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RH: MITOCHONDRIAL PHYLOGEOGRAPHY OF THE SABLE

**Colonization history of the sable *Martes zibellina* (Mammalia, Carnivora) on the
marginal peninsula and islands of northeastern Eurasia**

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 36 We examined the nucleotide sequences of the mitochondrial NADH dehydrogenase
 37 subunit 2 gene (976 base pairs) for 279 individuals of the sable *Martes zibellina*
 38 (Carnivora, Mustelidae), derived from diverse areas throughout the regions of the Ural
 39 Mountains to the Russian Far East on the Eurasian continent and the peripheral
 40 peninsula (Kamchatka) and islands (Sakhalin, Hokkaido, and southern Kurils). The
 41 demographic history of the sable and its migration history to the eastern peripheral

peninsula and islands were inferred using phylogeographic approaches. The analyses confirmed the previously found major lineages for the examined sables and further identified novel sub-lineages. Our data also support that a lineage, which is endemic to the eastern marginal islands (Sakhalin, Hokkaido, and southern Kurils), that was produced by the demographic expansion of an ancestral lineage in the Eurasian continent. The most recent common ancestor of the Sakhalin, Hokkaido, and southern Kuril sables was estimated to exist during the Late Pleistocene. We also determined that another lineage exists on Sakhalin and is shared by the Far East Primorsky population. Our results indicate multiple migration events onto Sakhalin from the continent and suggest the importance of the formation of several straits to the distribution of sable lineages. Meanwhile, Kamchatka is dominated by a sole lineage which would also have followed the demographic expansion on the Eurasian continent. The Russian Far East was indicated as the source area for lineage diversifications; in this region, genetic diversity was relatively high, which is consistent with previous studies.

Key words: Hokkaido, mitochondrial DNA, *Nd2*, phylogeography, sable, Sakhalin

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Climate oscillations during the Pleistocene imposed enormous constraints on boreal species, causing the reformation of their distributions and population genetic diversity (Hewitt 1996, 2000). Intensive glaciation forced boreal species to retreat from areas of high latitude, especially in northern parts of Europe and North America (Stewart and Lister 2001; Hewitt 2004; Lister 2004). Previous studies have presented plausible evidence of southern refugia in Europe and North America based on paleontological data and signatures of past demographic history left behind on the phylogeographic structure of present-day species (e.g., Fedorov and Stenseth 2002; Waltari et al. 2007; Provan and Bennett 2008). On the other hand, the majority of northeastern Eurasia was not covered by ice sheets during glacial periods (Grosswald 1980, 1998; Svendsen et al. 2004). Instead, the cold and dry climate led to coverage by tundra steppe-like vegetation; therefore, taiga forests have been fragmented as small patches in mainly southern Siberia (Abbott and Brochmann 2003; Semerikov et al. 2007; Binney et al. 2009). Many phylogeographic studies of boreal species in northeastern Eurasia have generally suggested the contraction of the ranges of boreal species into several refugia (e.g., southern Ural Mountains or southeastern Siberia) during glacial periods, followed by demographic expansion to form present-day distributions (Kvist et al. 2001, 2003; Goropashnaya et al. 2007; Oshida et al. 2005;

Fedorov et al. 2008; Korsten et al. 2009; Davison et al. 2011; Poyarkov and Kuzmin 2008; Hope et al. 2010; Malyarchuk et al. 2011, 2013; Sakka et al. 2010; Kryukov et al. 2012; Ohdachi et al. 2012; Todisco et al. 2012). However, how climate changes during the Pleistocene period influenced the demographic history of boreal species in northeastern Eurasia, particularly compared to Europe and North America, remains to be precisely determined.

Meanwhile, recent phylogeographic studies have shown that peripheral populations of Eurasian boreal mammals in areas such as the Kamchatka Peninsula and on Sakhalin, Hokkaido, and the southern Kuril Islands possess characteristic genetic structures compared to mainland populations (Iwasa et al. 2000, 2009; Matsushita et al. 2001; Inoue et al. 2007; Korsten et al. 2009; Bannikova et al. 2010; Davison et al. 2011; Malyarchuk et al. 2011, 2013; Abramson et al. 2012; Kinoshita et al. 2012; Ohdachi et al. 2012; Yu et al. 2012; Gus'kov et al. 2013; Hirata et al. 2013; Ishida et al. 2013). However, the unique colonization histories of these peripheral populations have not been sufficiently discussed in combination with the demographic population expansions that occurred on mainland Eurasia, with the exception of studies on a limited number of species (Iwasa et al. 2000; Poyarkov and Kuzmin 2008; Korsten et al. 2009; Davison et al. 2011; Abramson et al. 2012; Ohdachi et al. 2012; Hirata et al. 2013). Thus, the

specific process involved in the formation of these peripheral populations is not well understood.

The sable *Martes zibellina* (Mammalia, Carnivora, Mustelidae) is an arboreal species that is intimately associated with forest habitats in northern Eurasia; its distribution ranges widely from the Ural Mountains to the Russian Far East, and isolated populations occur on Sakhalin, Hokkaido, and the southern Kuril Islands along the coast of northeastern Eurasia (Murakami 2009). Its distribution includes the taiga forest zone in Siberia and extends to southern areas where coniferous and deciduous forests occur. Therefore, the population dynamics of the sable may have been synchronized with the repeated vegetational shifts in northern Eurasia during Pleistocene glacial periods. Because the sable exhibits substantial morphological variation across its distribution and because its population structure may have been affected by the many artificial translocations (augmentation, introduction, and/or reintroduction) since the early 20th century (Monakhov 2011; Powell et al. 2012), phenotypic analyses to classify local races and clarify the demographic history are difficult. In contrast, previous genetic analyses using mitochondrial DNA (mtDNA) sequences have revealed several patterns of intraspecific variation. In general, 3 major lineages have been recognized for most continental sables from Ural to Russian Far East

populations (Petrovskaya. 2007; Malyarchuk et al. 2010; Sato et al. 2011; Li et al. 2013; Rozhnov et al. 2013); these lineages are estimated to have diverged from each other during the late Middle Pleistocene (Sato et al. 2011; Li et al. 2013).

On the other hand, the Kamchatka population has been shown to possess only one of these 3 major lineages, and this population exhibits much lower genetic diversity compared to other continental populations (Petrovskaya. 2007; Malyarchuk et al. 2010; Rozhnov et al. 2013). Similarly, lower genetic diversity has also been observed in the Hokkaido population (Sato et al. 2011; Ishida et al. 2013). However, neither the source area nor the exact process of these migrations has been clarified to date. To elucidate the colonization history of the eastern marginal peninsular and insular populations and the related demographic history of the sable in continental Eurasia, more comprehensive sampling from both mainland and peripheral regions as well as in-depth analyses of population genetic structure are required.

The present study examines the comprehensive range of sables including mainland populations from the west (Ural), central (Krasnoyarsk), and east (Russian Far East) as well as most peripheral peninsular and insular populations from Kamchatka, Sakhalin, Hokkaido, and southern Kuril (Fig. 1). The examination of the Sakhalin and Kuril samples is a novel aspect of this study. We used mitochondrial NADH

dehydrogenase subunit 2 (*Nd2*) gene sequences in the phylogeographic analyses to address the following issues: 1) how marginal peninsular and insular populations were established in combination with the demographic history of mainland Eurasian populations, and 2) how the migration history of the peripheral peninsular and insular sable have been synchronized with other boreal species in northern Eurasia since the Pleistocene.

MATERIALS AND METHODS

A total of 279 individual sables were analyzed, as listed in Supporting Information S1. We determined partial nucleotide sequences of the mitochondrial *Nd2* gene (976 bp) for 209 individuals; homologous sequences for an additional 70 individuals were downloaded from the DDBJ/EMBL/GenBank international DNA database with accession numbers AB455741 and AB625980–626048 derived from Sato et al. (2009, 2011). Novel sequences were deposited in the DNA databases with accession numbers AB908319–AB908369 (Supporting Information S1). Sequences for other *Martes* species, including *M. americana* (AY598546), *M. foina* (AB564140), *M. martes* (AB564141), and *M. melampus* (AB455709), were also downloaded from the database and examined in this study. In the phylogeny (topology) inferences, *M. foina*

was used as an outgroup according to the phylogenetic hypothesis that this species is the most closely related to the clade of “true martens,” which includes *M. americana*, *M. martes*, *M. melampus*, and *M. zibellina* (e.g., Wolsan and Sato 2010; Sato et al. 2012).

PCR amplification and sequencing strategy.—Total genomic DNA was extracted from tissues preserved in ethanol using the conventional phenol–chloroform method (Sambrook and Russell 2001). Polymerase chain reaction (PCR) was performed in a final volume of 20 μ L, which consisted of 1 μ L template DNA, 2.5 mM MgCl_2 , 0.2 mM dNTPs, 0.05 μ M each primer, 1 $\times$ *Taq* polymerase buffer, and 0.5 units AmpliTaq Gold DNA polymerase (Applied Biosystems [ABI], Foster City, California). Thermal cycling parameters were as follows: one cycle of denaturation at 95°C for 2 min, 35 cycles of denaturation at 95°C for 30 s, annealing at 50°C for 30 s, extension at 72°C for 1 min, and a final cycle of extension at 72°C for 10 min. The primers used to amplify the *Nd2* gene were ND2-FelF (Yu and Zhang 2006) and ND2-melExtR (Sato et al. 2009). A negative control sample replacing DNA templates with a corresponding volume of water was also prepared for each PCR reaction. We did not observe any amplification in our negative control PCR analyses. The sequence reaction of the PCR products was conducted using the BigDye Terminator Cycle Sequencing kit v3.1 (ABI)

and the primers ND2-FelF and ND2-CarF (Yu and Zhang 2006), followed by automated sequencing on an ABI3130 Genetic Analyzer (ABI). The *Nd2* sequences generated in this study and collected from the DNA database were aligned by eye using ProSeq ver. 2.91 (Filatov 2002), as the absence of insertions and deletions made the alignment straightforward.

