samples/year)	Coordinates	Chromosomal rase
no.	code			
Khabarovsk krai				
1	EV_E_po_1	Polina Osipenko district, right bank of the Amgun River (8/2008)	52°26′ N, 136°34′ E	"Evoron"
	EV_E_po_2	In the same place (12/2016)		
1L	EV_E_po L	In the same place (66/2017–2021)		
	EV_E_ev	Solnechny district, Lake Evoron valley, bank of the Devyatka River, terra typica (27/1978)	51°22′ N, 136°31′ E	"Evoron"
	EV_E_odan	Solnechny district, bank of the mouth of the Odan River (22/1979)	51°24′ N, 136°16′ E	"Evoron"
3	EV_?_amg	Verkhne-Bureinsky district, upper reaches of the Amgun River, Bureinsky ridge (8/1976)	50°035′ N, 134°045′ E	?
4	EV_A_urg	Verkhne-Bureinsky district, vicinity of the village Ust-Urgal, eastern bank of the Bureya River, near the mouth of the Urgal River (52/2019)	51°07′ N, 132°31′ E	"Argy"
4L	EV_A_urg L	In the same place (8/2020)		
Amur oblast				
5	EV_A_argy	Zeisky district, bank of the Argy River, in the area of the junction of the Argy and Zeya rivers (18/2015)	54°40′ N, 129°06′ E	"Argy"
5L	EV A_argy L	In the same place (126/2017–2019)		
6	EV_?_argy	In the same place (10/1973)	No data	"Argy"

Depression, and Verkhne-Zeya Plain (Fig. 1a). Teeth of laboratory-bred voles from the Evoron-Chukchagir Lowland ($n = 66$), Verkhne-Zeya Plain ($n = 126$), and Verkhne-Bureinskaya Depression ($n = 8$) were also studied. A total of 357 teeth were studied. No anomalous teeth of laboratory-bred voles were included in the analysis. The analysis included both right and left teeth from 180 individuals.

Six samples of the Evoron vole from natural populations were formed (Table 1). Since some individuals studied in the present work were previously studied by two genetic methods (karyological (Kartavtseva et al., 2021a; b) and molecular genetic (Sheremetyeva et al., 2016, 2017, 2023), a complex numbering system was provided to designate individuals in these studies. Thus, no. 4582/136-19 designates the numbers of chromosomal/molecular study. In molecular genetic number, the last two digits indicate the year of capture or slaughter of the laboratory animals. Previously, the descriptions of individuals with these numbers were published in the indicated studies. Unkaryotyped voles have only a molecular number. The numbers of animals from laboratory groups include the letter "L." Previously, when studying meiosis of the offspring of Evoron voles from different geographic samples, a coding of animals was proposed (Bikchurina et al., 2023), which was used in the present study with a slight modification (Table 1). The first two letters (EV) encode the species name. For the chromosomal race "Evoron," the letter E was added (EV_E); for the chromosomal race "Argy," the letter A (EV_A). Small letters after the chromosomal race name encode the locality name. Six samples from five natural populations (Fig. 1) were confined to three geographic regions (I–III).

I—Evoron-Chukchagir Lowland (Khabarovsk Krai)

Two karyotyped samples from this region were studied (no. 1 and no. 2) (Table 1, Fig. 1; black circles). Each sample unites two samples collected at different times, located geographically close. Distance between the samples no. 1 and no. 2 in a straight line is approximately 100 km. The voles from these samples were assigned to the "Evoron" chromosome race, since identical pairs of chromosomes in them were involved in structural rearrangements leading to a change in the chromosome number (Kartavtseva et al., 2021b).

Sample no. 1 (EV_E_po) is composed of two samples (EV_E_po_1 and EV_E_po_2) taken in different years in the vicinity of the village of Polina Osipenko (Table 1). The collections were performed by I.V. Kartavtseva and I.N. Sheremetyeva. The morphotypes

M3 were determined by I.V. Kartavtseva and A.I. Stepanova.

Sample no. 2 also combines two samples from the western shore of Lake Evoron, collected at different time (Table 1). The first sample (1978), EV_E_ev (terra typica), the voles were captured by zoologists from the Gamaleya Research Institute of Epidemiology and Microbiology of the USSR Academy of Medical Sciences. The voles were karyotyped by Yu.M. Koval'skaya without indicating the animal numbers (Koval'skaya and Sokolov, 1980). The collection of crania is stored in the Zoological Museum of Moscow State University, Moscow. Morphotypes M3 were determined by A.A. Pozdnyakov. The second sample (1979), EV_E_odan, the capture site is located 12 km northwest of terra typica (previously, the Evoron railway station). The collection of crania is stored in the Zoological Institute of the Russian Academy of Sciences, St. Petersburg, collector F.N. Golenishchev. Five individuals were karyotyped by S.I. Radzhabli and O.L. Sablina, without indicating animal numbers (Meyer et al., 1996). The voles of this sample were assigned to the "Evoron" chromosome race (Kartavtseva et al., 2021b). The M3 morphotypes were determined by A.A. Pozdnyakov.

We conditionally attributed the sample no. 3, EV ? amg (Table 1, Fig. 1), taken in the upper reaches of the Amgun River, to the samples of the Evoron-Chukchagir Lowland, since the middle course of the Amgun River passes through this lowland. The material was collected during the expedition of the Gamaleya Research Institute of Epidemiology and Microbiology of the USSR Academy of Medical Sciences in the area of the Baikal-Amur Mainline (BAM) from July 4 to 8, 1979. The material was transferred by V.V. Nikolaev to the Zoological Museum of the Institute of Systematics and Ecology of Animals, Siberian Branch, Russian Academy of Sciences and was among the uninventoried and unidentified samples. During the analysis of these samples in the early 1990s, A.A. Pozdnyakov paid attention that the cranium sizes of the voles in this sample significantly exceeded those of the Maximowicz's vole. Since the collection site was closer to Lake Evoron than the known localities of the Maximowicz's vole, the material was classified as the Evoron vole, to which L.I. Galkina agreed. The M3 morphotypes were determined by A.A. Pozdnyakov.

II—Verkhne-Bureinskaya Depression (Khabarovsk Krai)

Sample no. 4 EV_A_urg (Table 1, Fig. 1) was collected in the vicinity of the mouth of the Urgal River. The samples were collected by I.V. Kartavtseva and I.N. Sheremetyeva, karyotyped by I.V. Kartavtseva (Kartavtseva et al., 2021b). M3 morphotypes were determined by I.V. Kartavtseva and A.I. Stepanova.

III—Verkhne-Zeya Basin in Amur Oblast

Sample no. 5, EV_A_argy (Table 1, Fig. 1), collected by I.V. Kartavtseva and I.N. Sheremetyeva (2015). Out of 11 captured voles, two ones had abnormal teeth that were not included in our analysis. The samples were collected by I.V. Kartavtseva and I.N. Sheremetyeva, karyotyped by I.V. Kartavtseva (Kartavtseva et al., 2021b). M3 morphotypes were determined by I.V. Kartavtseva and A.I. Stepanova.

