

Original Article

Phylogeography of Korean field mouse *Apodemus peninsulae* (Rodentia: Muridae): an update

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ABSTRACT

To better understand the evolutionary and demographic histories of the Korean field mouse *Apodemus peninsulae* we examined mitochondrial (mt) cytochrome b gene sequences of 200 specimens from 65 localities in China, Japan, Korea, Mongolia, and Russia. The phylogenetic and phylogeographic analyses revealed three major groups of haplotypes: “Chinese” (C), “Korean” (K) and “Russian” (R). C includes only the samples from southern and central China, K combines all samples from Korean Peninsula and some samples from Siberia, and R comprises all samples from Russian Far East, Japan, and most samples from Siberia. Both R and K also include the samples from Northern China and Mongolia. Coalescent-based approaches suggest a link between separation of these groups and intensive Kung-Huang Pleistocene uplift event of the Tibetan Plateau. The rapid expansion events in R are associated with marine isotope stages (MIS) 3 and 4, and in K with MIS 6; no signs of rapid expansion were found in C. The widespread settlement of the northeast occurred in two waves, close in time: 1) to Northern China and Korean Peninsula, and then 2) to most of Siberia, the Russian Far East and Japan; parts of Siberia, Mongolia and northern China were colonized twice.

Keywords: molecular phylogeny - Genetics; mtDNA - Genetics; phylogenetic - Phylogenetics; Muridae - Taxa; species diversity - Taxonomy; comparative sequence analysis - Phylogenetics

INTRODUCTION

Global climatic fluctuations in the Pleistocene Epoch are known to have had a deep impact on species' distribution and the genetic structure of the current species worldwide (Avice 2000, Hewitt 2000). Under the influence of climatic fluctuations, some species disappeared from large areas of their ranges, others colonized new territories, and some species survived in refugia, then spread again, and these events occur repeatedly (Hewitt 1999, 2004, Michaux *et al.* 2005). Associations between genealogies and the geography of postglacial populations are determined by the values of population expansion, vicariant events, dispersive power, and refugial isolation (Bennett *et al.* 1997). Although the dynamics and consequences of colonization are species-specific, European and comparatively well-studied fauna were characterized by some common features of postglacial migrations (Taberlet *et al.* 1998). Due to monsoons from south-east Asia,

the climatic fluctuations in Asia during the Pleistocene Epoch were not as extensive as those in Europe or America, although cold and arid weather resulting from the Quaternary uplift of the Tibetan plateau fatefully affected the evolution and distribution of plants and animals, resulting in the disappearance of many species (Li *et al.* 1979, Qiu *et al.* 2011). The phylogeographic histories of species with a wide Eurasian/Asian distribution have been less studied, partly because of the difficulties associated with collecting materials over vast expanses of their ranges. However, an analysis of the available data has revealed some regularities. (i) Some species have low levels of genetic variation, which are observed as small phylogenetic trees or star-like haplotype networks, and this can be explained by rapid expansion across a large geographic area; (ii) there is limited correspondence between haplotypes and geographic distribution, with no clear definition of the refugial area or recolonization

pathways; and (iii) an evidence of a clear phylogeographic gap or signs of population expansion that date back to the pre-Vistula period (Painter et al. 2007). It has been also estimated that species of small mammals with a large geographical range often are a complex of cryptic species or complexes of deeply divergent phylogenetic lineages within the species (Jaarola and Searle 2002, Chelomina and Atopkin 2010, Paupério et al. 2012, Petrova et al. 2015).

The fauna of small mammals of north-east Asia, whose range includes many geographically separated domains, is of crucial interest for evolutionary biology, historical faunal reconstructions, and understanding the direction of genetic differentiation. Species of the trans-Paleartic genus of wood and field mice *Apodemus* Kaup 1829, ecologically associated with the forest zones of temperate latitudes, represent a convenient model for phylogeographic reconstructions. They have a short generation period and high rates of mtDNA substitutions, limited dispersal abilities, and a close relationship with the forest resources that altogether enhances the resolution of the phylogeographic analysis (Serizawa et al. 2000). The age of origin of the genus *Apodemus* is dated to the Late Miocene, approximately 10 Mya. The first rapid radiation of the genus in this epoch, about 5–6 Mya, followed by an appearance of some Asian wood mice, including *A. peninsulae*, is assumed to be associated with changes in the flora from tropical to temperate. The second radiation occurred 2–3 Mya at the beginning of the Quaternary period (Serizawa et al. 2000, Sakka et al. 2010, Ge et al. 2019).

The phylogeography of *Apodemus* species has been studied for a long time; however, some questions remain to be resolved or are still disputable (e.g. Serizawa et al. 2000, 2002, Michaux et al. 2003, 2005, Chelomina and Suzuki 2006, Suzuki et al. 2008, Chelomina and Atopkin 2010, Sakka et al. 2010, Oh et al. 2011, Liu et al. 2012, 2018, Ge et al. 2019, Latinne et al. 2020). The Korean field mouse *Apodemus peninsulae* Thomas 1906 is widespread in Asia, being a common and mass species in its localities. The species inhabits the most northern areas of the Asian part of the *Apodemus* range: the south of Siberia and the Russian Far East, Mongolia, the Korean Peninsula, and the Japanese Islands, and also a vast territory in China (Pavlinov et al. 1995). In contrast to other *Apodemus* species, inhabiting broad-leaf forests, *A. peninsulae* (similar to *A. agrarius* Pallas 1771) is commonly observed in more open habitats such as shrubs, sparse bushes, or steppes, etc. (Sakka et al. 2010, Ge et al. 2019). The northern borders of its range along the coast of the Sea of Okhotsk reach the Magadan Region, while the southern ones reach the Tibetan Plateau; the eastern borders are the islands of Sakhalin and Hokkaido, and the western borders are the Altai Mountains (Gromov and Erbajeva 1995, Kostenko 2000). Morphological differentiation of the Korean field mouse is weakly expressed; although nine subspecies are well described in world reports, not all of them can be certainly recognized so far (Vorontsov et al. 1977, Pavlinov et al. 1995). The species is well known to have a high number of polymorphic B-chromosomes (e.g. Rubtzov et al. 2009, Borisov et al. 2010, 2018, 2020, 2021). Additionally, *A. peninsulae* is of high epidemiological importance as a vector of borreliosis and leptospirosis, haemorrhagic fever, and is a host for such heavy human pathogens as hantavirus (Lokugamage et al. 2002, Zhang et al. 2007, Ge et al. 2019) and encephalitis virus (transmission occurs via tick bites feeding on infected rodents),

the reason for one of the most dangerous neuroviral infections in humans (Belikov et al. 2014). Thus in terms of public health it is very important to study Korean field mouse dispersion, as well as their genetic diversity and distribution. 2.60

The existence of different phylogeographic lineages within the *A. peninsulae* has previously been shown, suggesting the isolation and differentiation of the populations in separate refuge areas, during a substantial period of Quaternary glacial ages. Such genetic structure could be linked to the presence of biogeographic barriers probably reinforced during the Quaternary climate change (Serizawa et al. 2002, Sakka et al. 2010). However, the sample sizes analysed in these works are clearly insufficient for such a vast area with a geographically complex landscape to make reliable conclusions. The territories of Siberia, eastern and western Transbaikalia, turned out to be poorly investigated. We attempted to partially fill the gap in this work. 2.61

The present study aimed to shed more light on *A. peninsulae*'s genetic structure and its connection with the geographical structure of the species-area, to depict a demographic history, to detect putative refugia, and to suggest possible ways of species' dispersal based on an analysis of an extended database, which includes our new sequences and those available from GenBank. 2.65

MATERIALS AND METHODS

Samples and cytochrome *b* gene amplification

In the present study we used liver tissue samples stored in ethanol. The specimens were collected by the authors in different localities of Mongolia and Siberia. Animals were treated in accordance with the guidelines of the American Society of Mammologists, and within the European Union legislation guidelines (Directive 86/609/EEC). A total of 71 *Apodemus peninsulae* individuals were sequenced for the cytochrome *b* gene (*Cytb*) (see Supporting Information, Table S1). Altogether 129 *Cytb* sequences from *A. peninsulae* available in GenBank were also added to this dataset, representing a total of 65 localities in China, Korea, Russia, Japan, and Mongolia (Fig. 1; Table 1). 2.80

Genomic DNA was extracted using the Invitrogen Genomic DNA Extraction kit according to the manufacturer's instructions from liver tissue preserved in 95% ethanol at –20°C. The *Cytb* was amplified using the universal primers L14724 (5'-CGA AGC TTG ATA TGA AAA ACC ATC GTT G-3'), H15915 (5'-AAC TGC AGT CAT CTC CGG TTT ACA AGA C-3'), L15162 (5'-GCA AGC TTC TAC CAT GAG GAC AAA TAT C-3'), L15408 (5'-ATA GAC AAA ATC CCA TTC CA-3'), and H15149 (5'-AAA CTG CAG CCC CTC AGA ATG ATA TTT GTA CTC A-3') (Irwin et al. 1991). Amplifications were performed through 30 cycles (3 min/94°C 'hot start', 1 min/95°C, 1 min/50°C, 2 min/72°C) with a final 10-min extension cycle at 72°C. Polymerase chain reaction (PCR) products were sequenced directly on an ABI 3130 Genetic Analyzer using the ABI BigDye Terminator v.3.1 Cycle Sequencing Kit (Applied Biosystems). Nucleotide sequences were initially assembled using SeqScape v.2.6 (Applied Biosystems, USA) and aligned in the MEGA 6.0 program (Tamura et al. 2013) using the ClustalW algorithm. The resulting sequences were submitted to GenBank; the accession numbers are presented in Table 1. Outgroup species were also added from GenBank (Table 1). 2.85

