Received: 3 June 2017 | Accepted: 8 September 2017

DOI: 10.1111/zsc.12261

ORIGINAL ARTICLE

WILEY Zoologica Scripta

Multilocus phylogeny and taxonomy of East Asian voles *Alexandromys* (Rodentia, Arvicolinae)

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Funding information
Russian Foundation for Basic Research, Grant/Award Number: 14-04-00163, 15-04-04602 and 16-04-00983; MSU Zoological Museum, Grant/Award Number: AAAA-A16-116021660077-3; Theriology laboratory of ZIN RAS, Grant/Award Number: AAAA-A17-117022810195-3

[Version of Record, published online on 20 October 2017; urn:lsid:zoobank.org:act:640F3AA1-6EEB-4068-8CCB-C64EFC30BAB0

Phylogenetic relationships, taxonomy and nomenclature issues within East Asian voles *Alexandromys* were addressed using comprehensive species samples, including all 12 valid species of the genus, and multilocus analysis. We examined the mitochondrial cytochrome b (*cytb*) gene and three nuclear genes in 36 specimens. Additionally, we examined a data set of 106 specimens using only the *cytb* gene. Our results did not confirm the aggregation of *A. kikuchii*, *A. montebelli* and *A. oeconomus* into a separate clade, namely the subgenus *Pallasiinus.* Analysis of incomplete lineage sorting using JML software highlighted both the cases of mitochondrial introgression and incomplete lineage sorting within the genus. Thus, the sister position of *A. sachalinensis* and *A. maximowiczii* in mitochondrial trees could be explained by mitochondrial introgression, while the sister position of *A. limnophilus* and *A. fortis* in mitochondrial trees could be successfully explained by incomplete lineage sorting. Very short genetic distances, together with an absence of monophyly, of the three species, *A. evoronensis*, *A. mujanensis* and *A. maximowiczii*, is supported by multiple morphological data, which indicates that these three taxa should be one species—*A. maximowiczii*. Analysis of genetic distances and tree topology revealed that three species of short-tailed voles—*A. middendorffii*, *A. mongolicus* and *A. gromovi*—are more closely related to each other than to other established species of *Alexandromys*. The lacustrine vole, *A. limnophilus,* is closely related to the group of short-tailed voles. Analysis of the type specimens of *limnophilus* and *flaviventris* confirmed that these taxa form one species together with *A. l. malygini*. Our results suggest that the mountains of western Mongolia are inhabited by a new taxon of short-tailed voles of the same rank as *middendorffii*, *mongolicus* and *gromovi*—*A. m. alpinus* ssp. n.

KEYWORDS

Alexandromys, multilocus analysis, phylogeny, taxonomy,

1 | INTRODUCTION

Voles of the *Alexandromys* Ognev, 1914 genus are widely distributed in the Eastern Palaearctic. One species, the root vole *A. oeconomus* (Pallas, 1776) penetrates to Western Europe, and east to the Alaska Peninsula and adjacent regions of North America. East Asian voles generally prefer wet habitats along rivers or lake shores, wetlands within taiga, steppe, semidesert and desert zones, often inhabiting higher elevations in mountains. Such discontinuous distributions can potentially lead to separation of various geographical forms, including those worthy of a taxonomic rank.

Due to the high level of morphological similarity in grey voles (tribe Arvicolini Gray, 1821), *Alexandromys* was not recognised as a monophyletic group for a long time. Following modern splitting tendency, the taxonomic status of *Alexandromys* was elevated from subgeneric within the genus of *Microtus* Schrank, 1798 to full generic rank (Abramson & Lissovsky, 2012). Currently, the genus *Alexandromys* is considered to include 12 species: *A. evoronensis* Kovalskaya et Sokolov, 1980; *A. fortis* Büchner, 1889; *A. gromovi* Vorontsov et al. 1988; *A. kikuchii* Kuroda, 1920; *A. limnophilus* Büchner, 1889; *A. maximowiczii* Schrenk, 1859; *A. middendorffii* Poljakov, 1881; *A. mongolicus* Radde, 1861; *A. montebelli* Milne-Edwards, 1872; *A. mujanensis* Orlov et Kovalskaya, 1978; and *A. oeconomus* and *A. sachalinensis* Vasin, 1955. Previously, these species were assigned to different subgenera—*Microtus*, *Pallasiinus* Kretzoi, 1964, proper *Alexandromys*—and even to a separate genus *Volemys* Zagorodnyuk, 1990 (Gromov & Erbajeva, 1995; Gromov & Polyakov, 1977; Meyer, Golenishchev, Radjabli, & Sablina, 1996; Pavlinov & Rossolimo, 1998; Zagorodnyuk, 1990).

Studies based on the mitochondrial cytochrome b (*cytb*) gene (Bannikova et al., 2010; Conroy & Cook, 2000) showed the existence of two separate phylogenetic lineages within East Asian voles: *Pallasiinus* (*A. kikuchii*, *A. montebelli*, *A. oeconomus*) and *Alexandromys* s. str., including the remaining nine species. Within *Alexandromys* s. str., two clusters (*A. maximowiczii* together with *A. sachalinensis*; and *A. middendorffii*, *A. mongolicus*, together with *A. gromovi*) obtained high support values. The sister position of *A. maximowiczii* and *A. sachalinensis* was supported in the study of the mitochondrial control region (Haring, Sheremetyeva, & Kryukov, 2011). Despite the phylogenetic signal in conventional morphological data being obscure, results of morphological analysis of the group (Lissovsky & Obolenskaya, 2011) highlighted some contradictive points in mitochondrial-based phylogeny. If the clade of short-tailed voles (*A. middendorffii*, *A. mongolicus* and *A. gromovi*) is in a good agreement with their morphological similarity, the association of *A. maximowiczii* and *A. sachalinensis* is contradictory. *Alexandromys sachalinensis* displays very high cranial similarity with another species of the genus, *A. fortis*.

