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Geographic variation of *Microtus middendorffii* (Cricetidae, Arvicolinae, Rodentia) sensu lato studied by craniometrical and mitochondrial features

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ABSTRACT. Morphometric variation of voles *Microtus middendorffii* sensu lato and *M. gromovi* was examined based on 221 skulls. Molecular variation was assessed on partial sequences of cytochrome C oxidase subunit I gene (657 bp) from 23 individuals of *M. middendorffii* s.l. The observed pattern of variation within *M. middendorffii* s.l. corresponds to polytypic species comprising a number of geographic races. The taxonomic rank of the Ural and Yamal race (*M. m. ryphaeus*) is not lower than the rank of *M. m. middendorffii* and *M. m. hyperboreus*. Essential morphological differences within the scope of this study were found for the sample from the Kochechum River. The voles of *M. gromovi* are very similar morphologically to *M. middendorffii*. Taxa *M. middendorffii*, *M. gromovi*, and *M. mongolicus* form the single clade on the mitochondrial based tree, with *M. gromovi* as a basal taxon.

KEY WORDS: *Microtus middendorffii*, *Microtus hyperboreus*, *Microtus gromovi*, geographic variation.

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Географическая изменчивость краниометрических и митохондриальных признаков *Microtus middendorffii* (Cricetidae, Arvicolinae, Rodentia) sensu lato

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РЕЗЮМЕ. Исследована выборка из 221 черепа представителей *Microtus middendorffii* sensu lato и *M. gromovi*. Генетические данные по участку гена цитохром Ц оксидазы (657 пар оснований) получены от 23 экземпляров *M. middendorffii* s.l. Наблюдаемая картина изменчивости внутри *M. middendorffii* s.l. более всего соответствует политипическому виду, представленному несколькими географическими формами. Ранг урало-ямальской формы (*M. m. ryphaeus*) не ниже, чем *M. m. middendorffii* и *M. m. hyperboreus*. Существенные, в масштабе исследования, морфологические отличия характеризуют выборку с р. Кочечум. Морфологически представители *M. gromovi* очень близки к *M. middendorffii*. Таксоны *M. middendorffii*, *M. gromovi* и *M. mongolicus* образуют единую кладу на митохондриальном дереве, базальное положение в этой кладе занимает *M. gromovi*.

КЛЮЧЕВЫЕ СЛОВА: *Microtus middendorffii*, *Microtus hyperboreus*, *Microtus gromovi*, географическая изменчивость.

Introduction

Debates on the taxonomic status of the Middendorff's vole (*Microtus middendorffii* Poljakov, 1881) and the north Siberian vole (*M. hyperboreus* Vinogradov, 1933) have a long history. It was reviewed in detail earlier (Meyer *et al.*, 1996; Litvinov, 2001; Volpert & Shadrina, 2002). The study comparing all previous opinions is, however, still absent. This makes the discussed concepts ambiguous and unreliable.

The discussion always focused on the species or subspecies rank of *M. hyperboreus*. The other taxa, mentioned from time to time, were classified a priori either to *M. m. middendorffii*, or to *M. m. hyperboreus*.

Morphological characters differentiating *M. m. middendorffii* and *M. m. hyperboreus* are described in a number of publications (Vinogradov, 1933; Ognev, 1950; Vinogradov & Gromov, 1952; Krivosheev, 1971; Pokrovskiy *et al.*, 1975; Gromov & Polyakov, 1977; Meyer *et al.*, 1996; Litvinov, 2001). Following these descriptions, different authors separated *M. m. middendorffii* from *M. m. hyperboreus* in collections. But it is impossible to find two publications where the composition of taxa distinguished on the base of the same characters would coincide (Ognev, 1950; Krivosheev, 1971; Gromov & Polyakov, 1977; Meyer *et al.*, 1996; Litvinov, 2001; Volpert & Shadrina, 2002). In other words, different authors starting from the same points referred the same specimens to different taxa. Therefore, the morphological variation of *M. middendorffii* sensu lato needs quantitative evaluation.

Another issue, which has not been addressed yet, is the morphological distinctiveness of *M. gromovi* Vorontsov et al., 1988. As inferred from the data on cytochrome *b* gene (Bannikova *et al.*, 2010) and the general habitus of this vole, it is very close to *M. middendorffii*. It is, therefore, important to evaluate the morphological similarity between these two species and estimate the probability of their morphological misidentification.

Thus, the main task of the present study is to give a quantitative estimation of variation in *M. middendorffii* s.l. and *M. gromovi*. We intentionally avoid discussing the nomenclatorial questions here and will use the established names.

Materials and methods

Specimens used in the morphometric study were taken from the collections of the Zoological Museum of Moscow State University (ZMMU), Zoological Institute of the Russian Academy of Science, St-Petersburg (ZIN), Institute of Systematics and Ecology of Animals, Siberian Branch of the Russian Academy of Science (ISEA), Institute of Plant and Animal Ecology, Ural Branch of the Russian Academy of Science (IPAE), Institute of Biological Problems of North, Far East Branch of the Russian Academy of Science (IBPN). The sample contained 221 intact skulls of *M. middendorffii* s.l. and *M. gromovi* (Appendix I).