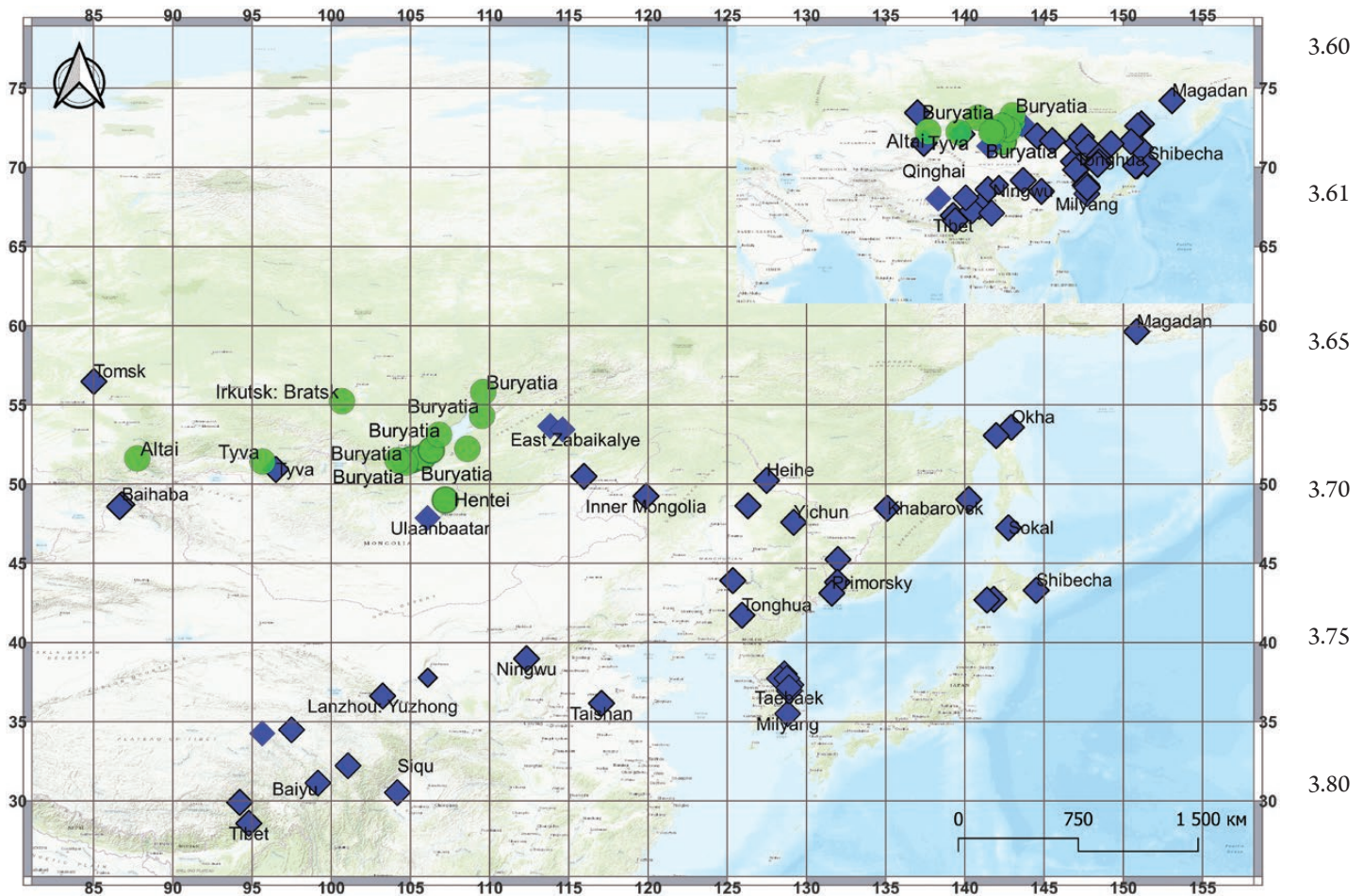


Figure 1. Sampling localities for the Korean field mouse. Circles are our data, and diamonds are GenBank data.

Data analysis

Haplotype (Hd) and nucleotide (Pi) diversities with their standard deviations within *Cytb* haplogroups and the distribution of nucleotide substitutions along the gene were calculated using DNASP v.5.1 (Librado and Rozas 2009).

To evaluate the intraspecific phylogenetic relationships among the samples, individual gene trees were reconstructed using Bayesian inference (BI) methods in MrBayes 3.1 (Ronquist and Huelsenbeck 2003), maximum likelihood (ML), and neighbour-joining (NJ) methods in MEGA 6.0. Three species as outgroup were used, *Apodemus mystacinus* (Danford and Alston 1877), *A. agrarius* (Pallas 1771), and *A. argentus* (Temminck 1844). The best-fit model of nucleotide substitution HKY+G+I was selected with jModelTest v.2.1.5 software (Darriba et al. 2012). Two parallel runs of Markov chain Monte Carlo (MCMC) analyses were performed for 10 million generations, with trees sampled every 1000 generations. The first 25% of the MCMC samples were discarded as burn-in, and the remaining samples were used to generate majority rule consensus trees. ML and NJ phylogenies were inferred using a HKY+G+I model of evolution and 1000 bootstrapping replicates in MEGA 6.0 (Tamura et al. 2013). Final trees were then viewed in FigTree 1.4.2 (available at <http://tree.bio.ed.ac.uk/software/fig-tree/>). The calculation of variable and parsimony-informative sites and genetic distances (Kimura 2-parameter model, K2P) was carried

out using MEGA 6.0. The time to the most recent common ancestor (TMRCA) of the *Cytb* sequences and 95% highest posterior density (HPD) were estimated using BEAST v.2.6.0 (Bouckaert et al. 2019). We chose Yule process tree priors, the HKY substitution model, and the strict clock model with a rate of 2.8% as estimated previously (Suzuki et al. 2015). Bayesian searches were conducted using the MCMC method for 10 million generations, of which the first 1 million were discarded as a burn-in. Sufficient sampling (ESS > 200) was confirmed in TRACER v.1.7 (available at <http://tree.bio.ed.ac.uk/software/tracer/>).

Phylogenetic networks were computed with a median-joining (MJ) algorithm implemented in NETWORK 4.6 (Bandelt et al. 1999) and the minimum-spanning trees (MST) algorithm in ARLEQUIN v.3.11 (Excoffier et al. 2005). Haplotype (Hd) and nucleotide (Pi) diversities with their standard deviations were calculated using the program DNASP v.5.1 (Librado and Rozas 2009). Population subdivisions was estimated using the hierarchical analysis of molecular variance (AMOVA) and genetic differences among populations were calculated by pairwise Fst test with 10 000 permutations in ARLEQUIN v.3.1. An Fst value ≥ 0.25 indicated that the gene flow was limited between two populations (Wright 1978). The historical population dynamics were analysed by mismatch distribution analyses using ARLEQUIN v.3.11 with

Table 1. Geographical locations and GenBank accession numbers of *Apodemus peninsulae* sequences used in the present study

Species	Geographic origin: country, province, city	Total number of animals	GenBank accession numbers	The associated studies	
4.5	<i>A. peninsulae</i>				4.60
	Southern China				
	Tibet	4			
	Milin		MK329420; MK329422	Ge et al., 2019	4.61
	Linzhi		MK329412; MK329413	Ge et al., 2019	
4.10	Central China				
	Sichuan	12			
	Rangtang		AM945779; AM945842; AM945840; AM945789; AM945790; AM945791; AM945798; AM945799; AM945843	Sakka et al., 2010	4.65
4.15	Baiyu		AY389001	Liu et al., 2004	
	Siqu		MG748198; MG748199	Liu et al., 2018	
	Shansi	1			
	Ningwu		MG748201	Liu et al., 2018	4.70
	Ningxia	11			
4.20	Xiji		AM945792–AM945797; AM945780; AM945781; AM945841; AM945787; AM945788	Sakka et al., 2010	4.75
	Shandong	1			
	Taishan		AY389002	Liu et al., 2004	
4.25	Qinghai	3			
	?		MG748193; MG748195; MG748239	Liu et al., 2018	
	Gansu	1			4.80
	Lanzhou		KP671850	Jeong et al., 2016	
4.30	Northern - Northeastern China				
	Jilin	2			
	Changchun		AY388999	Liu et al., 2004	4.85
	Tonghua		MK329530	Ge et al., 2019	
4.35	Heilongjiang	4			
	Haili		AY38900	Liu et al., 2004	
	Wudalianchi		MK329468	Ge et al., 2019	4.90
	Yichun		MG748168	Liu et al., 2018	
	Heihe		MK329471	Ge et al., 2019	
4.40	Inner Mongolia	6			
			KX066074; KX066075	Zuo et al., unpublished	
			MG748177–MG748179	Liu et al., 2018	4.95
			AY389003	Liu et al., 2004	
4.45	Northwestern China				
	Xinjiang	5			
	Baihaba		AM945782–AM945785	Sakka et al., 2010	
	?		MG748219	Liu et al., 2018	4.100
4.50	Japan				
	Hokkaido	4			
			AB032850	Serizawa et al., 2000	
			AB073788; AB073789; AB073790	Serizawa et al., 2002	4.105
4.55	Korea				
	South Korea	48			
			AB073809–AB073811	Serizawa et al., 2002	
			KT364347–KT364388	Kim and Park, 2015	
			JNS46584	Kim and Park, 2011	4.110
			HQ660074; HM034941	Oh et al., 2011	