Morphological studies performed on various species within the genus showed the following: morphological differences between *A. evoronensis*, *A. mujanensis* and *A. maximowiczii* are very shallow (Lissovsky & Obolenskaya, 2011; Meyer et al., 1996; Voyta, Golenishchev, & Tiunov, 2013); *A. mongolicus* consists of two morphologically distinct geographical forms (Lissovsky & Obolenskaya, 2011); the subspecies of the root vole *A. o. kharanurensis* Courant et al., 1999 is very distinct in cranial morphology (Lissovsky & Obolenskaya, 2011). The long discussion on the taxonomic status of *A. hyperboreus* Vinogradov, 1934 (Litvinov, 2001; Meyer et al., 1996; Volpert & Shadrina, 2002) likely ended after the morphological and genetic analysis of a larger data set (Lissovsky et al., 2010). This taxon should be considered as a junior synonym of *A. middendorffii*. Several taxonomic issues remain unresolved. The taxonomic integrity of *A. limnophilus* across the distribution range was predicted by karyological studies (Courant et al., 1999; Malygin, Orlov, & Yatsenko, 1990); morphological variation within this species was studied on the basis of very limited samples only (Lissovsky & Obolenskaya, 2011), while molecular studies did not address different geographical forms of the species. The putative taxon *M. arvalis baicalensis* Fetisov, 1941 occupies an indefinite taxonomic position, as its holotype was lost; meanwhile, this name could be a potential senior synonym for short-tailed voles from southern Siberia and adjacent regions.

In summary, it must be highlighted that despite that East Asian vole systematics and phylogeny being addressed earlier by various authors, many issues remain unclear. Moreover, all previous studies on *Alexandromys* with the application of genetic analyses used only sequences of mitochondrial DNA fragments (Bannikova et al., 2010; Conroy & Cook, 2000; Haring et al., 2011). Thus, this study aimed to elucidate the phylogenetic relationships in a multilocus approach and to clarify taxonomy and nomenclature issues within the genus *Alexandromys* analysing the most comprehensive species sample, including all recognised species of the genus. We also sequenced partial sequences of the cytochrome b gene from a number of old type specimens to solve some nomenclatorial issues.

2 | MATERIAL AND METHODS

Analysis was performed on the basis of two data sets. The main analysis included 36 specimens of *Alexandromys* voles (Table S1; Figure 1) that were studied using four genes, listed below. The second, larger data set with 106 specimens was analysed using the *cytb* gene only. This data set included sequences from type specimens of nominal taxa *limnophilus* and *flaviventris*, paratypes of *baicalensis*, and topotypes of *kharanurensis*. *Myodes rutilus* (Pallas, 1779), *Arvicola amphibius* (Linnaeus, 1758) and *Microtus arvalis* (Pallas, 1778) were used as an outgroup in each data set. Most samples were represented by fresh tissues fixed in ethanol; the second data set also included fragments of skin from specimens from old museum collections. The majority of examined specimens were identified on the basis of morphological features according to Lissovsky and Obolenskaya (2011). Some specimens were karyotyped (Table S1).

Sequences of the cytochrome b (*cytb*) gene (1,140 bp); exon 11 of breast cancer 1 nuclear gene (BRCA1) (alignment length 967 bp); intron of the nuclear protein kinase C iota (PRKCI) (alignment length 491 bp); and intron of the nuclear interleukin 1 receptor accessory protein-like 1 (ILRAPL1) (alignment length 561 bp) were analysed in this study.

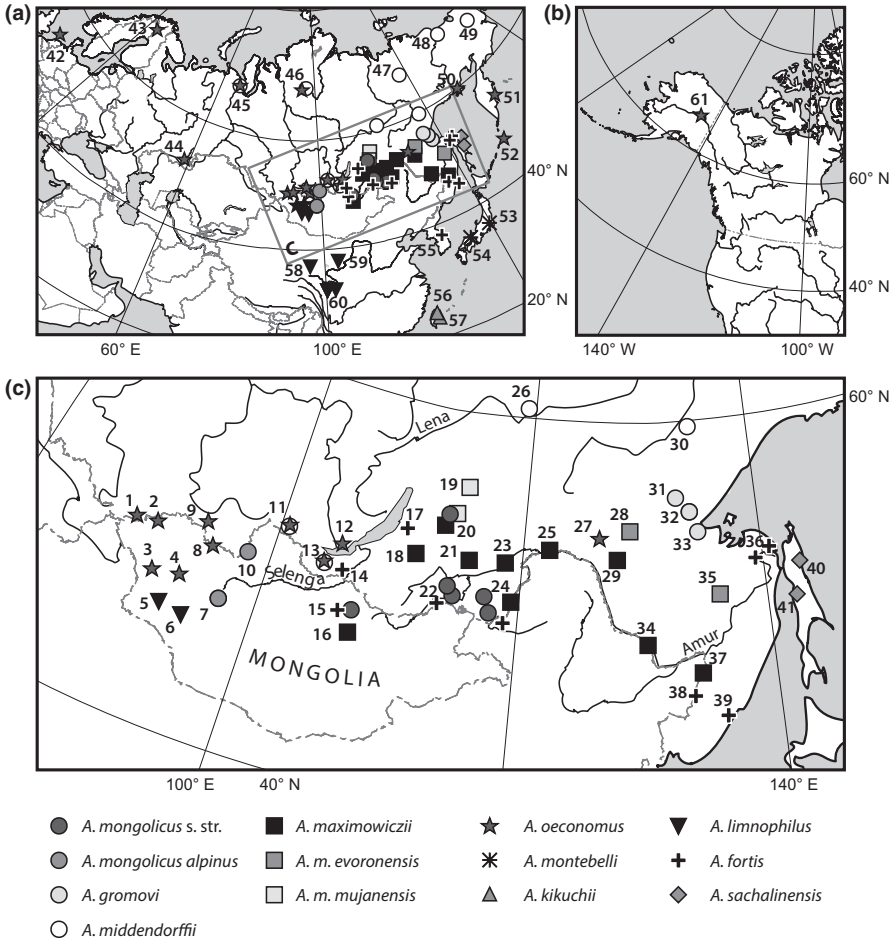

FIGURE 1 Map showing sampling localities of the species of *Alexandromys* used in this study. For details refer to Table S1

2.1 | DNA isolation, amplification and sequencing

Total genomic DNA was extracted from ethanol-fixed muscle tissues using a DNA-sorb-C kit (InterLabService Ltd., Moscow, Russia) and using QIAamp Tissue Kit (Qiagen, Germantown, MD, USA) from museum skin samples. The genes were amplified by polymerase chain reaction and sequenced using primers (Table S2): *cytb* – L14729 + H15906arvic (Lebedev, Bannikova, Tesakov, & Abramson, 2007); BRCA1 – F180_arv + R1240_arv (Bannikova, Sighazeva, Malikov, Golenishchev, & Dzuev, 2013); PRKCI – PRKCI-F + PRKCI-R (Matthee, van Vuuren, Bell, & Robinson, 2004); ILRAPL1 – IL1RAPL1_F + IL1 RAPL1_R (Carneiro, Blanco-Aguiar, Villafuerte, Ferrand, & Nachman, 2010). Amplicon length completely covered nuclear genes sizes; in the case of cytb, amplicon length was slightly shorter than complete gene, about 900 bp on average. *Cytb* from museum samples was amplified with several successive overlapping short fragments using the following primers: F75 + R322; F275 + R430; F389 + R654 and F646 + R817.