Fifteen measurements were taken with electronic caliper (with an accuracy of 0.01 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 the level of maxillary toothrows, orbital length and width, width of rostrum' base, orbital constriction, length of auditory bulla, 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 based on logarithmic measurements.

We used the skulls of voles of different ages. All skulls were divided into three age categories (Lissovsky & Obolenskaya, 2010) corresponded to obviously juvenile (1), obviously adult with developed crests on the skull (3), and all others (2).

We used hierarchical two-factor MANOVA with geographical sample and sex treated as factors (sex nested in sample), in order to evaluate significance of differences between sexes. For this purpose we studied five samples of individuals from age group 2 with approximately equal ratio of males and females.

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. 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 seven samples included in this analysis.

The samples for hierarchical cluster analysis included only specimens collected in the same locality (44 samples total). Only samples with n>3 were used in cluster analysis (20 samples). Cluster analysis was performed on the basis of a matrix of Mahalanobis distances using the unweighted pair group method with arithmetic mean (UPGMA). The bias induced by using samples of different sizes was corrected (Marcus, 1993).

An analysis of posterior probabilities was performed using canonical discriminant analysis. The learning sample was composed of specimens used in cluster analysis and divided into groups according to its result.

The ordination was performed using the axes of canonical space calculated with grouping variable containing geographical samples with n>3.

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 oxidase subunit 1 (COI) 657bp in length from 23 specimens of *M. middendorffii* s.l. from 8 geographical localities (Appendix II) was used for the study of genetic

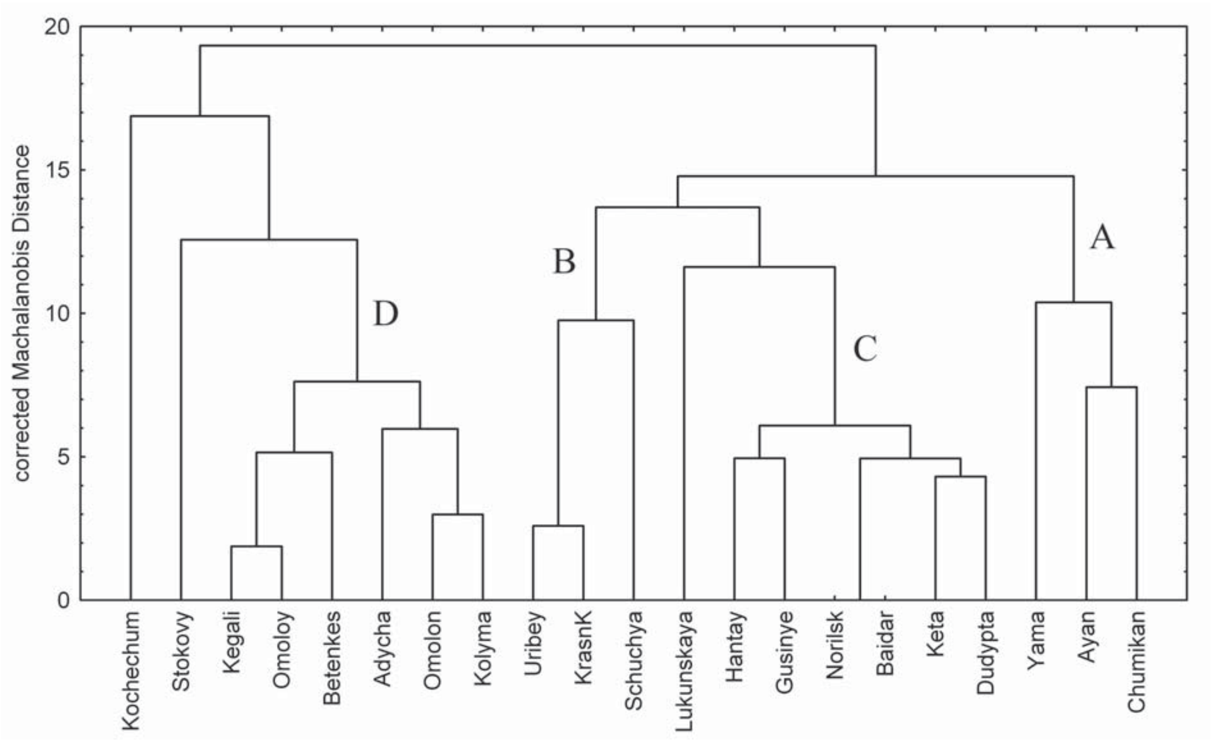

Figure 1. The dendrogram showing results of hierarchical cluster analysis of craniometric features of *Microtus middendorffii* s.l. and *M. gromovi* samples. For explanations of sample labels, refer to Appendix I.

differentiation. Analysis also included four specimens of *M. gromovi* from two localities and two specimens of *M. mongolicus* Radde, 1861 from one locality.

The specimens of *M. fortis* Büchner, 1889 and *M. maximowiczii* Schrenk, 1859, which together with previous species constitute the subgenus *Alexandromys* (Bannikova *et al*., 2010), were taken as an outgroup.