Phylogenetic and chronological analyses.—Reconstruction of the phylogenetic tree using the maximum likelihood (ML) criterion (ML—Felsenstein 1981) was conducted using the program MEGA ver. 5.05 (Tamura et al. 2007). The best-fit substitution model (TN93+I) was selected using the Bayesian Information Criterion (BIC) implemented in MEGA. Trees were obtained from heuristic searches using as-is sequence addition and NNI branch swapping; otherwise, default settings were used. Clade support was assessed using nonparametric bootstrap analyses (Felsenstein 1985) with 1,000 replicates with the same settings as the above ML heuristic search.

Reconstruction of the phylogenetic tree and estimation of divergence times by Bayesian inference (BI) were conducted using the program BEAST ver. 1.4.8 (Drummond and Rambaut 2007). The Model test function in MEGA was used to choose an appropriate substitution model (TN93+I) with the BIC. The dataset was analyzed in a

Bayesian uncorrelated log-normal relaxed-clock model using the coalescent model with constant population size as tree prior on phylogeny. We considered rate variation among different branches, where the rates on each branch were independently drawn from a log-normal distribution and were uncorrelated (Drummond et al. 2006). We used the program BEAUti, ver. 1.6.1 (provided in the BEAST package) to generate the input file for the BEAST program, using the substitution model for the sequence evolution, priors, and conditions of the Markov Chain Monte Carlo (MCMC) approach for estimating posterior distributions of the time to the most recent common ancestor (MRCA) of individual sables. Three independent MCMC analyses were run for 50×10^6 generations with trees sampled every 5,000 generations. Each log file was checked to confirm convergence to the stationary posterior distribution and sufficient effective sample size (ESS) of each parameter using the program Tracer ver. 1.6 (Rambaut and Drummond 2007). Then the log files of 3 independent runs were combined to provide each parameter estimate, with the first 25% of the sampled parameters discarded as burn-in. We obtained sufficient ESS values exceeding 200 for all parameters. A calibration point was set on the basis of the time estimate for the divergence between *M. foina* and the other *Martes* species in Sato et al. (2012). We adopted a normal distribution with a mean of 3.045×10^6 million years ago (mya) and standard deviation of 0.3555 to the

basal divergence of the examined taxa, such that the 95% confidence intervals ranged from 2.46–3.63 mya as shown in Sato et al. (2012). This calibration was also consistent with the estimate of Koepfli et al. (2008).

Network and phylogeographic analyses.—To infer the relationships of the obtained haplotypes, the median-joining network was reconstructed using the program Network ver. 4.6 (Bandelt et al. 1999). For the lineages inferred from the phylogenetic analysis, estimation of nucleotide diversity (π), analysis of mismatch distribution (Li 1977; Harpending 1994; Rogers 1995), and the neutrality test (Tajima 1989; Fu 1997) were conducted using the program ARLEQUIN ver. 3.5.1.3 (Excoffier et al. 2005). In the mismatch distribution analysis, the goodness-of-fit of the observed distribution to the expected distribution under the sudden-expansion model (Rogers 1995) was tested by computing the sum of squares deviation and the raggedness index. In the same program, haplotype diversity (h) and π were evaluated for each population defined geographically as in Fig. 1. We explored population structure using the program SAMOVA (spatial analyses of molecular variance—Dupanloup et al. 2002) to infer the genetic barriers within the distribution of the sable. This method implements a simulated annealing approach to define groups of populations that are geographically

homogeneous and maximally differentiated from the other populations. In this analysis, the number of groups (K) was a priori determined to range from 2 to 8. For each K value, 10,000 simulated annealing steps were performed starting from each of 200 sets of initial conditions, searching for the largest F_{CT} values (proportion of total genetic variance due to differences among groups of populations) as a predictor of the best grouping of populations (Dupanloup et al. 2002). In addition, we estimated pairwise fixation index (Φ_{ST}) values among populations in ARLEQUIN and constructed a neighbor-joining (NJ) tree using these values in MEGA.

Results

Sequence variation and phylogenetic inference.—In total, 51 haplotypes were identified in the 976 bp mitochondrial *Nd2* gene sequences among the 279 individuals. Haplotypes (Hap) 1–13 have been described previously (Sato et al. 2011), whereas Hap 14–51 were newly identified in the present study (74.5% [38/51] haplotypes are novel). Among the 51 haplotypes, we found 61 segregating sites, of which 36 were singleton sites and the remaining 25 were parsimony informative sites.

We constructed the ML phylogenetic tree (Fig. 2) and recognized 3 major lineages (R1+H1, R2, and R3) within the sable clade, as reported in Sato et al. (2011).

We do not present the Bayesian tree here, as it is the same as the ML tree; thus, we only present the posterior probabilities (Fig. 2). In the topology, the R3 lineage initially branched off from the other lineages, followed by R2 from the remainder. The R1+H1 lineage consisted of 3 sub-lineages (R1a, R1b+H1, and R1c), of which the R1b and R1c haplotypes were newly found in this study. The H1 lineage was exclusively composed of insular individuals from Sakhalin, Hokkaido, and the southern Kuril Islands. The range of each group of haplotypes was depicted in Fig. 3.

Statistical indices for genetic diversity and the demography are shown in Table 1. For all groups of haplotypes, except R1c, H1, and R3, at least one of the neutrality tests indicated negative values that significantly deviated from zero, implying rapid population growth (Table 1). In addition, the mismatch distribution for most groups of haplotypes, except R1, did not reject the sudden expansion model (Table 1).

Chronological inference.—The divergence times for each major node of the phylogenetic tree, estimated using BEAST, are shown in Fig. 2. The lineages of *Martes martes* and *M. zibellina* were estimated to have diverged 0.54 mya, with a 95% confidence interval (CI) of 0.27–0.80 mya. The most recent common ancestor (MRCA) for the sable clade was estimated to have existed 0.22 mya (CI = 0.12–0.34 mya), which

corresponds to the divergence time of the R3 lineage from the other sable lineages. Subsequent divergence of the R2 lineage from the R1+H1 clade occurred 0.20 mya ($CI = 0.10\text{--}0.30$ mya). The dates for the MRCA of each major lineage, R1+H1, R2, and R3, were estimated to be within 0.09–0.14 mya from the latter part of the Middle Pleistocene (0.126–0.781 mya) to the Late Pleistocene (0.01–0.126 mya). The MRCA of the R1b+H1 lineage was dated at 0.09 mya ($CI = 0.04\text{--}0.15$ mya). The MRCAs of the other R1 sub-lineages, R1a and R1c, and H1 were inferred to be around 0.02–0.06 mya, corresponding to the Late Pleistocene.

Geographic trends of the sable lineages.—The haplotype network was constructed to represent the locality compositions in each haplotype and their relationships (Fig. 4). The observed haplotypes in the continental lineages were widespread, from eastern to western regions of the sable distribution in Eurasia. However, only 13 of 46 continental haplotypes were shared among populations. Furthermore, 28 of 33 continental-tip haplotypes were unique to each population.

We also calculated the compositional variability of each group of haplotypes among local populations (Table 2). All individuals from Hokkaido and the southern Kuril Islands were of the H1 lineage, whereas Sakhalin individuals harbored 5

haplotypes; 1 was included within the H1 lineage and the other 4 were in the R2 lineage (Fig. 4; Table 2). Three R1 sub-lineages exhibited different compositions in each local population. For example, all Kamchatka individuals harbored only R1a, showing no other lineages. All individuals from Primorsky belonging to R1 lineage were typed as the R1a with no R1b or R1c haplotypes. In contrast, more than 40% of individuals from Ural were typed as R1b or R1c haplotypes, whereas no individuals exhibited the R1a haplotype. The Krasnoyarsk population possessed only 1 central haplotype (Hap 1) within the R1a lineage (Fig. 4); therefore, no variation was observed within the population in terms of the R1a lineage, a possible result of the founder effect as discussed below. The R1c sub-lineage consisted of only 2 haplotypes observed in Ural and Krasnoyarsk, and this sub-lineage was distantly genetically related to the other R1 haplotypes by at least 4 mutations (Fig. 4). In the R2 lineage, 14 of 20 haplotypes were detected from eastern populations, especially in Primorsky and Khabarovsk, whereas most individuals from the Ural Mountains and Krasnoyarsk showed Hap 10 and its descendants (Hap 40–43), except for 1e individual typed as Hap 35. In addition, the eastern continental Primorsky and Khabarovsk populations exhibited relatively higher nucleotide diversity among the R2 haplotypes ($\pi = 0.0208$ and 0.0203 , respectively; Table 2) compared to the Krasnoyarsk and Ural populations ($\pi = 0.0100$ and 0.0115 ,

respectively). The R2 haplotypes possessed by 10 of 15 Sakhalin individuals (Hap 7, 36, and 37, except 47) were genetically close to one another, and only Hap 7 was shared with one continental individual from Primorsky (Fig. 4). The R3 haplotypes were detected from 4 continental populations but at lower frequencies than the R1 and R2 haplotypes in every population (Table 2).

Genetic diversity of each local population.—Considering the total overall genetic variation across all lineages, the populations from the Ural Mountains, Primorsky, and Khabarovsk showed relatively higher genetic diversity, considering both haplotype and nucleotide diversities ($h = 0.85, 0.85, \text{ and } 0.91$, and $\pi = 0.0627, 0.0516$ and 0.0506 , respectively; Table 2). On the other hand, the genetic diversities of the Krasnoyarsk, Magadan, and Sakhalin populations were somewhat lower ($h = 0.76, 0.92$, and 0.81 , respectively and $\pi = 0.0415, 0.0426$ and 0.0427 , respectively), whereas values for the Kamchatka, Hokkaido, and Kuril populations were much lower ($h = 0.25, 0.39$, and 0.60 , respectively and $\pi = 0.0025, 0.0042$ and 0.0120 , respectively). However, some caution should be used when interpreting the genetic diversity for the Magadan population, which may have been affected by artificial translocations of sables from other regions (Petrovskaya 2007). Powell et al. (2012) summarized that the

reintroduction of the 361 sables from the Khabarovsk to Magadan in 1958 was successful. The highest haplotype diversity of the Magadan population ($h = 0.92$) may reflect such reintroductions. Taking this concern into account, the Ural population in western Russia and the Primorsky and Khabarovsk populations in the Russian Far East clearly possessed higher genetic variation.