Sample no. 6, EV_?_argy (Table 1, Fig. 1). Karyotypes not studied, collections of V.M. Sapaev (1973), bank of the Argy River. We found crania of five voles (defined by V.A. Kostenko as "Maximowicz's vole") in 2024 in the collection of V.A. Kostenko of the Federal Scientific Center of the East Asia Terrestrial Biodiversity, Far East Branch, Russian Academy of Sciences. In the monograph by Kostenko (2000, p. 124), it is indicated that the collection of V.M. Sapaev (Argy River) is stored at the Institute of Water and Environmental Problems, Far East Branch, Russian Academy of Sciences, Khabarovsk. However, according to a personal communication by B.A. Voronov (who worked with V.M. Sapaev), the collection was lost. Since we only captured the Evoron vole during a search for Maximowicz's vole in the Upper Zeya Plain, in the place of the field work of V.M. Sapaev at the mouth of the Agri River, we refer it to the Evoron vole in the present study. This sample was not karyotyped; therefore, we include a question mark in the sample code.

The straight line distance between the sample no. 4, as well as two samples no. 5 and no. 6, is about 450 km.

Laboratory Groups

We provide data on the founders (those that produced offspring) for each laboratory group of voles (Table 1), since their numbers, chromosomal and molecular genetic characteristics are available in the published articles (see Methods) and will be used in further studies. In the article title, we use the term "population" as the population of a given species in a specific location. Hereinafter, to emphasize a difference between laboratory samples and the samples obtained from nature, we will refer to laboratory samples as "laboratory groups."

Group 1L (EV_E_po L). The offspring were obtained from females nos. 0062/93-16, 0061/94-16 and male no. 0060/58-16 (kept together) from sample no. 1 (EV_E_po) as a result of breeding from 2018 to 2021 (F1–F3). One of the females died after giving birth. Subsequent offspring were obtained from one female and the same male.

Group 4L (EV_A_urg L). The only litter was obtained from the female no. 4646 and male no. 4651.

Group 5L (EV_A_argy L). The offspring were obtained from one female no. 3992/22-15 and two males nos. 3995/25-15 and 3996/26-15.

The laboratory breeding of voles was conducted by I.N. Sheremetyeva and M.V. Pavlenko at the basis of the experimental site of the Federal Scientific Center of the East Asia Terrestrial Biodiversity, Far East Branch, Russian Academy of Sciences. The conditions for breeding and maintaining the voles were published (Pavlenko et al., 2017).

The crania of voles from natural samples nos. 1, 4, 5, and 6 and all laboratory groups are stored in the Bioresource Collection of the Federal Scientific Center of the East Asia Terrestrial Biodiversity, Far East Branch, Russian Academy of Sciences (registration number 2797657).

Method of Morphotypic Analysis

Traditional method. A practice of distinguishing M3 morphotypes in grey voles has a long history. In the first study, in which the variability of M3 in the common vole was described (Rörig and Börner, 1905), the number of protruding angles on the inner and outer sides was taken into account (Fig. 2).

The scheme of the main morphotypes of the M3 Evoron vole (Fig. 2) demonstrates data obtained by complex and traditional methods.

This traditional method of describing the variants of M3 outline was used later as well, designating them with a fraction reflecting the number of salient angles in the tooth from the lingual (internal, from the tongue side) and labial (external, buccal) sides: 3/3, 4/3, 4/4, 5/4, etc. These morphotypes were also given special names: simplex (3/3), typica (4/3), duplicata (4/4), complex or variabilis (5-4/3-5). In the seminal work (Rörig and Börner, 1905), the number of protruding angles was indicated in a different order, from the labial (external, buccal) side, and the number of salient angles in the tooth from the lingual (internal, from the tongue side) side.

Complex method. Along with taking into account the number of salient angles, many researchers also paid attention to the number of closed fields of M3, denoting them with Roman numerals and uniting them in a table with folding classes that, in turn, were designated with Arabic numerals (Ognev, 1950; Angerman, 1973; Bol'shakov et al., 1980). When identifying morphotypes, a special attention in these studies was paid to the outline of the talon (Maleeva, 1976; Bol'shakov et al., 1980), but it was not analyzed separately. For some species, a geographic variability of M3 morphotypes was also traced (Bol'shakov et al., 1980; Guthrie, 1971; Markova et al., 2010, 2019; Tiunov et al., 2013).

It is obvious that according to these two traits, a combinatorial classification of molars, presented in the form of a table, is the most natural (Pokrovskii et al., 1975; Vasil'eva, 1978; Bol'shakov et al., 1980). This method is convenient for analyzing the variability of individual samples. It allows us to predict which morphotypes can still be found, since there are unfilled cells in the constructed tables. However, the obtained tabular data complicates a comparison of morphotype variability across different samples and do not allow for statistical analysis without significant modification.

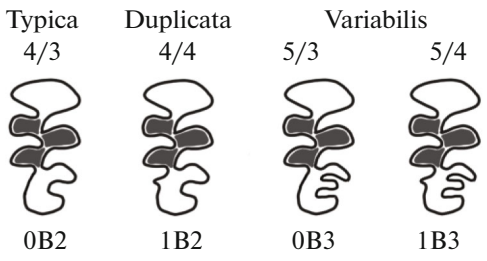

Fig. 2. Scheme of four primary occlusal surface morphotypes of M3 in *Alexandromys evoronensis* with designations used in two methods. The designations for the traditional method are above the tooth schemes; for the complex method, below the tooth schemes. A more detailed comparison of the morphotype designations for two methods is indicated in Table 1.

A new method based on the description of morphotypes by the variability of the pattern of the masticatory surface of the third upper (M3) molar (Pozdnyakov, 1993, 2003) allowed us to give a detailed characteristics of the morphotypic variability of molars in the species of the genus *Alexandromys: A. fortis*, *A. maximowiczii*, *A. mujanensis*, and *A. evoronensis*.

According to this method (Pozdnyakov, 1993), the number of closed fields in front of the talon, excluding the anterior unpaired loop, and the number of salient angles on the talon on both the buccal (external) and lingual (internal) sides were taken into account (Fig. 3). By the number of closed fields, classes were distinguished and designated with Latin letters: one closed triangle, **Y**; two, **A**; three, **B**; four, **C**; five, **D**. The triangles were numbered with Roman numerals, beginning from the anterior unpaired loop. Tooth shapes with fused fields IV and V, as well as I and II, were considered as separate classes (**E** and **b**, respectively). The designation of the identified morphotypes consists of the class designation and the number of salient angles on the talon on the external and internal sides (for example, morphotype **0B2** has class **B**, which indicates the absence of a salient angle on the external side and the presence of two angles on the internal side of the talon). In addition, the method allows us to include data on the variant of space fusion and tooth complexity coefficient in the analysis.