In specimens with lack of BOLD number in Appendix II, the gene region was amplified by PCR with the forward/reverse primer combination: TGT AAA ACG ACG GCC AGT TCT CAA CCA AYC AYA ARG AYA TYG G / CAG GAA ACA GCT ATG ACT ARA CTT CTG GRT GKC CRA ARA AYC A. Double-stranded polymerase chain reaction (PCR) usually entailed 30 thermal cycles as follows: 30 s denaturation at 95°C, 30 s annealing at 50°C and 50 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. Approximately 10–30 ng of the purified PCR product was used for sequencing with each primer by auto sequencing system 3730 DNA Analyzer (Applied Biosystems, Foster City, CA, USA) using ABI PRISMR BigDyeT Terminator v. 3.1.

Phylogenetic reconstruction was performed using a maximum likelihood (ML) algorithm. The selection of substitution model, phylogenetic tree reconstructions and genetic distances calculations were performed in Treefinder (Jobb, 2008). The robustness of the trees was assessed by bootstrap resampling (500 replications). Average intergroup genetic distances were calculated in MEGA version 4 (Tamura *et al*., 2007).

Results

Sexual dimorphism in the studied samples does not significantly differ from zero (Wilk's Lambda = 0.04, p = 0.08).

Hierarchical cluster analysis distinguishes several groups within the studied sample (Fig. 1). The first one includes three samples from the coast of the Sea of Okhotsk (cluster A). The second includes three samples from the Polar Ural Mts and Yamal Peninsula (cluster B). The third group unites samples from Taimyr Peninsula and one sample from the coast of Baidaratskaya Bay (cluster C). The sample from the right bank of the Khatanga River ("Lukunskaya") is adjacent to the cluster C, although it is separated from the latter by quite a large distance. The fourth group consists of samples from Verkhoyansk region, Omolon River and the upper stream of the Kolyma River (cluster D). The sample from the source of Kolyma River ("Stokovy") joins this cluster, but at a considerable distance. The sample from Kochechum River notably differs from all the rest.

The location of groups mentioned above in the ordination plane is shown at the Fig. 2. The distribution of the specimens in the space of several skull measurements is given at the Fig. 3.

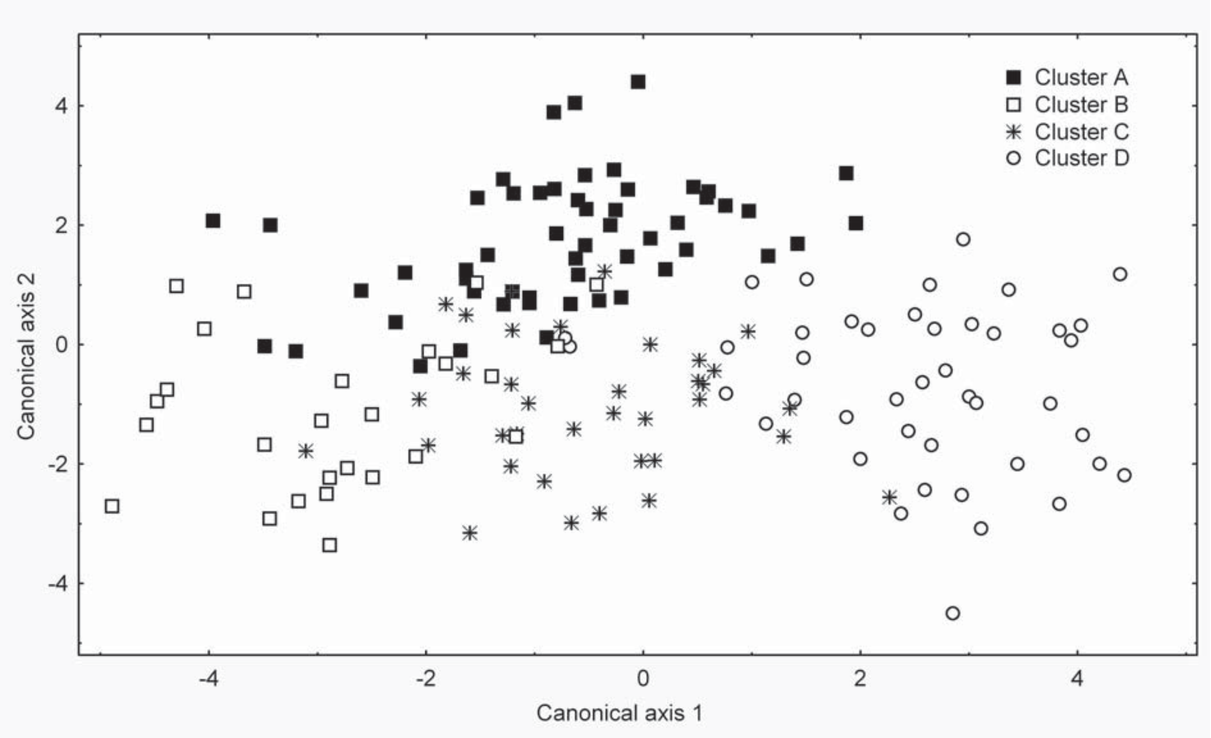

Figure 2. Distribution of *Microtus middendorffii* s.l. and *M. gromovi* specimens in the canonical hyperspace calculated based on between-sample differences. Symbols categories correspond to clusters from Fig. 1.

