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Genetic Structure Formation of Reed Vole Populations at the Northern Periphery of Their Distribution (*Alexandromys fortis*, Rodentia, Arvicolinae)

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Abstract—The genetic structure of the reed vole (*Alexandromys fortis* (Buchner 1889)) from the northern periphery of its distribution area was studied using the variability of the mtDNA control region. A high haplotype and nucleotide diversity has been shown in the northern part of the species range. The diversity is due to the presence of two lineages that form phylogenetic subclades within the NORTH lineage on dendrograms. The MAIN haplotypes have a wide geographic distribution. Basically, the distribution of the ISL haplotypes is confined to the islands of the Rimsky-Korsakov Archipelago (Bolshoy Pelis and Matve~~y~~ev) in the Sea of Japan and in the Barguzin Depression in Buryatia. They are also found in mainland populations, albeit with low frequencies, only in the south of the Russian Far East . The ISL haplotypes are noted to be close to those previously identified based on fossil material from cave deposits in the south of Primorsky ~~krai~~. Several alternative hypotheses concerning the ways of the formation of such a phylogeographic structure are considered. Small areas with local favorable environmental features are suggested to have persisted at the northern periphery of the reed vole distribution, where the species could have survived the Pleistocene and retained the ISL haplotypes that might have appeared earlier than the MAIN haplotypes. Those local areas can be considered as microrefugia, which could have played important roles in maintaining the high genetic diversity of the species in the southern part of the Russian Far East. Secondary colonization events by individuals with the MAIN haplotypes could have occurred already after the completion of the climatic minimum and the wide expansion of the species to the north from a southern macrorefugium. The existence of two macrorefugia, in which two subclades, MAIN and ISL, were formed, followed by random fixations of rarer ISL haplotypes in small isolated populations, is also hypothesized.

Keywords: phylogeography, mitochondrial DNA control region, variability, *Alexandromys fortis*, microrefugia

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The reed vole (*Alexandromys fortis* (Büchner 1889)) is a polytypic species distributed over a vast area of the Manchurian–Chinese subregion of the Eastern Palearctic (Gromov and Erbaeva, 1995; Batsaikhan and Tsytsulina, 2016). The area~~l~~ of *A. fortis* is represented by several large isolates (Fig. 1*A*) (Shenbrot, Krasnov, 2005), and on its periphery there are a number of small isolated populations: on the islands of Peter the Great Bay of the Sea of Japan (Chugunov and Katin, 1984; Kostenko, 2000; Sheremet~~i~~ev, 2001), in the northern part of Sakhalin Island (Voronov, 1992; Tiunov et al., 2009), and in the Barguzin ~~d~~epression in Buryatia (Gromov and Erbaeva, 1995). As an inhabitant of the forest and forest-steppe zone (Batsaikhan and Tsytsulina, 2016), this species is mainly confined to humid biotopes located along the banks of rivers, lakes, and swamps, as well as sea coasts, which explains its mosaic distribution. Seven subspecies of the reed vole are known: *A. fortis fortis* (Buchner 1889), described from the Ordos regions of China, distributed in Shanxi Province, Ningxia Hui Autonomous Region in the southern part of Inner Mongolia of China; *A.f. calamorum* (Thomas 1902), described from the environs of Nanjing (Jiangsu Province, China), distributed in the provinces of Anhui, Zhejiang, Jiangxi, Hunan, Hubei, Jiangsu, and around Shanghai; *A.f. michnoi* (Kast-

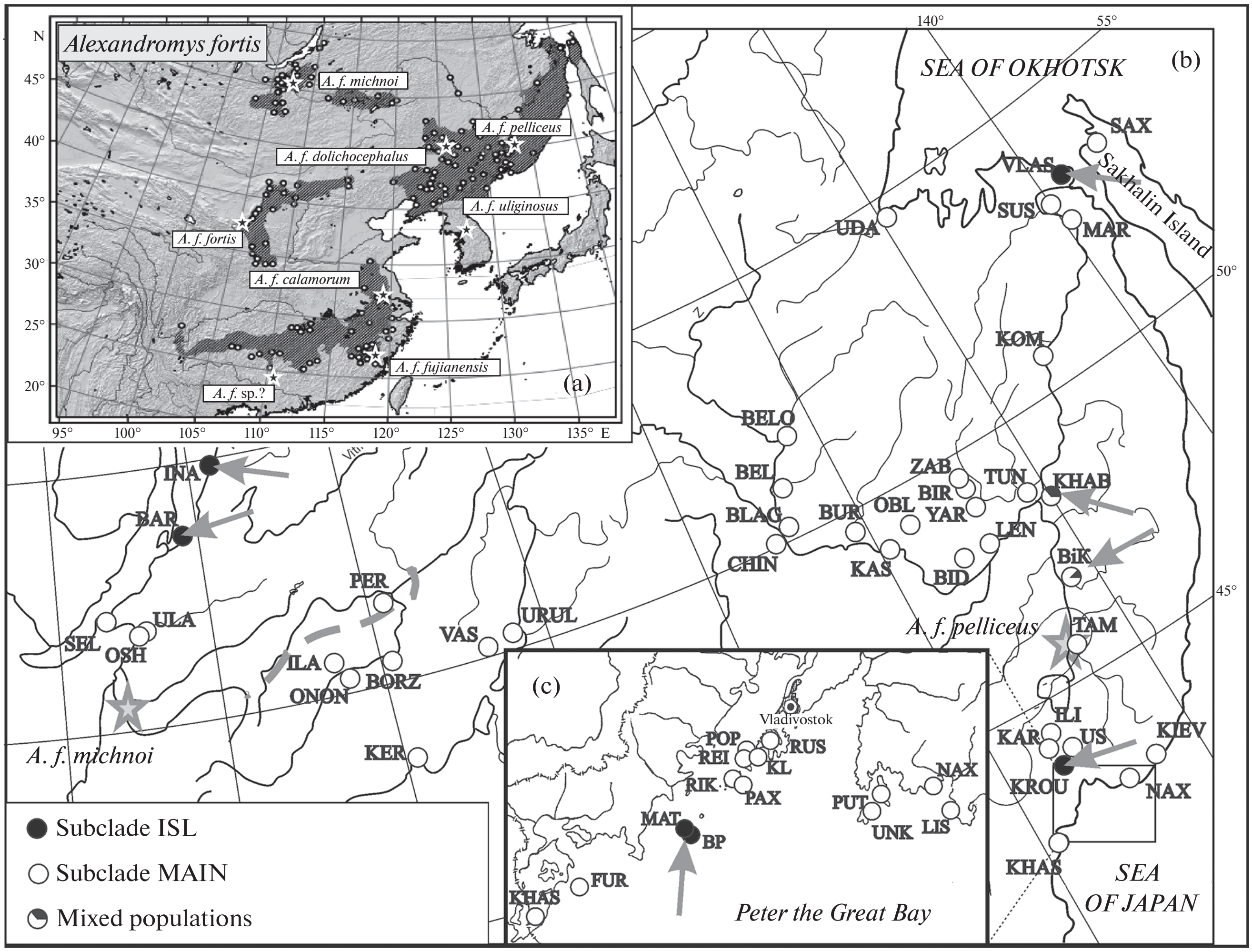


Fig. 1. (a) Area~~l~~ and (b, c) places of material collection of the reed vole. Range of the species reduced by Shenbrot, Krasnov (Shenbrot, Krasnov, 2005). Sample codes correspond to those in Table 1. An asterisk indicates the places of the original description of subspecies. The dotted line indicates the proposed boundary between the subspecies *A.f. michnoi* znd *A.f. pelliceus* in Transbaikalia. The arrow indicates the sites of detection of individuals with mtDNA of the ISL phylogroup.

schenko 1905), described from Southwestern Transbaikalia, near the town of Kyakhta in the Chikoi River basin, inhabiting Western and Eastern Transbaikalia; *A.f. pelliceus* (Thomas 1911), described from the floodplain of the Ussuri River, distributed in the southern part of the Russian Far East (Primorsky Krai, southern Khabarovsk Krai, Jewish Autonomous Oblast, and southern Amur oblast), in the provinces of Heilongjiang and Jilin, and in the northeastern part of Inner Mongolia of China; *A.f. dolichocephalus* (Mori 1930), described from the central part of Northeast China, lives in the provinces of Liaoning, Jilin (Jilin), and Inner Mongolia of China; *A.f. uliginosus* (James et Jonson 1955), described from the central part of the Korean Peninsula; and *A.f. fujianensis* (Hong 1981), described from Fujian, China. It is generally accepted that two morphologically weakly separated subspecies are found on the territory of Russia: *A.f. michnoi* and *A.f. pelliceus* (Gromov, Polyakov, 1977). Opinions differ regarding the boundaries of distribution of these subspecies (Vinogradov, 1933; Fetisov, 1940; Ognev, 1950; Lukashin, 1975).