Since the traditional method was previously used in the studies of the Evoron vole morphotypes (Koval'skaya and Sokolov, 1980; Meyer et al., 1996), we provide a table, in which data obtained by the complex method can be converted to traditional data (Table 2). This allowed us to compare the results obtained by two methods.

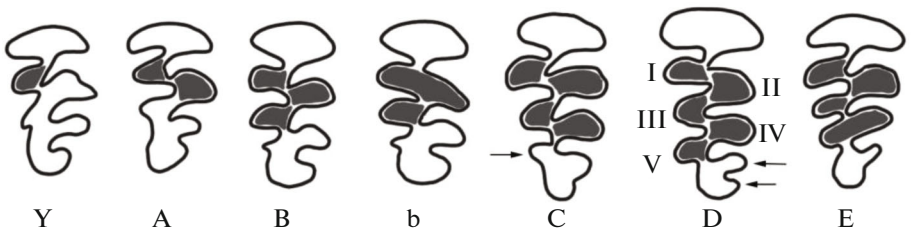

Fig. 3. Scheme of morphotypes of the third upper molar (M3) in the voles of the genus *Alexandromys* (according to: Pozdnyakov, 1993). Closed fields are filled in black; unpaired loop and talon are unfilled. Classes by the number of closed fields: one field, Y; two fields, A; three, B; four, C; five fields, D; b, with fused prisms I and II; E, with fused prisms IV and V. Arrows indicate protruding angles on the talon: C, on the outer (buccal) side; D, on the inner (lingual) side.

Identification of primary and reserve morphotypes. In this article, the **analysis of the frequency** of M3 morphotypes, applied previously (Maleeva, 1976; Bol'shakov et al., 1980), is adopted. Morphotypes are divided into **primary** (frequency 12% or more) and **reserve**, or rare (less than 11.9%) (in the laboratory group, previously not noted in natural samples). In turn, according to the frequency, the **primary** morphotypes are divided into ***overdominant*** (more than 36%), **dominant** (15–35.9%), and ***subdominant*** (12–14.9%).

Estimation of ranking of morphotype complexity. When developing the method for estimating the morphotype complexity, it was assumed that when obtaining one morphotype from another (understood as a transformation of a geometric figure), their indices of complexity should differ according to the number of transformations. Based on this, a scheme of correspondences between classes (from the morphotype designation) and specific numbers was developed: **A**–8, **b**—9, **B**—10, **C**—12, **E**—13. The morphotype complexity was calculated by summing this number with the numbers designating the complexity of the structure of the outer and inner surfaces of the teeth. For example, the complexities of the following morphotypes are expressed by numbers: **0B2**—12 (that is, 0 + 10 + 2), **1B3**—14 (that is, 1 + 10 + 3), **0E2**—15 (that is, 0 + 13 + 2), etc.

At the same time, many researchers, using the traditional methods, divide molars into simple and complex based on the outline of the masticatory surface of the vole molars, assuming that the spectrum of variability is continuous, and there are intermediate variants between them (Guthrie, 1971; Bol'shakov et al., 1980; Markova, 2013).

In the method we adopted, **simple** morphotypes included morphotypes with the values of 12 or less (that is, numbers 10–12); **complex** morphotypes, 14 or more (that is, numbers 14–16); **intermediate**, 13.

Asymmetry index. The M3 morphotypes on the right and left sides of an individual can be represented by both identical and different variants, which allows us to distinguish between symmetrical and asymmetrical pairs (or combinations) of morphotypes. The portion of asymmetrical individuals in the sample is represented by the asymmetry index (P_{as}) (Pozdnyakov, 2004). The number of different combinations of morphotypes on the left and right sides (N_s) was taken into account (Pozdnyakov, 2004). Small sample no. 3 was

Table 2. M3 morphotypes of the Evoron vole (*Alexandromys evoronensis*) according to generally accepted and complex methods

Generally accepted (Rörig and Börner, 1905)		Complex (Pozdnyakov, 1993)
Main plans of tooth structure	Number of salient angles on the lingual/labial sides of the tooth	The morphotype designation indicates the number of salient angles on the outer side of the talon, the number of closed fields in letter expression, and the number of salient angles on the inner side of the talon
Typica (principalis)	4/2	0A2
	4/3	1A2, 0B2, 0b2
Duplicata	4/4	2A2, 1B2, 1b2, 1C1, 0E1
Variabilis (complex)	4/5	1E1
Variabilis	5/3	0B3
Variabilis	5/4	2A3, 1B3, 0E2
	5/5	1E2, 2B3

not included in the main statistical analysis, but was used when analyzing the frequency of simple and complex teeth from different samples. Previously, the estimation of the asymmetry index of the first lower molar was applied to the species of the genera *Microtus* and *Alexandromys* (Kovaleva et al., 2019, 2021). The asymmetry analysis was conducted by A.A. Pozdnyakov.

Statistics. The level of significance of differences was estimated, applying the Kruskal–Wallis criterion, a nonparametric analogue of the rank analysis of variance, for each parameter. Each morphotype was divided into five traits, each of which was assigned a numerical rank (1, number of salient angles on the outer side of the talon; 2, letter designation, class; 3, upper or lower case letter of the class; 4, number of salient angles on the inner side of the talon; 5, tooth complexity according to the complexity coefficient: simple/intermediate/complex). Conducted by Stepanova A.I. in the STATISTICA 5 program (StatSoft, 1995). The calculations of the morphotype asymmetry index for the studied individuals were carried out in the Past 4.11 program by A.A. Pozdnyakov (Hammer et al., 2001).

Groups of vole samples. It is known that the vole samples taken in different years and population phases can differ in the frequency of dominant morphotypes (Bol'shakov et al., 1980); therefore, to estimate the influence of this factor, we divided each vole sample into two groups (different in the time of capture).

The first group of samples (1970s) includes the samples from the collections of the Zoological Institute of the Russian Academy of Sciences, Zoological Museum of Moscow State University, and Institute of Systematics and Ecology of Animals, Siberian Branch, Russian Academy of Sciences (collections of 1978 and 1979). These are collections of voles from the Evoron Lake valley (no. 2) and upper reaches of the Amgun River (no. 3), captured in years of high abundance (up to 80% of hits per 100 trap-nights) (Kuzikov et al., 1979; Kovalevskii et al., 1980).

However, we couldn't catch a single individual in the Evoron Lake valley for several years (from 2000 to 2005); only in 2006, Kartavtseva I.V. captured one vole at the fork in the road between the village Kharpichan and village Evoron (Kartavtseva et al., 2007). This individual was not included in the analysis, since the cranium was lost. This group of samples includes the voles captured in 1973 in the valley of the Argy River, a tributary of the Zeya River (no. 6), before the formation of the Zeya Reservoir here.

The second group of samples (2000s) includes three samples from river valleys: the lower reaches of the Argy (no. 5, 2015), middle reaches of the Amgun (no. 1, 2016), and the middle reaches of the Bureya (no. 4, 2019), with the frequency of abundance of 18.8, 3, and 10%, respectively.