In 17 cases out of 44, the posterior probability of attribution to one of the four classes (A, B, C, D) is bigger than 90%. Five of them are dubious from the geographical viewpoint. Nine specimens demonstrates a maximal posterior probability less than 60%.

The evolutionary model selected for COI corresponds to J2 (Jobb, 2008) with gamma (G=0.1235) distributed rates across sites and can be described in the following parameters. Base frequencies are: T=0.2637; C=0.2923; A=0.2695; G=0.1744. The probabilities of base substitutions: TC=0.2733; TA=CA=0.0173; TG=CG=0.0019; AG=0.6883. One hundred thirty one sites are variable within the analyzed fragment, among them 51 sites are variable within *M. middendorffii* s.l.

The ML tree is shown at the Fig. 4. The representatives of *M. middendorffii* s.l., *M. mongolicus*, and *M. gromovi* constitute a well supported clade, where *M. gromovi* occupies a basal position. There are two major clades inside *M. middendorffii* s.l. The first includes animals from the Polar Ural Mts and Yamal Peninsula, the second one houses all the rest. The last group in its part includes four minor groups which form two clades with weak bootstrap support. The ML distances between samples are listed in the Tab. 1.

Discussion

The studied sample is well structured both morphologically and genetically. Obviously, this structure is more complicated than it was supposed in the above-mentioned discussion on the status of *middendorffii* and *hyperboreus*. It should be noted that, the composition of morphological and genetical groups is consistent. However the ranks of differences between the same groups in morphological and genetical approaches do not correlate. Generally, the position of specimens in the space of canonical axes and poor predictive ability of posterior probabilities indicate on low level of morphological distinctions within the group under study.

The representatives of *M. gromovi* form distant isolated clade in our study, which is in agreement with results on another mitochondrial gene (Bannikova *et al.*, 2010). In the morphological analysis, *M. gromovi* corresonds to cluster A. It includes samples from Chumikan and Ayan that were earlier identified as representatives of this species (Frisman *et al.*, 2009; Bannikova *et al.*, 2010). The cluster A is fully within the morphological variation of studied sample.

Thus, as follows from our results, the voles *M. gromovi* morphologically are very similar with the group *M. middendorffii* s.l. It noteworthy that I.S. Poljakov (1881) identified the specimen from Ayan as *M. middendorffii*. Both the initial assignment (Vorontsov *et al.*, 1988) and further comparison (Sheremetyeva *et al.*, 2008; Frisman *et al.*, 2009) of *M. gromovi* with a morphologically distant species *M. maximowiczii* could be regarded as misunderstanding based on the similarity of chromosome numbers.