Table 1. Continued

Species	Geographic origin: country, province, city	Total number of animals	GenBank accession numbers	The associated studies	
5.5	Mongolia	16			5.60
	<i>Ulan Bator</i>		JQ664593–JQ664597	Bayarlkhagva <i>et al.</i> , 2013	
	<i>Hentei</i>		MF143532–MF143542	Atopkin, unpublished	5.61
	Russia				
5.10	<i>Far East</i>	15			
	Magadan		AB073795	Serizawa <i>et al.</i> , 2002	
	Sakhalin		AB073791–AB073793	Serizawa <i>et al.</i> , 2002	5.65
	Khabarovsk		AF427335–AF427338	Dekonenko and Ivanov, unpublished	
5.15	Primorye		AB073794; AB073796–AB073800	Serizawa <i>et al.</i> , 2002	
	<i>Siberia</i>	67			
	Transbaikal		AB073801–AB073805	Serizawa <i>et al.</i> , 2002	5.70
	Buryatia		ON986853–ON986882; ON986889–ON986896	Present study	
5.20	Irkutsk		ON986883–ON986888; ON986897–ON986898	Present study	
	Baikal region		OP429092	Present study	5.75
	Altai		AB073806; AB073808	Serizawa <i>et al.</i> , 2002	
			MF143521–MF143531	Atopkin, unpublished	
5.25	Tyva		AB073807	Serizawa <i>et al.</i> , 2002	
			ON986899; ON986900	Present study	
	Tomsk		AB073806	Serizawa <i>et al.</i> , 2002	5.80
	Outgroup				
5.30	<i>A. mystacinus</i>		MW287354	Mohammadi <i>et al.</i> , 2021	
	<i>A. agrarius</i>		AB303225	Suzuki <i>et al.</i> , 2008	
	<i>A. argenteus</i>		AB164581	Suzuki <i>et al.</i> , 2004	5.85

10 000 permutations. This distribution is usually multimodal in populations at demographic equilibrium, but it is unimodal in populations that had passed through a recent demographic expansion or through a range expansion with high levels of migration between neighbouring demes (Excoffier 2004). The sum of squared deviations (SSD) and the raggedness index (Rg), to determine whether the sequences deviated significantly from a model of population expansion, were also estimated in the ARLEQUIN v.3.11. The neutrality test statistic F_s (Fu 1997) were applied to detect recent population expansion; P -values were generated using 10 000 coalescence simulations in the ARLEQUIN v.3.11. The F_s statistic is sensitive to population demographic expansions, which generally lead to a negative F_s value. The time parameter (Tau) expressed in mutational units was estimated by generalized non-linear least squares using the ARLEQUIN v.3.11.

We used the Bayesian skyline plot (BSP; Drummond *et al.* 2005), as implemented in BEAST v.2.6.0, to estimate demographic variations in phylogenetic lineages over time. The BSP analyses were carried out using a strict clock model. We performed two independent MCMC runs of 10 million iterations each, sampling every 1000th step for each lineage. The results of the independent runs were combined with LogCombiner

v.2.1.0 after the removal of 25% burn-in. TRACER v.1.7 was used to verify that the runs were successful (ESS > 200) and to visualize plots of the female effective population sizes (N_e) over time. The start times (t) of expansion events were calculated using the equation $t = \tau/2\mu k$, where τ is the expansion parameter, μ is the evolutionary rate (substitutions per site per years), and k is the length of the analysed fragment (Suzuki *et al.* 2015). We used the time-dependent evolutionary rates of *Cytb* in small mammals: 2.8%, 4.7%, and 11% for Tau of approximately 7–8, 5, and 3, respectively (Suzuki 2021, Inoue *et al.* 2022).

RESULTS

Phylogenetic analysis and divergence time

The phylogenetic analysis of 200 *Cytb* sequences of *A. peninsulae* detected 794 conserved sites (80.04%) and 198 variable sites (19.96% of all sites). Among variable sites, 64.14% (12.8% of total) were parsimony informative across the 992 bp alignment. The K2P distances between haplotypes ranged from 0.00% to 5.1% (average 2.0%).

The phylogenies estimated by NJ, ML, and BI were consistent with each other, and the topology was generally supported (Fig. 2). All *A. peninsulae* samples formed a strongly supported (BS = 99,

5.60

5.61

5.65

5.70

5.75

5.80

5.85

5.90

5.95

5.100

5.105

5.110

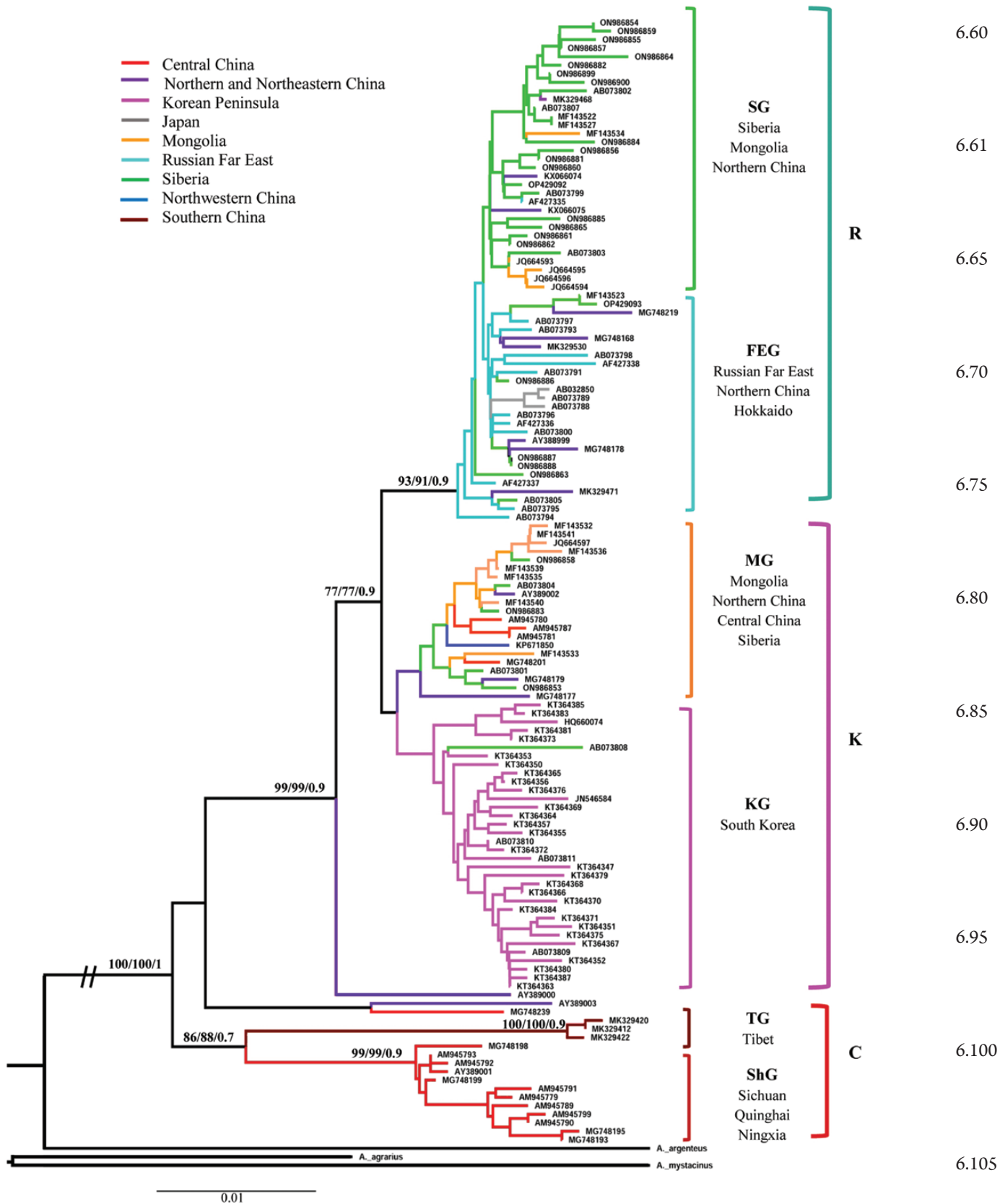


Figure 2. Evolutionary relationships of Korean field mouse *A. peninsulae* based on mitochondrial *Cytb* gene. Bootstrap values and posterior probabilities (NJ/ML/BI) are given as node labels.

PP = 1.0) monophyletic group. Phylogenetic trees clearly indicated three major groups of haplotypes. The first included all specimens from the Russian Far East and Japan, and most samples from Siberia, while the second included all samples from the Korean Peninsula and some samples from Siberia. Some localities of northern China, Siberia, and Mongolia are common for both haplotype groups. The third group of haplotypes consisted of samples only from China. Thus, 1, 2, and 3 haplotype groups can be conditionally called Russian (R), Korean (K), and Chinese (C), respectively. All samples from the Korean haplotype group are divided into two groups: one of which (KG) includes only Korean samples with one exception, and the other (MG) consists mainly of specimens from Mongolia; however, the subdivision is only slightly supported statistically. Within R, two groups of haplotypes can also be roughly distinguished: Siberian (SG) and Far Eastern (FEG), comprising mainly the samples from Siberia and the Russian Far East, respectively. The Chinese haplotype group clearly subdivided into Tibetan (TG, samples only from Tibet) and Sichuan (ShG, consisting mainly of samples from Sichuan, and also from Ningxia and Qinghai) groups. High statistical support was obtained for R ($BS \geq 91$, $P = 0.9$), TG and ShG ($BS \geq 99$, $P = 0.9$ for both), and also for C ($BS \geq 86$, $P = 0.7$) and R + K ($BS = 77$, $P = 0.9$). However, no statistical support was obtained for the separation between C and AY389003 + MG748239.