Genetic differentiation among local populations of sable.—The SAMOVA analysis revealed genetically distinct groups of sable populations based on intensity of gene flow (Table 3). F_{CT} values were especially high at $K = 2$ and 3, and slightly decreased as the number of groups increased. When $K = 2$, two insular populations on Hokkaido and the southern Kuril Islands were together separated from the other populations, and the genetic difference among groups was the highest of all groupings, explaining 33.37% of the total genetic variation. In the analysis of $K = 3$, the Hokkaido and southern Kuril populations were separated from one another. Increasing the K from 4 to 5 detected new separations for Kamchatka and Sakhalin. Mainland populations of Magadan, Khabarovsk, Primorsky, Krasnoyarsk, and Ural Mountains were grouped as 1 population until K was increased to 6. Populations from Hokkaido and the southern Kuril Islands were typed as the same group at $K = 2, 7$, and 8. The NJ tree using the Φ_{ST}

values among populations also revealed a trend toward a peripheral versus mainland arrangement, where eastern marginal peninsular and insular populations were also placed in a peripheral position in the NJ tree (Fig. 5).

DISCUSSION

We conducted phylogeographic analyses using 279 individual sables from a more comprehensive distribution area than has been previously examined. Three distinct major lineages, R1+H1, R2, and R3, were among the continental populations (but H1 was not observed in the continent), while 1 insular endemic lineage, H1, was observed on Sakhalin, Hokkaido, and the southern Kuril Islands. The existence of 3 mtDNA lineages on the Eurasian continent is also consistent with the results of previous studies that primarily focused on continental Far Eastern populations (Balmysheva and Solovenchuk 1999a, 1999b; Petrovskaya 2007; Malyarchuk et al. 2010; Sato et al. 2011; Li et al. 2013). In the present study, the large number of newly obtained individuals from more extensive geographic areas enabled us to determine that the R1+H1 lineage contains 3 separate sub-lineages, R1a, R1b+H1, and R1c. R1, R2, and R3 haplotypes appeared from eastern to western populations on the Eurasian continent, whereas the Kamchatka population was primarily composed of the R1a haplotypes (Fig. 3 and 4).

This observation is consistent with the results of Malyarchuk et al. (2010) where the Kamchatka population is almost exclusively composed of one major dominant lineage (A1 in Malyarchuk et al. 2010). Together, our study and these previous studies, which adopted different molecular markers and methodologies, have arrived at a congruent result; however, the present study provides further refined insight into the demographic history of sable populations on the Eurasian continent and the roles of the eastern peripheral peninsula and islands on the genetic diversity of isolated sable populations. Below, we focus on these 2 points and discuss the population history of the sable. Lastly, we compare the knowledge obtained for the sable with other boreal organisms, focusing on their migration histories to eastern marginal islands during the Pleistocene.

Demographic history of the sable on the Eurasian continent.—To determine the origin and process of diversification of sable lineages on the Eurasian continent, several studies have evaluated genetic diversity and demographic indices (Rozhnov et al. 2010, 2013; Sato et al. 2011; Li et al. 2013). Based on the mtDNA variations, they showed higher genetic diversity for the Ural or Russian Far East populations, suggesting that these regions are possible refugia in the glacial periods. The present analyses also clarified that populations in both Ural Mountains and Russian Far East have higher

genetic diversity (Table 2). On the other hand, the origin of the lineage expansion was only suggested in the Russian Far East, not in the Ural region. This is because 1) R1a is diverse in the Russian Far East and a founder effect was observed in the more western Krasnoyarsk region, 2) the Ural population has only derived R1b haplotypes (Hap 28-31) and does not contain the central haplotype (Hap 24) which is shared by more eastern Krasnoyarsk and Russian Far East populations, and 3) the Russian Far East population has higher genetic diversity in the R2 lineage and the Ural and Krasnoyarsk populations only have descendant haplotypes (Hap 40-42) from widely shared Hap 10. These results imply that the Russian Far East would have provided the sable population with important refugia for lineage diversifications. Furthermore, the population expansion was detected for R1a, R1b+H1, and H1 lineages, underpinning that the Russian Far East served as a source area for demographic expansions into eastern peripheral parts such as Kamchatka and Hokkaido. Note, however, that the discussions above do not refute the refugia hypothesis of the southern Ural region (Rozhnov et al. 2013). In fact, we observed higher genetic diversity in the Ural population and determined that the R1c lineage originated in this region. Further studies are needed to validate the western refugia hypothesis.

The effect of the artificial translocations of the sable.— Historically, sables, especially in continental populations, were heavily harvested, and therefore the significant range contraction was induced from 18th to early 20th centuries (Powell et al. 2012). Nearly 20,000 individuals were artificially translocated during 1901 to the 1980s (Powell et al. 2012). Therefore, there is a concern that this artificial translocation disturbs the natural genetic structure and hinders the discussion of their demographic history as described in the last section. However, it is likely that our results were not largely affected by the artificial translocation events. The present analysis revealed that 28 of 33 continental haplotypes that were “tip (terminal haplotype)” in the haplotype network were unique to each population (Fig. 4). Furthermore, most of haplotypes, which occurred in more than 3 populations, were located in the center of star-like clusters of haplotypes (Fig. 4). These phylogeographic structures suggest that genetic diversity was mainly generated by historical demographic events that have occurred gradually over time, rather than recent artificial translocations. We therefore assumed that the effects of augmentations, introductions, and/or reintroductions would be less likely in the present study.

Migration history of the sable on the eastern marginal peninsula and

islands.—Our study has revealed the characteristic patterns of genetic variation in peripheral peninsular and insular populations in northeastern Eurasia. The SAMOVA analysis also documented the genetic differentiation of peripheral populations from the other mainland populations (Table 3; Fig. 5). Previous studies have also reported lower genetic variation in the Kamchatka and Hokkaido populations compared to other continental populations (Petrovskaya 2007; Inoue et al. 2010; Malyarchuk et al. 2010; Sato et al. 2011; Rozhnov et al. 2013). The present findings revealed that the Kamchatka population was composed only of R1a haplotypes, whereas the neighboring population in Magadan harbors R1a, R1b, and R2. On the other hand, insular populations on Hokkaido and the southern Kuril Islands only contain H1, whereas the Sakhalin population harbors both H1 and R2. Populations in the neighboring Russian Far East exhibited higher genetic diversity as described above. Therefore, these results suggest that the eastern marginal peninsular and insular populations possess limited mtDNA lineages, further implying the involvement of founder effects by limited expanded lineages in the formation of the peripheral populations.

As suggested in the demographic analyses, the Kamchatka population appears to have been founded by the expansion event of the R1a sub-lineage from the southeastern part of the Russian Far East, while most of the insular populations are

inferred to have been formed as a result of the expansion of the R1b+H1 sub-lineage, from which the insular H1 lineage was generated (Figs. 2 and 4). The MRCAs of R1a and R1b+H1 were dated at 0.06 mya ($CI = 0.02\text{--}0.11$) and 0.09 mya ($CI = 0.04\text{--}0.15$). The colonization of the H1 lineage on the islands presumably occurred within the interval between the MRCAs for the R1b+H1 and H1 lineages (0.04–0.09 mya) in the Late Pleistocene age; this event could have prevented the migration of the sable lineage from Hokkaido to the southern Honshu islands of the Japanese archipelago by the Tsugaru Strait (Ohshima 1990, 1991, 1992; Millien-Parra and Jaeger 1999). In summary, the limited number of lineages in the peripheral regions (Kamchatka and Hokkaido) resulted from demographic expansions that began on continental Eurasia in the Late Pleistocene period.

The most interesting finding of our study is that the R2 haplotypes also occur on Sakhalin, but not on Hokkaido or the southern Kuril islands. Previous studies have suggested that the Hokkaido population has a monophyletic origin and was established by 1 migration event from the continent via Sakhalin (Hosoda et al. 1999; Sato et al. 2011). However, the presence of the R2 lineages on Sakhalin suggests that the migration event to Sakhalin happened at least twice. More frequent colonizations may also have been possible, taking into account the 2 divergent lineages (Hap 47 versus Hap 7, 36,

and 37) in the R2 lineage (Fig. 3). The Tatar (Mamiya) Strait located between the Eurasian continent and Sakhalin is narrower and shallower than La Perouse (Soya) Strait between Sakhalin and Hokkaido (Position Information Database, High Performance Computing System, Information Initiative Center, Hokkaido University, 2010, <http://www.hucc.hokudai.ac.jp/~x10795/Latlonele.html>, Accessed 30 March 2014), which could have allowed sable migrations to Sakhalin even after the emergence of La Perouse (Soya) Strait. Considering that one of the R2 haplotypes (Hap 7) observed on Sakhalin was shared by 1 Primorsky individual and that the H1 haplotype observed on Sakhalin diverged from the continental R1b haplotypes. As a result, we hypothesize that the H1 lineage initially migrated to the eastern marginal islands, followed later by the R2 lineage. The 2nd migration by the R2 lineage was not likely to have reached Hokkaido and the Kuril Islands due to the establishment of the La Perouse (Soya) Strait.

Comparative phylogeography of eastern marginal insular populations.—Boreal species exhibit complicated colonization histories on the Far Eastern marginal islands. The fauna of Sakhalin, Hokkaido, and the southern Kuril Islands is similar to those on the continent of the southeastern part of the Russian Far East, as land bridges appeared

during most glacial periods, allowing many organisms to migrate onto these islands (Dobson 1994; Millien-Parra and Jeager 1999; Kawamura 2007). Previous studies have provided insights into the phylogeographic history of Hokkaido mammals, demonstrating species-specific patterns of historical migrations from the continent (e.g., Mckay et al. 2012; Sato 2013). The present study and Sato et al. (2011) suggest that the mtDNA lineage of the sable in Hokkaido was established during the Late Pleistocene. This migration time estimate is consistent with that for the Korean field mouse (Sakka et al. 2010), but not with those for the Eurasian flying squirrel, the gray red-backed vole, and the mountain hare, whose migration times were estimated to occur during the late Middle Pleistocene (Yamada et al. 2002; Oshida et al. 2005; Abramson et al. 2012; Kinoshita et al. 2012). On the other hand, the brown bear *Ursus arctos* and the red fox *Vulpes vulpes* possess several distinctive mtDNA lineages on Hokkaido, suggesting repeated colonizations since the Middle to Late Pleistocene (Matsushashi et al. 1999, 2001; Inoue et al. 2007; Korsten et al. 2009; Hirata et al. 2013). For Sakhalin, the signature of repeated migrations from the continent has also been suggested for the brown bear and the mountain hare, indicating that the migration to Sakhalin from the continent occurred after the establishment of the Hokkaido lineage (Kinoshita et al. 2012; Hirata et al. 2013). The gray red-backed vole, Korean field mouse, and least

shrew may also have exhibited at least 2 migrations onto the island of Sakhalin (Pavlenko et al. 1989; Iwasa et al. 2000; Serizawa et al. 2002; Sakka et al. 2010; Abramson et al. 2012; Ohdachi et al. 2012). The similar pattern of coexistence of old and recent migrants in Sakhalin was also observed for the Siberian salamander (Matsui et al. 2008; Poyarkov and Kuzmin, 2008; Malyarchuk et al. 2011, 2013) and the carrion crow (Kryukov et al. 2012). The present study also revealed that the sable experienced at least 2 waves of migration from the continent, during which 2 lineages (H1 and R2) mingled on Sakhalin. Interestingly, nuclear *Mc1r* and *Tcf25* gene analyses have shown that the Hokkaido sable harbored an old endemic nuclear DNA lineage that likely colonized earlier than the modern mtDNA lineages on the island (Ishida et al. 2013). Hence, we conclude that the eastern peripheral insular populations of boreal species were constructed by multiple migration and colonization events.

