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Morphological and genetic variation of narrow-headed voles *Lasiopodomys gregalis* from South-East Transbaikalia

Andrey A. Lissovsky*, Ekaterina V. Obolenskaya & Tatyana V. Petrova

ABSTRACT. The sample of 115 skulls and 28 sequences of cytochrome *b* gene of narrow-headed voles *Lasiopodomys gregalis*, mainly from South-East Transbaikalia was studied. Geographic variation of craniometric features was not found in the studied sample. Such morphological variation contradicts deep mitochondrial divergence between voles from the South and North of the region under discussion.

KEY WORDS: narrow-headed voles, *Lasiopodomys gregalis*, South-East Transbaikalia.

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Морфологическая и генетическая изменчивость узкочерепных полевок *Lasiopodomys gregalis* Юго-Восточного Забайкалья

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РЕЗЮМЕ. Изучена выборка из 115 черепов и 28 последовательностей гена цитохрома *b* узкочерепной полевки *Lasiopodomys gregalis*, главным образом, из Юго-Восточного Забайкалья. Показано, что географическая изменчивость краниометрических признаков в изученной выборке не выражена. Это не соответствует глубокой митохондриальной дивергенции полевок юга и севера региона.

КЛЮЧЕВЫЕ СЛОВА: узкочерепные полевки, *Lasiopodomys gregalis*, Юго-Восточное Забайкалье.

Introduction

Morphological variation of narrow-headed vole *Lasiopodomys gregalis* (Pallas, 1779) was studied in detail (Dupal, 2000; Golenishchev & Petrovskaya, 2002; Dupal & Abramov, 2010). According to these studies, morphologically homogeneous population inhabits the major part of the distribution range of the species. Some studies found clinal variation of craniometrical features. Several geographical samples were found to be slightly different from the major part of the species; these samples were different depending on the features and geographic area analyzed. Nobody found, however, morphological peculiarity of narrow-headed voles from South-East Transbaikalia.

Meanwhile pilot genetic study found considerable mitochondrial difference between voles from South-East Transbaikalia and other distribution range (Abramson *et al*., 2006).

The aim of this study was to examine mitochondrial and morphological variation of narrow-headed voles from South-East Transbaikalia and to evaluate concordance between mitochondrial and morphological data.

Materials and methods

Narrow-headed vole is a species that was formerly included in the genus *Microtus* Schrank, 1798 within the separate subgenus *Stenocranius* Kastschenko, 1901 (Gromov & Polyakov, 1977). Molecular data suggest that this taxon is close to species of the genus *Lasiopodomys* Lataste, 1887. Furthermore, this latter genus is separate from the *Microtus* clade (Abramson *et al*., 2009; Bannikova *et al*., 2010). Thus, following Abramson & Lissovsky (2012), we use the name *Lasiopodomys gregalis*.

Specimens used in the morphometric study were taken from the collection of the Zoological Museum of Moscow State University. The sample contained 115 intact skulls of *L. gregalis* (Appendix 1).

Fifteen measurements were taken (with an accuracy of 0.1 mm) from each skull as follows: condylobasal length, minimal distance between maxillary toothrows, diastemal length, alveolar length of maxillary toothrow, zygomatic breadth, maximal width between lateral edges of auditory bullae, skull height at maxillary toothrows level, orbital length and width, width of rostrum' base, orbital constriction, length of auditory bul-