The K2P distances between haplotype groups (Fig. 2) are ranged from 4.56% when compared TG with Russian and Korean haplotype groups to 1.34% when Korean haplotype subgroups were compared with each other. Most of the differences appeared to be fixed when compared ShG and TG between themselves and with R and K. Numerous fixed mutations resulted in five certain amino acid substitutions when comparing C with R and K: Pro → Leu (4th codon), Leu → Pro (149th and 278th codons), Ile → Thr (176th codon), and Val → Gly (287th codon). In contrast, only two fixed nucleotide differences were revealed between R and K.

Divergence timing data (Fig. 3) indicated that the earliest split within *A. peninsulae* occurred about 0.86 (0.680–1.080, HPD 95%) Mya between the south-west C and north-east R + K haplotype groups. Approximately 0.61 (0.405–0.832, HPD 95%) Mya, Chinese haplotypes were subdivided into the Tibetan (TG) and Sichuan (ShG) groups. Later, about 0.42 (0.312–0.536, HPD 95%) Mya, the Korean and Russian haplotype groups were separated, and the MG/KG and SG/FEG subdivision occurred about 0.34 (0.255–0.432, HPD 95%) and 0.25 (0.186–0.313, HPD 95%) Mya, respectively.

Phylogeography

Median-joining haplotype network (Fig. 4) is strictly supported by phylogenetic analysis showing the genealogical relationships among *Cytb* haplogroups of the Korean field mouse. By phylogeographic pattern they are divided into four, major subdivided mtDNA lineages: conditionally 'mixed', north-eastern, south-western, and north-western lineages. The first lineage consists of three highly divergent haplotypes from Heilongjiang (L3—AY389000), Qinghai (L2—MG748239), and Inner Mongolia (L1—AY389003). The south-west lineage subdivided into Tibet and Sichuan lineages; the first includes specimens from the Tibetan Plateau and the second comprises specimens from Sichuan, Qinghai, and Ningxia (TG and ShG groups, respectively).

The north-west lineage, splitting from the north-east lineage, is represented only by Xinjiang specimens with a single haplotype (L4—MG748219). The north-eastern lineage includes all the remaining samples and is represented by two large and clearly differentiated phylogeographic groups, R and K, which correspond to those on the phylogenetic tree (see Fig. 2). Similar to the phylogenetic analysis, there is a weak region-specific subdivision within the K and R groups. Genetic differentiation indices F_{st} between major phylogeographical groups were the following: 0.730, 0.848, and 0.460 ($P < 0.001$) for C/K, C/R, and K/R, thus indicating a high level of genetic differentiation.

There were 130 different *Cytb* haplotypes defined in the dataset. The overall haplotype (Hd) and nucleotide diversity (π , %) were 0.992 and 1.987, respectively (Table 2). All three representative phylogeographical groups (ShG, K, and R) show high genetic diversity, with approximately equal values of haplotype diversity ($Hd \geq 0.900$), and twice higher nucleotide diversity in the K compared to both the ShG and R ($\pi = 1.21\%$ vs. $\pi = 0.52$ – 0.67%). In addition, the values of the temporal coefficient Tau are also significantly higher for K (Table 2). Moreover, the patterns of nucleotide diversity distribution along the gene, as well as a pattern of haplotype frequency (Supporting Information, Fig. S1), are significantly different between the phylogeographical groups. Comparison of MG and KG showed higher values of parameters of genetic diversity (especially nucleotide) and Tau in KG. When comparing SG and FEG, the values of genetic diversity parameters were higher in FEG, while the Tau values were almost the same (Table 2).

Historical demography

The mismatch analysis of the *Cytb* sequences was performed for each haplotype groups, and the rapid expansion model was not rejected in all datasets. In general, the distribution of pairwise genetic differences was unimodal, with low SSD and Rg values. The F_s tests for selective neutrality showed significant negative values ($P < 0.05$) in all datasets except ShG (Table 2; Fig. 5, left). The BSP (Fig. 5, right) showed specific median lines and a rather similar underlying trend (at HPD 95%) in population dynamics over time for different haplotype groups. Both K and R showed signs of sudden expansion; however, only K demonstrated signs of population decline in the present. The slight signs of population growth with no strong signs of expansion in the last 70 000 years were estimated for the ShG, suggesting that the hypothesis of a stable effective population size cannot be rejected.

To estimate the timing of expansion events, we used different evolutionary rates according to Tau values (Table 2). The start time of the expansion event in FEG and SG at an evolutionary rate about 4.7% was estimated to be 54 000 and 59 000 years ago, corresponding to MIS (marine isotope stage) 3 (30–57 kya) and MIS 4 (57–71 kya). The start times of the expansion event in MG and KG at an evolutionary rate of about 2.8% was estimated to be 142 000 and 172 000 years ago, corresponding to MIS 6 (130–191 kya). At the same evolutionary rate, the start of the R and K expansion occurred 120 000 and 220 000 years ago, which correspond to MIS 5 (72–130 kya) and MIS 7 (191–243 kya), respectively.

Population genetic analysis

For a deeper understanding of the nature of genetic diversity distribution over the species' range, a comparative analysis of

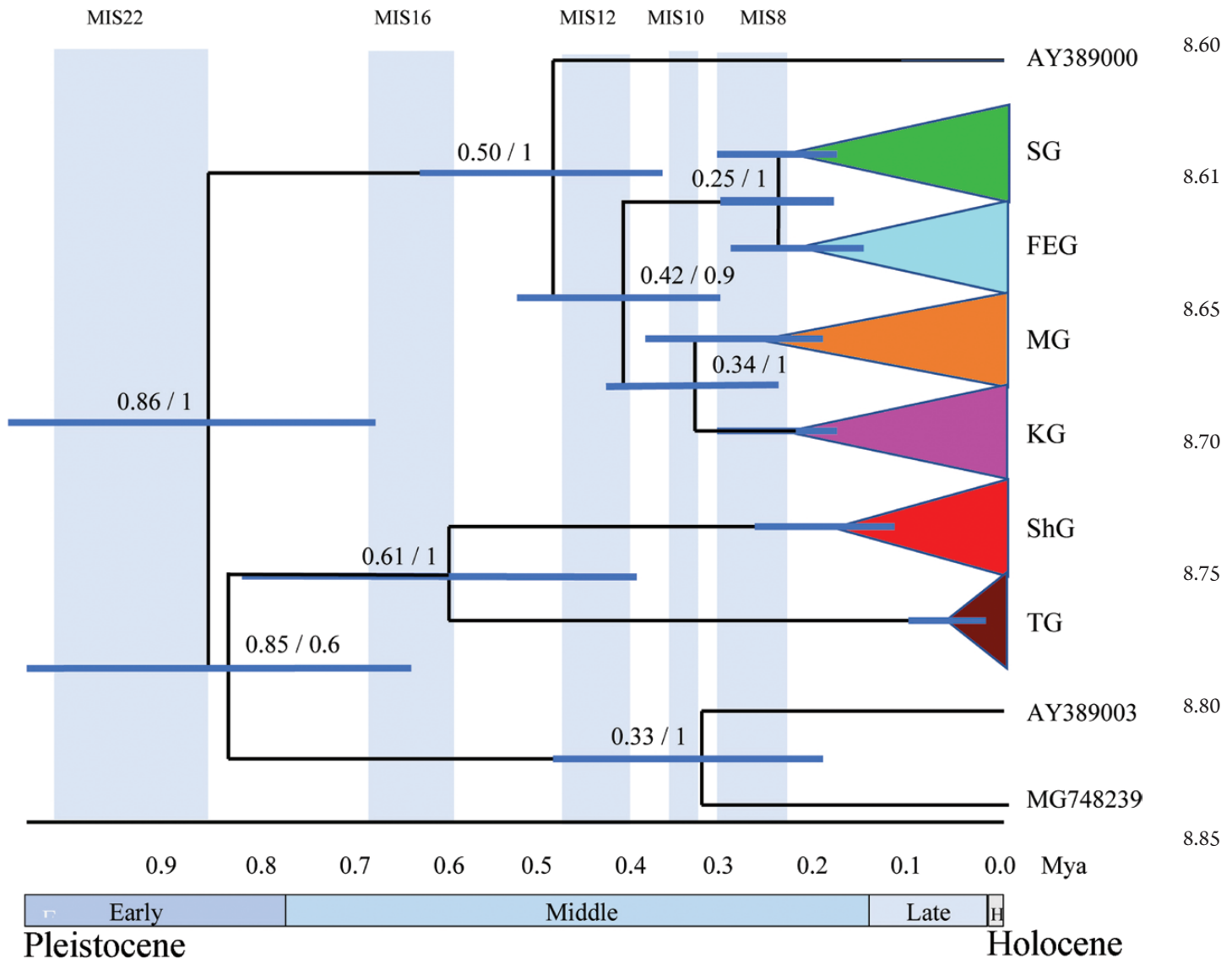


Figure 3. Chronogram of *Apodemus* based on *Cytb* sequences. Branch lengths represent time; node bars indicate the 95% CI for the clade age; the median ages and Bayesian posterior probabilities are given as node labels.

individual geographical populations was carried out. The results showed that the populations of Qinghai, Ningxia, and Inner Mongolia are genetically the most diverse, while the populations of the Far East (mainland and especially Sakhalin and Hokkaido Islands) and Tibet are the least genetically diverse (Table 3). Demographic growth of the populations of Korea, Mongolia, and the Far East mainland was supported by statistically significant neutrality test values, while the populations of Qinghai and Ningxia were the most stable.