Photographing of teeth was carried out under the stereomicroscope SteREODiscovery V12 (Carl Zeiss) using the Axio CamMRc digital camera; image merging was performed in the Combine ZM program; measurements (in mm), in the Axio Vision 4.8.2. When processing the material, the equipment of the Center for Collective Use "Biotechnology and Genetic Engineering" of the Federal Scientific Center of the East Asia Terrestrial Biodiversity, Far East Branch, Russian Academy of Sciences (Vladivostok) was used. Photography and image processing were conducted by A.I. Stepanova.

RESULTS

General Characteristics of M3 Morphotypes of the Evoron Vole

In the studied samples out of six local populations of the Evoron vole, 16 morphotypes were found for M3, 10 of which were new (Table 2, marked with an asterisk), previously not described for the species (Pozdnyakov, 1993).

In general, seven **primary** morphotypes were identified for the species. This number varies from two to five in different samples. Four common **primary** morphotypes were found in three samples (Table 3, Fig. 4). These morphotypes have three closed triangular fields (class **B**) with a different number of salient angles on the talon: **0B2, 0B3, 1B2**, and **1B3**. According to the traditional classification, such morphotypes can be classified as typica, duplicata, and variabilis (Table 1). The frequency of the **primary** morphotypes in each of the studied samples varied from ***overdominant*** to **dominant**, ***subdominant***, and even **reserve**. Only one complex morphotype of class **B** (**1B3**), as the **primary** one, was present in five out of six studied natural samples.

The **primary (*subdominant*)** variant **2B3** was found only in one non-karyotyped sample (no. 3, EV_?_amg), located in the upper reaches of the Amgun River (photo is absent).

The class **E** morphotypes, with fused fields IV and V (Fig. 5), were found with varying frequencies in natural samples. Two morphotypes with such class as ***subdominant*** (**0E2** and **1E2**) were detected in one sample (no. 3). Reserve morphotypes were found in three samples: **0E2** in samples no. 4 and no. 5, **1E2** in samples no. 1 and no. 4, **1E1** in sample no. 5.

Out of nine **reserve** morphotypes, seven were found for the first time (**0A2, 1A2, 0b2, 2A2, 1C1, 1E1, 2A3**) for individuals from the laboratory groups. The first three morphotypes were detected in laboratory-bred voles from the samples no. 1 and no. 5; the last four morphotypes, only in laboratory-bred voles from the sample no. 5. Rare morphotype **1b2** was found only in natural sample no. 1 (EV_E_po) and laboratory-bred (EV_E_po L) of the "Evoron" chromosome race. Morphotype **0E1** was found only in natural sample no. 4 (EV_A_argy) of the "Argy" chromosome race (Table 3).

Table 3. Variability of the third upper molar (M3) morphotypes of *Alexandromys evoronensis* in different samples

Complexity coefficient		Morphotype	Geographic regions								
			I				II		III		
			EV_E_po		EV_E_ev	EV_?_amg	EV_A_urg		EV_A_argy		EV?_argy
			no. 1	1 L	no. 2	no. 3	no. 4	4 L	no. 5	5 L	no. 6
Simple	10	0A2*	0	0.053	0	0	0	0	0	0.008	0
	11	1A2*	0	0.053	0	0	0	0	0	0.031	0
	11	0b2*	0	0.092	0	0	0	0	0	0	0
	12	2A2*	0	0	0	0	0	0	0	0.031	0
	12	**0B2**	**0.2**	*0.145*	0.061	0	**0.212**	***0.9***	**0.222**	**0.318**	0.1
Intermediate	13	2A3*	0	0	0	*0*	0	0	0	0,023	0.1
	13	**0B3**	0	0.053	**0.306**	*0.125*	0.115	0	0.111	0.078	***0.5***
	13	**1B2**	***0.4***	***0.447***	**0.082**	*0*	**0.154**	0.1	**0.222**	**0.287**	**0.3**
Complex	14	**1B3**	**0.25**	0.092	***0.408***	***0.5***	***0.423***	0	**0.222**	0.101	0
	14	1C1*	0	0	0	0	0	0	0	0.023	0
	14	0E1	0	0	0	0	0.038	0	0	0.047	0
	15	2B3*	0	0	0	*0.125*	0	0	0	0	0
	15	1E1*	0	0	0	0	0	0	0.111	0.016	0
	15	0E2	0	0	***0.143***	*0.125*	0.019	0	0.111	0.039	0
	16	1E2*	0.05	0	0	*0.125*	0.038	0	0	0	0

W, natural population; L, laboratory group. Bold font, **primary** morphotypes: **dominant,** ***overdominant*****,** and ***subdominant***. No, sample numbers; *n*, number of studied teeth.

Frequencies of M3 Morphotypes in Samples from Different Geographic Regions

Evoron-Chukchagir Lowland (I), chromosome race "Evoron"

The voles from the sample no. 1 are characterized by the predominance of three **primary** morphotypes: **1B2, 0B2**, and 1B3 (Table 3). The combined sample no. 2 includes three primary morphotypes: **1B3** (Fig. 4d), 0B3 (Fig. 4b), and **0E2**.

In natural sample no. 1, rare class **b** morphotypes were found obtained as a result of the fusion of the first and second triangular prisms of the tooth. The morphotype **0b2** (Fig. 5e) was present with a higher frequency in the natural sample (0.1) as compared to that

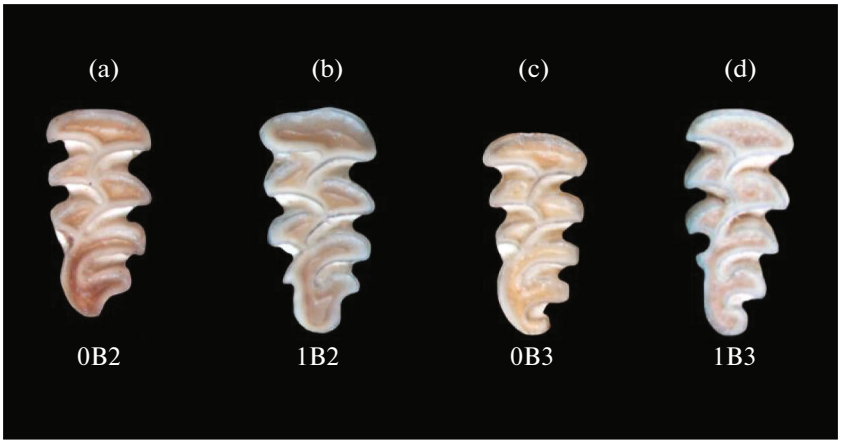

Fig. 4. Primary morphotypes of M3 in *Alexandromys evoronensis* with different complexity coefficients (cc): (a) no. 4642, male, EV_A_urg L, (simple, cc = 12); (b) no. 4314, male, EV_E_po (intermediate, cc = 13); (c) no. 4157, male, EV_A_argy L (intermediate, cc = 13); (d) no. 4163 female, EV_A_argy L (complex, cc = 14).