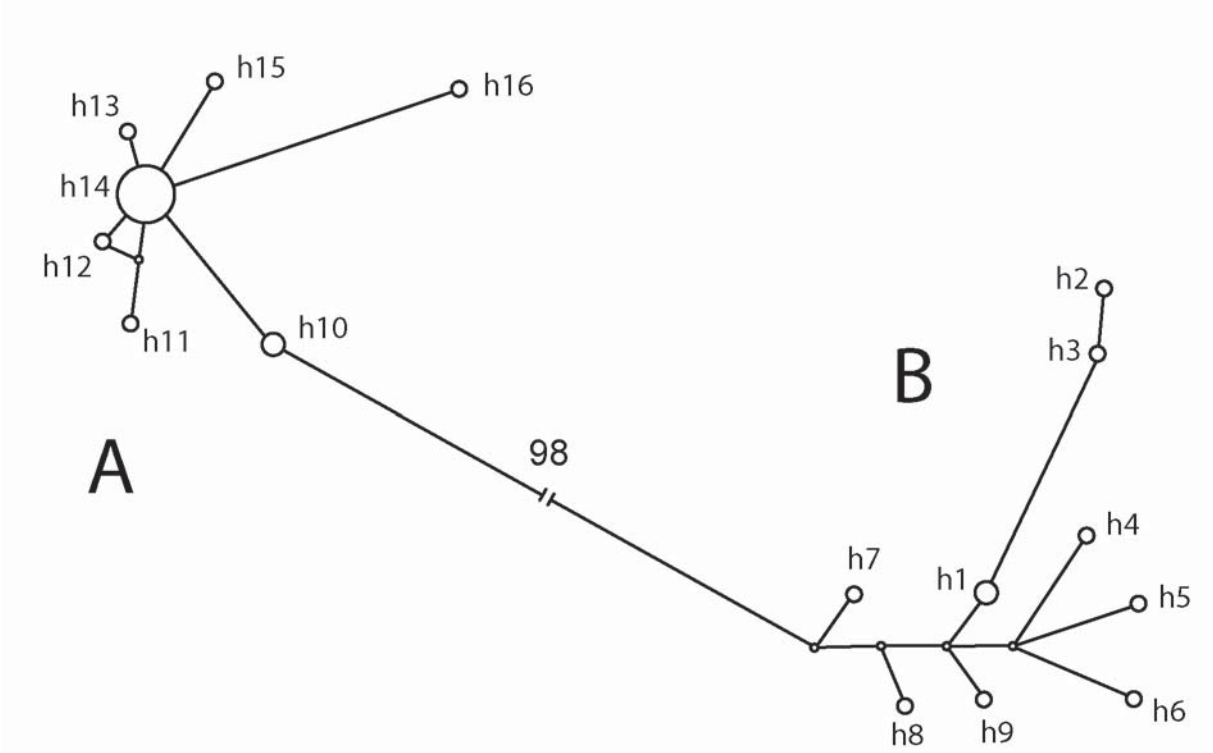

Figure 1. Maximum parsimony network of *L. gregalis* cytochrome *b* haplotypes from Transbaikalia. Haplotype labels refer to Appendix 2. The size of circles is proportional to the haplotype frequency.

la, width of auditory bulla, alveolar length of mandibular toothrow, distance between the base of incisor and the apex of mandibular articular process. All calculations were performed on logarithmic measurements.

We used the skulls of voles of different ages. All skulls were divided into three age categories corresponding to obviously juvenile (1), obviously adult with developed crests on the skull (3), and all others (2).

In order to exclude age bias from morphometric analysis, we used an orthogonal projection of initial data along the vector of age variation (Burnaby, 1966). The vector of age variation was calculated as the first eigenvector of the between-group covariance matrix computed with MANOVA, in which the variable containing age gradations was used as a grouping variable. We used only the first and the third age classes during calculations of the covariance matrix in order to avoid an error induced by inaccuracy in determining the second age class. There were five samples included in this analysis.

The samples for hierarchical cluster analysis included only specimens collected in the same locality (45 samples total, Appendix 1). Only samples with $n>3$ were used in cluster analysis (16 samples). Cluster analysis was performed on the basis of a matrix of Mahalanobis distances using the unweighted pair group method with arithmetic mean. The bias induced by using samples of different sizes was corrected (Marcus, 1993).

The following approach was applied as an ordination method: first, the eigenvectors of the within-group covariance matrix (with 16 large geographic samples as groups) of the dataset with reduced age was calculated. Secondly, the initial data matrix was multiplied with the matrix of the eigenvectors. Thus the initial data was rotated into the space of intergroup variation without distortion of the initial space.

Craniometric data were processed using standard modules of STATISTICA 8.0 (StatSoft 2007) and several custom algorithms written by the first author using Statistica Visual Basic programming language.

A fragment of mitochondrial gene cytochrome *b* from 28 voles from 11 geographical localities (Appendix 2) was used for the study of genetic variation. The gene region (891 bp) was amplified by polymerase chain reaction (PCR) using primer combination L14728 (Lebedev *et al*., 2007) / H15985 (Ohdachi *et al*., 2001). PCR entailed 30 thermal cycles as follows: 30 s denaturation at 94°C, 45 s annealing at 55°C and 1 min 20 s extension at 72°C. All PCR experiments included negative controls. PCR products were visualized on 1.5% agarose gel and then purified using Omnix DNA purification kit. Both strands were directly sequenced using the ABI PRISM BigDye Terminator v. 3.1.