We amplified *cytb*, PRKCI and ILRAPL1 genes under the following conditions: 94°C for 3 min, 42 cycles of 94°C for 20 s, 55°C for 20 s and 72°C for 40 s and 1 repeat of 72°C for 3 min. PCR conditions for BRCA1 were as follows: 94°C for 3 min, 42 cycles of 94°C for 20 s, 60°C for 20 s and 72°C for 40 s and 1 repeat of 72°C for 3 min. Short *cytb* fragments were amplified under the following conditions: 94°C for 5 min, 40 cycles of 94°C for 15 s, 55°C for 20 s and 72°C for 30 s and 1 repeat of 72°C for 5 min.

2.2 | Phylogenetic analysis

The nucleotide sequences were assembled, edited and aligned using Geneious 8.1.8 (http://www.geneious.com; Kearse et al., 2012). Nuclear genes demonstrated some heterozygous nucleotide positions that were determined as double peaks (with a height of one peak of 0.6 of another peak height or more) on paired chromatograms. Sixty per cent of BRCA1 sequences had heterozygous positions; 2.9 positions per such sequence on average. For ILRAPLE1, these ciphers were 13% and 1.8 positions on average; for PRKCI, these ciphers 36% and 1.8 positions on average. Haplotypes of nuclear genes were reconstructed with output probability threshold of 0.9 using PHASE v2.1 (Stephens & Donnelly, 2003) and implemented in DnaSP v5.10.01 (Librado & Rozas, 2009).

The best-fit of several substitution models for each locus was assessed using Treefinder (Jobb, 2011) under the

corrected Akaike information criterion (AICc). If the specific model was not implemented in MrBayes or *BEAST, the next most parameterised model was selected. A Bayes factor comparison (Nylander, Ronquist, Huelsenbeck, & Nieves-Aldrey, 2004) for *cytb* and BRCA1 showed that the codon-partitioned model was better than the single partition model, and thus, we used codon-partitioned models in all analyses. The PRKCI and ILRAPL1 introns were analysed as a single partition each.

A Bayesian analysis of gene trees on the basis of four genes separately was performed in MrBayes 3.2.6 (Ronquist et al., 2012) with 50,000,000 generations (the standard deviations of split frequencies were below 0.004; potential scale reduction factors were equal to 1.0; stationarity was examined in Tracer v1.6 (Rambaut, Suchard, Xie, & Drummond, 2014)), two runs with five independent chains, a sampling frequency of 5,000 and the next most complex model after Treefinder results available in MrBayes (Ronquist, Huelsenbeck, & Teslenko, 2011). The heating parameter was selected in preliminary runs following Ronquist et al. (2011). It was set to 0.02 in the analyses of BRCA1, ILRAPL1 and PRKCI and to 0.1 in the analysis of *cytb*.

Multilocus phylogenetic reconstruction on the basis of three nuclear genes was performed using the species-tree coalescent-based method implemented in *BEAST v2.4.5 (Bouckaert et al., 2014). The strict clock model and lognormal relaxed clock model were used separately. Results of three independent runs of 100,000,000 generations, constructed under the Yule process and with the majority of parameters estimated, were examined using Tracer v1.6 (Rambaut et al., 2014), and concatenated using LogCombiner, discarding the first 20% as burn-in. Trees were then summarised with TreeAnnotator v2.2.1 as the maximum clade credibility tree.

"Species-tree" approach allows to estimate species-tree in contrast to individual gene trees that can differ substantially from each other and from the species-tree because of incomplete lineage sorting (Heled & Drummond, 2010; Joly, McLenachan, & Lockhart, 2009). Another source of difference between individual gene trees is an interspecies hybridisation. In our case, nuclear gene-based species-tree fitted morphological pattern better than mtDNA-based tree (see Introduction). Thus, we considered mitochondrial introgression as one of the possible hypothesis of such incongruence between nuclear and mitochondrial data sets. We tested the mitochondrial introgression vs. incomplete lineage sorting hypothesis using the program JML v1.3.0 (Joly, 2012; Joly et al., 2009). JML uses as input posterior distributions of species-trees and population sizes from *BEAST. The method tests whether the minimum distance between sequences of two species is smaller than the distance calculated under a scenario that does not account for hybridisation. We performed an additional MCMC run with both the mitochondrial and nuclear genes together using species-tree coalescent-based method in *BEAST with 100,000,000 generations to estimate parameters for the JML analysis. Nuclear-based species-tree set from previous analysis and mitochondrial sequences was used as input data. We conducted the JML analysis using three relative mutation rates for the "locusrate" parameter: the mean value and the lower and upper boundary values of the 95% credible interval from *BEAST output.

3 | RESULTS

Nuclear genes proved to have similar rates after the analysis of all genes under the species-tree method: BRCA1:ILRAPL1:PRKCI = 1.14 [0.87–1.4]:1.05 [0.77–1.34]:1 [0.72–1.3]. Mitochondrial *cytb* was notably faster: 7.2 [6.48–8.09] relative to the average nuclear rate.

All four trees constructed on the basis of the *cytb,* and three nuclear genes had different topology (Figure 2; Figs S1–S4). There was no difference in species-tree topology of supported branches between trees constructed under strict clock and relaxed clock assumptions (Figure 3). The only phenomenon common for all trees obtained was the existence of the monophyletic *Alexandromys* lineage. At the lower scale, there were two clusters that appeared on nearly all trees (Figures 2 and 3; Figs S2 and S3). The first clade comprises of three recognised species: *A. maximowiczii*, *A. evoronensis* and *A. mujanensis*. The second contained several species of short-tailed voles (*A. middendorffii*, *A. mongolicus*, *A. gromovi* and new one from western Mongolia described below). Genetic distances between the taxa are listed in Table 1.