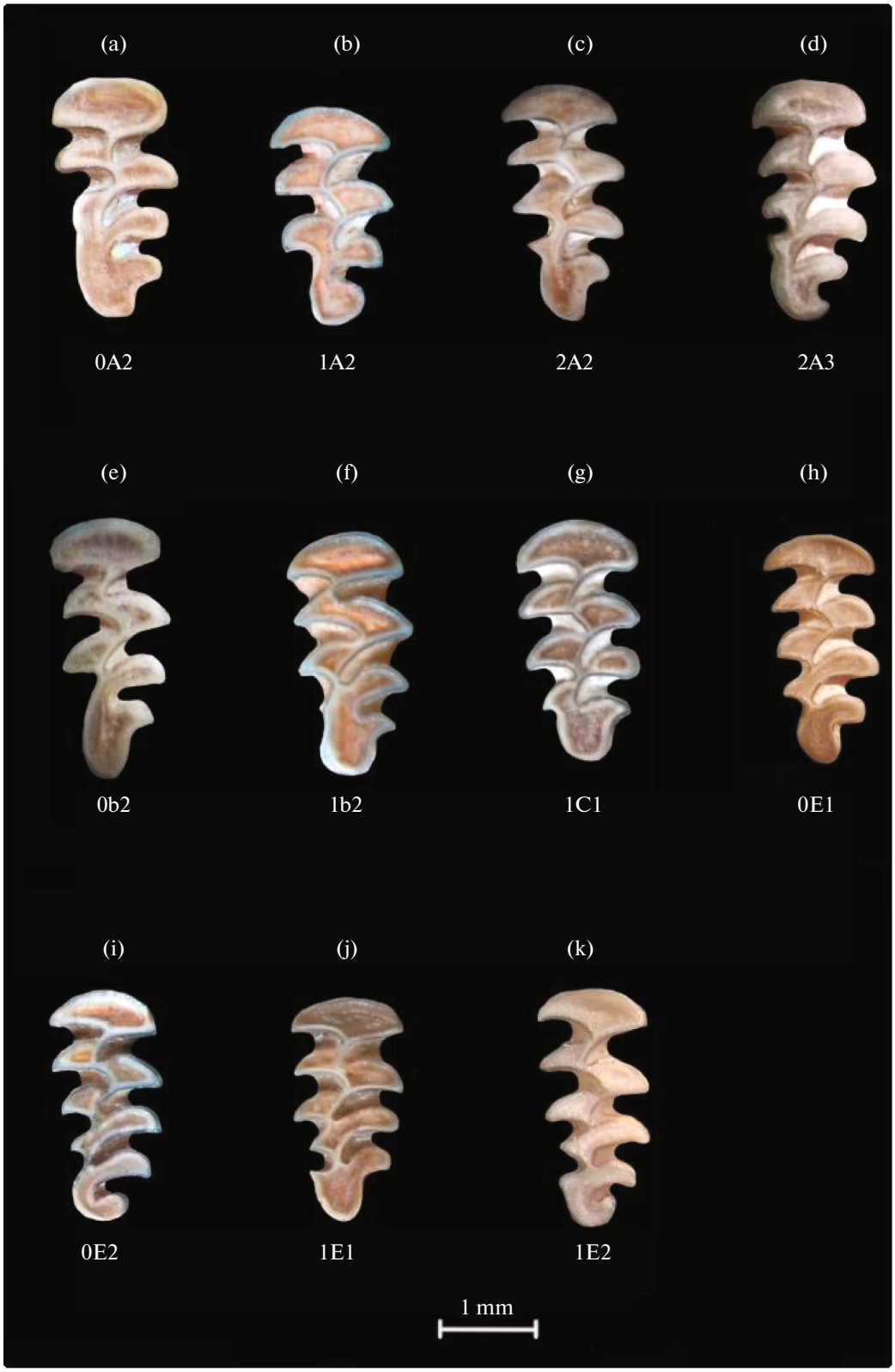

Fig. 5. Morphotypes of adult *Alexandromys evoronensis* individuals of classes **A**, **b**, **C**, and **E** with different complexity coefficients (cc): (a) **0A2**, no. 4464/329-18, female EV_A_argy L, simple (cc = 10); (b) **1A2**, no. 4504/8-19), male EV_A_argy L, simple (cc = 11); (c) **2A2**, no. 4581/135-19, male EV_A_argy L, simple (cc = 12); (d) **2A3**, no. 4339/33-18, male EV_A_argy L, simple (cc = 13); (e) **0b2**, no. 4597/269-19, male EV_E_po L, simple (cc = 11); (f) **1b2**, no. 4305 female EV_E_po, simple (cc = 12); (g) **1C1**, no. 4582/136-19, male EV_A_argy L, complex (cc = 14); (h) **0E1**, no. 4090, female EV_A_argy L, complex (cc = 14); (i) **0E2**, no. 4069, male EV_A_argy, complex (cc = 15); (j) **1E1**, no. 3999/29-15, female EV_A_argy (cc = 15); (k) **1E2**, no. 70-90, female EV_A_urg (cc = 16).