A maximum parsimony haplotype network was constructed with Network 4.6 (Bandelt *et al*., 1999) using the median joining method.

Field material was gathered in Zabaikalskiy Kray (former Chitinskaya Region and Aginskiy Buryat Autonomous District) within Krasnokamenskiy, Kalgan-

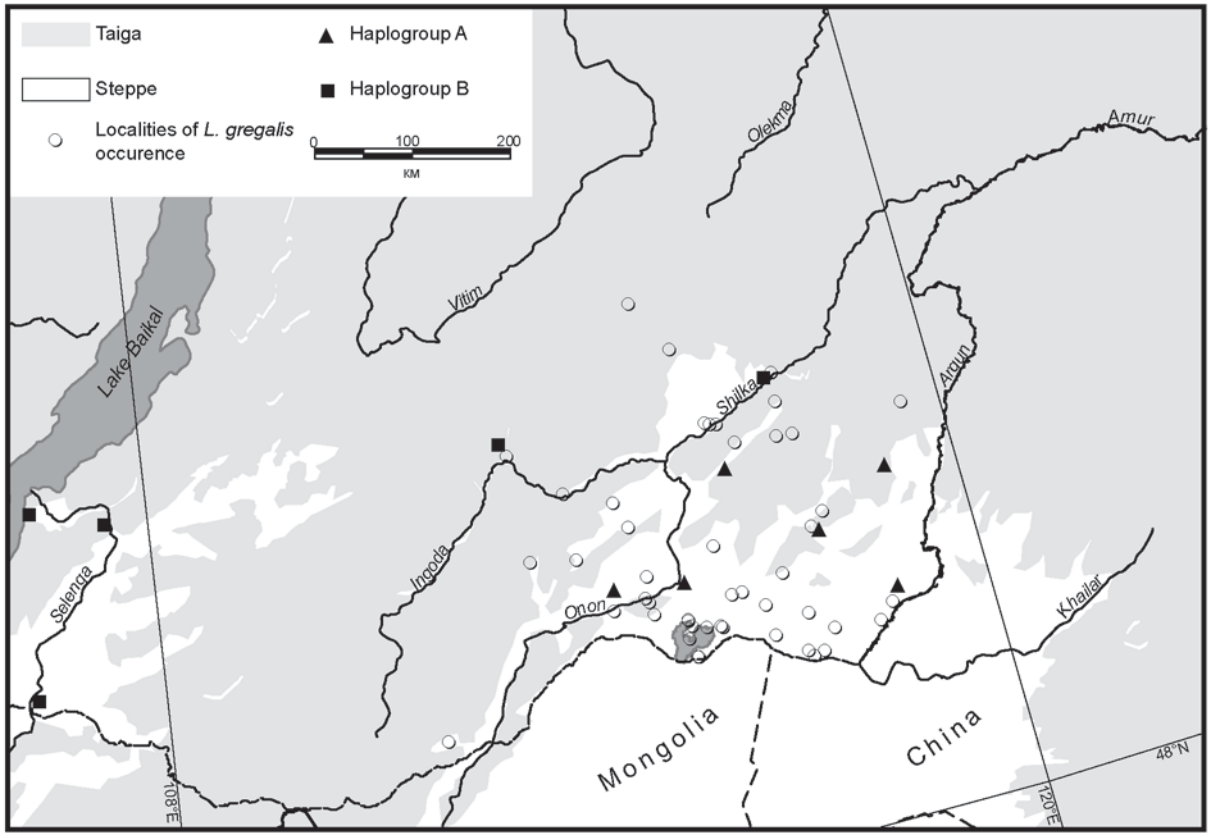

Figure 2. Distribution of *L. gregalis* in South-East Transbaikalia. Localities where specimens were studied genetically are shown.

skiy, Aginskiy, Alexandrozavodskiy and Sretenskiy districts (2005, 2007, 2011), Russia.

The map of distribution of narrow-headed voles in South-East Transbaikalia was constructed on the basis of localities of the specimens from the following collections: Zoological Museum of Moscow State University; Zoological Institute of the Russian Academy of Sciences, Saint-Petersburg; Institute of Systematics and Ecology of Animals, Siberian Branch of the Russian Academy of Sciences; Zoological Museum of Irkutsk State University.