The pairwise estimations of F_{st} among populations range widely from negative values to almost 1 (Table 4). Most populations are strongly differentiated ($F_{st} > 0.25$) indicating highly restricted gene flow. The populations of Sichuan, Qinghai, and Tibet are the most differentiated from the others ($F_{st} = 0.612$ – 0.888) and have fixed nucleotide substitutions. The populations of Korea and Ningxia (with one exception) are also clearly differentiated from all populations, while Far Eastern populations (both mainland and islands) are strictly differentiated (besides

those listed above) only from Altaic and Mongolian populations. High levels of gene flow are often observed within geographically close populations of North China, Siberia, and the Far Eastern mainland (e.g. populations of Transbaikalia and north-east China, $F_{st} < 0.00$). Interestingly, the F_{st} value between the island populations (Sakhalin and Hokkaido) and the population of the Korean Peninsula is several times higher than in comparison with the mainland population of the Russian Far East. The results are well illustrated by the number of direct links between haplotypes (based on MST reconstruction) across species' range, which vary greatly among different geographical populations (Supporting Information, Fig. S2).

The pattern of the nucleotide diversity distribution along the *Cytb* in different populations is different, but all types can be combined into several main groups: Ningxia-, Qinghai-, and Sichuan-like. The first group is characterized by a peak diversity in the central part (450 bp) of the gene sequence, the second group has a conserved region that clearly divides the sequence

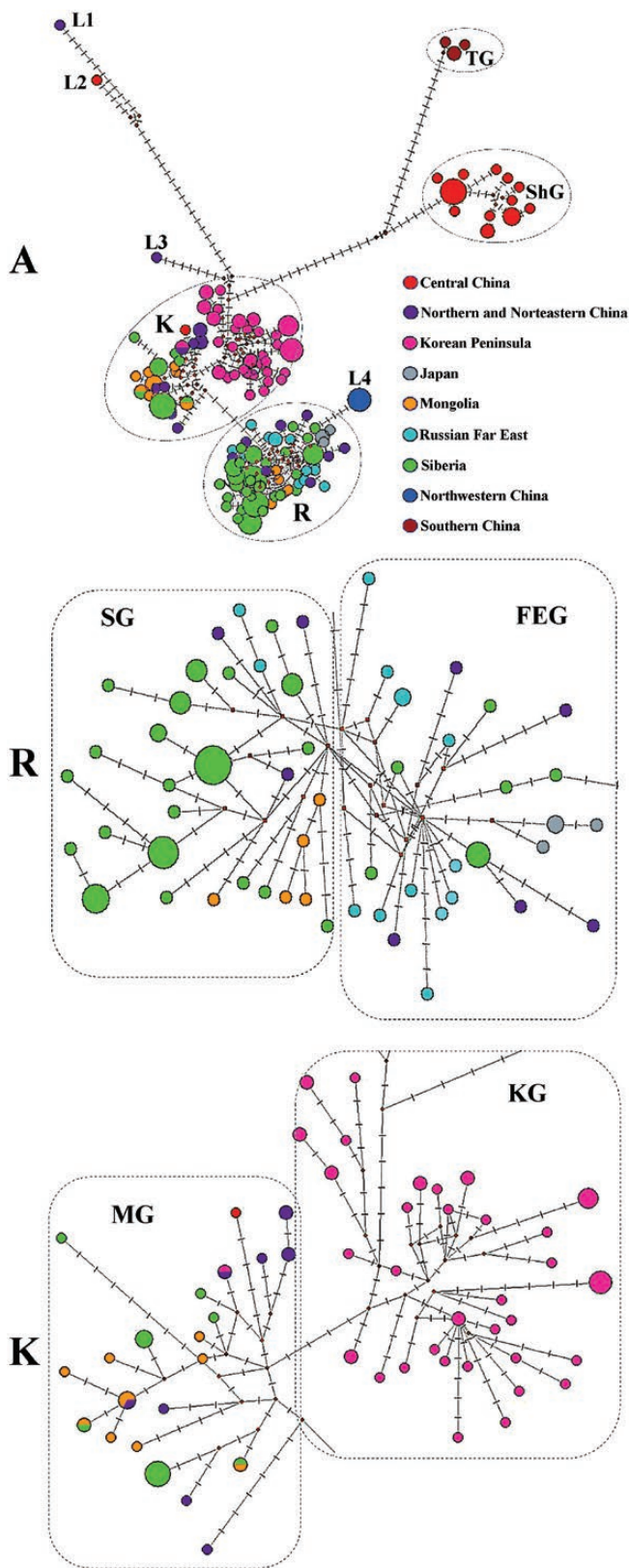


Figure 4. Median-joining network of all of the Korean field mouse *Cytb* haplotypes (A), and of Russian (R) and Korean (K) phylogeographic groups on a large scale. L1 represents AY389003, L2—MG748239, L3—AY389000, and L4—MG748219 sequence (see Table 1). Size of circles is proportional to the haplotype frequency. Dashes indicate mutational steps. Dots represent undetected haplotypes.

into two parts, and the third group (the largest) is characterized by a peak at the beginning (160 bp) of the sequence (Supporting Information, Fig. S3). 9.60

DISCUSSION 9.61

This study executed comprehensive phylogeographic analyses to infer the evolutionary history of the Korean field mouse *A. peninsulae* and to provide insights into the processes that shaped its distribution pattern, first of all in the north-eastern part of the species area. 9.61

Phylogenetic patterns and dating 9.65

The intraspecific mtDNA phylogeny revealed a clear hierarchical pattern of divergence with an acceptable geographical structure, suggesting *A. peninsulae* resettlement from south-west China (see Fig. 2, the tree base) to the north-east, up to the Russian Far East and Japan (Fig. 2, the tree top). This result is in good agreement with the existing ideas that in the Late Pliocene, when climate became arid, *Apodemus* probably expanded to northern China and Mongolia (Ge et al. 2019). The main divergence usually is due to geological events and Pleistocene climatic changes, often resulting in geographical isolation of populations, and this is profoundly marked in the species' genetic structure (Avice 2000). 9.70

For the first time, we have dated major divergent events within the Korean field mouse and have estimated their association with the most significant geological events in south-west China during the Eopleistocene, as well as with global climate change. The divergence time of the earliest *A. peninsulae* splits, R + K/C (~0.86 Mya) and ShG/TG (~0.61 Mya), estimated in this study may have been associated with Kun-Huang (1.2–0.6 Mya) movements known as one of the most intense uplift events in the Tibetan Plateau (Fig. 3; Zheng et al. 2000, Zhisheng et al. 2001, Fan et al. 2012), and also with MIS 22 (866–1030 kya) and MIS 15 (563–621 kya) on the global scale of climate change, respectively. It is significantly later than the period of the most ancient Danube glaciation in Europe (1.5–1.8 Mya) in the Early Pleistocene, when Asian and European races of the pygmy wood mouse *Apodemus uralensis* Pallas 1811 separated (Chelomina and Atopkin 2010) and European continental *A. sylvaticus* Linnaeus 1758 populations were split into two main genetic lineages, non-overlapping in their geographical distributions (Michaux et al. 2005). The timing of R/K, KG/MG, and SG/FEG separations (~0.25–0.42 Mya) may have been associated with the glacial period of MIS 11 (374–424 kya), MIS 10 (337–374 kya), and MIS 8 (243–300 kya), respectively. These results are in good agreement with data obtained from *A. speciosus* in the Japanese archipelago (Suzuki et al. 2015), suggesting a similar response of wood mice to climate change in East Asia. 9.80

Phylogenetic analysis, supported by phylogeographic reconstructions, have revealed highly divergent lineages of *A. peninsulae*, which is also characteristic of other species of different taxonomic groups (reptiles, amphibians, fish, insects, and rodents) that are widespread in East Asia, and often with pronounced north–south discontinuities (Ding et al. 2011, Petrova et al. 2015, Chen et al. 2017, Lebedev et al. 2018, Song et al. 2018, Tang et al. 2022). In addition, the phylogenetic pattern of Korean wood mice with different levels of differentiation 9.105

Table 2. Genetic diversity and parameters of the demographic expansion for each phylogeographic group. Three Tibetan haplotypes of TG, as well as 'L' haplotypes (see text), were not analysed separately, but the corresponding samples were taken into account in the analysis of the total sample. *N*, sample size; *S*, number of polymorphic sites; *h*, number of haplotypes; *Hd*, haplotype diversity; *Pi*, nucleotide diversity; *F_s*, Fu's statistical tests of neutrality; *SSD*, sum of squared deviations; *Rg*, raggedness index; *Tau*, time parameter of the demographic expansion; *SD*, standard deviation; *P*, *P*-value.