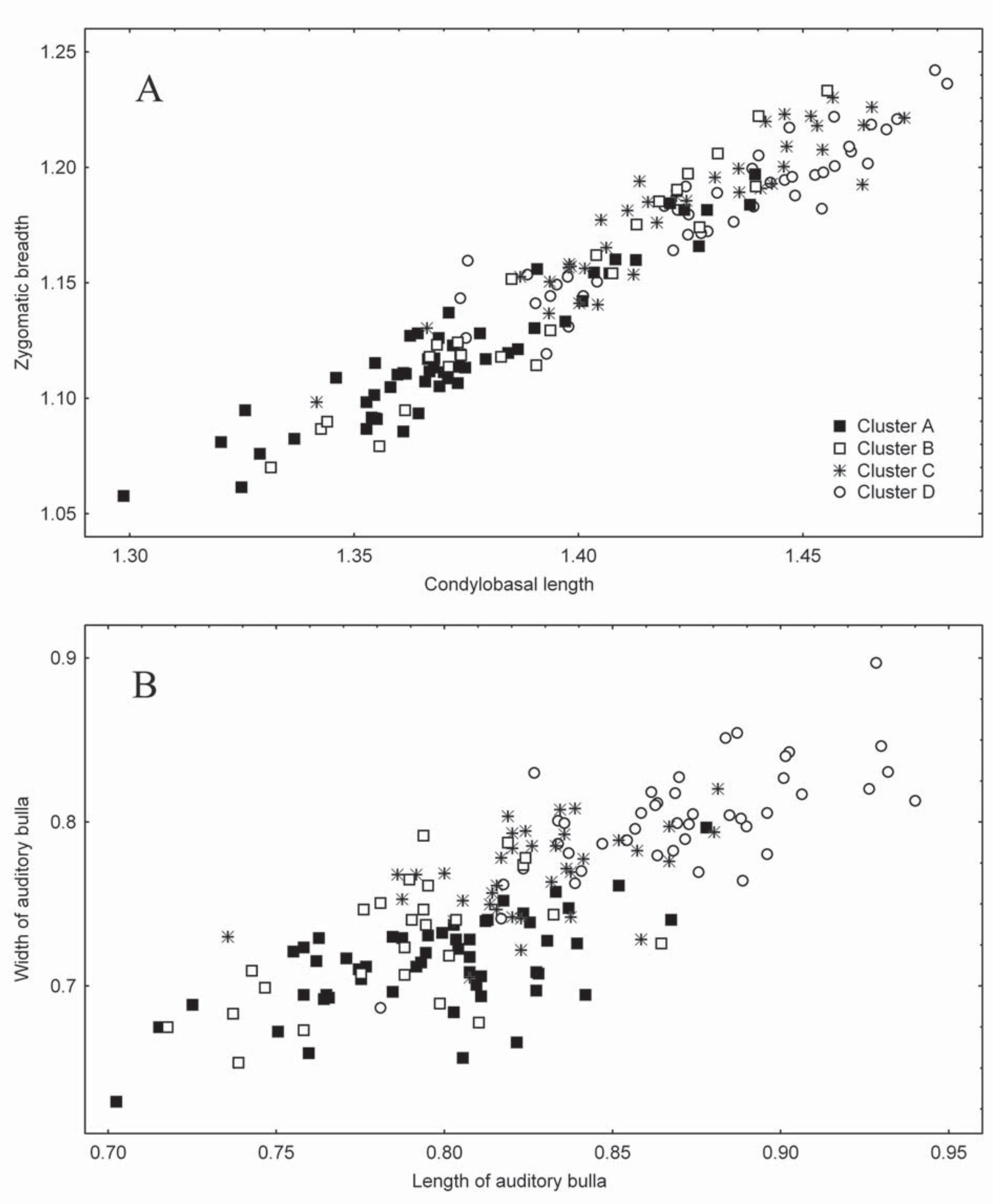

Figure 3. Distribution of *Microtus middendorffii* s.l. and *M. gromovi* specimens in the plane constituted by cranial features. The axes are in common logarithm scale. Symbols categories correspond to clusters from Fig. 1.

The variation of *M. middendorffii* s.l. demonstrates the existence of several groups. The voles inhabiting the Polar Ural Mts and Yamal Peninsula display strong genetical isolation. It is also well separated morphologically (cluster B). Obviously, this group has a taxonomic rank not lower than races *middendorffii* sensu stricto or *hyperboreus*. The name *M. m. ryphaeus* Heptner, 1948 is considered as the senior synonym for the voles from the area under discussion. Thus, this name could be assigned to