Results

All haplotypes of Transbaikalian narrow-headed voles constituted two groups, divided by 98 substitutions (Fig. 1). Such difference roughly corresponds to p-distance of 11%. Geographic distribution of the two haplogroups representatives is shown in Fig. 2. Representatives of the haplogroup A distributed to the South from Shilka River and in steppe along Onon River. Voles bearing haplotypes of the haplogroup B inhabit western Transbaikalia and steppe to the North of Shilka and Ingoda Rivers.

The first two axes of the space of maximized intersample morphological differences explain 41 and 28% of total variance respectively. Specimens from different parts of the range form the single cloud within this space (Fig. 3). Distribution of specimens from two regions of Transbaikalia, outlined above, completely overlaps. Cluster analysis of craniometric features does not separate voles from these two regions of Transbaikalia also (Fig. 4).

Discussion

Our results do not show concordance between the deep mitochondrial divergence of Transbaikalian narrow-headed voles and their cranial morphology. While the extent of mitochondrial differences between haplogroups A and B is comparable to the divergence between subgenera *Alexandromys* and *Pallasiinus* (Bannikova *et al*., 2010), craniometric data does not display any geographic variation.

This discordance can be explained in two different ways. The first way means that voles from northern and southern parts of South-East Transbaikalia (corresponding to haplogroups A and B) belong to two sister taxa separated long time ago from each other. In this case, these taxa are sibling species, since they have no morphological distinction. Another possible explanation is mitochondrial artifact — conservation of ancient mito-

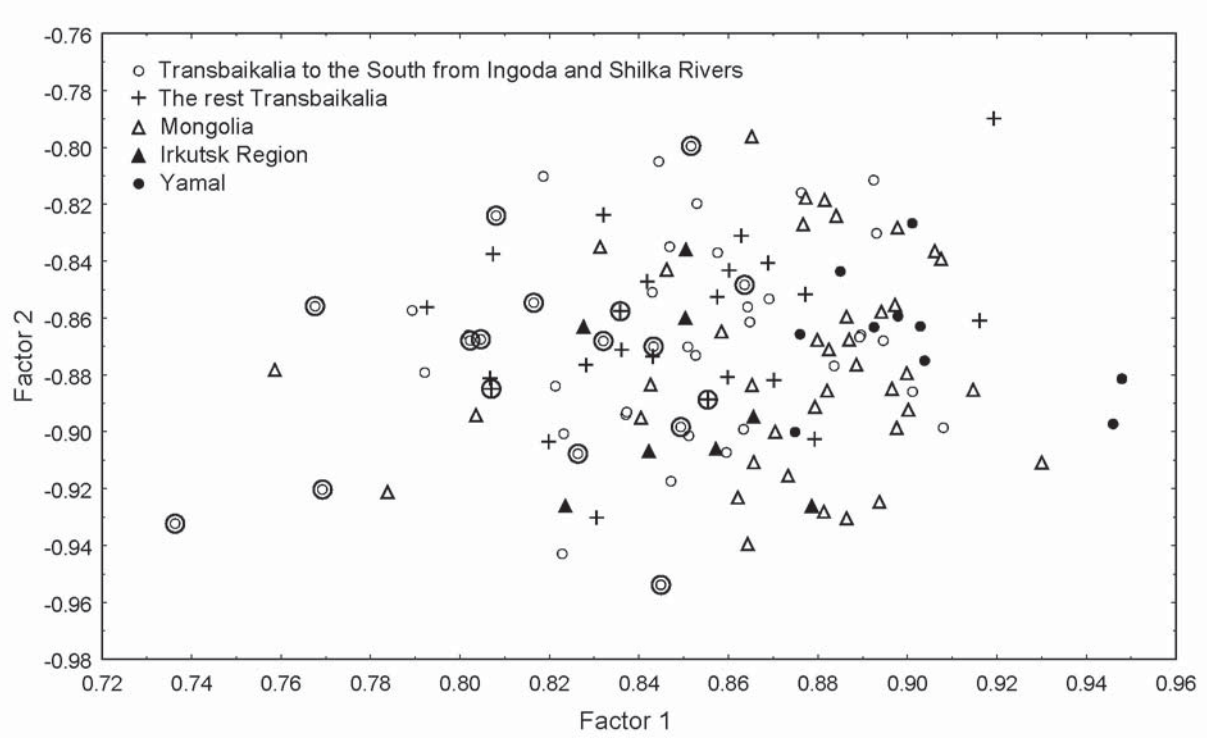

Figure 3. Distribution of *L. gregalis* specimens in the space of maximized differences between geographical samples. The specimens, studied genetically, are outlined with circle.