Due to its wide range, large number, and diversity of isolated populations, the reed vole is of great interest for phylogeographic studies (Chelomina and Sheremetyeva, 2007; Sheremetyeva et al., 2006; Haring et al., 2011; Guskov and Sheremetyeva, 2012; Guo et al., 2012; Gao et al., 2017; Lissovsky et al., 2018), which, however, do not yet fully cover the range of the species. The most extensive work on the phylogeographic structure of *A. fortis* was undertaken by Gao et al. (Gao et al., 2017), who analyzed 86 animals from six provinces of China and identified three groups (NORTH, SOUTH, and GX) with a clear geographical confinement. The relationships between subspecies of the reed vole living in the central part of the range were also studied. At the same time, the phylogenetic relationships of the two subspecies of *A. fortis* living in the northern part of the range (on the territory of Russia) remain unclear. In addition, a number of isolated populations on the periphery of the range still remain unexplored.

The purpose of this work is to study the genetic structure of the reed vole (*A. fortis*) at the periphery of the northern part of the range according to the results of the analysis of the mitochondrial DNA control region variability.

MATERIALS AND METHODS

In this work 142 individuals of *A. fortis* were used, which were caught in 55 local populations (including 13 insular ones) in the north of the range: in the southern part of the Russian Far East, in Zabaykalsky Krai, Buryatia, Mongolia, and China (Table 1, Figs. 1*B,* 1*C*). Samples of our own collections are stored in the collection of mammalian tissues of the Federal Scientific Center *of East Asia Terrestrial* Biodiversity, Far East Branch, Russian Academy of Sciences, Vladivostok.

DNA was isolated by salt extraction (Aljanabi and Martinez, 1997) from alcohol-fixed muscles and liver. A detailed procedure for the preparation of the reaction mixture, the scheme of the PCR reaction, and the preparation of samples for sequencing were described earlier (Sheremetyeva et al., 2015). The nucleotide sequence of the control region was determined on an ABI Prizm 3130 automated sequencer at the Center for Shared Use of the Federal Scientific Center *of East Asia Terrestrial Biodiversity*, Far East Branch, Russian Academy of Sciences, Vladivostok. From all reed voles from our collections, complete nucleotide sequences of the control region were obtained, which were included in Genbank/NCBI under the numbers MZ056579–MZ056719. In addition, the analysis included 38 nucleotide sequences of the control region of reed voles from Russian populations HM135815-HM135852 (Haring et al., 2011), as well as 86 nucleotide sequences of the control region of voles from China Genbank/NCBI KJ207290-KJ207373, FJ597650-FJ597731, and GU474450-GU474511 (Guo et al., 2012; Gao et al., 2017). As an outgroup, we chose the root vole (*A. oeconomus*) ~~no.~~ HM135920 (Haring et al., 2011).

The resulting sequences were edited and aligned using the BioEdit 7.0.9.0 program (Hall, 1999). The sequence length varied from 925 to 958 bp, and after alignment it was 905 bp. Phylogenetic trees were constructed using the Maximum Likelihood method using the MEGA X program (Kumar et al., 2018). We used the Hasegawa–Kishino–Yano model with a G-distribution (BIC=8847.319), the reliability of clustering was assessed using bootstrap analysis (1000 repetitions). Haplotype networks were constructed using the Network 10.0.0.0 program with the "median joining" method (Bandelt et al., 1999). When constructing phylogenetic trees and networks, deletions were not taken into account. Calculation of the indicators of genetic diversity (nucleotide (π) and haplotype (h) diversity, number of variable sites (Vs), average number of pairwise nucleotide differences (k)) and plotting of the p distribution of pairwise nucleotide differences between haplotypes were performed using the DnaSP 6.00 program (Rozas et al., 2017). Calculation of neutrality statistics (Tajima's D and Fu's F) and analysis of the demographic and spatial expansion were carried out using the Arlequin 3.5 program (Excoffier and Lischer, 2010).

RESULTS

In a sample of 142 individuals of *A. fortis* not previously studied, 116 haplotypes were found, of which 111 were identified for the first time. Taking into account the haplotypes described earlier (Haring et al., 2011; Guo et al., 2012; Gao et al., 2017), their total number for the species is 209, and the number of variable sites is 169 (Table 2). In general, the species has a high haplotype (94%) and nucleotide (1.63%) diversity.

ML phylogenetic reconstruction demonstrated separation of all haplotypes of *A. fortis* into three isolated clades with high bootstrap supports (Fig. 2). These clades correspond to the NORTH, SOUTH, and GX phylogenetic lineages identified earlier in China (Gao et al., 2017). All haplotypes of ~~Far Eastern~~ reed voles from the territory of Russia identified in the course of this work belonged to the NORTH lineage.

Three subclades can be distinguished within the SOUTH lineage: HN, FJ-1, and FJ-2 (Figs. 2, 3). The haplotypes of these groups, as well as the GX lines, have a clear geographical localization. At the same time, haplotypes belonging to the highly differentiated FJ-1 and FJ-2 subclades were found in individuals from one local population in Fujian Province, China (Gao et al., 2017). The indicators of the haplotype and nucleotide diversity in the subclades of the SOUTH line and within the GX line do not exceed 0.723 and 0.0053, respectively, which is significantly lower than for the species as a whole (Table 2).

Within the NORTH lineage, both on the phylogenetic tree and on the median network, two subclades can be distinguished: MAIN and ISL (Fig. 3). At the same time, the indices of haplotype diversity in the MAIN and ISL subclades remain high (0.972 and 0.957, respectively), while the values of nucleotide diversity are lower (0.0082 and 0.0065, respectively) than for the species as a whole (Table 2). The distribution of haplotypes in the MAIN and ISL subclades does not have a clear geographical localization. In the northern part of the species range, individuals with haplotypes of the MAIN subclade predominantly live. The proportion of voles with haplotypes of the ISL subclade is only 11% of all individuals of the NORTH line.

Table 1. Material for the study of the mtDNA control region of *Alexandromys fortis*