Specimens	<i>N</i>	<i>S</i>	<i>h</i>	<i>Hd</i> ± <i>SD</i>	<i>Pi</i> , % ± <i>SD</i>	<i>F_s</i> (<i>P</i>)	<i>SSD</i> (<i>P</i>)	<i>Rg</i> (<i>P</i>)	<i>Tau</i>
Total	200	198	130	0.992 ± 0.002	1.987 ± 0.102				
Chinese (ShG)	20	23	12	0.900 ± 0.053	0.522 ± 0.048	-2.2908 (0.169)	0.0158 (0.65)	0.0227 (0.95)	7.287
Korean (K)	81	108	55	0.985 ± 0.005	1.208 ± 0.059	-24.3200 (0.000)	0.0033 (0.40)	0.0039 (0.80)	12.268
Russian (R)	87	91	56	0.977 ± 0.008	0.673 ± 0.040	-25.1203 (0.000)	0.0006 (0.95)	0.0095 (0.90)	6.667
MG (Mongolian)	33	41	21	0.956 ± 0.022	0.666 ± 0.045	-7.2647 (0.006)	0.0093 (0.25)	0.0222 (0.40)	7.879
KG (Korean)	48	73	34	0.980 ± 0.010	0.884 ± 0.046	-16.9452 (0.000)	0.0030 (0.45)	0.0117 (0.25)	9.546
SG (Russian)	56	51	32	0.953 ± 0.015	0.526 ± 0.033	-17.6717 (0.000)	0.0039 (0.55)	0.0189 (0.45)	5.824
FEG (Russian)	31	54	27	0.984 ± 0.016	0.664 ± 0.068	-16.8405 (0.000)	0.0036 (0.20)	0.0161 (0.20)	5.498

between individual lineages preceding the last glacial maximum may indicate the predominance of the vicarious model in the evolutionary history of *A. peninsulae*, which is widely accepted for the Pleistocene fauna, including that of East Asia (Ding *et al.* 2011, Song *et al.* 2018, Tang *et al.* 2022).

Phylogeography and historical demography

Quaternary environmental changes, occurring in 100-Kyear cycles, have influenced the population dynamics and genetic structure of many terrestrial mammal species (Hewitt 2000, 2004, Sakka *et al.* 2010). At that, populations in refugia often reflect long-term stability, while populations on colonized regions are usually characterized by rapid population expansion (Sawyer and Cook 2016). In this study, we have demonstrated the different demographic histories of the three main phylogeographic lineages of the Korean wood mice. Because the rate of mtDNA evolution in animals is variable and time-dependent, especially during the early stages of divergence, and estimates based on genealogy may exceed estimates from phylogenetic studies on geological timescales by one to two orders (e.g. Ho *et al.* 2005, 2015, Ho and Larson 2006, Suzuki *et al.* 2015, Suzuki 2021), here we calculated the timing of a population expansion based on *Tau* values. We have identified evidence of sudden expansion of most haplotype groups of the Korean field mouse, reflecting global climate change during the Quaternary glacial cycles. The major expansion events in *A. peninsulae* populations occurred before LGM (~20 kya) in periods of MIS 6 (C, MG, and KG) and MIS 3–4 (R, SG, and FEG), i.e. first (131–172 kya) in the south-west, and then (71–59 kya) in the north-east part of the species' range, which reflects the direction of the probable dispersal of the wood mice. In the Japanese archipelago, *A. speciosus* (Temminck 1844) and grassland *Myodes* voles experienced rapid expansion due to environmental changes during MIS 4 and MIS 3 (Honda *et al.* 2019, Inoue *et al.* 2022). The striped field mouse *A. agrarius* Pallas 1771 (sympatric with *A. peninsulae* in the eastern part of its range) also showed evidence of a rapid expansion during MIS 4–3 (Kozyra *et al.* 2021), although another report suggested that the transcontinental expansion of *A. agrarius* was a relatively recent event that occurred after the LGM (Yalkovskaya *et al.* 2022).

The available data indicate that during most of the Pleistocene, other small mammals (such as voles and lemmings) common in Siberia and the Far East were also assessed as successful species

(Fedorov *et al.* 2008, Petrova *et al.* 2015). Given these data, the reasons for the population decline in the recent history of group K are of some interest. It can be assumed that climate humidification and the wide distribution of woody vegetation at the Pleistocene–Holocene boundary were more pronounced on the Korean Peninsula, which contributed to the reduction of habitats in the Late Holocene, since the Korean mouse prefers more open landscapes compared to other species of wood mice (Sakka *et al.* 2010, Ge *et al.* 2019). Chinese phylogeographical groups did not experience recent population expansion; however, population growth was constantly low during the Holocene. Although the species inhabiting south China have different population demography histories, many of them had experienced population expansion before LGM, and estimates are greatly varied. *Apodemus draco* Barrett-Hamilton 1900 of the Tibetan Plateau experienced population expansion approximately 52–13 kya, or 14–4 kya, i.e. before or after LGM (Fan *et al.* 2012), while population expansions of *A. ilex* (Temminck 1844) were roughly 89–23 kya (Liu *et al.* 2012). At the same time, population stability was indicated for south China populations of *Eothenomys melanogaster* Milne-Edwards 1871 in the post-glacial (Lv *et al.* 2018).

Analysis of haplotype and nucleotide diversity (Table 2) can also provide insight into the demographic history of populations and consider inferences about past demographic events. Thus, high values of both parameters (which have been estimated for most geographic populations) reflect a large population size and extended range. The high gene and low nucleotide diversities (which is more consistent with the Tibetan and insular populations) are the result of long-term isolation of the population with its relatively small size. The low values of both parameters (not observed in our study) would indicate that population was originated from an ancestral population with low effective population size survived a period of depression (Avice 2000, Painter *et al.* 2007, Galbreath *et al.* 2009). Thus, the obtained genetic diversity parameters reject the bottleneck hypothesis for all populations, as well as their origin from a small ancestral population for almost all, suggesting that this species was successful during most of the Pleistocene and that climate humidification and extensive tree vegetation development in the Pleistocene–Holocene boundary contributed to the increase in range. This is consistent with the statement that the main patterns of post-glacial changes in the diversity of Palearctic mammals were not

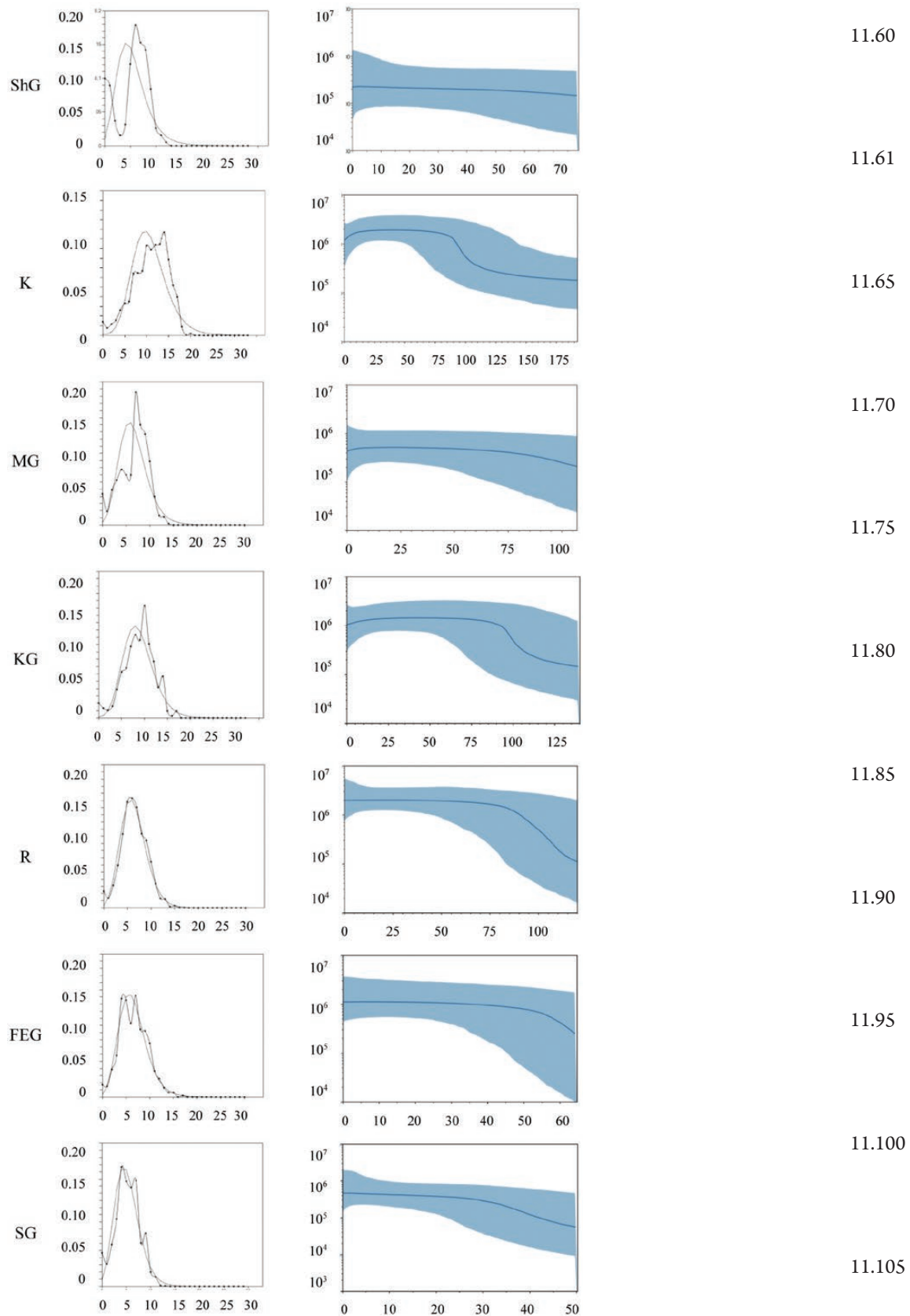


Figure 5. Historical demography analyses of the Korean field mouse: left—mismatch distribution; right—the Bayesian skyline plots for Sichuan (ShG), Korean and Mongolian (K), Mongolian only (MG), Korean only (KG), Russian (R), Far Eastern (FEG), and Siberian (SG) groups of haplotypes. For mismatch distribution the solid line indicates the observed and the dashed line expected number of pairwise differences; for the Bayesian skyline plots the central thick line indicates the median value of effective population size (Y-axis) through the time (X-axis, thousand years ago); the shaded area denotes the 95% highest posterior probability intervals.