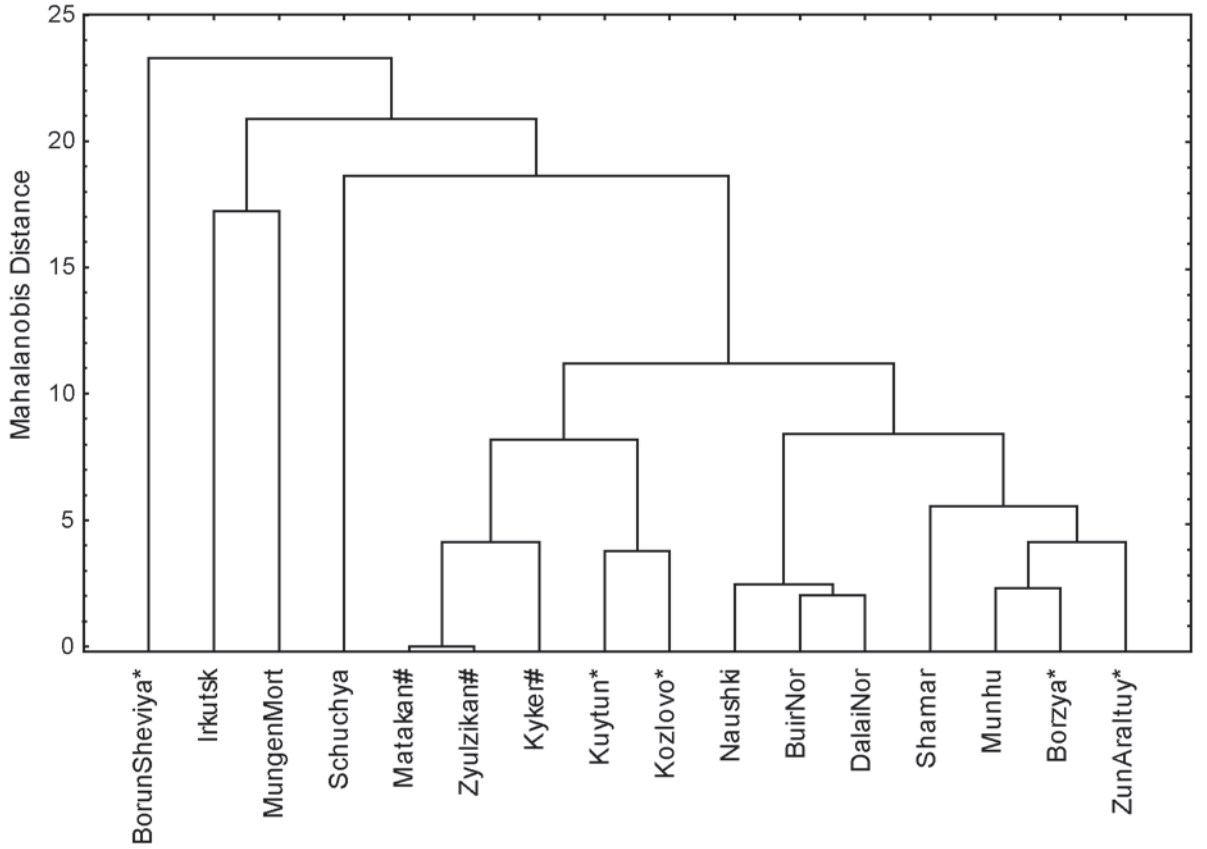

Figure 4. Dendrogram for hierarchical cluster analysis of craniometric features of *L. gregalis* samples. Sample labels refer to Appendix 1. Samples from the territory of South-East Transbaikalia lying to the south of Ingoda and Shilka Rivers are marked by asterisk; to the north, by the number sign.

chondrial lineage within South-East Transbaikalia. It is possible for example as a result of preferred exchange of males between southern and northern populations together with limited exchange of females. Selection of one of these two hypotheses will be possible after analysis of nuclear genes.