There was no difference in the specimen composition of the terminal clades, roughly corresponding to accepted species, in trees constructed on the basis of nuclear and mtDNA. However, there was a difference in relative phylogenetic position of some taxa for these two data sets. The first case concerns the relative position of *A. sachalinensis* and *A. maximowiczii*. In mitochondrial trees, *A. sachalinensis* and *A. maximowiczii* sensu lato are sister species, whereas nuclear trees did not contain such a clade. Another difference between mitochondrial and nuclear trees concerned the phylogenetic position of *A. limnophilus*. Mitochondrial trees arranged this species as sister to *A. fortis*. Conversely, the nuclear species-tree (Figure 3) unites *A. limnophilus* with the short-tailed voles with bayesian posterior probabilities (bpp) of 0.91–0.96.

The phylogenetic position of some particular specimens is worth mentioning. Sequences obtained from holotypes of *A. limnophilus* and *A. flaviventris* occurred in the same clade as other representatives of *A. limnophilus*, including *A. l. malygini* (Figure 2). Topotypes of *A. kharanurensis* fell within Asian *A. oeconomus* without any separation. Two paratypes

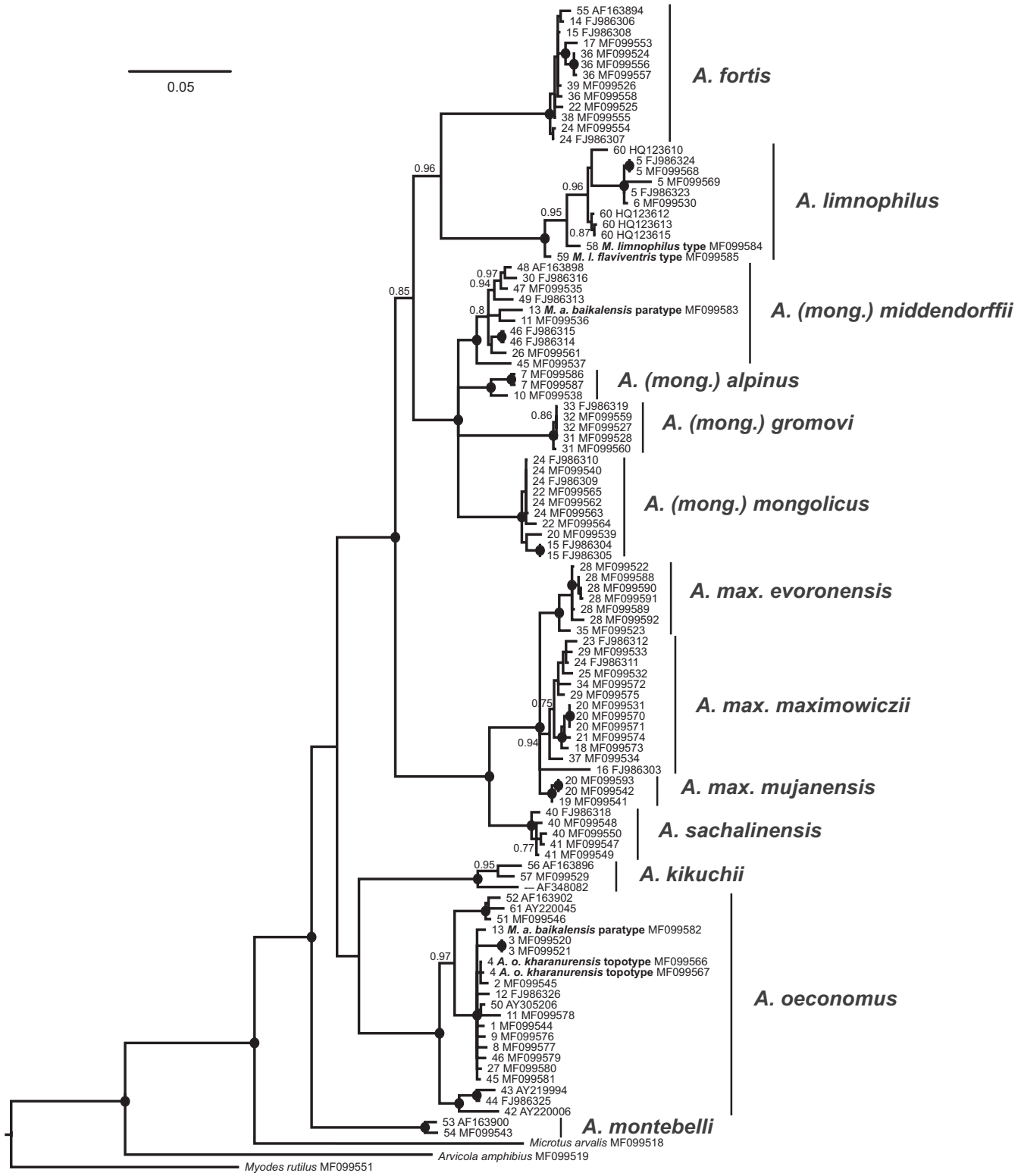

FIGURE 2 Maximum clade credibility tree of Bayesian analysis based on full set of cytochrome b sequences of *Alexandromys* voles. Bayesian probabilities below 0.75 are not shown; interval of 0.75–0.97 is shown with numbers above branches; probabilities over 0.98 are indicated at nodes with black circles. Each label contains Map ID and GenBank ID (Figure 1; Table S1). Type specimens are highlighted

of *baicalensis* occurred in different clades. One of the specimens was placed within the clade of *A. middendorffii*, and another in *A. oeconomus*.

According to JML testing, a major part of the discordance between mitochondrial and nuclear data could be explained by incomplete lineage sorting. Several cases are, however,

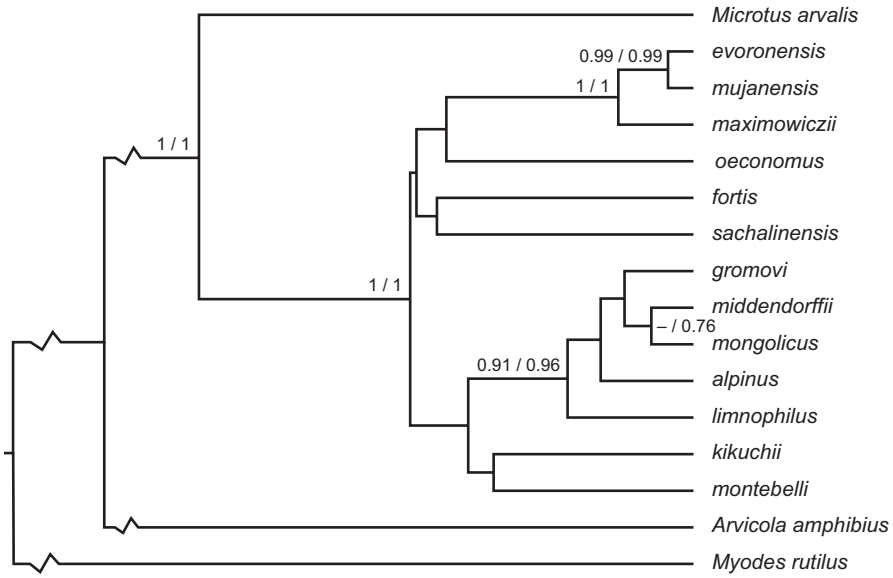

FIGURE 3 Phylogenetic tree of *Alexandromys* voles constructed using "species-tree" approach on the basis of three nuclear genes. Bayesian probabilities below 0.75 are not shown. Numbers on branches indicate Bayesian probabilities for strict/relaxed clock models used in analyses