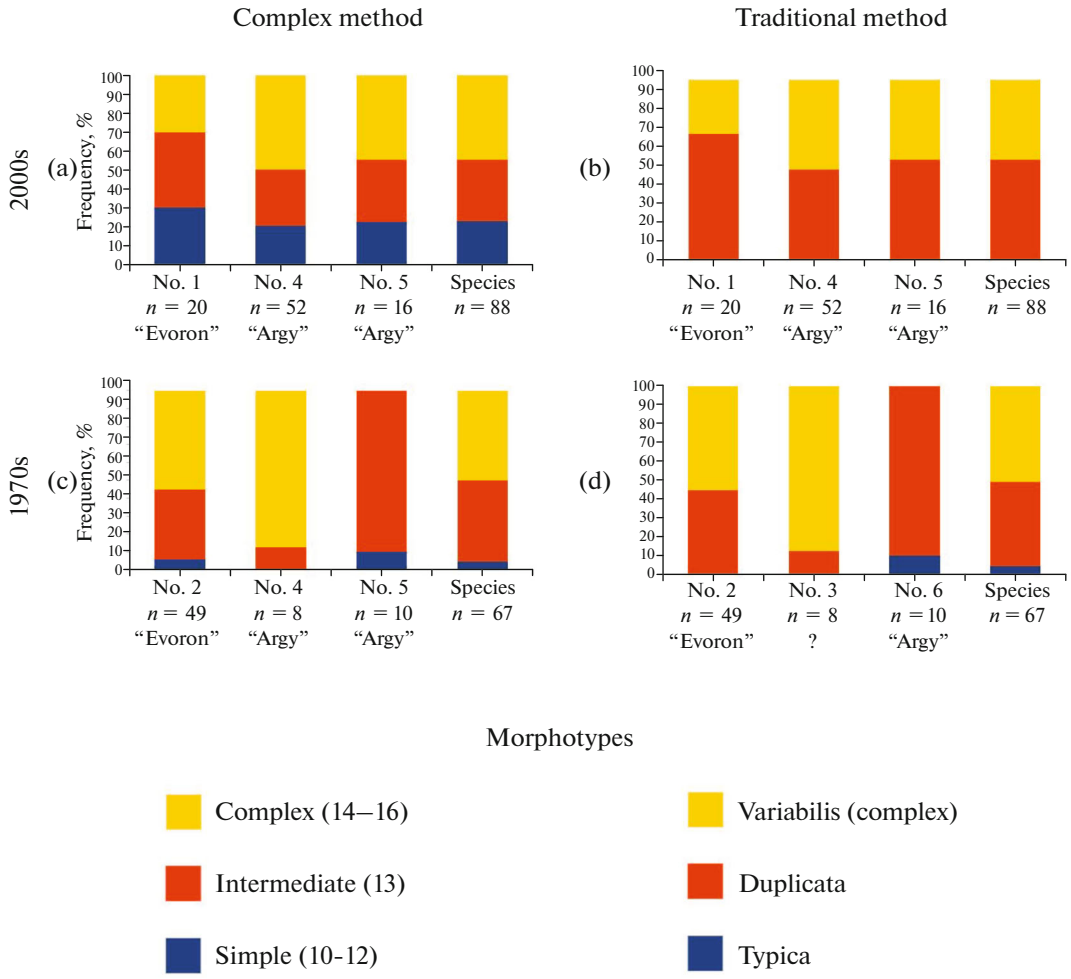

Fig. 6. Frequencies of simple (typica), intermediate (duplicate), and complex (variabilis) morphotypes of six samples (nos. 1–6) of the Evoron vole from two time periods. Data obtained using: (a) and (b), complex method; (c) and (d), traditional method. The complexity coefficient of M3 morphotype of the "Evoron" and "Argy" chromosomal races is given in brackets. ?, karyotypes not studied.

in the laboratory group (0.053). Another rare morphotype with this class, **1b2** (Fig. 5f), possessing a greater number of salient angles on the talon, also appeared in the laboratory group. These morphotypes were not found in other samples.

During the laboratory breeding of the voles from this sample (1L), the frequency of the primary M3 morphotypes was different (Table 3); particularly, two rare simple morphotypes of class **A** (**0A2** and **1A2**) were identified, characterized by the presence of two closed triangular prisms and the fusion of the third triangular prism with the talon.

In the Evoron-Chukchagir Lowland, class **E** morphotypes (with fused IV and V fields) were found in the sample no. 2 from the Evoron Lake valley. The ***subdominant*** morphotype **0E2** with the frequency of 0.143 (Fig. 6) was the third most common morphotype, while it was not detected in the voles of the sample no. 1 from the Amgun River valley. The morphotype **1E2** of this class was found as a reserve morphotype with the frequency of 0.035 in the sample no. 2.

In the samples from the Evoron-Chukchagir Lowland, three out of eight detected morphotypes (**0B2, 1B2**, and **1B3**) were noted in both samples (no. 1 and no. 2); moreover, these morphotypes with different frequency vary from primary to reserve (Table 3). Out of other five morphotypes, two were identified in the sample no. 2 and three in the sample no. 1.

For three generations of voles from the laboratory group of the sample no. 1, eight morphotypes were identified (reserve **0A2, 1A2**, and **0b2**, not found in natural samples no. 1 and no. 2), that is, two morphotypes more than in the natural sample.

The founders of this laboratory group, two females (one with the morphotype **1B2**, the other with unknown morphotype) were bred at the same time with the male 4050/34-16 (with the morphotype **0B2**). Both females in the first litter simultaneously gave

birth to 16 offspring, which had seven morphotypes (the male morphotype predominated). In the second generation, the number of morphotypes decreased to six, the male morphotype predominated. In the third generation, one pair reproduced, the offspring of which had abnormal teeth, the morphotype of which could not be determined.

Verkhne-Bureinskaya Depression (II), chromosome race "Argy"

In the natural population of the Evoron vole at the mouth of the Urgal River (sample no. 4), morphotypes **1B3**, **0B2**, and **1B2** predominated (Table 3). Class E morphotypes are represented by three reserve morphotypes: **0E1, 0E2**, and **1E2**.

Four out of five laboratory-bred animals of the first generation of one pair had the primary morphotype of the mother (**0B2)** and one vole had the morphotype of the father and mother (**1B2/0B2**).

Upper Zeya Basin (III), chromosome race "Argy"

For natural population of the lower reaches of Argy River, two samples collected at different times were studied (Table 3). Specimens of the sample no. 6 (1973) were captured before the flooding of the Upper Zeya Plain and formation of the Zeya Reservoir. Four M3 morphotypes were noted for these voles: two **primary** (**1B2** and **0B3**) and two **reserve** (**0B2** and **2A3)**.

In 2015, after a significant rise in the banks of the Zeya Reservoir and flooding of the Argy River estuary, the voles were captured from this population, for which three **primary** morphotypes (**0B2, 1B2,** and **1B3**) and three **reserve** morphotypes (**0B3, 1E1**, and **0E2**) were the main morphotypes. A comparison of the morphotypes in two samples indicates a change in the frequency of morphotypes and emergence of two new morphotypes in the sample no. 2.

A maximal number of morphotypes (twelve) was observed for the 5L laboratory animals with an increased portion of two **dominant** morphotypes: **0B2** (0.318) and **1B2** (0.287). Despite a large diversity of morphotypes, variants caused by the fusion of the first and second triangular fields (class **b)** were absent in both natural sample and laboratory group. For laboratory individuals, the presence of abnormal teeth was detected in all generations of laboratory breeding, ranging from 11 to 30% (at the average, 21%). It should be noted that one out of two founder males had abnormal teeth (changed tooth size and shape, not allowing to determine the morphotype, increased spaces between teeth). Parental morphotypes with another frequency are present in all generations of laboratory-bred voles. Four class **A** morphotypes (with two closed triangles) and complex talon were also identified in laboratory animals.

Comparison of simple and complex M3 morphotypes using two methods

The frequencies of **simple** M3 morphotypes in the voles of the "Evoron" chromosome race from the Evoron-Chukchagir Lowland from two different time samples (no. 1 and no. 2) differed according to data on the analysis of two methods (Fig. 6). According to the complex method, **complex** morphotypes predominated in natural sample no. 2 (southern) (Fig. 6b), the frequency of which was higher than in the sample no. 1 (northern) (Fig. 6a). The results obtained by the traditional method confirm data on the predominance of **complex** morphotypes in the sample no. 2; however, the **simple** morphotypes identified by the complex method were not detected when using the traditional method. Thus, the use of complex method allowed us to discover that individuals with **complex** teeth predominated in the Evoron-Chukchagir Lowland in the 1970s; in the 2000s, the frequency of complex teeth morphotypes decreased, but the frequency of **simple** teeth morphotypes increased.