As was hypothesized by Obolenskaya (2010), Shilka and Onon Rivers can be a barrier to narrow-headed voles dispersion, similarly to Northern *Ochotona hyperborea* and Manchurian *O. mantchurica* pikas (Lissovsky *et al*., 2008) and striped hamsters *Cricetulus b. barabensis* and *C. b. pseudogriseus* (Lebedev & Lissovsky, 2008). Later, the importance of Shilka as a strong zoogeographical barrier was questioned after a detailed study of striped hamsters distribution (Korablyov *et al*., 2010). The latter authors found Unda River, instead of Shilka, as a border between *Cricetulus b. barabensis* and *C. b. pseudogriseus* distribution. Our data on distribution of narrow-headed voles from two haplogroups, presented herein, allow hypothesizing Shilka River as possible barrier of voles dispersion. However since both banks of Onon River are inhabited by voles with A haplotypes, this river does not play a zoogeographical role for the species under discussion. Probably, forests along the right bank of Ingoda River limit dispersion of voles in this region.

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Appendix 1. The list of specimens used in morphometrical analysis. Information is in the following order: the name of the sample in quotes (only for the samples, used in cluster analysis): locality and geographical coordinates: the specimen museum ID-s.

«Kyker»: Russia, Zabaikalskiy Kray, Tungokochenskiy District, Kyker Village; 53.16° N, 115.81° E: S-23258, S-23259, S-23260, S-23261, S-23262, S-23264, S-23265, S-23266, S-23256.

«Matakan»: Russia, Zabaikalskiy Kray, Sretenskiy District, Matakan River; 52.26° N, 117.64° E: S-182034, S-182033, S-182031.

«Zyulzikan»: Russia, Zabaikalskiy Kray, Nerchinskiy District, Zyul'zikan Village; 52.67° N, 116.28° E: S-23315, S-23254, S-23253.

«—»: Russia, Zabaikalskiy Kray, Nerchinskiy District, vicinities of Nerchinsk; 51.95° N, 116.56° E: S-25672.

«—»: Russia, Zabaikalskiy Kray, Nerchinskiy District, vicinities of Chita; 52.04 N, 113.53 E: S-25438.

«—»: Russia, Zabaikalskiy Kray, Nerchinskiy District, Kalinino Village; 52.02° N, 116.79° E: S-25667.

«BorunSheviya»: Russia, Zabaikalskiy Kray, Aginskiy District, valley of Borun-Sheviya; 51.43° N, 114.95° E: S-90776, S-90777, S-90773.

«—»: Russia, Zabaikalskiy Kray, Borzinskiy District, 42 km from Borzya to Solov'evsk; 50.1° N, 116.14° E: S-90758, S-90757, S-90765, S-90761.

«DalaiNor»: China, Manchuria Province, Dalai-Nor Lake, mouth of Urshun River; 48.96° N, 117.73° E: S-90754, S-90755.

«Kozlovo»: Russia, Zabaikalskiy Kray, Kalganskiy District, Kozlovo Village; 51.21° N, 118.93° E: S-178592, S-178593, S-178594, S-178595, S-178596, S-178590, S-178591.

«Kuytun»: Russia, Zabaikalskiy Kray, Krasnokamenskiy District, 7 km S from Kuytun Village; 50.12° N, 118.67° E: S-180440, S-180441, S-180443, S-180442, S-180444, S-180445, S-180446, S-180447.

«ZunAraltuy»: Russia, Zabaikalskiy Kray, Borzinskiy District, Zun-Araltuy Lake; 50.05° N, 117.37° E: S-90747, S-42816, S-42813, S-42810, S-42800, S-42806.

«—»: Russia, Zabaikalskiy Kray, Aleksandrovozavodskiy District, valley of Gazimur River; 50.81° N, 117.71° E: S-90779.

«—»: Russia, Zabaikalskiy Kray, Aginskiy District, Tsagan-Nor Lake; 50.7° N, 115.22° E: S-90774.

«—»: Russia, Zabaikalskiy Kray, Borzinskiy District, Tsagan-Oluy Village; 50.46° N, 117.15° E: S-90762, S-90763.

«—»: Russia, Zabaikalskiy Kray, Byrkinskiy District, valley of Urulunguy River; 50.12° N, 116.1° E: S-90748.

«—»: Zabaikalskiy Kray, Borzinskiy District, Nikolay-Torom Lake; 49.86° N, 117.7° E: S-90768.

«—»: Russia, Zabaikalskiy Kray, Borzinskiy District, Chumrostuy place, 12 km from Kharanor station; 50.212° N, 116.8° E: S-90760, S-90767.