better explained by a hybridisation scenario. All three runs of JML selected pairs of *A. maximowiczii–A. sachalinensis* (p min:mean:max of different specimen pairs: 0.04–0.07:0.02–0.07:0.01–0.09) and *A. maximowiczii–A. mujanensis* (0.07–0.09:0.05–0.09:0.03–0.08) had significantly shorter within-pair distances for *cytb* than could be suggested after simulations on nuclear genes. A run with maximal "locusrate" value added a pair of specimens of *A. maximowiczii–A. evoronensis* to this list (0.08).

4 | DISCUSSION

The multilocus analysis of a complete set of *Alexandromys* species presented here do not add significantly to the resolution of the phylogeny of the genus. The main results were related to composition of taxa at the species level that can input more to taxonomy than to phylogenetics. However, we can speculate that as incomplete lineage sorting events dominate in our data set, a moderate increase in the number of nuclear genes will not resolve the phylogeny too. Investigation of multiple loci using NGS techniques may be more promising.

4.1 | General comparison of tree topologies

The topology of the mitochondrial tree (Figure 2; Fig. S1) is in general concordance with previous studies (Bannikova et al., 2010; Conroy & Cook, 2000; Martínková & Moravec, 2012). However, *A. kikuchii*, *A. montebelli* and *A. oeconomus* did not form a separate clade in our trees. We relate this to more intensive sampling in our study, as the general scheme of analysis was similar to that used in previous work. It should be noted, however, that although the mentioned clade was postulated previously (Bannikova et al., 2010), it never obtained high branch support values (Bannikova et al., 2010; Conroy & Cook, 2000). In our study, we did not obtain a clade containing these three species in nuclear trees. Thus, our data do not support the concept of dividing *Alexandromys* into two lineages: *Alexandromys* s. str. and *Pallasiinus* Kretzoi, 1964.

The different position of *A. sachalinensis* and *A. maximowiczii* in mitochondrial- and nuclear-based trees needs special attention. A close phylogenetic relationship between these species was previously found (Meyer et al., 1996). A. Pozdnyakov (1996) considered that this conclusion was based mainly morphological features. Moreover, Meyer et al. (1996) discussed the morphological similarity between *A. sachalinensis* and *A. maximowiczii* in the structure of enamel loops of the teeth and anterior part of spermatozoids, while discussion of karyotype structure in the same study implied similarity between *A. sachalinensis* and *A. fortis*. Hybridisation between all three species was unsuccessful (Meyer et al., 1996), but studies based on mtDNA supported the idea of a close phylogenetic relationship between *A. sachalinensis* and *A. maximowiczii* (Bannikova et al., 2010; Haring et al., 2011). Cranial study prejudiced morphological similarity between the latter pair of species; the skull of *A. sachalinensis* is more similar to *A. fortis* (Lissovsky & Obolenskaya, 2011).

Our study of nuclear genes does not resolve the phylogenetic relationships of *A. sachalinensis*. However, our JML results allow us to suggest that the sister position of *A. maximowiczii* and *A. sachalinensis* on the mitochondrial DNA tree most likely appear due to recent hybridisation with mitochondrial introgression. Future intensive sampling of *A. sachalinensis* could determine whether inherent mtDNA of *A. sachalinensis* persist in the population of this species, as well as when the introgression event could have taken place. Phylogenetic relationships of both *A. maximowiczii* and *A. sachalinensis* should be resolved using more

TABLE 1 Genetic distances between *Alexandromys* taxa. Distances (±*SD*) calculated on the basis of cytochrome b gene; minimal cytochrome b based interspecies distance (MID), simulated by JML; and distance calculated on the basis of BRCA1 gene are shown. Short-tailed voles (*A. middendorffii*, *A. mongolicus* and *A. gromovi*) are abbreviated as *A. mongolicus* s.l

	cytb	MID	BRCA1
A. oeconomus–A. maximowiczii s.l.	25.2 ± 7.8	9.9	1.3 ± 0.8
A. oeconomus–A. fortis	23.9 ± 8.0	9.2	1.6 ± 1.0
A. oeconomus–A. mongolicus s.l.	22.2 ± 8.2	9.4	2.2 ± 1.2
A. oeconomus–A. kikuchii	17.6 ± 1.6	10.7	2.0 ± 1.3
A. oeconomus–A. montebelli	19.5 ± 7.6	10.4	1.8 ± 1.2
A. fortis–A. maximowiczii s.l.	22.4 ± 5.6	9.7	1.4 ± 1.0
A. sachalinensis–A. fortis	20.4 ± 4.3	10.3	1.1 ± 0.6
A. fortis–A. limnophilus malygini	16.2 ± 2.0	11.6	1.4 ± 0.8
A. sachalinensis–A. maximowiczii s.l.	7.0 ± 2.3	6.8	1.8 ± 1.2
A. l. malygini–A. mongolicus s.l.	18.8 ± 5.1	12.6	0.4 ± 0.3
A. m. evoronensis–A. maximowiczii s.s.	3.0 ± 1.5	2.1	0.3 ± 0.2
A. m. mujanensis–A. maximowiczii s.s.	2.0 ± 0.8	1.7	0.2 ± 0.2
A. mongolicus s.s.*–A. middendorffii*	8.0 ± 2.3	5.8	0.5 ± 0.3
A. mongolicus s.s.*–A. gromovi*	12.0 ± 3.1	6.8	0.7 ± 0.4
A. mongolicus s.s.*–A. m. alpinus*	8.2 ± 2.7	6.1	0.5 ± 0.3
A. middendorffii–A. gromovi	10.3 ± 2.7	6.1	0.5 ± 0.4
A. oeconomus (Asia)*–A. oeconomus* (Europe)	4.7 ± 1.4	—	0.4 ± 0.3
A. oeconomus (Asia)*–A. oeconomus* (Beringia)	4.1 ± 0.6	—	0.2 ± 0.2

intensive gene sampling; however, they are not as close as was supposed on the basis of mtDNA study.