Code samples	Sample (number of samples)	Coordinates	Number of haplotypes	Phylogroup
	A. f. pelliceus (Thomas 1911)			
Island populations				
	Islands of Peter the Great Bay (Sea of Japan)			
PUT*#	Putyatin Island (*n* = 3)	42.83° N, 132.42° E	3	MAIN
LIS*#	Lisy Island (*n* = 4)	42.76° N, 132.91° E	4	MAIN
RUS#	Russky island (*n* = 1)	43.00° N, 131.85° E	1	MAIN
POP*#	Popov Island (*n* = 2)	42.95° N, 131.72° E	2	MAIN
KING*#	Reyneke Island (*n* = 2)	42.90° N, 131.72° E	1	MAIN
KL*#	Klykov Island (*n* = 3)	42.94°N, 131.77°E	3	MAIN
RIK*#	Rikord Island (*n* = 5)	42.87° N, 131.65° E	5	MAIN
FUR#	Furugelm Island (*n* = 2)	42.47° N, 130.92° E	2	MAIN
MAT*#	Matveev Island (*n* = 8)	42.67° N, 131.43° E	7	ISL
BP#	Bolshoy Pelis Island (*n* = 5)	42.66° N, 131.46° E	4	ISL
PAX#	Pakhtusova Island (*n* = 4)	42.90° N, 131.65° E	3	MAIN
UNK#	Unkovsky Rocks (*n* = 1)	42.82° N, 132.37° E	1	MAIN
	Sakhalin Island			
SAX	Zaliv Pomr’ (*n* = 3)	53.69° N, 142.59° E	3	MAIN
Mainland populations				
	~~Primorskii~~ krai			
KHAS*#	Khasansky district, vicinity of the village of Khasan (*n* = 9)	42.43° N, 130.65° E	9	MAIN
NAX*#	Vicinity of Nakhodka (*n* = 4)	42.88° N, 132.74° E	2	MAIN
US*#	Vicinity of Ussuriysk (*n* = 1)	43.63° N, 132.22° E	1	MAIN
KROU*	Vicinity of the village of Krounovka (*n* = 1)	43.70° N, 131.60° E	1	ISL
KAR*	Karantinnaya honeydew (*n* = 1)	40.68° N, 131.47° E	1	MAIN
ILI*	Vicinity of the village of Ilyichevka (*n*=1)	44.20° N, 131.92° E	1	MAIN
TAM	Lesozavodsky district, vicinity of the village of Tamga (*n* = 4)	45.57° N, 133.61° E	4	MAIN
KIEV	Lazovsky district, vicinity of the village of Kievka (*n* = 4)	42.84° N, 133.69° E	3	MAIN
	Khabarovsk ~~region~~			
KHAB	Vicinity of Khabarovsk, village of Galkino (*n* = 14)	42.78° N, 134.28° E	13	MAIN (8), ISL (5)
BIK	Vicinity of Bikin (*n* = 8)	46.83° N, 134.25° E	8	MAIN (7), ISL (1)
KOM *	Vicinity of Komsomolsk-on-Amur (*n* = 3)	50.50° N, 136.99° E	3	MAIN
SUS*	Vicinity of the village of Susanino (*n* = 2)	52.73° N, 140.11° E	2	MAIN
VLAS*	Vicinity of the village of Vlasievo (*n* = 1)	53.42° N, 140.91° E	1	ISL
UDA*	Uda River (*n* = 2)	54.70° N, 135.26° E	2	MAIN
MAR*	Vicinity of the village of Mariinsky (*n* = 1)	51.71° N, 140.21° E	1	MAIN
ZAB	Zabelovsky Cluster of the Bastak Reserve (*n* = 2)	48.94° N, 133.12° E	2	MAIN
	Jewish Autonomous Oblast			
TUN	Vicinity of the village of Danilovka, Tunguska River (*n* = 2)	48.59° N, 134.60° E	2	MAIN
BIE	Vicinity of Birobidzhan (*n* = 1)	48.73° N, 133.04° E	1	MAIN
BID	Vicinity of the village of Bidzhan (*n* = 8)	47.99° N, 131.96° E	7	MAIN
LEN	Vicinity of the village of Leninskoe (*n* = 2)	47.93° N, 132.60° E	2	MAIN
SMALL*	Bira River, Zheltyi Yar (*n* = 2)	48.57° N, 133.05° E	1	MAIN
OBL	Vicinity of the city of Obluchye (*n* = 5)	48.93° N, 130.70° E	5	MAIN

Code samples	Sample (number of samples)	Coordinates	Number of haplotypes	Phylogroup
	Amur ~~o~~blast			
BUR	The floodplain of the lower reaches of the Bureya River (*n* = 9)	49.71° N, 129.69° E	9	MAIN
BLAG*	Vicinity of Blagoveshchensk (*n* = 4)	50.31° N, 127.48° E	4	MAIN
KAS*	Vicinity of the village of Kasatkino (*n* = 1)	48.97° N, 130.07° E	1	MAIN
BEL	Vicinity of the city of Belogorsk (*n* = 1)	50.89° N, 128.65° E	1	MAIN
BELO	Vicinity of the village of Beloyarovo (*n* = 1)	51.60° N, 128.77° E	1	MAIN
	Northern China			
CHIN	Vicinity of the ~~village~~ of Heihe (*n* = 4)	50.25° N, 127.54° E	4	MAIN
HLJ**	Vicinity of Jiamusi, Province of Heilongjiang (*n* = 3)	47.50° N, 133.50° E	3	MAIN
FU**	Vicinity of Fuyuan Township, Province of Heilongjiang (*n* = 2)	48.35° N, 134.28° E	2	MAIN
	A. f. michnoi (Kastschenko 1905)			
	Buryatia			
ULA	Vicinity of Ulan-Ude (*n* = 9)	51.82° N, 107.41° E	9	MAIN
OSH*	Vicinity Ulan-Ude, village of Oshurkovo (*n* = 13)	51.95° N, 107.48° E	12	MAIN
SEL	Delta of the Selenga River, vicinity of the village of Stepnoi Dvorets (*n* = 1)	52.15° N, 106.34° E	1	MAIN
BAR	Vicinity of the village of Barguzin (*n* = 1)	53.60° N, 109.70° E	1	ISL
INA	Barguzin Depression, vicinity of the village of Ina-Soel (*n* = 1)	53.76° N, 110.23° E	1	ISL
	Zabaykalsky Krai			
ONON	Onon River, east of the mouth of the Ilya River, Narin-Kundui (*n* = 3)	50.43° N, 113.79° E	3	MAIN
BORZ	Ononsky district, vicinity of the village of Ust Borzya, Borzya River (*n* = 4)	50.62° N, 115.66° E	4	MAIN
URUL	Priargunsky district, Urulyungui River (*n* = 1)	50.32° N, 118.99° E	1	MAIN
VAS	Borzinsky district, village of Vasilyevsky khutor (*n* = 2)	50.59° N, 117.80° E	1	MAIN
ILA	Ilya (*n* = 2)	50.81° N, 113.58° E	2	MAIN
PER	Vicinity of the village of Pervomaisky (*n* = 1)	51.65° N, 115.80° E	1	MAIN
	Dornod Province, Mongolia			
KER	50 km northeast of Choibalsan, the lower course of the Kerulen River (*n* = 1)	48.36° N, 115.35° E	1	MAIN
	A. f. fortis (Buchner 1889)			
NX**	Ningxia Hui Autonomous Region, China (*n* = 20)	38.20° N, 106.20° E	3	MAIN
NIN**	" (*n* = 1)	36.60° N, 105.32° E	1	MAIN
	A. f. dolichocephalus (Mori 1930)			
JL**	Jilin Province, China (*n* = 1)	43.50° N, 125.60° E	1	MAIN
	A. f. calamorum (Thomas 1902)			
DON**	Dongting Lake, Hunan Province, China (*n* = 164)	29.32° N, 112.95° E	30	HN
HN**	" (*n* = 19)	29.10° N 112.50° E	3	HN
	A. f. fujianensis (Hong 1981)			
FJ**	Provnice of Fujian, China (*n* = 20)	27.10° N, 117.20° E	5	FJ–1(2), FJ–2(3)
	A. f. subspecies			
GX**	Guangxi Zhuang Autonomous Region, China (*n* = 20)	25.20° N, 110.10° E	10	GX

* Sample material partially used by Haring et al. (2011), ** Data from Gao et al. (2017), # Material used in the work of Sheremetyeva (2020).

Table 2. Indicators of the genetic diversity of phylogroups of *Alexandromys fortis*

Index	GX	SOUTH			NORTH		All
		FJ–1	FJ–2	HN	MAIN	ISL	
n	20	5	15	163	184	23	410
N	11	2	3	33	139	21	209
Vs	16	2	2	30	120	29	169
$h \pm$ SD	0.726 ± 0.092	0.535 ± 0.016	0.514 ± 0.014	0.693 ± 0.026	0.972 ± 0.009	0.957 ± 0.034	0.9428 ± 0.0068
$k \pm$ SE	4.74 ± 2.42	0.80 ± 0.68	0.68 ± 0.07	2.81 ± 1.49	7.48 ± 3.51	5.85 ± 2.90	14.436
$\pi \pm$ SD	0.0053 ± 0.0003	0.0008 ± 0.0001	0.0007 ± 0.0006	0.0031 ± 0.0018	0.0082 ± 0.0004	0.0065 ± 0.0003	0.0163 ± 0.0003
Tajima's D (P)	0.65(>0.10)	–0.001(>0.10)	–0.02(>0.10)	–1.61(<0.05)	–2.32(0.000)	–1.99(<0.05)	–1.45(>0.10)
Fu's F(P)	–20.03(0.000)	–5.41(0.000)	–6.40(0.000)	–26.48(0.000)	–24.59(0.000)	–12.95(0.000)	–34.36(0.000)

n – sample size. N – number of haplotypes. Vs – number of variable sites. k – average number of pairwise nucleotide differences. h – haplotype diversity. π - nucleotide diversity. Tajima's D – Tajima's test coefficient. Fu's F – Fu's test coefficient; SD – standard deviation. S.E. – standard error. P – p-value.