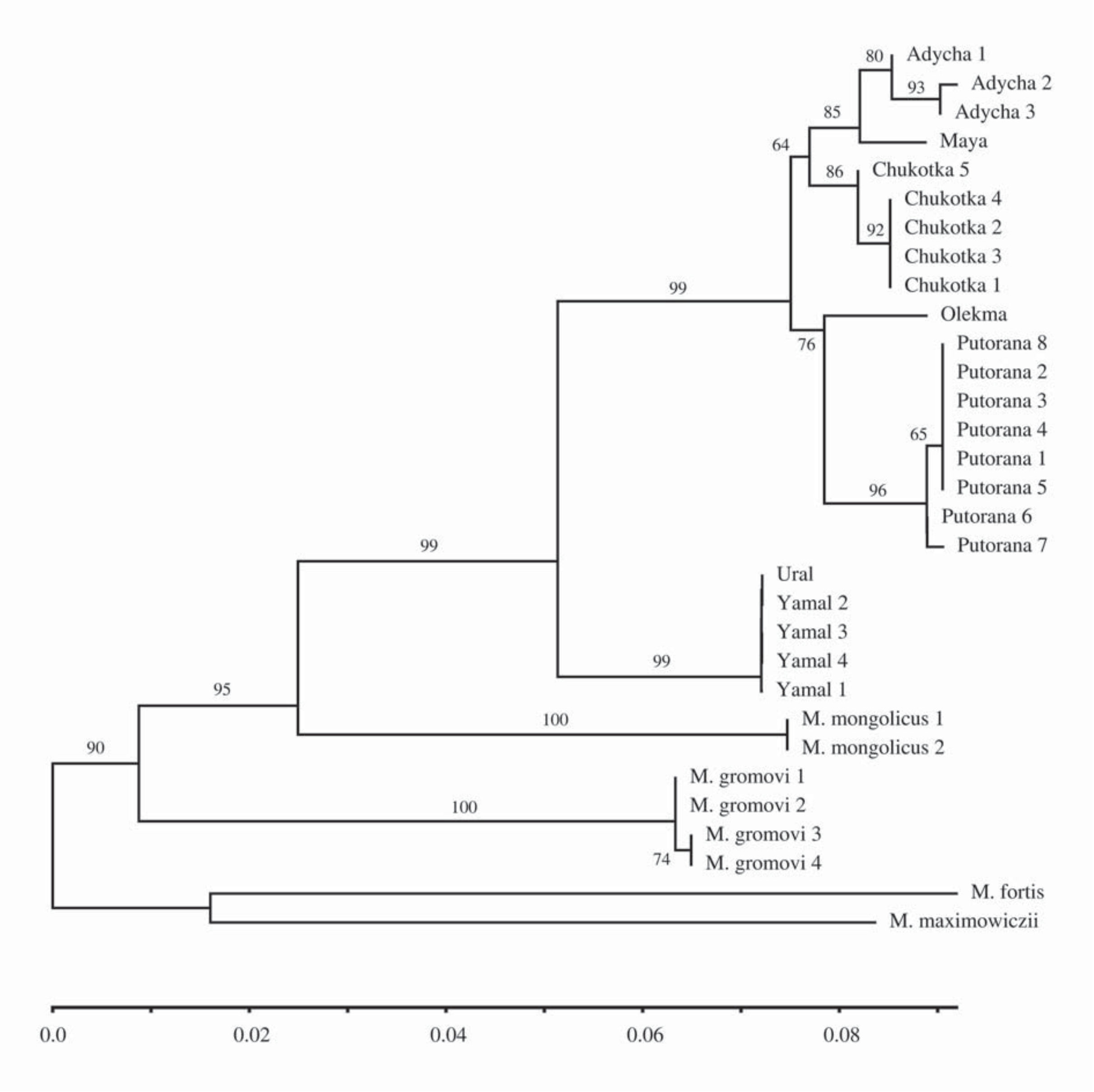

Figure 4. Maximum-likelihood tree of *Microtus* specimens constructed for cytochrome C oxidase 1st subunit. Numbers on branches indicate bootstrap support; values less than 60 are not shown. For explanations of taxa labels, refer to Appendix II.

voles from the Polar Ural Mts and Yamal Peninsula prior to a special study.

Genetical differences between *middendorffii* s.s. (Taimyr Peninsula) and *hyperboreus* s.s. (basin of Adycha River) are notably lower as compared to the distance between them and *M. m. ryphaeus*. Morphologically these two races (clusters C and D) differ well in the scale of present study.

Our results suggest that the range of *hyperboreus* race covers not only the basin of Adycha River, but Verkhoyansk Range, lower Maya River basin, upper Kolyma basin, and Omolon basin.

The samples constituting the race of *middendorffii* s.s. occupy Taimyr Peninsula and Putorana Plateau. Geographically consistent pattern of specimens' arrangement into morphological clusters is disturbed by the inclusion of the sample from Baidaratskaya Bay into the race under discussion instead of *M. m. ryphaeus* as it is expected from its geographical position. This phenomenon requires additional investigation. If subsequently supported, it may infer a sympatric or parapatric distribution of *middendorffii* and *ryphaeus* in the west of the range.

Two morphological samples ("Stokovy", "Lukunskaya") are distant from all groups, although, their positions on the tree unite them with geographically nearest cluster. However, the sample from Kochechum River is morphologically distinct from all other voles,

Table 1. Average genetic ML distances (%) between samples in analysis. For samples designation see Appendix II.

	Maya	Chukotka	Adycha	Olekma	Putorana	Yamal+ Ural	*gromovi*	*mongolicus*	*maximowiczii*	*fortis*
Maya	0									
Chukotka	1.9	0								
Adycha	1.4	2.0	0							
Olekma	2.7	2.3	2.8	0						
Putorana	2.9	2.5	2.9	2.2	0					
Yamal+Ural	5.8	5.4	5.9	5.8	6.0	0				
gromovi	13.5	13.1	13.6	13.5	13.7	11.9	0			
mongolicus	11.4	10.9	11.4	11.4	11.5	9.7	12.1	0		
maximowiczii	17.2	16.8	17.3	17.2	17.4	15.6	14.8	15.8	0	
fortis	18.1	17.6	18.1	18.1	18.2	16.4	15.6	16.7	14.3	0

therefore it is impossible to attribute it to one of the clusters.

It should be noted that, according to genetical results, voles from Chukot Peninsula could be placed in the race *hyperboreus*. Similarly, the specimen from Olekma River could be attributed to the *middendorffii* race. However, both these groupings demonstrate a weak bootstrap support and large ML distances segregating samples under discussion with corresponding races. We have only a few skulls in both cases, so it is impossible in the frame of our methods to discuss the degree of their morphological similarity or isolation.

Summing up this part of the study, we can state that the taxonomic pattern inside *M. middendorffii* is far from final description. It is quite probable that the pattern described here is somewhat biased by the abundance of material. Indeed, there is no doubt of the three taxa existence: *M. m. middendorffii*, *M. m. hyperboreus* and *M. m. ryphaeus*. At the same time, a number of local samples, based on a few specimens only, warrant a rank, similar to one of the first two taxa. These samples are from Kochechum River, Chukot Peninsula, and Olekma River. It is very probably, thus, that variation of *M. middendorffii* corresponds to a pattern of polytypic species with numerous local races. More studies are needed to elucidate this issue.

Another question, which is difficult to avoid, concerns the species/subspecies taxonomic rank of observed taxa. From morphological point of view, the degree of similarity between them is very high. They are also similar to another species, *M. gromovi*. Therefore, there is no grounds for a "search for separate species". In genetic approach we see quite low difference between *M. m. middendorffii* and *M. m. hyperboreus*. So there are no reasons for further discussion of full species rank of these two taxa. Quite different is the issue of *M. m. ryphaeus*. The genetic distance between this taxon and other forms of *M. middendorffii* is too small for a species rank in showing "accelerated molecular evolution" of *Microtus* voles (Bannikova *et al*., 2010). If, however, the clustering of voles from Baidaratskaya Bay with *M. m. middendorffii* reflects an affinity, rather than an error of the technique, this point will need a reconsideration.