Sample no. 6 (1970s) of the chromosome race from the Argy River valley population mainly includes **intermediate** morphotypes (Figs. 6c and 6d). In the sample no. 5 (2000s) from this population, **complex** and **simple** morphotypes (with a predominance of **complex** ones) were manifested, the frequency of which was determined using a **complex** method (Fig. 6a).

Sample no. 4 of the chromosomal race "Argy" from the population of the Bureya River valley did not differ in the frequency of **complex** M3 morphotypes from the sample no. 5 of the Argy River valley.

Sample no. 3 from the upper reaches of the Amgun River (karyotype unknown) includes **complex** morphotypes (Figs. 6c and 6d). The results obtained by two methods did not differ.

In general for the species (Figs. 6a and 6c), according to data of a complex analysis, the frequency of **complex** teeth decreased insignificantly (from 50 to 45%), of **intermediate** morphotypes decreased (from 45 to 33%), and of **simple** morphotypes increased significantly (from 4 to 23%) in the 2000s as compared with the 1970s. Modern samples (nos. 1, 4, 5) differ significantly ($p = 0.001$) from the samples of the 1970s (nos. 2, 3, 6) in the complexity of the talon structure, in the number of salient angles on the inner side of the tooth (in modern ones, this index is lower).

The traditional analysis detected weak differences for the species (different time samples) in the frequencies of M3 morphotypes of different complexity (Figs. 6b and 6d).

Comparison of morphotypic variability of two chromosomal races

By the complexity of morphotypes estimated by the traditional method, no differences were found

Table 4. General characteristics of chromosomal and morphotypic variability of M3 in samples of the chromosomal races "Evoron" and "Argy" of the Evoron vole

Trait	"Evoron"			"Argy"		
	EV_E_ev no. 2	EV_E_po no. 1		EV_A_urg no. 4	EV_A_argy no. 5	
	W	W	L	W	W	L
n	49	18	76	52	16	129
N_m	5	5	8	7	6	11
N_s	8	6	8	10	6	19
P_{as}	16.67	7.14	0	14.29	0	32.31
2*n*	38–40	40–41	40–41	34, 36, 37	34, 36	34, 36–37
NF	55–57, 59	54–57	56–57	51, 54–56	52, 54–56	54–56

W, natural samples; L, laboratory groups, no., sample numbers correspond to the numbers in Table 2. *n*, number of studied teeth; N_m, number of morphotypes; N_s, frequency of morphotype combinations; P_{as}, asymmetry index; 2*n*, number of chromosomes; *NF*, number of chromosome arms (according to: Kartavtseva et al., 2021).

between two chromosomal races. But in the results obtained using the complex method, the presence of two class **b** morphotypes was demonstrated in the samples of the "Evoron" chromosomal race from the Evoron-Chukchagir Lowland (**1b2** in the natural sample and **0b2** in the laboratory group of a single population (no. 1)). Despite the fact that 67 teeth from natural samples and 134 teeth from laboratory groups of voles of the "Argy" chromosomal race were studied, no class **b** morphotypes were detected. The "Evoron" and "Argy" chromosomal races have significant differences ($p = 0.0078$) in the fusion of the prisms of the first and second triangles (class **b**). The class **b** morphotype, characterized by the prism fusion, was noted only in the sample no. 1. Such differences were noted in both natural and laboratory animals.

Comparison of samples by chromosomal and morphotypic variability of M3

Each sample was characterized by its own values of chromosomal and morphotypic variability (Table 4). Individuals from the samples from natural populations and laboratory group of the "Evoron" chromosomal race had a smaller number of identified morphotypes (N_m) than individuals from the samples from natural populations and laboratory group of the "Argy" chromosomal race. The samples of chromosomal races also differed in the frequency of morphotype combinations. The number of morphotype combinations (N_s) and asymmetry index (P_{as}) were higher in those samples, in which the number of studied teeth was higher; therefore, we did not take into account this index in this comparative analysis. The largest number of morphotypes ($N_m = 7$) and frequency of their combinations ($N_s = 10$) (Table 4) were detected in the sample no. 4 from the Verkhne-Bureinskaya Depression of the "Argy" chromosomal race. The lowest values of these parameters were noted for two samples no. 1 and no. 2 from the Evoron-Chukchagir Lowland of the "Evoron" chromosome race, collected in different years.

The voles of the chromosome races differed in chromosomal characteristics (2*n*, NF) (Table 4). Three structural rearrangements were detected for individuals of the "Evoron" chromosome race: two fusions of chromosomes by telomeres and one fusion with centromeres (Kartavtseva et al., 2021). Six structural rearrangements were detected for individuals of the "Argy" chromosome race: four fusions with telomeres (one of the fusions involved three chromosomes) and two fusions with centromeres (Kartavtseva et al., 2021). Our study demonstrated that the voles from natural samples and laboratory group of the "Evoron" chromosome race have lower morphotypic variability of M3, including the asymmetry index, as compared to the voles from natural samples and laboratory group of the "Argy" chromosome race. Thus, chromosomal races have morphotypic differences (in the number of morphotypes, their combinations, asymmetry index, and frequency of combinations).

Comparison of samples by chromosomal and molecular genetic variability

Previously, data were obtained indicating that the karyotype of individuals from the Evoron-Chukchagir Lowland contains a maximal number of acrocentric chromosomes (26) for the species (Kartavtseva et al., 2021) that were involved in the chromosome fusion. These rearrangements resulted in a decrease in the chromosome number from 42 to 38 in the "Evoron" chromosomal race and to 34 in the "Argy" chromosomal race. Based on this, it was suggested that the voles of the "Evoron" chromosomal race have an ancestral karyotype (Kartavtseva et al., 2021). How-

ever, data from mtDNA control region (Sheremetyeva et al., 2023) allowed us to reveal the most ancient haplotype in the Verkhne-Bureinskaya Depression sample (the "Argy" chromosomal race), rather than in the Evoron-Chukchagir Lowland. These data called into question the previously suggested hypothesis based on karyological data.

DISCUSSION

The studies of the morphotypic variability of voles from the tribe Arvicolini demonstrated the presence of an association between the parameters characterizing this variability and climatic indices (Pozdnyakov and Litvinov, 1994; Pozdnyakov, 2003, 2004; Montuire and Brunet-Lecomte, 2004; Nappi et al., 2006; Markova et al., 2010; Renvoisé et al., 2012; Montuire et al., 2019; Kovaleva et al., 2019, 2021), as well as morphotypic changes over time (Kawamura, 1988; Borodin, 2009). In general, this can indicate an association between the variability of M3 in voles of this tribe and environmental conditions (Bol'shakov et al., 1980), including a set of physical conditions (that can be quantified and that affect morphology indirectly, through the growth rate) and nutritional conditions (that also affect morphology indirectly, through a change in physiological loads) in this complex. From this point of view, the identified peculiarities (by the frequency of the primary morphotypes) of the Evoron vole can indicate different environmental conditions and different nutritional conditions. It is known that a change in nutrition influence the morphotypic variability of rodent molars (Vorontsov, 1967).