Table 3. Indicators of demographic expansion of phylogroups of *Alexandromys fortis*

Index	GX	SOUTH			NORTH	
		FJ–1	FJ–2	HN	MAIN	ISL
τ	6.6	0.0	0.7	2.1	6.2	4.7
θ_0	0.00	0.00	0.00	0.54	2.05	1.42
θ_1	13.32	99999	99999	25.63	50.70	92.34
SSD(P)	0.012(0.57)	0.32(0.000)	0.006(0.57)	0.002 (0.38)	0.005(0.87)	0.009(0.27)

τ - expansion time in mutational units. θ – mutational parameters at the initial (θ_0) and final (θ_1) stages of population growth. SSD – sum of squared deviations between the observed and expected distribution of pairwise nucleotide differences. P – p-value.

The value of Tajima's D for all subclades except the lineage GX was negative, but it was significant only for the lineage groups NORTH. The results of Fu's F test for selective neutrality for all subclades were not only negative, but also highly significantly different from zero, which testifies in favor of the hypothesis of an increase in the abundance in the past (Table 2).

Distribution of the pairwise nucleotide differences between haplotypes of voles for groups HN, MAIN, and ISL had a unimodal form, while only for the group HN does the peak fall at the beginning of the scale (Fig. 4). The distribution of pairwise nucleotide differences between haplotypes of individuals in a population from Fujian Province is characterized by a bimodal distribution, which is a consequence of the mixing of subclade haplotypes FJ-1 and FJ-2. The presence of a peak in the region of minimal differences in subclades HN, FJ-1, and FJ-2 involves sudden population growth with the founder effect.

Small values of the conditional expansion time τ, as well as low and statistically unreliable values of the sum of deviations SSD, testify in favor of the hypothesis of population growth for the populations of all the studied subclades except for FJ-1 (Table 3).

Distribution of haplotypes of phylogenetic subclades in the continental southern part of the Russian Far East. To determine the phylogenetic relationships of haplotypes of *A. fortis,* a median network was built in the southern part of the Russian Far East (Fig. 5). The haplotype variants found in the individuals studied belong to two subclades: MAIN and ISL. At the same time, the proportion of individuals with haplotypes of the MAIN subclade is significantly higher in comparison with ISL (91.2 and 8.8%, respectively). ISL haplotypes forming a separate group were found in samples from the vicinity of the cities of Khabarovsk (KHAB) and Bikin (BIK), as well as in a sample from the lower Amur region (near the village of ~~Vlas'evo~~, VLAS) and western Primorye (near the village of Krounovka, KROU) (Table 1). The haplotypes of the MAIN subclade are grouped into networks in a structure close to stellate; most of them were unique (i.e., found in only one individual), but three haplotypes (H1, H2, and H3) were found in three or more individuals from different samples that are separated from each other. Haplotype H1 on the network has a central position. In general, the haplotypes of this subclade did not form groups according to their geographic location.

Distribution of haplotypes of phylogenetic subclades on islands of the Far East. The median network (Fig. 6) constructed for haplotypes of reed voles from island populations also revealed their belonging to two subclades: MAIN and ISL. The ISL subclade includes

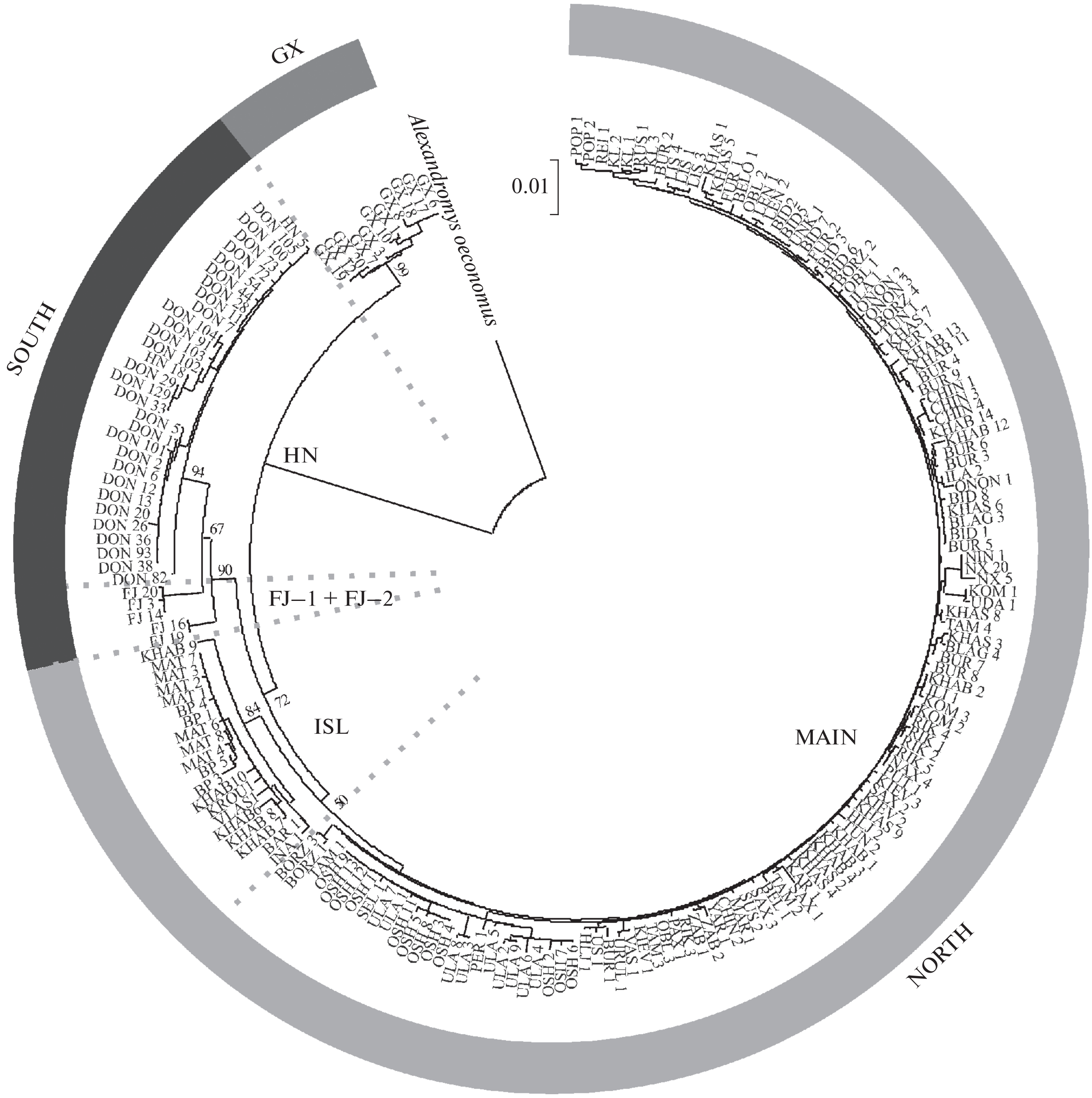


Fig. 2. Dendrogram of phylogenetic relationships of the mtDNA control region of the reed vole. GX, SOUTH, and NORTH are phylogenetic lineages (according to Gao et al., 2017). HN, FJ–1, and FJ–2 are groups within the SOUTH lineage; MAIN and ISL are groups within the NORTH lineage.

haplotypes of voles from the Matveev (MAT) and Bolshoy Pelis (BP) Islands of Rimsky-Korsakov Archipelago of the Sea of Japan, and the MAIN group includes haplotypes of voles from all other islands of Peter the Great Bay of the Sea of Japan and Sakhalin Island.