«—»: Zabaikalskiy Kray, Borzinskiy District, Macievskaya station, valley of Bugutur; 49.68° N, 117.47° E: S-45297, S-45298.

«Borzya»: Russia, Zabaikalskiy Kray, Borzinskiy District, Borzya railway station; 50.38° N, 116.51° E: S-25454.

«—»: Russia, Zabaikalskiy Kray, Ononskiy District, vicinities of Kulusutay; 50.23° N, 115.67° E: S-25465.

«—»: Russia, Zabaikalskiy Kray, Zabaikalskiy District, vicinities of Matsievskaya station; 49.72° N, 117.25° E: S-182077.

«—»: Russia, Zabaikalskiy Kray, Chitinskiy District, Tasey Lake, vicinities of source Kholoya River; 52.3° N, 113.14° E: S-37834.

«Schuchya»: Russia, Yamalo-Nenetskiy Autonomous Area, Yamal Peninsula, middle course of Schuchya River; 67.37° N, 68.71° E: S-111820, S-111822, S-111805, S-111826, S-111825, S-111814, S-32106, S-32138.

«—»: Russia, Yamalo-Nenetskiy Autonomous Area, Yamal peninsula, Schuchya River, mouth of Kheyakhe River; 67.07° N, 68.2° E: S-96937.

«—»: Russia, Yamalo-Nenetskiy Autonomous Area, Yamal peninsula, Seyakha River; 69.921° N, 71.785° E: S-100705.

«Irkutsk»: Russia, Irkutsk region, Irkutskiy District, vicinities of Granovshina Village; 52.47° N, 104.28° E: S-25444, S-25445, S-25446.

«—»: Russia, Irkutsk region, Alarskiy District, Alar' Village; 53.07° N, 102.54° E: S-140559, S-140560.

«Naushki»: Russia, Buryatia Republic, Kyakhtinskiy District, vicinities of Naushki Village; 50.38° N, 106.27° E: S-179179, S-179182, S-179177.

«—»: Mongolia, Khentii Aymak, left bank of Onon river; 48.93° N, 110.04° E: S-107110.

«—»: Mongolia, Khurkha River, tributary of Onon; 48.58° N, 110.61° E: S-39942, S-39858.

«BuirNor»: Mongolia, Dornod Aymak, east bank of Buir-Nuur Lake; 47.89° N, 117.87° E: S-119843, S-39850, S-39854.

«—»: Mongolia, Khentii Aymak, Khentey Range, Eren-Daba-Nuruu pass; 48.83° N, 111.67° E: S-137828.

«—»: Mongolia, Khentii Aymak, Kerulen River, vicinities of Idermeg; 47.55° N, 111.22° E: S-128156.

«MungenMort»: Mongolia, Khentey Range, vicinities of Mungen-Mort; 47.84 N, 107.85 E: S-110443, S-110444, S-110445.

«Munhu»: Mongolia, Sukhe-Batorskiy Aymak, Munkhu-Khany Somon; 46.95 N, 112.02 E: S-39941, S-39946.

«Shamar»: Mongolia, Selenge Aymak, vicinities of Shamar; 50.1° N, 106.2° E: S-149509, S-149510, S-149511, S-149512, S-149513, S-149515, S-149516, S-149517, S-149518, S-149519, S-127966, S-127965, S-137829.

«—»: Mongolia, Sukhe-Batorskiy Aymak, 20 km E from Politin-Khuduk frontier post, Shiliyn-Bogd-Ula; 45.47° N, 114.57° E: S-137830, S-137831.

«—»: Mongolia, Sukhe-Batorskiy Aymak, 80 km NE from Erden-Tsagan; 46.4° N, 115.9° E: S-111950.

«—»: Mongolia, Dornod Aymak, frontier post Tereg, S from Khermiyn-Ula; 46.86° N, 117.67° E: S-137827.

«—»: Mongolia, Kerulen River, 13 km E from Chaybalsan; 48.1° N, 114.66° E: S-41866.

«—»: Mongolia, Urgyn-Gol River 12 km SW from Yugodzer; 45.87° N, 115.22° E: S-39844.

«—»: Mongolia, Central of Khangay, upper Chulutuin River; 47.66° N, 97.68° E: S-39846.

«—»: Mongolia, Dornod Aymak, 80 km SE Bayan Tumen; 47.35° N, 114.62° E: S-39855.