We assume that not only the repeated appearances of land bridges between islands and the continent, but also the latitudinal climate cline on these peripheral islands have likely played important roles in preserving several lineages that colonized during different ages. The modern vegetation of Hokkaido Island is classified as a “pan-mixed forest” consisting of a sub-arctic needle-leaved and temperate broad-leaved forest (Tatewaki 1958), whereas the taiga zone forest composed of larch and spruce

species is considered to have advanced southward during the last glacial period (Ono 1990; Ohshima, 1991; Igarashi and Zharoh 2011; Kito and Ohkuro 2012), in a manner similar to northern continental Asia (Mokhova et al. 2009; Stebich et al. 2009). On the other hand, central Sakhalin is recognized as an important vegetation boundary, known as the Schmidt line (Miyabe and Tatewaki 1937). Phylogeographic analyses using nuclear and cytoplasmic markers for larch, spruce, and fir *Abies* species have revealed that central Sakhalin is a major area of introgression between old island colonists and subsequently migrated lineages (Khatab et al. 2008; Aizawa et al. 2007, 2009; Polezhaeva et al. 2010; Semerikova et al. 2011). In the present study, the H1 lineage was observed in a relatively southern area on Sakhalin, whereas the R2 lineage occurred in the north (Fig. 1). Such an observation might reflect the environmental boundary in the central Sakhalin area. We suggest that such a transitional forest zone and its periodic shift have also significantly affected the distribution of boreal mammals on Sakhalin. To clarify the demographic history of the sable on the eastern peripheral islands of Eurasia in more detail, phylogeographic analyses with more comprehensive sampling and multiple genes are required. Such studies could illuminate the past repeated expansion histories of continental boreal species during the Pleistocene, as the signatures of past expansions on the continent might have been erased by more recent expansion events,

while eastern peripheral islands would maintain such vestiges of old expansions.

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SUPPORTING INFORMATION

SUPPORTING INFORMATION S1.— Sample information of sables used in this study.

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Figure legends

Fig. 1.—Sampling localities for sables examined in this study. The map on the left gives a continental-scale view. The square indicates the inset shown on the right, the area of the southern Russian Far East and marginal islands. The numbers in square brackets after the name of a region indicate the number of examined individuals. We present each population in the text based on these sampling localities: Ural, Krasnoyarsk, Magadan, Kamchatka, Khabarovsk, Primorsky, Sakhalin, Hokkaido, and southern Kuril Islands. Open circles represent localities that only possess H1 lineage haplotypes.

Fig. 2.—The maximum-likelihood (ML) phylogenetic tree inferred from the 976 bp nucleotide sequences of the mitochondrial *Nd2* gene for 279 individual sables and other related species in the genus *Martes*. *Martes foina* was used as the outgroup. The Bayesian tree was the same as the ML tree in topology and therefore is not shown. Numbers above branches show bootstrap proportions in the ML analysis (left) and posterior probabilities in the Bayesian inference analysis (right). Numbers below branches represent divergence time estimates (means) with their 95% confidence intervals in parentheses. Only bootstrap values higher than 50% are shown. Lineage

names are indicated on the right side of the phylogeny: R1, R1a, R1b, R1c, H1, R2, and R3.

Fig.3.—Geographic distributions of the a) major 3 lineages of the sable, R1+H1, R2, and R3, and b) sub-lineages of the R1+H1 lineage. The R1b+H1 sub-lineage is shown separately by the R1b and H1 haplotype distributions for to be pragmatic, although R1b cannot be called “lineage” because of its paraphyletic relationships to H1. Range shapes of the distributions for each lineage were depicted according to the existence of the haplotypes in each population shown in Fig. 1.

Fig. 4.—A median-joining network reconstructed from the 976 bp nucleotide sequences of the mitochondrial *Nd2* gene for 279 sable individuals. Numbers next to nodes show the haplotype numbers that correspond to those in Fig. 2. Node sizes are proportional to haplotype frequencies. Each node indicates the proportion of sampling localities showing the haplotypes. Slashes on branches between nodes indicate mutations. Lineage names are indicated as in Fig. 2.

Fig. 5.—Neighbor-joining network based on the pairwise fixation index (Φ_{ST}) values

among populations defined in Fig. 1. K represents the number of groups set a priori by the authors in the SAMOVA analysis, which corresponds to values in Table 3.

TABLE 1.—Statistics for demographic analyses. An asterisk indicates $P < 0.05$.

Lineage	Sample numbers	Haplotype numbers	P_i	Tajima's D		
R1a	86	8	0.0050	-1.5461	*	-
R1b	24	9	0.0170	-1.6127	*	-
R1c	8	2	0.0054	1.1665		-
H1	30	5	0.0076	-1.0883		-
R1	118	19	0.0193	-1.7198	*	-
R1b + H1	54	14	0.0173	-1.7514	*	-
R1 + H1	148	24	0.0241	-1.6590	*	-1
R2	110	20	0.0236	-1.0849		-
R3	21	7	0.0172	-0.7473		-
all	279	51	0.0547	-1.3016		-2

TABLE 2.—Statistics of sable populations within respect to haplotype compositions. The number “1” represents percent frequencies in each population), “2” represents haplotype diversity, “3” nucleotide diversity (π), and

H1	R1a	R1b	R1c
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Population	1	2	3	1	2	3	1	2	3	1	2
Kamchatka	0			15	0.25	0.0025	0			0	
				(100.0)							
Magadan	0			5	0.70	0.0080	5	0.80	0.0180	0	
				(45.5)			(45.5)				
Khabarovsk	0			24	0.66	0.0082	6	0.73	0.0120	0	
				(31.2)			(7.8)				
Primorsky	0			30	0.30	0.0032	0			0	
				(37.5)							
Krasnoyarsk	0			12	0.00	0.0000	5	0.40	0.0040	3	0.00
				(46.2)			(19.2)			(11.5)	
Ural	0			0			8	0.64	0.0204	5	0.00
							(29.6)			(18.5)	
Sakhalin	3	0.00	0.0000	0			0			0	
	(20.0)										
Hokkaido	22	0.39	0.0042	0			0			0	
	(100.0)										
Kuril	5	0.60	0.0120	0			0			0	

(100.0)

TABLE 3.—Population grouping of sable populations by SAMOVA analysis.

Number of groups (<i>K</i>)	2	3	4	5	6	7	8
Kamchatka	I	I	I	I	I	I	I
Magadan	I	I	II	II	II	II	II
Khabarovsk	I	I	II	II	III	III	III
Primorsky	I	I	II	II	III	IV	IV
Krasnoyarsk	I	I	II	II	III	II	V
Ural	I	I	II	II	III	V	VI
Sakhalin	I	I	II	III	IV	VI	VII
Hokkaido	II	II	III	IV	V	VII	VIII
Kuril	II	III	IV	V	VI	VII	VIII
FSC ^a	0.1505	0.1571	0.1275	0.1044	0.0989	-0.0200	-0.044
FST ^a	0.4340	0.4202	0.3841	0.3534	0.3273	0.2354	0.233

FCT ^a	0.3337	0.3121	0.2941	0.2780	0.2535	0.2504	0.267
Among group	33.37	31.21	29.41	27.80	25.35	25.04	26.7
Among populations within group	10.03	10.80	9.00	7.54	7.38	-1.50	-3.35
Within populations	56.60	57.98	61.59	64.66	67.27	76.46	76.6

^a: All FSC, FST and FCT values were statistically significant ($P < 0.05$).

FIG. 1.

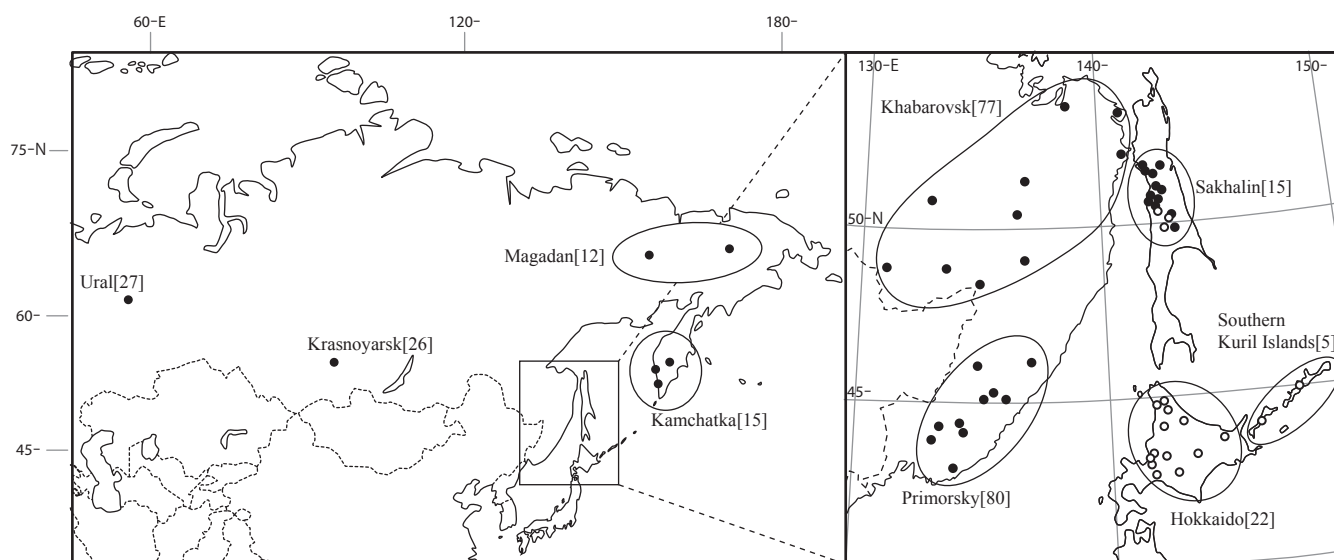


FIG. 2.