Island vole haplotypes belonging to the MAIN subclade form four groups on the network. The first group included individuals from the Rikord (RIK), Pakhtusova (PAX), and Putyatin (PUT) islands. The same group includes two haplotypes (H1 and H2) that are often found in voles in the mainland populations of the Far East, while the H1 haplotype was preserved in the population of Putyatin Island, and the H2 haplotype, on Pakhtusova Island. It should be noted that the voles of Rikord and Pakhtusova islands have one common haplotype. This is probably due to the fact that the ancestral vole population of these islands was the same. The second group included haplotypes of individuals from Sakhalin Island, while two of them differ

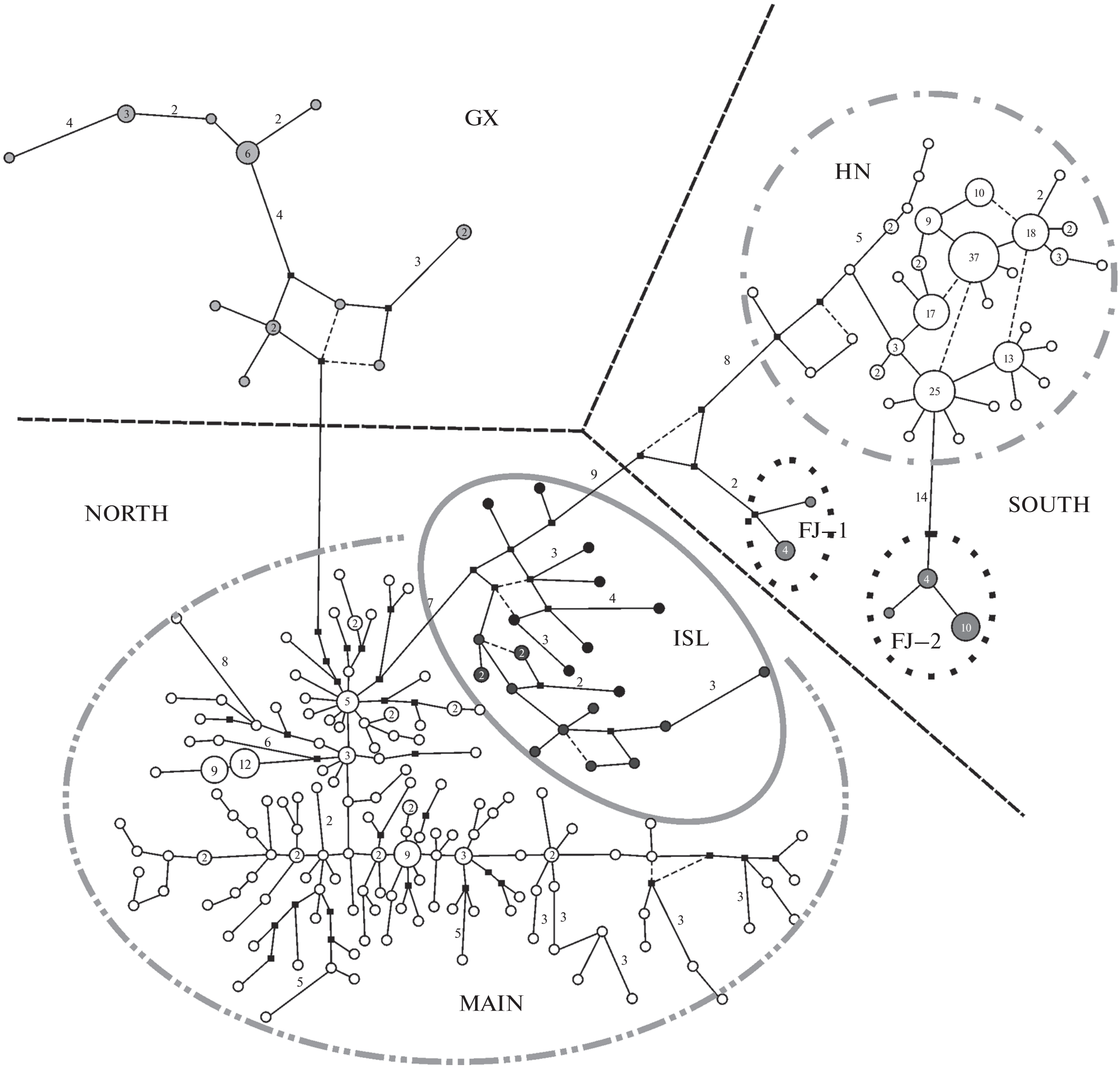


Fig. 3. Phylogenetic network of haplotypes of the mtDNA control region of the reed vole. GX, SOUTH, and NORTH are phylogenetic lineages (according to Gao et al., 2017). HN, FJ–1, and FJ–2 are groups within the SOUTH line; MAIN and ISL are groups within the NORTH line.

from the common haplotype of Rikord and Pakhtusov islands by only two substitutions, while the differences between Sakhalin haplotypes are quite large (up to six nucleotide substitutions). The third group is formed by haplotypes of voles from the islands of Lisy (LIS), Unkovsky Rocks (UNK), and Furugelm Island (FUR), which is far from them. Individuals of the Lisy Islands and the Unkovsky Rocks have a common haplotype. The fourth group consists of haplotypes of individuals from four nearby islands of the Empress Eugenia archipelago: Russky (RUS), Popov (POP), Reynecke (REI), and Klykov (KL).

Distribution of haplotypes of phylogenetic subclades in Transbaikalia. Most of the haplotypes of the studied animals from Transbaikalia (Buryatia, Zabaykalsky Krai) also belong to the MAIN subclade (Fig. 7). On the phylogenetic network, they formed two groups in accordance with their geographical affiliation: Eastern and Western Transbaikalia. Only one individual from Eastern Transbaikalia (near the village of Pervomaisky, PER) had a haplotype close to individuals from Western Transbaikalia. Haplotypes of the ISL subclade were found only in both individuals caught in Buryatia, in the Barguzin Depression (vicinity the village of Barguzin, BAR, and in the vicinity of the village of Ina-Soel, INA). Unfortunately, these samples were too small, and it is impossible to state that there are no voles with the haplotype of the MAIN subclade.

DISCUSSION

The results of our analysis of the variability of the nucleotide sequences of the control region of *A. fortis* confirmed the presence of the three phylogenetic lineages (NORTH, SOUTH, and GX) identified earlier (Gao et al., 2017). At the same time, as noted in this work, the GX phylogenetic lineage is the most ancient. The NORTH phylogenetic lineage is evolutionarily the youngest and most common; it is revealed over most of the range.

In this work, we have shown for the first time that the NORTH lineage is divided into two sister phylogenetic subclades, which we designate as MAIN and ISL. The haplotypes of the first of them have a wide geographical distribution, while the haplotypes of the second are confined to the islands of the Rimsky-Korsakov Archipelago of the Sea of Japan (Bolshoy Pelis and Matveev) and the Barguzin Depression in Buryatia, and are also found with low frequency in mainland populations in the southern part of the Russian Far East, most of all in the lower Amur basin. It should be noted that the haplotypes of the ISL subclade were not found in China, but this may be due to the small number of samples and individuals studied. The populations of the Bolshoy Pelis and Matveev Islands, as well as, possibly, the Barguzin Depression, currently do not have contact the populations of the main part of the range, retaining one (ISL) mtDNA type.