«—»: Mongolia, Khentii Aymak, Bain-Gol River, tributary of Khurkha River; 48.43° N, 110.37° E: S-39862.

Appendix 2. The list of specimens used in genetic analysis.

Locality	Haplotype	Museum ID	GenBank ID
Buryatia Republic, Kabanskiy District, Istomino Village	h1	BPI-2029	KF751101
Buryatia Republic, Kabanskiy District, Istomino Village	h1	BPI-2032	KF751102
Buryatia Republic, Kabanskiy District, Istomino Village	h2	BPI-2033	KF751103
Buryatia Republic, Kabanskiy District, Istomino Village	h3	BPI-2035	KF751104
Buryatia Republic, Kyakhtinskiy District, vicinities of Naushki Village, 50,367° N, 106,25° E	h4	S-179177	KF751098
Buryatia Republic, Kyakhtinskiy District, vicinities of Naushki Village, 50,367° N, 106,25° E	h5	S-179178	KF751099
Buryatia Republic, Ulan-Udinskiy District, Oshurkovo vVillage, 51,933° N, 107,433° E	h6	BPI-1989	KF751100
Zabaikalskiy Kray, Sretenskiy District, Matakan River, 52,383° N, 117,9° E	h7	S-182032	KF751078
Zabaikalskiy Kray, Sretenskiy District, Matakan River, 52,383° N, 117,9° E	h8	S-182034	KF751079
Zabaikalskiy Kray, Chitinskiy District, vicinities of Ugdan Village	h9	coll_8	KF751077
Zabaikalskiy Kray, Aginskiy Buryatskiy District, Kharganashi River, 50,669° N, 114,667° E	h10	S-191190	KF751088
Zabaikalskiy Kray, Aginskiy Buryatskiy District, Kharganashi River, 50,669° N, 114,667° E	h11	S-191191	KF751089
Zabaikalskiy Kray, Aginskiy Buryatskiy District, Kharganashi River, 50,669° N, 114,667° E	h12	S-191192	KF751090
Zabaikalskiy Kray, Aginskiy Buryatskiy District, Kharganashi River, 50,669° N, 114,667° E	h10	S-191193	KF751091
Zabaikalskiy Kray, Aleksandrovo-Zavodskiy District, Aleksandrovskiy Zavod, 55,861° N, 117,931° E	h13	S-191194	KF751087
Zabaikalskiy Kray, Baleyskiy District, vicinities of Baley Village	h14	ZIN-96277	KF751085
Zabaikalskiy Kray, Baleyskiy District, vicinities of Baley Village	h14	ZIN-96283	KF751086
Zabaikalskiy Kray, Kalganskiy District, vicinities of Kozlovo Village 51,35° N, 118,217° E	h14	S-178590	KF751096
Zabaikalskiy Kray, Kalganskiy District, vicinities of Kozlovo Village 51,35° N, 118,217° E	h14	S-178593	KF751092
Zabaikalskiy Kray, Kalganskiy District, vicinities of Kozlovo village 51,35° N, 118,217° E	h14	S-178591	KF751093
Zabaikalskiy Kray, Kalganskiy District, vicinities of Kozlovo Village 51,35° N, 118,217° E	h14	S-178592	KF751094
Zabaikalskiy Kray, Kalganskiy District, vicinities of Kozlovo Village 51,35° N, 118,217° E	h14	S-178594	KF751095
Zabaikalskiy Kray, Krasnokamenskiy District, vicinities of Kuytun Village, 50,2° N, 118,083° E	h14	S-180440	KF751080
Zabaikalskiy Kray, Krasnokamenskiy District, vicinities of Kuytun Village, 50,2° N, 118,083° E	h14	S-180441	KF751081
Zabaikalskiy Kray, Krasnokamenskiy District, vicinities of Kuytun Village, 50,2° N, 118,083° E	h14	S-180442	KF751082
Zabaikalskiy Kray, Krasnokamenskiy District, vicinities of Kuytun Village, 50,2° N, 118,083° E	h14	S-180443	KF751083
Zabaikalskiy Kray, Krasnokamenskiy District, vicinities of Kuytun Village, 50,2° N, 118,083° E	h15	S-180446	KF751084
Zabaikalskiy Kray, Ononskiy District, vicinities of Ust'-Borzya Village, 50,0° N, 115,0° E	h16	S-180439	KF751097