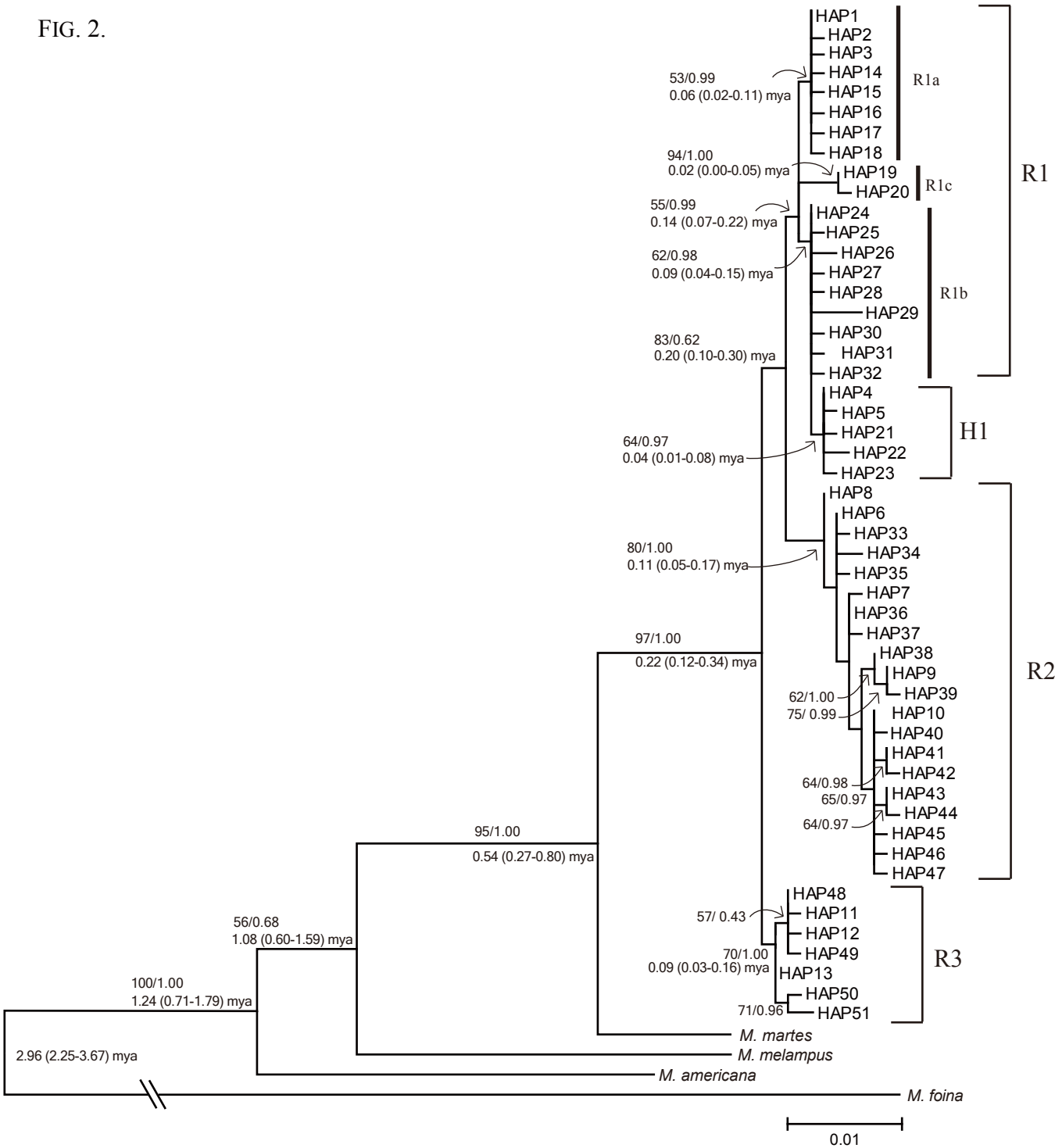


FIG. 3

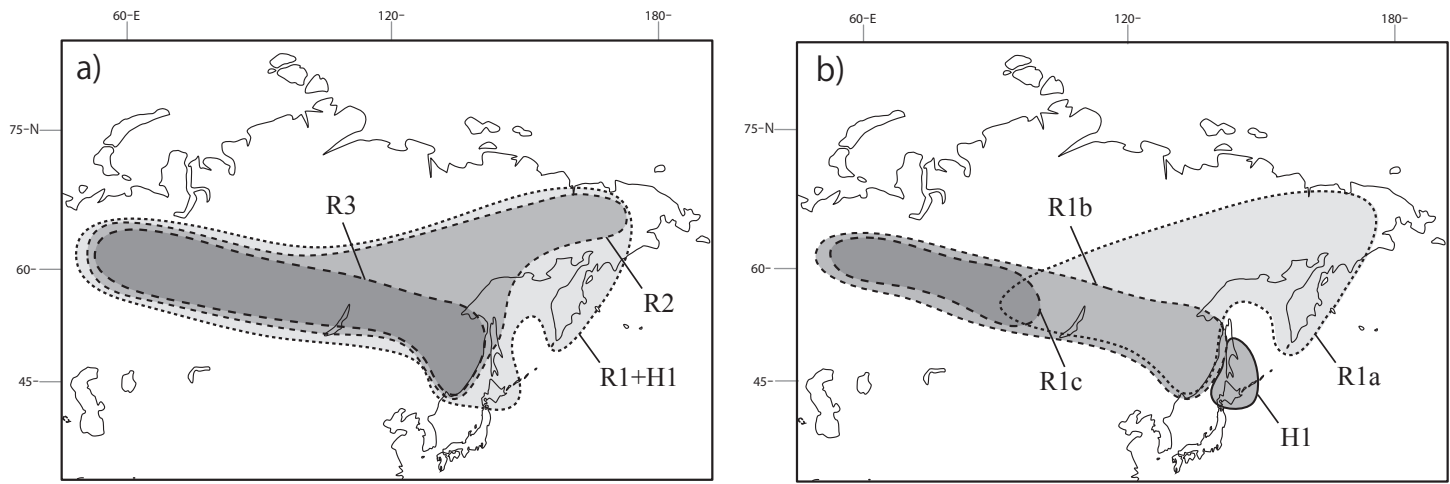


FIG. 4.

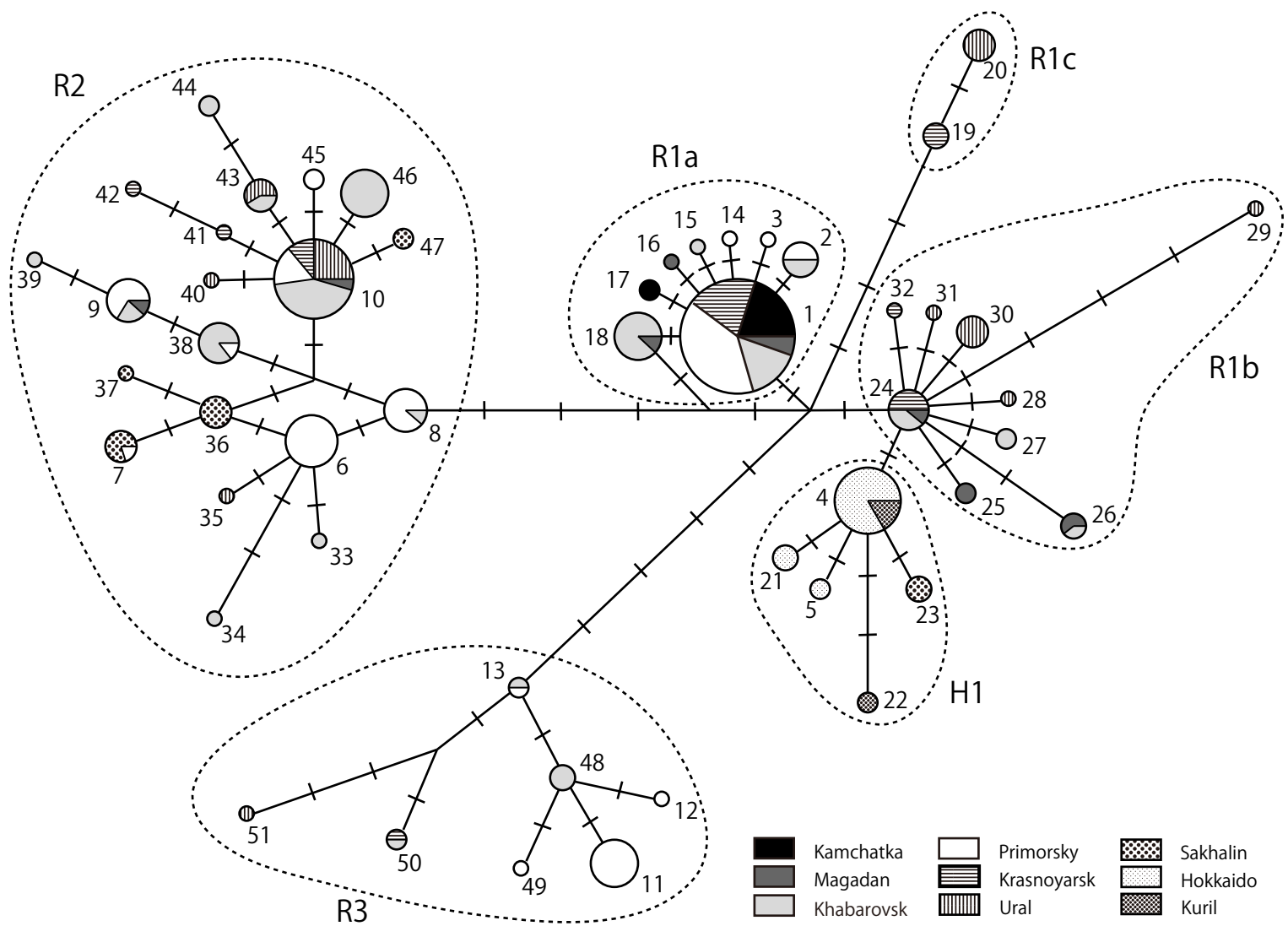
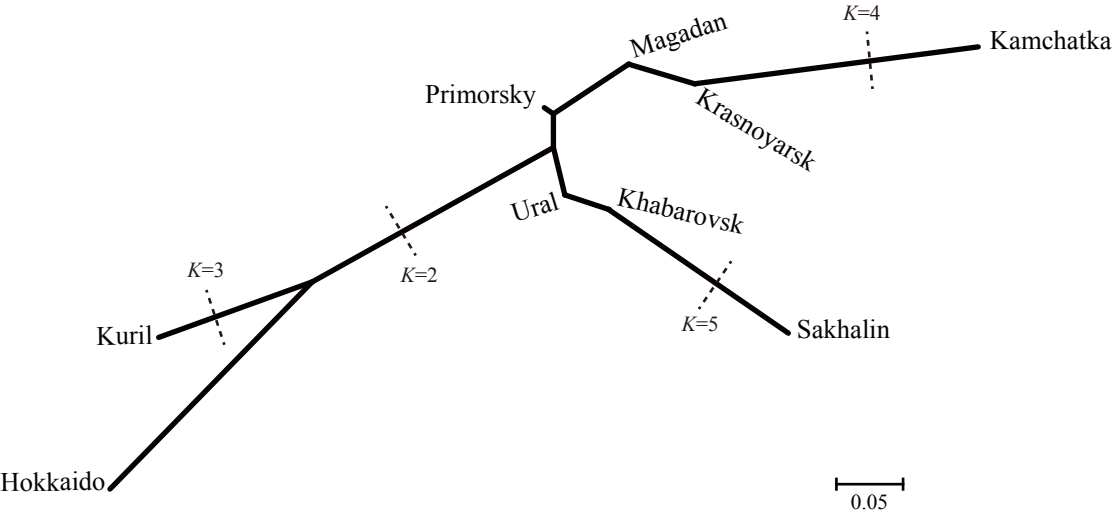