The literature, including that devoted to the mammals of Northeast Asia (Matsuhashi et al., 2001; Abramson et al., 2012; Ye et al., 2015), contains examples of similar genogeographic patterns, when rare phylogenetic lines (both along with the main line and fixed), are not found in the main part of the range. Traditionally, such a phylogeographic picture is explained by fluctuations in the boundaries of species ranges in the Pleistocene due to climate change. The colonization of certain areas of the ranges occurs with lines that have formed in different refugia. As is known, sharp climate fluctuations in the Pleistocene, especially during the last glacial maximum (21000–18000 years ago), strongly influenced the geographic distribution and genetic diversity of many species of the temperate zone in the Northern Hemisphere (Hewitt, 2000). Despite the absence of a major Quaternary glaciation in East Asia, climatic fluctuations in this area were very significant. Thus, it is known that the climate of the northern part of subtropical China (between 32° and 45° N) was at least 7–10°C colder and drier than the current climate (Xiangjun and Yinshuo, 1991). As a result of climate change, the ranges of many species of the temperate zone have been reduced from their northern part to macrorefugia in the south, where the regional climate was acceptable for existence. After the last glacial maximum, many species repopulated the northern territories they previously occupied, and in some cases the expansion

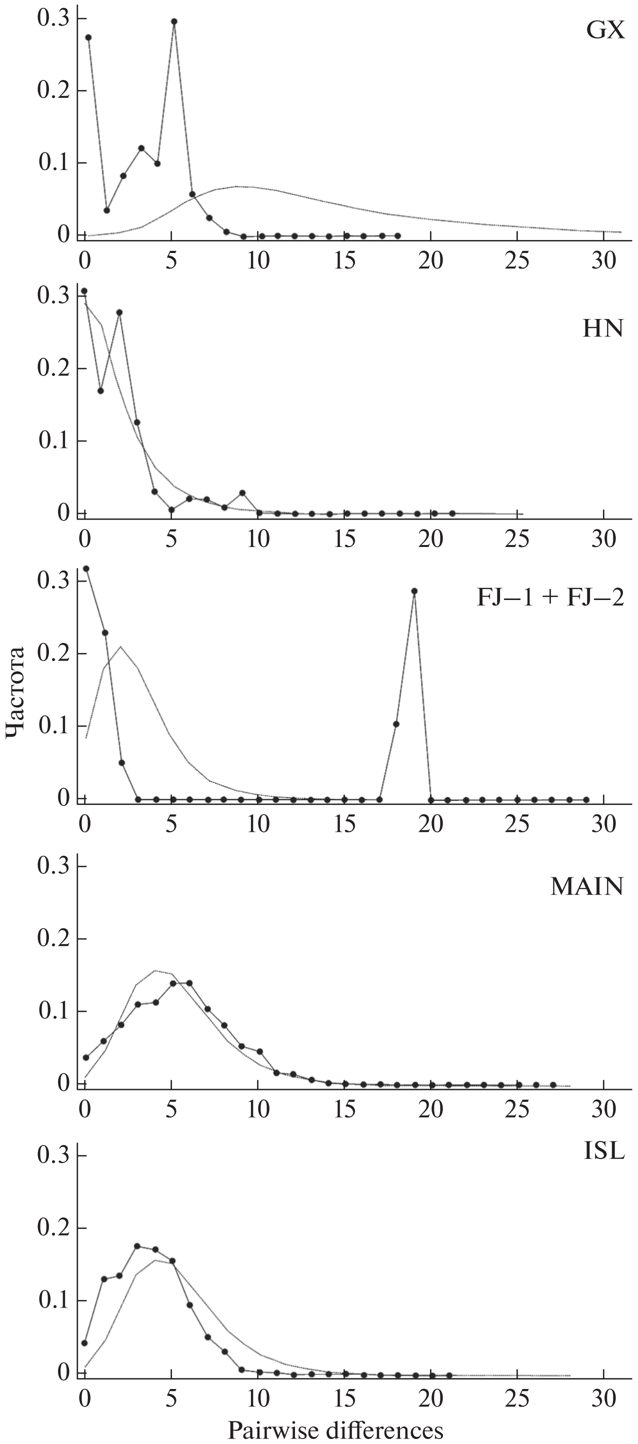
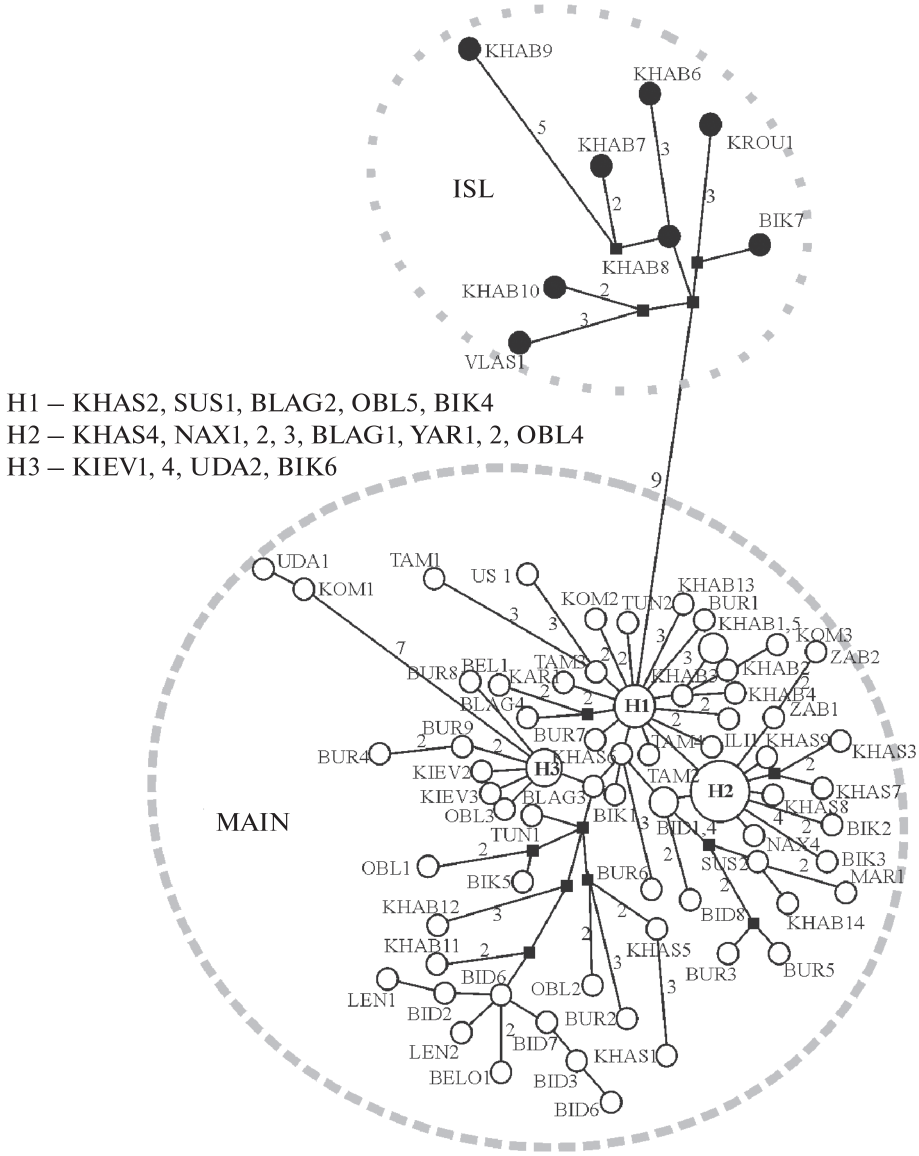


Fig. 4. Frequency (ordinate) of pairwise nucleotide differences (abscissa) in phylogenetic groups of the reed vole using a population growth-decline model. The observed frequency is indicated by a solid line, and the expected distribution is indicated by a dotted line.



H1 – KHAS2, SUS1, BLAG2, OBL5, BIK4
H2 – KHAS4, NAX1, 2, 3, BLAG1, YAR1, 2, OBL4
H3 – KIEV1, 4, UDA2, BIK6

Fig. 5. Phylogenetic network of mtDNA haplotypes of *Alexandromys fortis* in the Far Eastern part of the range (mainland). The sizes of the circles are proportional to the number of samples with a given haplotype. Haplotypes are designated according to sample codes in Table 1. The numbers on the branches of the network correspond to the number of nucleotide substitutions exceeding 2.

occurred much faster than the models predicted (Clark et al., 2003; Magri, 2008). It is known that many modern representatives of East Asian fauna spread from glacial refugia located in Northeast China and the Korean Peninsula (Xie and Zhang, 2005; Zhang et al., 2008; Sakka et al., 2010; Aizawa et al., 2012; Kim et al., 2018; Lee, et al., 2018; Choi et al., 2020).