4.2 | Geographic distribution of vole species

According to the conventional viewpoint, *Alexandromys* includes a number of species with restricted distribution (Gromov & Erbajeva, 1995; Musser & Carleton, 2005; Shenbrot & Krasnov, 2005). Thus, *A. evoronensis* and *A. mujanensis* are always listed as species known from their type localities only; although *A. gromovi* has not yet been included in checklists as a separate species, it was also only known from type locality for a long time. Middendorf's vole is described from a narrow polar belt of Siberia. Meanwhile, intensive sampling of the last decade displayed much wider distribution of the *Alexandromys* species. The main reason for such "range expansion" is a special interest to the group under discussion.

The main changes concern two groups of voles: *A. maximowiczii*, *A. evoronensis* and *A. mujanensis*; and short-tailed voles. *Alexandromys maximowiczii* inhabits wet meadows along rivers and lakes; recent studies found this species in Ussuri River basin (Lissovsky & Obolenskaya, 2011; Sheremetyeva, Kartavtseva, Frisman, Vasil'eva, & Adnagulova, 2015; Figure 1: 37) that appeared to be the easternmost part of the species range. New records on *A. evoronensis* and *A. mujanensis* result in notable changes in the distribution patterns. Besides the terra typica of *A. evoronensis* (Figure 1: 35), it was found at the sides of the Amgun River (Sheremetyeva, Kartavtseva, Voyta, & Tiunov, 2010), Bureya River (Sheremetyeva, Kartavtseva, Vasil'eva, & Frisman, 2016) and at the Zeya plain (Figure 1: 28). Thus, the known distribution ranges of *A. maximowiczii* and *A. evoronensis* are separated by a narrow band of the Tukuringra Range (distance between the closest records is about 100 km) that holds patchy suitable habitats for these voles. A new record of *A. mujanensis* (Figure 1: 20) puts this species as close to *A. maximowiczii* distribution as possible (distance between the closest records is about 83 km). Thus, it is difficult to say that the three species in question represent three remote isolates. Their distribution should be studied thoroughly to find possible range junctions.

The most dramatic "range expansion" concerned *A. middendorffii*. This species formerly considered an arctic inhabitant is now known to be a widespread vole (Dokuchaev & Dorogoy, 2005; Lissovsky et al., 2010; Sheremetyeva et al., 2010; Figure 1: 11, 13, 26, 30, 49). The distribution of *A. gromovi* covers at least the eastern part of the Stanovoy Range and the Dzhugdzhur Range (Lissovsky et al., 2010; Sheremetyeva et al., 2010; Figure 1: 31–33). The Mongolian vole was also confirmed in the north-westernmost part of the range (Figure 1: 20). Thus, although distribution ranges of *A. middendorffii*, *A. gromovi* and *A. mongolicus* are still allopatric, distribution borders of these species are situated very close to each other.

4.3 | Taxonomic status of *A. evoronensis* and *A. mujanensis*

Trees constructed on the basis of both mitochondrial and nuclear data sets are similar in very close phylogenetic proximity of *A. maximowiczii*, *A. evoronensis* and *A. mujanensis*.

Our results of the JML test found that mtDNA-based genetic distances are significantly shorter in the pair *A. maximowiczii–A. mujanensis*, than the distances calculated on the basis of analysis of posterior distributions of nuclear species-trees from *BEAST with known ratio of mitochondrial to nuclear mutation rates. Such result suggests hybridisation with mitochondrial introgression scenario (Joly et al., 2009). The same result was obtained for *A. maximowiczii–A. evoronensis* pair but at lower confidence level. It should be noted that in the analysis of the larger taxa set with *cytb* (Figure 2), *A. maximowiczii* is not monophyletic relative to *A. evoronensis* and *A. mujanensis*. Monophyly is broken by the specimen of *A. maximowiczii* from Hentiyn Nuruu, Mongolia. Similar results showing paraphyly of *A. maximowiczii* related to *A. evoronensis* and *A. mujanensis* were obtained with the control region of mtDNA (Haring et al., 2011).

Genetic distances between these three taxa calculated using both mitochondrial and nuclear data sets (Table 1) are notably shorter than distances between recognised species of *Alexandromys*. In *cytb,* these distances are even shorter than intraspecific distances within *A. oeconomus*; in nuclear BRCA1, these sets of distances are comparable.

Two of the species from the group under discussion, *A. evoronensis* and *A. mujanensis*, were described as separate species on the basis of different chromosome structure (Kovalskaya & Sokolov, 1980; Orlov & Kovalskaya, 1978). Laboratory experiments showed that offspring of interspecies hybridisation in these three species are sterile (Meyer et al., 1996). The results of those experiments seem to contradict our results of JML test implying gene flow between *A. maximowiczii* and two other species, especially *A. mujanensis*. There are two possible explanations of such contradiction. In the first case, establishment of postzygotic reproductive isolation could be very recent and took place after hybridisation events suggested by JML test. In the second case, laboratory hybridisation experiments may not reflect real natural situation. Indeed, supposed postzygotic reproductive isolation is a result of chromosomal rearrangements. Laboratory experiments cited above used limited number of specimens from one population per species. Meanwhile, all the three species share notable chromosomal variation (Kartavtseva et al., 2008; Lemskaya et al., 2015; Sheremetyeva, Kartavtseva, & Vasil'eva, 2017); thus, gene flow could occur through some populations that were not involved in the hybridisation study.

The shallow difference between Maximowicz's vole and two other species was earlier found in numerous morphological and allozyme studies (Frisman, Korobitsyna, Kartavtseva, Sheremetyeva, & Voyta, 2009; Lissovsky & Obolenskaya, 2011; Meyer et al., 1996; Pozdnyakov, 1996; Voyta et al., 2013). Thus, it is clear that *A. evoronensis* and *A. mujanensis* represent taxa at a very low level of speciation. The only reason to increase their taxonomic status to independent species lies in the results of experimental hybridisation that is in conflict with other data sets. Thus, species status for the taxa in question would be justified if one considers postzygotic reproductive isolation of the same taxonomic weight as speciation time and previous gene flow. Taking into consideration the discussion above, we suggest recognising *A. evoronensis* and *A. mujanensis* as subspecies of *A. maximowiczii*: *A. m. evoronensis* and *A. m. mujanensis*.