FIG. 5.



Population	Sample code	Haplotype	Sampling Locality	Accession numbers
Kamchatka	15_mi	Hap1	Milkovsky district, Kamchatka territory	AB908319 ^a
	19_mi	Hap1	Milkovsky district, Kamchatka territory	AB908319 ^a
	25_mi	Hap1	Milkovsky district, Kamchatka territory	AB908319 ^a
	39_mi	Hap1	Milkovsky district, Kamchatka territory	AB908319 ^a
	41_mi	Hap1	Milkovsky district, Kamchatka territory	AB908319 ^a
	55c	Hap1	Sobolevsky district, Kamchatka territory	AB908319 ^a
	56c	Hap1	Sobolevsky district, Kamchatka territory	AB908319 ^a
	57c	Hap1	Sobolevsky district, Kamchatka territory	AB908319 ^a
	60c	Hap1	Sobolevsky district, Kamchatka territory	AB908319 ^a
	25_ub	Hap1	Ust-Bolsheretsky district, Kamchatka territory	AB908319 ^a
	26_ub	Hap1	Ust-Bolsheretsky district, Kamchatka territory	AB908319 ^a
	29_ub	Hap17	Ust-Bolsheretsky district, Kamchatka territory	AB908335 ^a
	33_ub	Hap17	Ust-Bolsheretsky district, Kamchatka territory	AB908335 ^a
	34_ub	Hap1	Ust-Bolsheretsky district, Kamchatka territory	AB908319 ^a
	35_ub	Hap1	Ust-Bolsheretsky district, Kamchatka territory	AB908319 ^a
Magadan	26b	Hap26	Balygychan, Srednekansky district, Magadan region	AB908344 ^a
	29b	Hap16	Balygychan, Srednekansky district, Magadan region	AB908334 ^a
	34b	Hap1	Balygychan, Srednekansky district, Magadan region	AB908319 ^a
	35b	Hap18	Balygychan, Srednekansky district, Magadan region	AB908336 ^a
	37b	Hap10	Balygychan, Srednekansky district, Magadan region	AB908328 ^a
	46b	Hap1	Balygychan, Srednekansky district, Magadan region	AB908319 ^a
	50b	Hap26	Balygychan, Srednekansky district, Magadan region	AB908344 ^a
	51b	Hap24	Balygychan, Srednekansky district, Magadan region	AB908342 ^a
	111b	Hap1	Balygychan, Srednekansky district, Magadan region	AB908319 ^a
	CHUK2	Hap9	Chukotka territory	AB908327 ^a
	CHUK3	Hap25	Chukotka territory	AB908343 ^a
	CHUK4	Hap25	Chukotka territory	AB908343 ^a
Khabarovsk	AK2169	Hap9	Evoron lake, Solnechny district, Khabarovsk territory	AB625980 ^b
	AK204	Hap1	Solnechny district, Khabarovsk territory	AB625981 ^b
	AK205	Hap1	Solnechny district, Khabarovsk territory	AB625982 ^b
	AK206	Hap1	Solnechny district, Khabarovsk territory	AB625983 ^b
	6346_kh	Hap27	Nanaysky district, Khabarovsk territory	AB908345 ^a
	6347_kh	Hap27	Nanaysky district, Khabarovsk territory	AB908345 ^a
	6352_kh	Hap38	Nanaysky district, Khabarovsk territory	AB908356 ^a
	6357_kh	Hap8	Nanaysky district, Khabarovsk territory	AB908326 ^a
	6358_kh	Hap48	Nanaysky district, Khabarovsk territory	AB908366 ^a
	6364_kh	Hap33	Nanaysky district, Khabarovsk territory	AB908351 ^a

6369_kh	Hap48	Nanaysky district, Khabarovsky territory	AB908366 ^a
5888_kh	Hap48	Verkhnebureinsky district, Khabarovsky territory	AB908366 ^a
5889_kh	Hap9	Verkhnebureinsky district, Khabarovsky territory	AB908327 ^a
5891_kh	Hap46	Verkhnebureinsky district, Khabarovsky territory	AB908364 ^a
5894_kh	Hap46	Verkhnebureinsky district, Khabarovsky territory	AB908364 ^a
5902_kh	Hap39	Verkhnebureinsky district, Khabarovsky territory	AB908357 ^a
5903_kh	Hap18	Verkhnebureinsky district, Khabarovsky territory	AB908336 ^a
5904_kh	Hap10	Verkhnebureinsky district, Khabarovsky territory	AB908328 ^a
5912_kh	Hap46	Verkhnebureinsky district, Khabarovsky territory	AB908364 ^a
5916_kh	Hap1	Verkhnebureinsky district, Khabarovsky territory	AB908319 ^a
5970_kh	Hao13	Verkhnebureinsky district, Khabarovsky territory	AB908331 ^a
5977_kh	Hap18	Verkhnebureinsky district, Khabarovsky territory	AB908336 ^a
5980_kh	Hap1	Verkhnebureinsky district, Khabarovsky territory	AB908319 ^a
12-06	Hap10	spring Ulculusun, Obluchie district, Jewish region	AB908328 ^a
12-07	Hap18	Malaya Kamenushka river, Obluchie district, Jewish region	AB908336 ^a
12-08	Hap1	spring Maslovsky, Obluchie district, Jewish region	AB908319 ^a
12-09	Hap18	spring Maslovsky, Obluchie district, Jewish region	AB908336 ^a
12-10	Hap10	spring Maslovsky, Obluchie district, Jewish region	AB908328 ^a
12-11	Hap18	Malaya Kamenushka river, Obluchie district, Jewish region	AB908336 ^a
12-12	Hap46	spring Maslovsky, Obluchie district, Jewish region	AB908364 ^a
12-13	Hap46	spring Maslovsky, Obluchie district, Jewish region	AB908364 ^a
12-14	Hap24	spring Maslovsky, Obluchie district, Jewish region	AB908342 ^a
12-15	Hap46	spring Maslovsky, Obluchie district, Jewish region	AB908364 ^a
12-16	Hap46	Malaya Kamenushka river, Obluchie district, Jewish region	AB908364 ^a
12-17	Hap18	Malaya Kamenushka river, Obluchie district, Jewish region	AB908336 ^a
12-18	Hap10	Malaya Kamenushka river, Obluchie district, Jewish region	AB908328 ^a
12-19	Hap18	spring Maslovsky, Obluchie district, Jewish region	AB908336 ^a
12-20	Hap18	spring Maslovsky, Obluchie district, Jewish region	AB908336 ^a
12-21	Hap10	spring Maslovsky, Obluchie district, Jewish region	AB908328 ^a
12-22	Hap46	spring Maslovsky, Obluchie district, Jewish region	AB908364 ^a
12-23	Hap18	spring Maslovsky, Obluchie district, Jewish region	AB908336 ^a
12-24	Hap18	spring Maslovsky, Obluchie district, Jewish region	AB908336 ^a
12-25	Hap34	upper reaches of Yan river, Khabarovsky territory	AB908352 ^a
12-26	Hap10	upper reaches of Yan river, Khabarovsky territory	AB908328 ^a
12-27	Hap15	upper reaches of Yan river, Khabarovsky territory	AB908333 ^a
12-28	Hap24	upper reaches of Yan river, Khabarovsky territory	AB908342 ^a
12-29	Hap46	upper reaches of Yan river, Khabarovsky territory	AB908364 ^a
12-30	Hap46	upper reaches of Yan river, Khabarovsky territory	AB908364 ^a
3370	Hap38	Khabarovsky territory, Nikolaevsky district	AB908356 ^a
3371	Hap2	Khabarovsky territory, Nikolaevsky district	AB908320 ^a
3372	Hap38	Khabarovsky territory, Nikolaevsky district	AB908356 ^a