Let us take up a reliability of cranial characters for determinations of races. Different authors, regardless of preferred taxa composition, proposed cranial features to descriminate between *M. m. middendorffii* and *M. m. hyperboreus*. These features included elongated or rounded shape of auditory bullae, zygomatic breadth, skull length, and development of skull crests (Ognev, 1950; Vinogradov & Gromov, 1952; Krivosheev, 1971; Pozdnyakov *et al*., 1998; Litvinov, 2001). It should be, however, kept in mind that both the shape of auditory bullae and zygomatic breadth, length of the skull, and crests development are age-dependent. Young voles show rounded bullae and relatively small zygomatic breadth. Thus, the identifying voles on the basis of skull or bullae shape involves the additional risk to confuse age and taxonomic variation. For example, zygomatic breadth and skull length demonstrate complete overlapping between the taxa (Fig. 3). The bullae shape (proportion of length to width) shows continuous linear row of variation. The largest bullae are characteristic for *M. m. hyperboreus* (Fig. 3), as was also postulated by previous authors.

To compare our conclusions with previously published results, it is necessary to analyse the taxonomic composition in these studies. The majority of authors included the voles from the Polar Ural Mts and Yamal Peninsula into the taxon *middendorffii* (Ognev, 1950; Vinogradov & Gromov, 1952; Gileva, 1972; Pokrovskiy *et al*., 1975; Gromov & Polyakov, 1977). The sample from the Yama River (included in this study in *M. gromovi*) was considered within the taxon *hyperboreus* (Yudin *et al*., 1976). A number of authors included specimens from the southern Taimyr (Dudypta River) into the race *hyperboreus* (Ognev, 1950; Vinogradov & Gromov, 1952; Gromov & Polyakov, 1977). The Taimyr sample was analysed in our study and, within its frame, unambiguously belongs to *middendorffii*.

The data on free hybridization in captivity, given as a strong argument to uniting the taxa *middendorffii* and *hyperboreus* by some authors (Pokrovskiy *et al*., 1975), were related to taxa *M. m. middendorffii* and *M. m. ryphaeus* (at least to the Yamal population) (Volpert & Shadrina, 2002). It is these races that shawed the similarity in karyotypes (Gileva, 1972). The difference in the location and abundance of nucleolar organizer was shown for the representatives of *M. m. middendorffii* and *M. m. hyperboreus* (Meyer *et al*., 1996).

The concept of northern lowlands from the Yana River to the Kolyma River inhabited by *middendorffii*, whereas the range of *hyperboreus* occurring either more to the south or at higher altitudes, can be quite frequently met in the literature (Vinogradov & Gromov, 1952; Krivosheev, 1971; Gromov & Polyakov, 1977; Meyer *et al*., 1996; Pozdnyakov *et al*., 1998; Litvinov, 2001; Volpert & Shadrina, 2002). This viewpoint has been illustrated by quantitative data (Pozdnyakov *et al*., 1998; Litvinov, 2001). We had no data on voles from the lower stream of the Kolyma and Indigirka rivers which showed maximal morphological divergence from other voles (Pozdnyakov *et al*., 1998; Litvinov, 2001). Thus we could not evaluate the correspondence between taxa in the cited paper and those studied in the present study. The future data on this issue will give an important progress in resolving the taxonomy of Middendorff's vole.

Along with recent faunistic records (Boyeskorov *et al.*, 1993; Dokuchaev & Dorogoy, 2005; Abramson *et al*., 2009), our results notably change the concept of the range of *M. middendorffii*. In addition to the southward and eastward expansion of the known range, worth noting is investigation of several particular parts of the range. The spatial contact between the races *M. m. middendorffii* and *M. m. ryphaeus*; *M. m. hyperboreus* and *M. gromovi* are of the major interest. Another point is the identification of Middendorff's vole in the remote regions, as the mouth of Podkamennaya Tunguska, Olekma, and Maya Rivers. All these records likely indicate the occurrence of voles of this group throughout the major part of Siberia.

The last point we want to discuss is the topology of the genetic tree as regards the inter-species relationships. The relative positions of *M. middendorffii*, *M. gromovi* and *M. mongolicus* on the tree remained unclear after the previous study (Bannikova *et al*., 2010). We used another mitochondrial gene, and obtained the good bootstrap support for the branching pattern of these species. Thus, the splitting of *M. gromovi* is basal relative to the divergence of *M. middendorffii* and *M. mongolicus*. At the same time, from craniometrical point of view, the pair of species *M. middendorffii* and *M. gromovi* is hardly distinguishable.

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Appendix I. 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, museum, the specimens number in parenthesis.