4.4 | Taxonomic status of *A. baicalensis*

The nominal taxon *Microtus arvalis baicalensis* Fetisov, 1941 was described as a subspecies of the common vole *M. arvalis*. The holotype (ID 231, collected on 22.7.1936 on "Ordak Golets") was kept in the collection of the East-Siberian University, now State Irkutsk University (IGU). Fetisov (1941) mentioned 26 specimens of *M. arvalis* collected by him in 1936. An earlier publication (Fetisov, 1937) contains a list of exact places where the series was collected: Tsagan-Chelutay (51.505 N; 106.172 E), Ortsak (51.292 N; 103.785 E; this is the correct name for "Ordak": "d" and "ts" are similar letters in Russian), Khan-Ula (51.182 N; 103.982 E) and Khatyn-Ula (undefined). The holotype is absent in both the collection of IGU and the inventory documents. It is known that A. Fetisov moved some specimens he collected to larger museums. However, we did not find the specimens in the ZMMU or ZIN collections. The only two specimens related to the topic were found in the ZIN collection. These are voles initially identified as *M. arvalis* collected by Fetisov on 9.7.1936 (ZIN 25840) and 14.7.1936 (ZIN 25841) at Snezhnaya River. Taking into account that the difference in collection date is a few days, they should be collected at Khan-Ula Golets (distance between Ortsak and Khan-Ula is about 18 km), the only site situated at this river. As Fetisov (1937, 1941) mentioned voles collected in 1936 in the region of Snezhnaya River in the original description of *Microtus arvalis baicalensis*, the latter two specimens (25,840 and 25,841) should be designated as paratypes (ICZN, 1999 Art. 72.4.1.1, 72.4.5).

Voles of *M. arvalis* do not inhabit high altitudes of East Siberia, thus Ognev (1950) referred to *M. a. baicalensis* as a junior synonym of *A. mongolicus*. If this species identification was correct, this name could be a senior synonym to Mongolian voles of western or central Mongolia. It should be noted that Ognev did not list any exact museum specimen of *M. a. baicalensis* in the publication.

Our analysis found that two paratypes of *M. a. baicalensis* belong to different species: one is *A. middendorffii* and another is young specimen of *A. oeconomus*. Such identification is concordant with teeth morphology of these two specimens. The second case could be considered as accidental collector's identification mistake—the tail length of the adult root vole is notably larger than values provided by Fetisov (1941), so probably adult root voles were absent in

the type series of *M. a. baicalensis*. However, our identification of *A. middendorffii* explains this confusion. Specimens of *A. middendorffii* are very similar to *M. arvalis* in terms of dental morphology (Gromov & Erbajeva, 1995; Gromov & Polyakov, 1977). Distribution of *A. middendorffii* and *A. mongolicus* is allopatric, and thus, it is less probable that the type series included both species. Consequently, we can hypothesise that the holotype of *M. a. baicalensis* also belonged to *A. middendorffii*.

4.5 | New vole from western Mongolia

The existence of a clade including short-tailed voles (*A. middendorffii*, *A. mongolicus* and *A. gromovi*) in both mitochondrial and nuclear gene trees deserves special attention. This clade contains the fourth branch that has not been described earlier (Figures 2 and 3). This fourth branch includes three specimens from north-western Mongolia and the adjacent Tuva Republic, Russia, and corresponds to "western *A. mongolicus*" of Lissovsky and Obolenskaya (2011). This is a group of voles inhabiting the mountain tundra west of the Selenga River, previously referred to as *A. mongolicus* by all authors. According to morphological data (Lissovsky & Obolenskaya, 2011), this western Mongolian taxon is distributed in the Khangai and Tarbagatai Mountains of Mongolia, extreme south-eastern Altai Mountains of Russia (Mountains east of Chuyskaya Steppe); our genetic data adds the extreme south-eastern Tuva along the Mongolian border to the distribution range. Representatives of this taxon under discussion have distinct morphological peculiarities, compared to *A. mongolicus* s. str. and *A. middendorffii* (Lissovsky, Kadetova, & Obolenskaya, accepted). They can be distinguished from *A. mongolicus* s. str. by well-separated seven dentin fields in the first lower molar m_1, together with a well-developed re-entrant labial angle on the anteroconid of m_1 (Lissovsky et al., accepted; Pozdnyakov, 1996). The voles of the western Mongolian taxon differ from *A. middendorffii* by a flat interorbital surface, while adult *A. middendorffii* has characteristic relief in this part of skull with two flatten temporal crests that rise in nasal direction and form a wedge-shaped fossa in front of orbits (Lissovsky et al., accepted). Our genetic results show that the western Mongolian taxon has the same level of genetic segregation as *A. middendorffii*, *A. mongolicus* and *A. gromovi* (Figures 2 and 3; Table 1). The karyotype of western Mongolian voles was described by Yatsenko, Malygin, Orlov, and Yanina (1980); these authors did not find notable difference in structure from *A. mongolicus* s. str. There are no nominal taxa of the species group belonging to *A. mongolicus* s.l. described from the territory of western Mongolia or near it. The nominal taxon *M. a. baicalensis*, as shown above, belongs to *A. middendorffii*. Thus, we describe this new taxon below in this paper after discussion of its taxonomic rank.

4.6 | Taxonomic status of short-tailed voles

Four taxa of short-tailed voles that were listed above are small or medium size voles, inhabiting wet alpine habitats across Siberia from the Ural to Pacific coast, and high altitude steppes in the region of eastern Mongolia. Distribution ranges of the four taxa are allopatric with closely approximating borders.

This group of voles has a rich history of taxonomic relocations that was previously described in detail (Bannikova et al., 2010; Lissovsky et al., 2010). Briefly, *A. middendorffii* and *A. mongolicus* were suspected to be close relatives of *M. arvalis* (Gromov & Erbajeva, 1995; Gromov & Polyakov, 1977; Ognev, 1950); *A. gromovi* was described as a subspecies of *A. maximowiczii* and was elevated to the species rank compared with the latter species (Sheremetyeva, Kartavtseva, Voyta, Kryukov, & Haring, 2009). Although *A. middendorffii* and *A. mongolicus* were allocated to the subgenus *Alexandromys* mainly on the basis of karyological features (Meyer et al., 1996; Pavlinov & Rossolimo, 1998; Pozdnyakov, 1996), the close phylogenetic unity of the short-tailed voles was finally demonstrated in mtDNA studies (Bannikova et al., 2010; Conroy & Cook, 2000; Lissovsky et al., 2010). Morphological study supports such unity: the cranial shape of *A. middendorffii* is very similar to *A. gromovi* (Lissovsky & Obolenskaya, 2011; Lissovsky et al., 2010), while the cranial shape of *A. mongolicus* s.l. is somewhat different, but also similar to the previous two taxa (Lissovsky & Obolenskaya, 2011).