Primorsky	3373	Hap38	Khabarovsky territory, Nikolaevsky district	AB908356 ^a
	3374	Hap10	Khabarovsky territory, Nikolaevsky district	AB908328 ^a
	3375	Hap1	Khabarovsky territory, Nikolaevsky district	AB908319 ^a
	3376	Hap1	Khabarovsky territory, Nikolaevsky district	AB908319 ^a
	3377	Hap10	Khabarovsky territory, Nikolaevsky district	AB908328 ^a
	3378	Hap10	Khabarovsky territory, Nikolaevsky district	AB908328 ^a
	3379	Hap2	Khabarovsky territory, Nikolaevsky district	AB908320 ^a
	3380	Hap10	Khabarovsky territory, Nikolaevsky district	AB908328 ^a
	3381	Hap1	Khabarovsky territory, Nikolaevsky district	AB908319 ^a
	3382	Hap2	Khabarovsky territory, Nikolaevsky district	AB908320 ^a
	3383	Hap38	Khabarovsky territory, Nikolaevsky district	AB908356 ^a
	3384	Hap10	Khabarovsky territory, Nikolaevsky district	AB908328 ^a
	3385	Hap46	Khabarovsky territory, Nikolaevsky district	AB908364 ^a
	3386	Hap10	Khabarovsky territory, Nikolaevsky district	AB908328 ^a
	3387	Hap1	Khabarovsky territory, Nikolaevsky district	AB908319 ^a
	3388	Hap24	Khabarovsky territory, Nikolaevsky district	AB908342 ^a
	3389	Hap10	Khabarovsky territory, Nikolaevsky district	AB908328 ^a
	3390	Hap10	Khabarovsky territory, Nikolaevsky district	AB908328 ^a
	3391	Hap38	Khabarovsky territory, Nikolaevsky district	AB908356 ^a
	3392	Hap38	Khabarovsky territory, Nikolaevsky district	AB908356 ^a
	3393	Hap26	Khabarovsky territory, Nikolaevsky district	AB908344 ^a
	LAPKI2	Hap50	Tuguro-Chumikansky district, Khabarovsky territory	AB908368 ^a
	LAPKI3	Hap43	Tuguro-Chumikansky district, Khabarovsky territory	AB908361 ^a
	LAPKI4	Hap44	Tuguro-Chumikansky district, Khabarovsky territory	AB908362 ^a
	LAPKI5	Hap44	Tuguro-Chumikansky district, Khabarovsky territory	AB908362 ^a
	LAPKI6	Hap43	Tuguro-Chumikansky district, Khabarovsky territory	AB908361 ^a
	AK1309	Hap7	Sal'da river, Pozharsky district, Primorsky territory	AB625984 ^b
	AK1310	Hap11	Sal'da river, Pozharsky district, Primorsky territory	AB625985 ^b
	AK1311	Hap6	Sal'da river, Pozharsky district, Primorsky territory	AB625986 ^b
	AK1312	Hap6	Sal'da river, Pozharsky district, Primorsky territory	AB625987 ^b
	AK1274	Hap8	Amgu vil., Maksimovka river, Primorsky territory	AB625988 ^b
	AK1275	Hap2	Amgu vil., Maksimovka river, Primorsky territory	AB625989 ^b
	AK1276	Hap1	Mel'nichnoe vil., Bol'shaya Ussurka river, Primorsky territory	AB625990 ^b
	AK1277	Hap1	Mel'nichnoe vil., Bol'shaya Ussurka river, Primorsky territory	AB625991 ^b
	AK1278	Hap1	Mel'nichnoe vil., Bol'shaya Ussurka river, Primorsky territory	AB625992 ^b
	AK1279	Hap1	Mel'nichnoe vil., Bol'shaya Ussurka river, Primorsky territory	AB625993 ^b
	AK1280	Hap1	Mel'nichnoe vil., Bol'shaya Ussurka river, Primorsky territory	AB625994 ^b
	AK1281	Hap1	Mel'nichnoe vil., Bol'shaya Ussurka river, Primorsky territory	AB625995 ^b
	AK1282	Hap1	Mel'nichnoe vil., Bol'shaya Ussurka river, Primorsky territory	AB625996 ^b
	AK1283	Hap6	Mel'nichnoe vil., Bol'shaya Ussurka river, Primorsky territory	AB625997 ^b
	AK1284	Hap1	Mel'nichnoe vil., Bol'shaya Ussurka river, Primorsky territory	AB625998 ^b

AK1292	Hap8	Mel'nichnoe vil., Bol'shaya Ussurka river, Primorsky territory	AB625999 ^b
AK1293	Hap6	Mel'nichnoe vil., Bol'shaya Ussurka river, Primorsky territory	AB626000 ^b
AK1324	Hap9	Primanka river, Krasnoarmeysky district, Primorsky territory	AB626001 ^b
AK1394	Hap6	Primanka river, Krasnoarmeysky district, Primorsky territory	AB626002 ^b
AK1395	Hap1	Primanka river, Krasnoarmeysky district, Primorsky territory	AB626003 ^b
AK1396	Hap6	Primanka river, Krasnoarmeysky district, Primorsky territory	AB626004 ^b
AK1397	Hap3	Primanka river, Krasnoarmeysky district, Primorsky territory	AB626005 ^b
AK1398	Hap8	Primanka river, Krasnoarmeysky district, Primorsky territory	AB626006 ^b
AK1399	Hap6	Primanka river, Krasnoarmeysky district, Primorsky territory	AB626007 ^b
AK1400	Hap1	Primanka river, Krasnoarmeysky district, Primorsky territory	AB626008 ^b
AK1574	Hap11	Primanka river, Krasnoarmeysky district, Primorsky territory	AB626009 ^b
AK1575	Hap12	Primanka river, Krasnoarmeysky district, Primorsky territory	AB626010 ^b
AK1576	Hap8	Primanka river, Krasnoarmeysky district, Primorsky territory	AB626011 ^b
AK1654	Hap1	Primanka river, Krasnoarmeysky district, Primorsky territory	AB626012 ^b
AK1655	Hap1	Primanka river, Krasnoarmeysky district, Primorsky territory	AB626013 ^b
AK1689	Hap9	Primanka river, Krasnoarmeysky district, Primorsky territory	AB626014 ^b
AK1690	Hap6	Primanka river, Krasnoarmeysky district, Primorsky territory	AB626015 ^b
AK1691	Hap1	Primanka river, Krasnoarmeysky district, Primorsky territory	AB626016 ^b
AK1692	Hap6	Primanka river, Krasnoarmeysky district, Primorsky territory	AB626017 ^b
AK1693	Hap6	Primanka river, Krasnoarmeysky district, Primorsky territory	AB626018 ^b
AK1694	Hap1	Primanka river, Krasnoarmeysky district, Primorsky territory	AB626019 ^b
AK739	Hap8	Sitca river, Terneysky district, Primorsky territory	AB626020 ^b
AK1944	Hap6	Primanka river, Krasnoarmeysky district, Primorsky territory	AB908324 ^a
AK1945	Hap1	Primanka river, Krasnoarmeysky district, Primorsky territory	AB908319 ^a
AK1946	Hap11	Primanka river, Krasnoarmeysky district, Primorsky territory	AB908329 ^a
AK1947	Hap1	Primanka river, Krasnoarmeysky district, Primorsky territory	AB908319 ^a
AK1948	Hap45	Primanka river, Krasnoarmeysky district, Primorsky territory	AB908363 ^a
AK1958	Hap8	Primanka river, Krasnoarmeysky district, Primorsky territory	AB908326 ^a
AK1959	Hap1	Primanka river, Krasnoarmeysky district, Primorsky territory	AB908319 ^a
AK1960	Hap6	Primanka river, Krasnoarmeysky district, Primorsky territory	AB908324 ^a
AK1961	Hap6	Primanka river, Krasnoarmeysky district, Primorsky territory	AB908324 ^a
AK1962	Hap11	Primanka river, Krasnoarmeysky district, Primorsky territory	AB908329 ^a
AK1963	Hap11	Primanka river, Krasnoarmeysky district, Primorsky territory	AB908329 ^a
AK1964	Hap8	Primanka river, Krasnoarmeysky district, Primorsky territory	AB908326 ^a
AK1965	Hap1	Primanka river, Krasnoarmeysky district, Primorsky territory	AB908319 ^a
AK1966	Hap45	Primanka river, Krasnoarmeysky district, Primorsky territory	AB908363 ^a
AK1210	Hap10	Koksharovka vil., Chuguevsky district, Primorsky territory	AB626021 ^b
AK1211	Hap1	Koksharovka vil., Chuguevsky district, Primorsky territory	AB626022 ^b
AK1212	Hap10	Koksharovka vil., Chuguevsky district, Primorsky territory	AB626023 ^b
AK1213	Hap9	Koksharovka vil., Chuguevsky district, Primorsky territory	AB626024 ^b
AK1214	Hap1	Koksharovka vil., Chuguevsky district, Primorsky territory	AB626025 ^b