Thus, the most complex primary morphotypes of M3 were found in individuals from the upper reaches of the Amgun River and lower reaches of the Argy River. The Evoron vole from the upper reaches of the Amgun River (Kuzikov et al., 1979) lives in the permafrost zone in a small, moist area of the Bureinsky Ridge, surrounded by the larch forest. The lower reaches of the Argy River are also located in the permafrost zone and contains the northernmost habitat of the species. The climatic conditions of the listed habitats cannot be considered favorable for the Evoron vole.

Since a higher frequency of complex morphotypes was identified for the grey voles living in colder conditions (Pozdnyakov, 2003), this explanation can be also valid for the sample of Evoron voles in the upper reaches of the Amgun River.

The voles inhabiting the lower reaches of the Argy River, not fat from where it flows into the Zeya River, for the sample of which a predominance of complex morphotypes due to the class **E** morphotypes was noted, were captured at the edge of the larch forest with a slight predominance of wild roses and minimal amount of cereal plants. At the same time, a year prior to the capture (after severe flooding and uplift of the banks of the Zeya and Argy Rivers), the voles were displaced to a high bank of the Argy River. Here, we captured the voles among the roots of trees and shrubs, while in the Evoron-Chukchagir Lowland, we captured them in moist, mixed-grass meadows.

The study of samples of the Evoron vole collected at different times revealed a change in morphotypes towards simplifying the tooth surface pattern in all three geographically isolated populations. Such variability is possibly associated with the climate change and transition to other feeds. It is known that climate change and transition to other feeds for the isolated population of the Japanese mouse *Apodemus speciosus* (Temminck, 1845) on the Russian island of Kunashir led to the emergence of new molar traits for the species (Kartavtseva et al., 2023). It can be assumed that we are observing a change in trophic specialization patterns (despecialization) in isolated vole populations, which were previously indicated (Markova et al., 2019).

The emergence of a larger number of phenotypes and more complex morphotypes in the laboratory group can be explained by the expression of recessive genes and increased homozygosity of offspring as a result of inbreeding. According to the epigenetic theory of evolution (Vasil'ev, 2005), it is believed that in milder conditions of keeping, there is an increase in the range of variability due to a decrease in the functional load. Previously, phenotypic variability in molars was demonstrated for small invasive isolated populations of *Microtus rossiaemeridionalis* Ognev, 1924, which could be caused by a sharp increase in the frequencies of reserve morphotypes (Markova et al., 2019).

A lower morphotypic variability of M3 in the voles of the "Evoron" chromosomal race is consistent with chromosomal variability (as compared to the "Argy" chromosomal race). Thus, the voles of the "Evoron" chromosomal race have lower chromosomal variability (a smaller number of chromosomes involved in structural rearrangements). However, according to molecular genetic data, the Evoron vole population of the Evoron-Chukchagir Lowland is not more ancient. The voles of the Verkhne-Bureinskaya Depression of the "Argy" chromosomal race are a more ancient population.

The results of the analysis of mitochondrial DNA of the Evoron vole populations from three geographic regions of the Russian Far East (Sheremetyeva et al., 2023) indicated a low level of their genetic differentiation, which confirms their recent isolation. However, differentiation between two populations from the Evoron-Chukchagir Lowland ("Argy") and Bureya Depression in Khabarovsk krai ("Evoron"), geographically located closer to each other (approximately 300 km in a straight line), was larger than differentiation between two more distant populations of the "Argy" race (the Bureya Depression in

Khabarovsk krai and the Upper Zeya Plain in Amur oblast) (approximately 500 km in a straight line). In general, there was a consistency between mitochondrial DNA control region variability and karyotype variability across different chromosomal races. According to the chromosome analysis data, the voles with more ancient karyotype variants persist in the Evoron-Chukchagir Lowland (the "Evoron" chromosomal race), while according to data on molecular genetic analysis, the voles with the most ancient mitochondrial haplotype persist in the Verkhne-Bureinskaya Depression population (the "Argy" chromosomal race). It is possible that the voles of the Verkhne-Bureinskaya Depression (that possess the original karyotype variant) initially migrated to the Evoron-Chukchagir Lowland from the Verkhne-Bureinskaya Depression along the southern spurs of the Bureinsky Ridge. It is possible that the voles of yet unstudied Verkhne-Bureinskaya Depression populations can have the original karyotype or chromosomal rearrangements typical for individuals from the Evoron-Chukchagir Lowland.

CONCLUSIONS

Thus, as a result of studying the masticatory surface of the third upper cheek tooth ($n = 357$) in six natural samples of two chromosomal races ("Evoron" and "Argy") of the Evoron vole using a traditional approach, six M3 morphotypes were detected, while using a complex approach, sixteen morphotypes were identified (ten of which were new). Thus, the complex method allowed us to characterize in more details of a complex "geometric figure" of the masticatory surface of this tooth.

Each sample was characterized by its own set of frequencies of seven primary morphotypes, the number of which varied from two to five. The number of reserve morphotypes in natural samples was lower (from 0 to 5) than in laboratory groups (from 5 to 10). The traditional method revealed no differences between the M3 morphotypes of two chromosomal races ("Evoron" and "Argy"). The use of a complex method allowed us to detect significant differences between the chromosomal races. For individuals of the "Evoron" chromosomal race (as compared with individuals of the "Argy" chromosomal race), M3 morphotypes with fused first two prisms and weaker morphotypic variability were detected. The chromosomal races also differed in the number of M3 morphotypes, their combinations, asymmetry index, and frequency of combinations.

A comparison of M3 complexity coefficients in two groups of samples taken in different years (1970s and 2000s) revealed a chronological trend of an increase in the portion of simple teeth over the 40-year study period. Thus, an increase in the portion of simple morphotypes was observed in all samples taken in the 2000s.

A low morphotypic variability of M3 in voles of the "Evoron" chromosomal race (as compared to the "Argi" chromosomal race) is consistent with chromosomal data. The lowest number of chromosomes involved in structural rearrangements and possessing an ancestral karyotype variant for the species was detected namely for individuals of the "Evoron" chromosomal race. However, mtDNA research data suggest that the original karyotype variant can be also found in the voles of the Verkhne-Bureinskaya Depression. The complex method was convenient for understanding the nature of morphotypic variability of M3 in isolated populations of the Evoron vole. We believe that the applied complex method can be used in further studies of intraspecific variability of the voles of the genus *Alexandromys*.

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ETHICS APPROVAL AND CONSENT TO PARTICIPATE

The study was performed according to the approved national guidelines for the care and use of laboratory animals and was approved by the Animal Care and Use Ethics Committee of the Federal Scientific Center of the East Asia Terrestrial Biodiversity, Far East Branch, Russian Academy of Sciences (approved by protocol no. 3 dated February 21, 2023).

CONFLICT OF INTEREST

The authors of this work declare that they have no conflicts of interest.

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