The earliest find of *A. fortis* (600–700 ka BP) is known from the Early Pleistocene deposits of the Choukoutien Cave in Central China (Zheng and Li, 1990), so this species has undoubtedly undergone repeated significant changes in its distribution and abundance, following global climatic fluctuations during the Pleistocene. It is interesting that *A. fortis* is noted in Late Pleistocene deposits on Miyako Island (Japan), although it does not occur in the recent fauna of the island (Kaneko and Hasegawa, 1995). Kawamura (2014) suggested that *A. fortis* migrated from the continent to Miyako Island in the Middle Pleistocene. During this period, the range of the reed vole was much wider than the resent one, and 30000–24000 years ago, it was a common, widespread species in the southern part of the Far East (Alekseeva and Golenishchev, 1986; Panasenko and Tiunov, 2010) and was found in Southwestern Transbaikalia (Tologoi, upper sequence) (Alekseeva, 2005). Starting from 24000–21000 years ago, the abundance of the species sharply decreased until the beginning of the

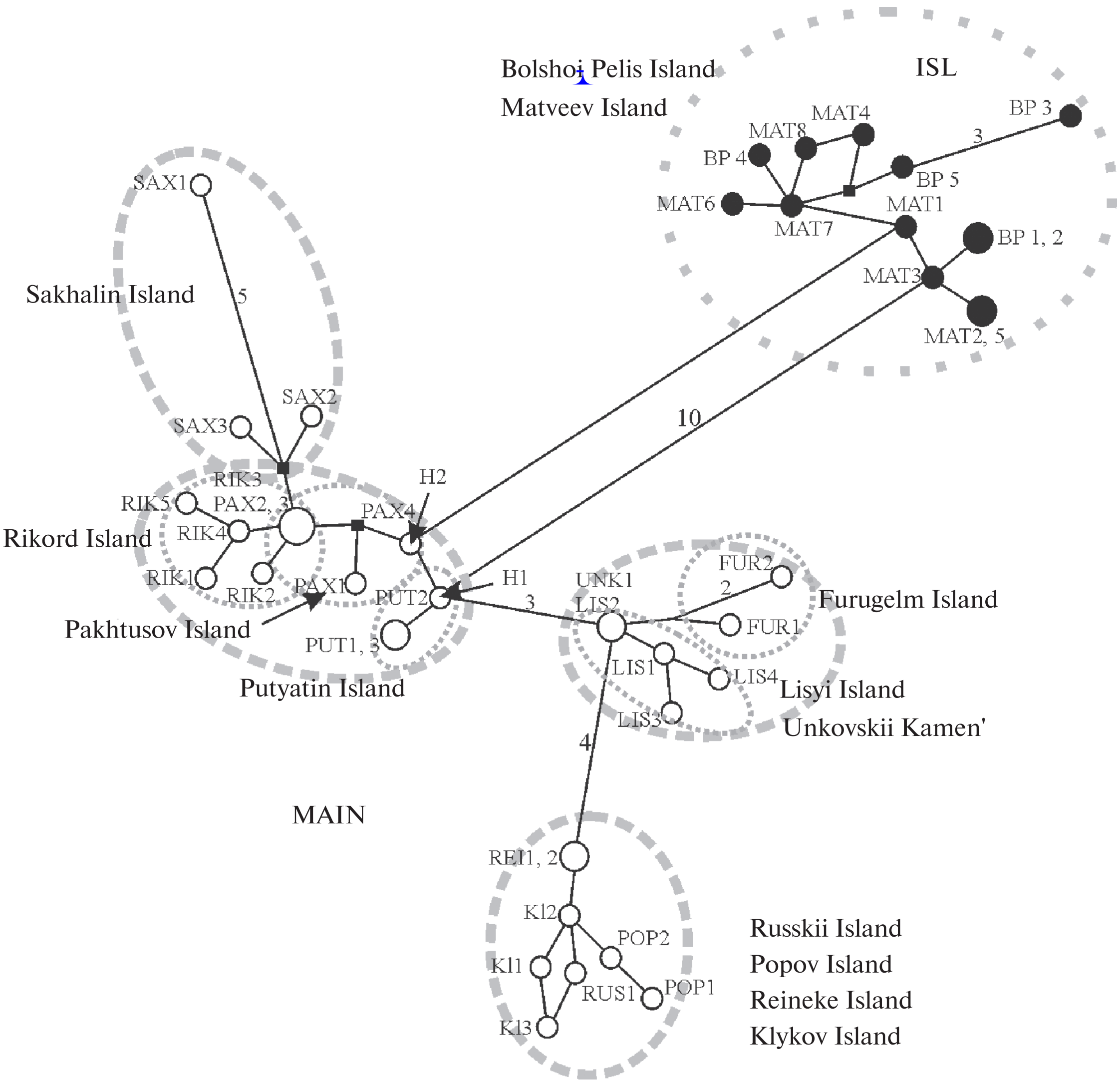


Fig. 6. Phylogenetic network of mtDNA haplotypes of *Alexandromys fortis* from the islands of Peter the Great Bay and Sakhalin. The sizes of the circles are proportional to the number of samples with a given haplotype. Haplotypes are designated according to sample codes in Table 1. The numbers on the branches of the network correspond to the number of nucleotide substitutions exceeding 2.

Holocene (10 ka BP) due to cooling (Panasenko and Tiunov, 2010); instead of the reed vole, Maximowicz's vole and lemmings begin to predominate in the excavations. During this period, the last climatic minimum was noted; Most of the reed vole populations probably shifted much further south, where they remained in refugia along with other species (Aizawa et al., 2012; Kim et al., 2018; Sakka et al., 2010; Zhang et al., 2008). In most of Transbaikalia, populations of *A. fortis* were destroyed by a huge ice-dammed lake (Vitim Sea), which existed during the Sartan glaciation, 28000–12500 years ago (Yenikeev, Staryshko, 2009). After 10000 years ago, a sharp rise in numbers began (Panasenko and Tiunov, 2010) with restoration of the range of the reed vole. After the degradation of the Vitim Sea, the territory of Transbaikalia, which was freed from it, was possibly recolonized by reed voles from the southern regions in two ways: the first path passed along the Selenga River basin, and the second along the Amur River and its tributaries. So the populations of *A. fortis* from Eastern and Western Transbaikalia could have formed independently of each other. This hypothesis is confirmed by morphological data, according to which the voles living in Eastern and Western Transbaikalia belong to different subspecies (Fetisov, 1940): in Western Transbaikalia only the Mikhno vole (*A.f. michnoi*), and in Eastern Transbaikalia there is a form close to the Far Eastern subspecies (*A.f. pelliceus*). In addition, the differences between *A. fortis* Eastern and Western Transbaikalia are also indicated by data on the variability of heterochromatic blocks in chromosomes (Kovalskaya et al., 1991).