	AK1215	Hap9	Koksharovka vil., Chuguevsky district, Primorsky territory	AB626026 ^b
	AK1216	Hap10	Koksharovka vil., Chuguevsky district, Primorsky territory	AB626027 ^b
	AK1269	Hap1	Koksharovka vil., Chuguevsky district, Primorsky territory	AB626028 ^b
	AK1285	Hap13	Koksharovka vil., Chuguevsky district, Primorsky territory	AB626029 ^b
	AK1286	Hap10	Koksharovka vil., Chuguevsky district, Primorsky territory	AB626030 ^b
	AK1287	Hap8	Koksharovka vil., Chuguevsky district, Primorsky territory	AB626031 ^b
	AK1288	Hap11	Koksharovka vil., Chuguevsky district, Primorsky territory	AB626032 ^b
	AK1336	Hap11	Koksharovka vil., Chuguevsky district, Primorsky territory	AB626033 ^b
	AK1644	Hap1	Koksharovka vil., Chuguevsky district, Primorsky territory	AB626034 ^b
	AK1645	Hap9	Koksharovka vil., Chuguevsky district, Primorsky territory	AB626035 ^b
	AK1646	Hap10	Koksharovka vil., Chuguevsky district, Primorsky territory	AB626036 ^b
	AK1699	Hap11	Koksharovka vil., Chuguevsky district, Primorsky territory	AB626037 ^b
	AK1700	Hap11	Koksharovka vil., Chuguevsky district, Primorsky territory	AB626038 ^b
	AK1701	Hap11	Koksharovka vil., Chuguevsky district, Primorsky territory	AB626039 ^b
	AK1734	Hap11	Koksharovka vil., Chuguevsky district, Primorsky territory	AB908329 ^a
	AK1735	Hap9	Koksharovka vil., Chuguevsky district, Primorsky territory	AB908327 ^a
	AK1736	Hap1	Koksharovka vil., Chuguevsky district, Primorsky territory	AB908319 ^a
	AK1737	Hap1	Koksharovka vil., Chuguevsky district, Primorsky territory	AB908319 ^a
	AK1831	Hap49	Anuchinsky district, Primorsky territory	AB908367 ^a
	AK1832	Hap1	Anuchinsky district, Primorsky territory	AB908319 ^a
	5925_kh	Hap14	Lazovsky district , Primorsky territory	AB908332 ^a
	5932_kh	Hap38	Lazovsky district , Primorsky territory	AB908356 ^a
	5938_kh	Hap2	Lazovsky district , Primorsky territory	AB908320 ^a
	5959_kh	Hap2	Lazovsky district , Primorsky territory	AB908320 ^a
Krasnoyarsk	1_kr	Hap24	Sayansky district, Krasnoyarsky territory	AB908342 ^a
	2_kr	Hap10	Sayansky district, Krasnoyarsky territory	AB908328 ^a
	3_kr	Hap19	Sayansky district, Krasnoyarsky territory	AB908337 ^a
	4_kr	Hap19	Sayansky district, Krasnoyarsky territory	AB908337 ^a
	5_kr	Hap10	Sayansky district, Krasnoyarsky territory	AB908328 ^a
	6_kr	Hap1	Sayansky district, Krasnoyarsky territory	AB908319 ^a
	7_kr	Hap42	Sayansky district, Krasnoyarsky territory	AB908360 ^a
	8_kr	Hap1	Sayansky district, Krasnoyarsky territory	AB908319 ^a
	9_kr	Hap1	Sayansky district, Krasnoyarsky territory	AB908319 ^a
	10_kr	Hap1	Sayansky district, Krasnoyarsky territory	AB908319 ^a
	11_kr	Hap41	Sayansky district, Krasnoyarsky territory	AB908359 ^a
	12_kr	Hap24	Sayansky district, Krasnoyarsky territory	AB908342 ^a
	13_kr	Hap10	Sayansky district, Krasnoyarsky territory	AB908328 ^a
	14_kr	Hap1	Sayansky district, Krasnoyarsky territory	AB908319 ^a
	15_kr	Hap50	Sayansky district, Krasnoyarsky territory	AB908368 ^a
	16_kr	Hap1	Sayansky district, Krasnoyarsky territory	AB908319 ^a
	17_kr	Hap32	Sayansky district, Krasnoyarsky territory	AB908350 ^a

Ural	18_kr	Hap1	Sayansky district, Krasnoyarsky territory	AB908319 ^a
	19_kr	Hap24	Sayansky district, Krasnoyarsky territory	AB908342 ^a
	20_kr	Hap19	Sayansky district, Krasnoyarsky territory	AB908337 ^a
	21_kr	Hap1	Sayansky district, Krasnoyarsky territory	AB908319 ^a
	22_kr	Hap24	Sayansky district, Krasnoyarsky territory	AB908342 ^a
	23_kr	Hap1	Sayansky district, Krasnoyarsky territory	AB908319 ^a
	24_kr	Hap1	Sayansky district, Krasnoyarsky territory	AB908319 ^a
	25_kr	Hap1	Sayansky district, Krasnoyarsky territory	AB908319 ^a
	26_kr	Hap1	Sayansky district, Krasnoyarsky territory	AB908319 ^a
	ZI18U	Hap28	Troitsko-Pechorsky district, Komi Republic	AB908346 ^a
	ZI20	Hap10	Troitsko-Pechorsky district, Komi Republic	AB908328 ^a
	ZI21U	Hap10	Troitsko-Pechorsky district, Komi Republic	AB908328 ^a
	ZI26U	Hap20	Troitsko-Pechorsky district, Komi Republic	AB908338 ^a
	ZI30U	Hap30	Troitsko-Pechorsky district, Komi Republic	AB908348 ^a
	ZI31U	Hap43	Troitsko-Pechorsky district, Komi Republic	AB908361 ^a
	ZI34U	Hap35	Troitsko-Pechorsky district, Komi Republic	AB908353 ^a
	ZI35U	Hap10	Troitsko-Pechorsky district, Komi Republic	AB908328 ^a
	ZI37U	Hap29	Troitsko-Pechorsky district, Komi Republic	AB908347 ^a
	ZI38U	Hap40	Troitsko-Pechorsky district, Komi Republic	AB908358 ^a
	ZI44U	Hap31	Troitsko-Pechorsky district, Komi Republic	AB908349 ^a
	ZI47U	Hap30	Troitsko-Pechorsky district, Komi Republic	AB908348 ^a
	ZI54U	Hap43	Troitsko-Pechorsky district, Komi Republic	AB908361 ^a
	ZI57U	Hap43	Troitsko-Pechorsky district, Komi Republic	AB908361 ^a
	ZI61U	Hap30	Troitsko-Pechorsky district, Komi Republic	AB908348 ^a
	ZI63U	Hap51	Troitsko-Pechorsky district, Komi Republic	AB908369 ^a
	ZI69U	Hap30	Troitsko-Pechorsky district, Komi Republic	AB908348 ^a
	ZI28U	Hap10	Troitsko-Pechorsky district, Komi Republic	AB908328 ^a
	ZI39U	Hap10	Troitsko-Pechorsky district, Komi Republic	AB908328 ^a
	ZI43U	Hap10	Troitsko-Pechorsky district, Komi Republic	AB908328 ^a
	ZI48U	Hap20	Troitsko-Pechorsky district, Komi Republic	AB908338 ^a
	ZI50U	Hap10	Troitsko-Pechorsky district, Komi Republic	AB908328 ^a
	ZI51U	Hap10	Troitsko-Pechorsky district, Komi Republic	AB908328 ^a
	ZI53U	Hap20	Troitsko-Pechorsky district, Komi Republic	AB908338 ^a
	ZI55U	Hap20	Troitsko-Pechorsky district, Komi Republic	AB908338 ^a
	ZI58U	Hap30	Troitsko-Pechorsky district, Komi Republic	AB908348 ^a
	ZI71U	Hap20	Troitsko-Pechorsky district, Komi Republic	AB908338 ^a
Sakhalin	GK1020	Hap37	Sakhalin Island	AB908355 ^a
	GK1021	Hap47	Sakhalin Island	AB908365 ^a
	GK1022	Hap23	Sakhalin Island	AB908341 ^a
	GK1023	Hap7	Sakhalin Island	AB908325 ^a
	GK1024	Hap36	Sakhalin Island	AB908354 ^a

Hokkaido	GK1025	Hap23	Sakhalin Island	AB908341 ^a
	GK1026	Hap23	Sakhalin Island	AB908341 ^a
	GK1027	Hap7	Sakhalin Island	AB908325 ^a
	GK1028	Hap36	Sakhalin Island	AB908354 ^a
	GK1029	Hap7	Sakhalin Island	AB908325 ^a
	GK1030	Hap36	Sakhalin Island	AB908354 ^a
	GK1031	hap36	Sakhalin Island	AB908354 ^a
	GK1032	Hap7	Sakhalin Island	AB908325 ^a
	GK1033	Hap47	Sakhalin Island	AB908365 ^a
	GK1034	Hap36	Sakhalin Island	AB908354 ^a
	HS3863	Hap5	Nukabira Onsen, Hokkaido Island	AB626040 ^b
	HS3864	Hap4	Nukabira Onsen, Hokkaido Island	AB626041 ^b
	HS3865	Hap4	Nukabira Onsen, Hokkaido Island	AB626042 ^b
	HS4701	Hap5	Nishiokoppe, Hokkaido Island	AB626043 ^b
	HS4705	Hap4	Nopporo, Hokkaido Island	AB626044 ^b
	HS4715	Hap4	Higashimokoto, Hokkaido Island	AB626045 ^b
	TH43	Hap4	Otoineppu, Hokkaido Island	AB626046 ^b
	TH44	Hap4	Soeushinai, Horokanai, Hokkaido Island	AB626047 ^b
	TH53	Hap4	Toikanbetsu, Hokkaido Island	AB626048 ^b
	TH401	Hap4	Teshio, Hokkaido Island	AB455741 ^c
	HS4800	Hap4	Chitose, Hokkaido Island	AB908322 ^a
	HS4869	Hap4	Tsukigata, Hokkaido Island	AB908322 ^a
	HS4870	Hap4	Tobetsu, Hokkaido Island	AB908322 ^a
	HS4871	Hap4	Tsukigata, Hokkaido Island	AB908322 ^a
	HS4872	Hap4	Tsukigata, Hokkaido Island	AB908322 ^a
	HS4856	Hap21	Tsukigata, Hokkaido Island	AB908339 ^a
	HS4890	Hap4	Hidaka, Hokkaido Island	AB908322 ^a
	HS4924	Hap4	Mikasa, Hokkaido, Japna	AB908322 ^a
	HS4966	Hap21	Tobetsu, Hokkaido Island	AB908339 ^a
	HS4993	Hap4	Tobetsu, Hokkaido Island	AB908322 ^a
	HS4994	Hap4	Tobetsu, Hokkaido Island	AB908322 ^a
	HS4995	Hap21	Tobetsu, Hokkaido Island	AB908339 ^a
Kuril	1_ku	Hap4	Kunashir Island, Kuril Islands	AB908322 ^a
	2_ku	Hap4	Kunashir Island, Kuril Islands	AB908322 ^a
	3_ku	Hap4	Kunashir Island, Kuril Islands	AB908322 ^a
	4_ku	Hap22	Iturup Island, Kuril Islands	AB908340 ^a
	5_ku	Hap22	Iturup Island, Kuril Islands	AB908340 ^a

^a Sequence generated in this study.

^b Sequence published in Sato et al. (2011).

^c Sequence published in Sato et al. (2009).