Short-tailed voles form a stable compact clade in all analyses. Low bpp values on the species-tree reflect six haplotypes of *A. middendorffii* in the PRKCI gene that occupied an unresolved position within *Alexandromys*. Genetic distances between these four taxa in *cytb* are larger than in the case of *A. maximowiczii* (*A. m. maximowiczii*, *A. m. evoronensis* and *A. m. mujanensis*) described above. However, both mitochondrial and nuclear genes agree on two times shorter distances between taxa of short-tailed voles than between established species (Table 1). Thus, short-tailed voles comprise a group of very phylogenetically close and morphologically similar taxa with parapatric distribution.

Clearly, the taxonomic rank of the four taxa of short-tailed voles does not correspond to the taxonomic rank of established species such as *A. fortis* or *A. maximowiczii*. The observed pattern is more characteristic for so-called species complexes or groups of recently evolved taxa. Such complexes could be described as superspecies as in Abramson and Lissovsky (2012). Taking into account, the very short nuclear genetic distances between the four taxa compared to other *Alexandromys* species, and the absence of nuclear monophyly in these four taxa, one can unite short-tailed voles into one species. The choice of taxonomic decision depends mainly on the accepted species concept. As we

should describe a new taxon with definite taxonomic status, we choose a species rank for the short-tailed voles. The senior synonym for this species is *A. mongolicus*. Thus, we describe a new taxon from western Mongolia as a subspecies of *A. mongolicus* s.l. The morphological comparison of different species of *Alexandromys* was described in another publication (Lissovsky et al., accepted), so we cite it here.

Alexandromys mongolicus alpinus ssp. n. Lissovsky A.A., Yatsentyuk S.P., Petrova T.V., Abramson N.I.

ZooBank registration: urn:lsid:zoobank.org:act:640F3AA1-6EEB-4068-8CCB-C64EFC30BAB0.

Detailed description could be found in the supporting information (Appendix S1).

4.7 | Phylogenetic position and taxonomy of *A. limnophilus*

A lacustrine vole *A. limnophilus* inhabits wet habitats in extra dry surroundings from the Qaidam to Gobi Desert. According to Musser and Carleton (2005), the junior synonyms for this name are *A. flaviventris* Satunin, 1903; *A. malcolmi* Thomas, 1911; and *A. malygini* Courant et al. 1999. Representatives of these nominal taxa were never checked for genetic proximity. We had no data on *A. malcolmi*; however, we analysed *cytb* sequences derived from type specimens of *A. limnophilus* and *A. flaviventris*. The main study was conducted on the basis of specimens of *A. l. malygini* from Mongolia. Our results confirmed that *limnophilus*, *flaviventris* and *malygini* belong to the same clade, thus supporting the current taxonomic concept. We found some polymorphism in *cytb* sequences of *A. limnophilus*. This result is expected, as we previously found a morphological difference between *A. l. malygini* and *A. l. limnophilus* (Lissovsky & Obolenskaya, 2011). Although we found taxonomical integrity of *A. limnophilus*, it is premature to discuss taxonomy, unless a type specimen of *A. malcolmi* is evaluated.

The topology of mtDNA-based trees in both previous (Bannikova et al., 2010) and present (Figure 2; Fig. S1) studies contradict our nuclear DNA-based results (Figure 3). Both hypotheses are supported by similar bpp values. However, our JML study revealed that the position of *A. limnophilus* on the mitochondrial tree could be successfully explained by incomplete lineage sorting, if the nuclear data set reflects the true phylogenetic pattern. Thus, there are no unresolved conflicts between both sets of genes; we can hypothesise that *A. limnophilus* is a sister to short-tailed voles. This hypothesis is indirectly supported by morphological similarity of the voles in question (Lissovsky & Obolenskaya, 2011).

4.8 | Taxonomic status of *A. o. kharanurensis*

Our trees constructed on the basis of mtDNA confirm previous studies (Brunhoff, Galbreath, Fedorov, Cook, & Jaarola, 2003) in the existence of three clades within *A. oeconomus*: roughly European, Siberian and Beringian. Nuclear genes display a more homogenous cluster for the root vole as a whole. Thus, from a phylogenetic point of view, the root vole represents a compact clade.

Our previous morphological study (Lissovsky & Obolenskaya, 2011) suggested that *A. o. kharanurensis* forms a distinct group within *Alexandromys* voles. None of the genes used in the present study supported distinct position of *A. o. kharanurensis*. The phenomenon of morphological separation of *A. o. kharanurensis* could be explained by additional information obtained from the collector of the specimens studied. All specimens of *A. o. kharanurensis* in the collection of Zoological Museum of Moscow University originated from animals kept in captivity (V. Malygin, personal communication). This information was not indicated in the museum documentation. Captive mammals often have somewhat disproportional skulls, so this could be the reason for the separate position of *A. o. kharanurensis* in the morphological study.

ACKNOWLEDGEMENTS

We would like to thank I. Fefelov, T. Sirokhina (Irkutsk) for the help with Irkutsk collection, L. Voyta (St Petersburg) for the invaluable help during manuscript preparation, Y. Kovalskaya (Moscow). J. Cook (Museum of Southwestern Biology, Albuquerque), C. Conroy (Museum of Vertebrate Zoology, Berkeley), A. Kadetova, E. Nikanorov, Y. Redkin, S. Podolskiy, A. Romanov provided us with some samples for molecular analysis. Two anonymous reviewers made a number of valuable comments on the earlier version of the manuscript. This study supported by the Russian Foundation for Basic Research, Grant 14-04-00163 (for AAL and SPY), 15-04-04602 (for NIA and TVP), and 16-04-00983 (FNG); research project of MSU Zoological Museum (AAAA-A16-116021660077-3) and research project of the Theriology laboratory of ZIN RAS (AAAA-A17-117022810195-3).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Lissovsky AA, Petrova TV, Yatsentyuk SP, et al. Multilocus phylogeny and taxonomy of East Asian voles *Alexandromys* (Rodentia, Arvicolinae). *Zool Scr*. 2018;47:9–20. https://doi.org/10.1111/zsc.12261