Table 3. Genetic diversity and parameters of the demographic expansion for separate geographical populations. For column headers see [Table 2](#). Significant values of neutrality test statistics are signed with a star

Region	N	S	h	Hd ± SD	Pi, % ± SD	F _s (P)	SSD	Rg
Korea (KOR)	49	75	35	0.980 ± 0.010	0.891 ± 0.044	-18.027 (0.000)*	0.002	0.01
Altai (ALT)	16	33	7	0.692 ± 0.124	0.607 ± 0.242	1.536 (0.775)	0.04	0.077
Irkutsk Reg., Russia (IRK)	18	29	9	0.895 ± 0.044	0.650 ± 0.117	0.381 (0.566)	0.063	0.135
Buryatia Rep., Russia (BUR)	28	46	15	0.931 ± 0.029	1.236 ± 0.070	0.872 (0.653)	0.033	0.056
Mongolia (MNG)	15	36	14	0.990 ± 0.028	1.129 ± 0.139	-4.486 (0.026)*	0.018	0.02
Northeast China (NEC)	6	37	6	1.000 ± 0.096	1.331 ± 0.324	-0.549 (0.345)	0.081	0.133
Inner Mongolia Aut. Reg., China (NM)	6	59	6	1.000 ± 0.096	2.312 ± 0.616	0.180 (0.319)	0.077	0.116
Russian Far East, mainland (RFE)	11	28	11	1.000 ± 0.039	0.616 ± 0.082	-6.094 (0.002)*	0.007	0.029
Far East Islands: Sakhalin and Hokkaido (FEI)	8	13	6	0.929 ± 0.084	0.486 ± 0.074	-0.092 (0.428)	0.092	0.272
Transbaikalia (TRB)	5	29	5	1.000 ± 0.126	1.391 ± 0.221	0.074 (0.323)	0.739	0.2
Sichuan Prov., China (SC)	13	53	11	0.974 ± 0.039	1.127 ± 0.433	-1.704 (0.171)	0.013	0.024
Qinghai Prov., China (QH)	3	37	3	1.000 ± 0.272	2.484 ± 1.141	2.080 (0.548)	0.27	0.444
Ningxia Hui Aut. Reg., China (NX)	11	37	5	0.782 ± 0.107	1.972 ± 0.258	7.203 (0.994)	0.128	0.115
Tibet Aut. Reg., China (TAR)	4	3	3	0.833 ± 0.222	0.151 ± 0.055	-0.287 (0.221)	0.006	0.083

Table 4. Genetic differentiation among the geographical populations of *Apodemus peninsulae*. Pairwise F_{st} values are below diagonal, a number of fixed differences/shared mutations are above diagonal; insignificant indices are marked by a star; extremely high indices and fixed differences are in bold. For regions' abbreviation see [Table 3](#).

	KOR	ALT	IRK	BUR	MNG	NEC	NM	RFE	FEI	TRB	SC	QH	NX	TAR
KOR	-	0/19	0/16	0/16	0/14	0/10	0/20	3/7	3/6	0/15	1/15	12/11	0/15	25/0
ALT	0.54	-	0/18	0/20	0/20	0/12	0/18	0/7	0/3	0/17	1/8	14/3	0/7	32/0
IRK	0.547	0.138*	-	0/22	0/17	0/13	0/17	0/4	0/1	0/16	1/8	13/2	0/7	31/0
BUR	0.406	0.120*	0.081*	-	0/23	0/15	0/23	0/8	0/1	0/19	1/9	13/2	0/9	31/0
MNG	0.351	0.345	0.361	0.110*	-	0/15	0/21	0/4	0/1	0/19	1/11	11/4	0/11	31/1
NEC	0.475	0.208*	0.115*	0.084*	0.240*	-	0/21	0/8	0/2	0/13	1/15	7/5	0/10	30/1
NM	0.379	0.197*	0.177*	0.034*	0.085*	-0.014*	-	0/9	0/4	0/18	1/21	1/11	0/19	21/1
RFE	0.53	0.26	0.133*	0.119*	0.331	0.027*	0.109*	-	0/6	0/5	4/7	18/6	5/4	35/0
FEI	0.545	0.347	0.255	0.187*	0.375	0.119*	0.136*	0.130*	-	0/4	6/2	20/2	6/3	38/0
TRB	0.364	0.171*	0.155*	-0.041*	0.015*	-0.006*	-0.089*	0.115*	0.215*	-	1/10	13/4	0/10	31/0
SC	0.743	0.785	0.787	0.705	0.705	0.693	0.612	0.773	0.775	0.681	-	0/21	0/31	17/0
QH	0.737	0.777	0.778	0.67	0.661	0.58	0.428	0.756	0.759	0.562	0.094*	-	2/15	23/1
NX	0.507	0.563	0.57	0.449	0.388	0.4	0.273	0.528	0.508	0.323	0.278	0.228*	-	19/0
TAR	0.821	0.883	0.875	0.774	0.801	0.81	0.684	0.888	0.926	0.811	0.749	0.723	0.614	-

extinctions, but radical shifts in species' ranges, when most of the Pleistocene mammalian fauna retreated to the east (Řičánková et al. 2015).

Refugia and migration routes

Our phylogeographic reconstructions revealed several different phylogenetic lineages of the Korean field mouse, as well as an extremely non-uniform level of differentiation between individual geographical populations and high differences in their genetic diversity (Tables 3, 4). Such results usually suggest isolation and differentiation of populations in multiple refuges that may be caused by the presence of biogeographic barriers such as mountains, rivers, and deserts (Avise 2000). In East Asia, the Lesser Hinnan Mountains and the Manchurian–Korean Mountains are known to be an effective barrier to animal migration (Driscoll et al. 2009), and the uplift of the Qinghai–Tibet

Plateau, leading to extension of the Gobi Desert, has caused changes in the distribution of many plants and animals in China, including *Apodemus* species (this study; Liu et al. 2004, 2012, Zhang et al. 2008, Sakka et al. 2010, You et al. 2010, 2010, Fan et al. 2012). In our study, populations of the Korean Peninsula, and especially Sichuan, Qinghai, and Tibet, were shown indeed to be highly differentiated (Table 4). An isolation of the Korean *A. peninsulae* populations was reported earlier and also it was observed for other species of the Korean Peninsula, including the congeneric striped field mouse *A. agrarius* (Serizawa et al. 2002, Lee et al. 2008, Zhang et al. 2008, Lattine et al. 2020). At the same time, close relationships between the animal populations of the Russian Far East and north-east China (that fit with our data; Table 4; Supporting Information, Fig. S2) were noted, which indicate the absence of strong isolation of this region (Lee et al. 2008, Oh et al. 2013). Water bodies, especially

seas, are known to be strong biogeographical barriers. However, the connections between mainland Asia and nearby islands, including Japan, appeared during most glacial periods, allowing many organisms to migrate on to these islands (Kinoshita *et al.* 2015). Our results confirm earlier observations of close relationships between populations of the Korean field mouse from the Russian Far East and Japan, suggesting colonization of the islands (Sakhalin and Hokkaido) with small ancestral populations located in eastern mainland Russia (Serizawa *et al.* 2000, 2002, Sakka *et al.* 2010) (Tables 3, 4; Supporting Information, Fig. S2).

Available phylogeographic studies suggest that East Asian species may have survived in one or more Pleistocene refugia. Evidence for the Ice Age refugia in East China (where a relatively mild climate has persisted) was supported by genetic data on many vertebrate and insect taxa, but identifying refugia is always a challenge (Fu *et al.* 2005, Zhang *et al.* 2008, Ding *et al.* 2011, Song *et al.* 2018, Tang *et al.* 2022). It is generally accepted that a characteristic feature of glacial refugia should be high species' diversity. However, given a widely accepted vicariant model, richness can indicate either glacial refugia or areas recolonized by genetic lineages from different refugia in the postglacial period, including mixing and hybridization of different phylogenetic lineages (e.g. Ding *et al.* 2011, Flanders *et al.* 2011, Song *et al.* 2018, Deng *et al.* 2019, Zuykova *et al.* 2019, Tang *et al.* 2022). Recent studies of plant chloroplast DNA in China has shown that only uniqueness can reliably identify refugia (Deng *et al.* 2019). In this regard, we believe that the pattern of nucleotide diversity distribution along the *Cytb* gene can also be considered as a test for the population uniqueness.

Thus, Qinghai, Ningxia, and Sichuan are most likely potential Pleistocene refugia for the Korean field mouse due to high genetic diversity and stability of their populations, and also specific patterns of distribution of nucleotide diversity in the *Cytb* gene (Table 3; Supporting Information, Fig. S3). In addition, these populations (ShG) occupy a basal position on the phylogenetic tree (Fig. 2). Taken together, this gives grounds to consider them centres of distribution of *A. peninsulae*. Large-scale dispersal may be accompanied by the emergence of new Pleistocene refugia in colonized territories, such as Inner Mongolia and Transbaikalia, whose populations are genetically highly diverse (Table 3). Based on the specificity of the distribution of nucleotide diversity (Supporting Information, Fig. S3), the Korean Peninsula, Altai, and the Russian Far East mainland can also be considered putative refugia, although they are much less diverse. These assumptions are in good agreement with the available data.