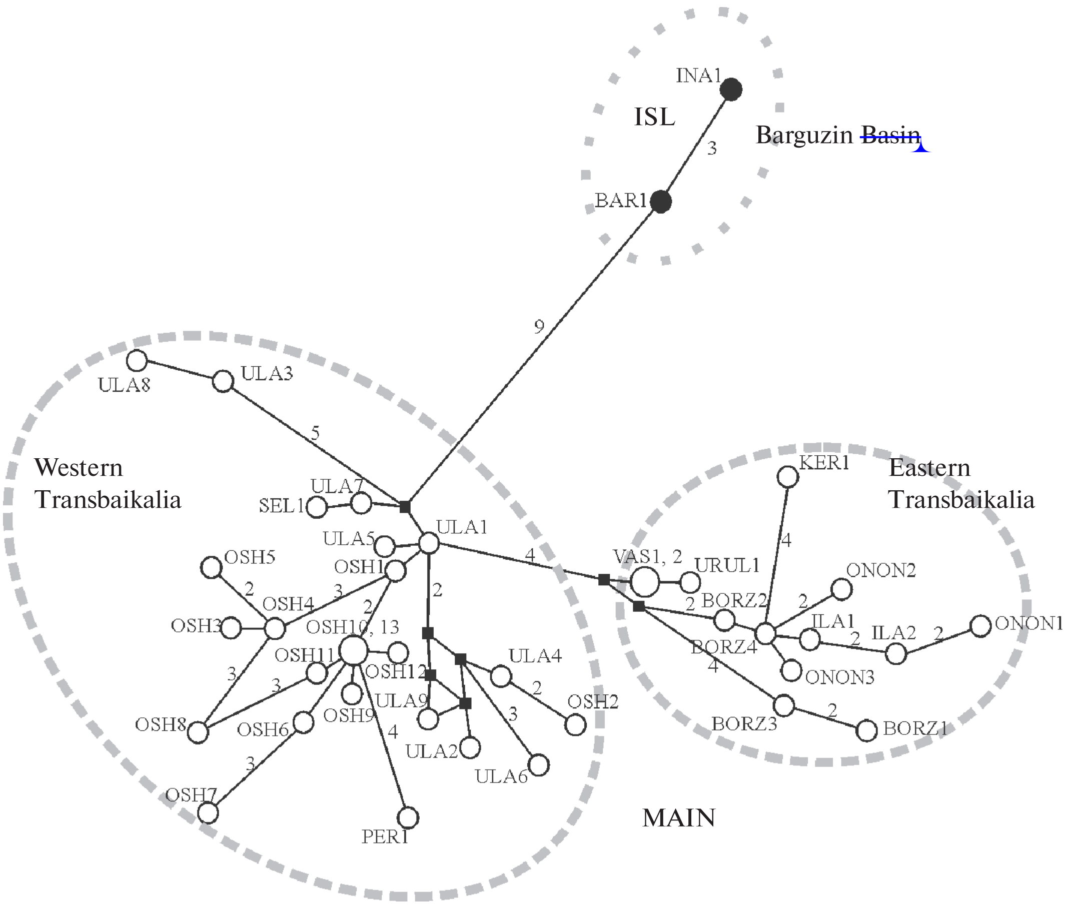


Fig. 7. Phylogenetic network of mtDNA haplotypes of *Alexandromys fortis* in the Transbaikalian part of the range. The sizes of the circles are proportional to the number of samples with a given haplotype. Haplotypes are designated according to sample codes in Table 1. The numbers on the branches of the network correspond to the number of nucleotide substitutions exceeding 2.

Our data on the variability of the control region in the reed vole confirmed the previously published results indicating the existence of a large macrorefugium in Northeast China (Gao et al., 2017). The existence of two subclades MAIN and ISL in the NORTH phylogenetic lineage and the uneven distribution of the corresponding lines can be considered in the light of several hypotheses: on the one hand, as evidence of an older (ancestral) polymorphism, which (taking into account the small genetic distance between the ISL and MAIN subclades) allows a nonrefugial origin of their haplotypes due to the accidental loss of intermediate variants. On the other hand, it can be assumed that the marginal areas of the range were populated from two refugia, in which haplotypes of the MAIN and ISL subclades were formed independently, and the uneven distribution of them can be explained by genetic-automatic processes. For example, a decrease in the occurrence of haplotypes of the ISL subclade over most of the range over time and their random fixation in small isolated populations.

In the case of the reed vole, we have the opportunity to detail the history of the formation of the genetic structure of the species, using for comparison data from the analysis of ancient DNA from fossil samples. Previously, we compared ancient mtDNA, which was isolated from paleomaterial taken from layers of different ages in the Medvezhyi Klyk Cave (Haring et al., 2015), and mtDNA from reed voles from modern populations of the islands of Peter the Great Bay, Sea of Japan (Sheremetyeva, 2020). As a result, it was shown that all ancient haplotypes, as well as modern ones, are divided into two subclades, MAIN and ISL, with fixed differences at four sites (the length of the analyzed fragment for ancient haplotypes is 344 bp). At the same time, it was noted that all ancient haplotypes of the ISL subclade, similar to the haplotypes of modern voles of the Rimsky-Korsakov ~~a~~rchipelago, were identified in older remains (>40000 and >30000 years ago). It is possible that voles inhabiting the territory of the southern part of Primorsky ~~krai~~ in the period of 30000–24000 years ago had mainly haplotypes of the ISL subclade (Sheremetyeva, 2020), but were subsequently "displaced" by haplotypes of the MAIN subclade. As suggested above, this could have happened as a result of random genetic-automatic processes. But it seems possible for us to consider phylogenetic patterns in *A. fortis* also from the standpoint of the microrefugia or “mysterious refugia” hypothesis (Rull, 2009). The existence of multiple microrefugia has been suggested by several authors in different animal species in continental East Asia (Bao et al., 2015; Zeng et al., 2015; Ye et al., 2019). An important characteristic of a microrefugium is a stable microclimate that differs enough from the climatic conditions of the surrounding region to facilitate the conservation of the species (Hampe and Jump, 2011). This hypothesis suggests their small size as they are localized and surrounded by inappropriate habitats. Microrefugia can be found in enclosed areas, such as in deeply indented river and lake valleys. These valleys provide a microclimate conducive to the survival of species (Stewart and Lister, 2001). Additionally, microrefugia can be located on the coast, where the climate is more humid and with less seasonal variability (Stewart et al., 2010). At the same time, according to the results of studies, microrefugia are quite difficult to identify even by genetic data. It should also be noted that not all species are able to survive in microrefugia (Hylander et al., 2015), since small isolated populations are particularly susceptible to negative impacts, inbreeding, and demographic fluctuations in numbers (Primak, 2002). However, the reed vole is able to exist for a long time even in very small populations due to the mechanisms of population density regulation (Katin, 1989). We can observe such small populations even now on the small islands of Peter the Great Bay. Most likely, this feature has deep evolutionary roots, since it is also characteristic of other species of gray voles (Lomolino, 1986).

Following the theory of microrefugiums, it can be assumed that, during the last climatic minimum, when the main range of reed voles shifted south, a small part of individuals remained in their former (located to the north) habitats with a stable microclimate, primarily on the sea coast, where meadow communities remained, and it is in these small isolates that the ISL subclade haplotypes are preserved. We can observe evidence of the existence of microrefugia on the isolated offshore islands of Peter the Great Bay (Matveev and Bolshoy Pelis), namely those that had previously separated from the mainland (Velizhanin, 1976; Sheremetiev, 2001). Traces of the existence of microrefugia can also be found on other islands of the Rimsky-Korsakov Archipelago in Peter the Great Bay. On at least two islands of Durnovo and De Livrona, reed voles showed features of the morphotypic variability of the anteroconid form of the first lower molar compared to other island and mainland populations (Vinokurova et al., 2022). The presence of microrefugia in the reed vole can also be assumed in the basin of the lower reaches of the Amur River and in the more continental, northwestern part of the range, in the intermontane basins of Transbaikalia, such as the Barguzin~~skaya~~, where the populations contain individuals with haplotypes of the ISL subclade (Fig. 1). Thus, microrefugia could contribute to the preservation of haplotypes of the ISL subclade in some marginal populations both during the period of the climatic minimum, when most populations of the species disappeared in the northern part of the range, and during the Holocene, when these territories were recolonized by voles with haplotypes of the MAIN subclade. However, it remains unclear why during the long isolation of these small populations remote from each other (i.e., with a low effective abundance of animals), they did not accumulate noticeable differences in the haplotypes of the ISL subclade. Perhaps this is due to the peculiarities of the biology of the species.

Thus, several hypotheses are possible to explain the genetic variability of the reed vole revealed in this work in the territory of Transbaikalia and the Far East. Some of them are more likely to explain the existence of haplotypes of the ISL and MAIN subclades within the NORTH lineage, while the role of microrefugia could have been to preserve the haplotypes of the ISL subclade during the climatic minimum and after its completion with a wide expansion of the species to the north. To test these hypotheses, this work needs to be continued both with the study of material from previously unstudied localities and with the involvement of additional molecular markers in the analysis.

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All applicable international, national, and/or institutional guidelines for the care and use of animals have been followed.

The authors declare that they have no conflicts of interest.

CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest.

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