Indeed, it has been reported that the Mongolian Plateau experienced relatively severe climatic conditions during the Quaternary glacial oscillations, and evidently served as a refugium and the centre of distribution for some species, e.g. the desert hamster *Phodopus roborovskii* Satunin 1903 and the mesobuthid scorpions (Lv *et al.* 2016); the Qinghai-Tibet Plateau is also considered a refugium for *Apodemus* species (Liu *et al.* 2012). Phylogeographic studies of some species of insects point to Sichuan as one of the refugia (micro or large scale) and the source of population lineages of northern China (Song *et al.* 2018, Tang *et al.* 2022). It has also been shown that the Altai Mountains are an important refugium of the last glacial biota that was widespread in northern Eurasia before the transition

from the Pleistocene to the Holocene, due to the presence of light forest areas (Hais *et al.* 2015). In East Asia, *A. peninsulae* refugia have been suggested in South Korea due to the warm mountainous climate, and in the Russian Far East and Northeast China, where there were no strong climatic fluctuations during the Pleistocene epoch (Zhisheng *et al.* 2001, Lee *et al.* 2008, Sakka *et al.* 2010, Qiu *et al.* 2011, Latinne *et al.* 2020).

Previously, based on the pattern of genetic diversity distribution among populations it has been hypothesized that *A. peninsulae* may have colonized South Siberia in the same way as *A. agrarius*, i.e. via the Russian Far East (Sakka *et al.* 2010). The presented data allow us to propose two schemes of possible migration routes of the Korean field mouse, which could have been used by the species to spread to the vast territories of north-east Asia. In concordance with Sakka's suggestion, initially the mouse colonized the Russian Far East, and then spread to southern Siberia. (Fig. 6A). According to the second scenario, in the Pleistocene, the Russian Far East and Siberia were inhabited independently of each other and, probably, from the same refugial sources (Fig. 6B). In both cases, most of the territory was colonized by migrants from the southern regions of China, while the Korean Peninsula did not play a noticeable role in the settlement of the north-eastern territories. Our data suggest that the populations of Ningxia, the Korean Peninsula, and Inner Mongolia may have been the result of rapid migration from Ningxia, while the populations of north-east China, Mongolia, and Siberia may have been largely shaped by migrants from Sichuan; similarly, migration from Qinghai may have contributed to the populations of the Russian Far East and Altai. In any case, the Korean Peninsula and the Russian Far East and Japan were settled once, while parts of Siberia, Mongolia, and Northern China were settled twice. As a result, a certain landscape of the distribution of genetic diversity has formed to date, supporting the two-stage scenario of the colonization of Siberia (Fig. 6C).

Taxonomic interpretation

The obtained comprehensive results indicate that phylogeographic data can be used to clarify the intraspecific taxonomy of the Korean field mouse. Although Corbet (1978) recognized only two subspecies of *A. peninsulae* in continental Asia, in total, *A. peninsulae* populations were recently classified into nine subspecies (*A. p. peninsulae*, *A. p. nigritalus*, *A. p. giliacus*, *A. p. praetor*, *A. p. sowerbyi*, *A. p. quinghaiensis*, *A. p. rufulus*, *A. p. majusculus*, and *A. p. major*) the first six of them were considered as the most valid (Vorontsov *et al.* 1977, Musser *et al.* 1993, Chelomina 2005). It was also suggested earlier by molecular data analysis the existence of two subspecies in the mainland of East Asia: *A. p. peninsulae* in Korea, Manchuria, and eastern Siberia, and *A. p. sowerbyi* in central China (Sichuan) (Serizawa *et al.* 2002). These data are in good agreement with our results based on the analysis of the *Cytb* sequence obtained from a much larger sample, which show high genetic heterogeneity between *A. peninsulae* haplotype groups throughout the species' range. Based on strong differentiation, along with the presence of numerous fixed mutations (both nucleotide and amino acid) between the South and Central Chinese (Tibetan, Qinghai, Sichuan) populations and the rest, we can assume the existence of two subspecific groups or geographical races of the Korean field mouse, which can be conditionally named south-western and north-eastern. Given the recommendation we do not exclude that

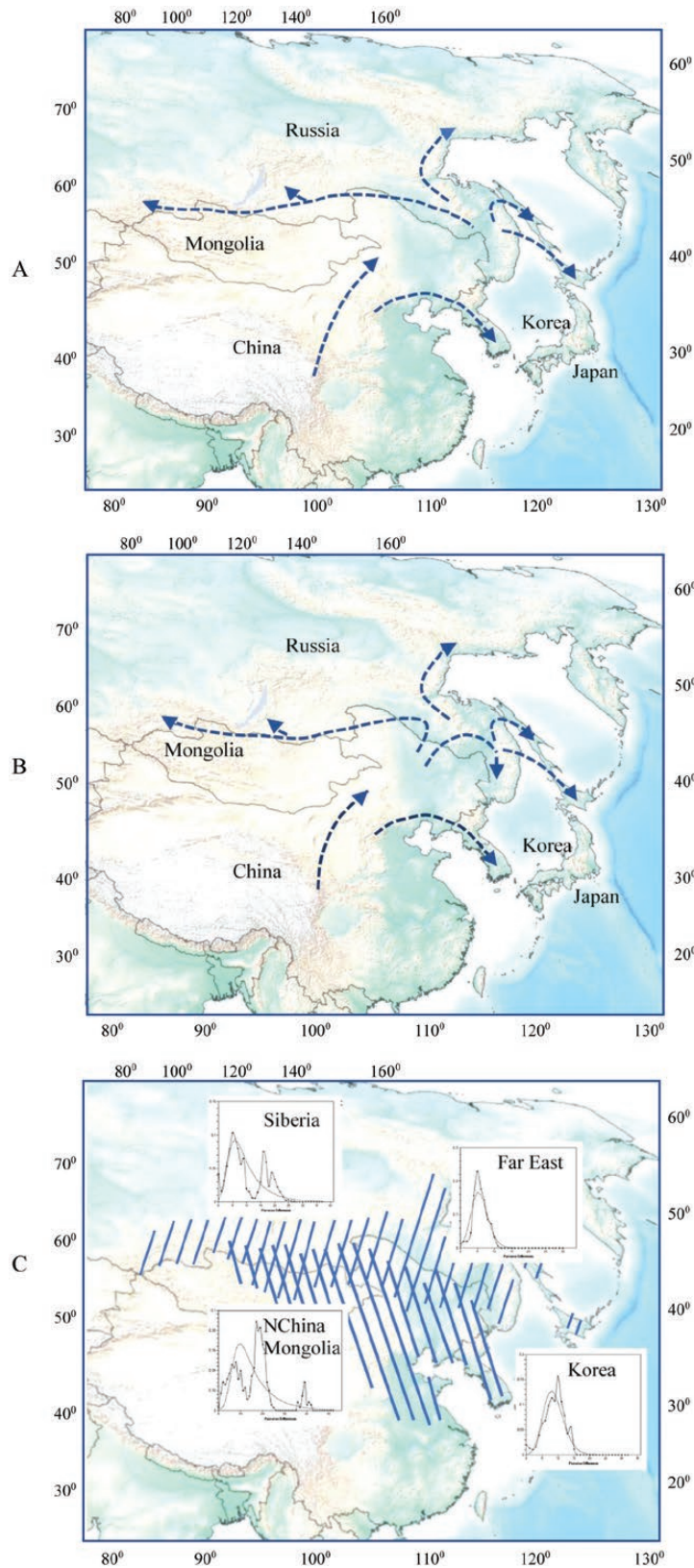


Figure 6. Possible migration routes of Korean wood mouse according to settlement of southern Siberia through the Far East (A), or independently of the Far East (B) (see text for more details). Hatching of thin and thick lines denotes the territories of the R and K phylogroups, respectively. The graphs show mismatch analysis data for four geographic areas (see Supporting Information, Fig. S4 for the large-scale plots).

these groups could also be regarded as independent species. This conclusion is consistent with the frequent consideration of widely distributed species, including those from East Asia, genetically distinct forms, or cryptic species (Chen *et al.* 2017).

CONCLUSION

Thus, on the basis of modern phylogenetic approaches and a detailed genetic analysis of various geographical populations, new data have been obtained that have significantly expanded and refined the existing ideas about historical demography and diversity of the Korean field mouse. The significant results of our study are the strong phylogenetic support for the phylogeographic haplogroups of *A. peninsulae*:

- extremely high differentiation with the absence of common haplotypes and the presence of fixed substitutions between south-western and north-eastern populations, suggesting their possible belonging to different geographical races or species;
- a clear differentiation with several common haplotypes and fixed nucleotide differences between geographically close and partially sympatric K and R;
- pronounced restriction of gene flow between the Korean Peninsula and other populations, in contrast to the high gene-flow between the Far Eastern and most geographic populations of Siberia and North China throughout their vast range;
- the correspondence of intraspecific phylogeny and demographic history to major geological events in Central and East Asia, and global climate changes in the Pleistocene;
- the existence of multiple centres of *A. peninsulae* biodiversity in different parts of the species' range, some of which can be considered Pleistocene refugia;
- two waves of recent colonization of the north-eastern part of the species' range, when the Korean Peninsula was colonized in the first wave, and most of Siberia and the Far East in the second wave, and some areas of Siberia, Mongolia, and Northern China were colonized twice;
- a pattern of the distribution of nucleotide diversity in the gene sequence as a reliable tool for determining refugia and migration routes.

To further advance our understanding of the genetic diversity and evolution of this ecologically important species of natural and urbanized landscapes, with a long evolutionary history and a vast area, which has a high epidemiological significance for humans, and to confirm our present findings, additional samples are needed, primarily from various regions of China.

SUPPLEMENTARY DATA

Supplementary data are available at *Zoological Journal of the Linnean Society* online.

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CONFLICTS OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY

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