«KrasnK» — Yamalo-Nenetskiy Autonomous District, Polar Ural Mts., railway station Krasniy Kamen, 66.55 N, 65.45 E, IPAE (12);

«Baidar» — Yamalo-Nenetskiy Autonomous District, south of Baidaratskaya Guba Bay, 68.2 N, 67.2 E, IPAE (6);

«Schuchya» — Yamalo-Nenetskiy Autonomous District, south of Yamal Peninsula, middle part of Schuchya River, 67.365 N, 68.708 E, ZMMU (8);

«Uribey» — Yamalo-Nenetskiy Autonomous District, center of Yamal Peninsula, Yuribey River, 68.48 N, 71.18 E, IPAE (7);

«Norilsk» — Krasnoyarskiy Kray, vicinities of Norilsk, 69.371 N, 88.397 E, ISEA (4);

«Hantay» — Krasnoyarskiy Kray, Putorana Plateau, Khantayskoe Lake, 68.267 N, 90.796 E, ISEA (7);

«Keta» — Krasnoyarskiy Kray, Putorana Plateau, Keta Lake, 68.834 N, 91.632 E, ZIN (8);

«Gusinye»— Krasnoyarskiy Kray, Putorana Plateau, Gusiniye Lakes, 68.3 N, 93.6 E, ZMMU (7);

«Dudypta» — Krasnoyarskiy Kray, south-east of Taimyr Peninsula, Dudypta River near mouth of Kamennaya River, 71.443 N, 94.104 E, ZMMU (5);

«Kochechum» — Krasnoyarskiy Kray, Turukhanskiy District, vicinities of Tola village, Kochechum River, 64.542 N, 100.222 E, ZIN (7);

«Lukunskaya» — Krasnoyarskiy Kray, Lukunskaya River — right tributary of Khatanga River, 72.529 N, 105.166 E, ISEA (5);

«Omoloy» — Republic of Yakutia-Sakha, Bulunskiy District, Omoloy River, 70.696 N, 133.265 E, ZIN (10);

«Chumikan» — Khabarovskiy Kray, Uda River, 25 km from Chumikan, 54.61 N, 135.01 E, ZMMU (27);

«Adycha» — Republic of Yakutia-Sakha, Verkhoyanskiy District, Adycha River, 67.532 N, 135.436 E, ZIN (6);

«Betenkes» — Republic of Yakutia-Sakha, Verkhoyanskiy District, Adycha River, Betenkes village, 67.579 N, 135.672 E, ZIN (9);

«Ayan» — Khabarovskiy Kray, Ayano-Mayskiy District, Ayan Village, 56.464 N, 138.161 E, ZMMU (21);

«Stokovy» — Magadan Region, Kulu River basin, Stokovoye, 61.848 N, 147.662 E, IBPN (6);

«Yama» — Magadan Region, Maymadzhinskiy Range, upper Yama River, 60.755 N, 151.786 E, ZMMU (9);

«Kolyma» — Magadan Region, Srednekanskiy District, right bank of Kolyma River, 62.591 N, 152.379 E, ZMMU (4);

«Omolon» — Chukot Autonomous Province, vicinities of Omolon village, 65.237 N, 160.555 E, ZIN (10);

«Kegali» — Magadan Region, Omolon River basin, near Kegali village, 64.358 N, 161.955 E, ISEA (5);

Republic of Komi, 134 km from Seyda railway station, 67.239 N, 63.043 E, ZMMU (1);

Yamalo-Nenetskiy Autonomous District, Eastern slope of Polar Ural Range, upper Sukhaya Synya River, 65.559 N, 63.073 E, ZIN (2);

Yamalo-Nenetskiy Autonomous District, Polar Ural, 60 km by railway from Labytnangi, 66.922 N, 65.74 E, ZMMU (1);

Yamalo-Nenetskiy Autonomous District, 12 km to NW from Labytnangi, 66.734 N, 66.266 E, ZIN (2);

Yamalo-Nenetskiy Autonomous District, south of Yamal Peninsula, Longotyugan River, 66.5 N, 67.44 E, IPAE (3);

Yamalo-Nenetskiy Autonomous District, north-west part of Yamal Peninsula, Sedoty-yakha River, 69.584 N, 67.699 E, ZIN (1);

Yamalo-Nenetskiy Autonomous District, south of Yamal Peninsula, vicinities of Schuchye village, 67.365 N, 68.708 E, ZMMU (2);

Yamalo-Nenetskiy Autonomous District, Krasnoselkupskiy District, Taz River, Tserkovenskoye village, 65.51 N, 82.133 E, ZIN (1);

Krasnoyarskiy Kray, vicinities of Norilsk, 1 km to the S from Nadezhda airport, 69.308 N, 87.981 E, ZIN (1);

Krasnoyarskiy Kray, Turuchanskiy District, Mirnoe research station, 62.37203 N, 89.061899 E, ZMMU (1);

Krasnoyarskiy Kray, south-east of Taimyr Peninsula, Kresty village near mouth of Dudypta River, 70.853 N, 89.924 E, ZIN (1);

Krasnoyarskiy Kray, Putorana Plateau, near mouth of Irekteken River, 68.3 N, 93.8 E, ZMMU (3);

Republic of Yakutia-Sakha, Olenek River near mouth of Pur River, 71.809 N, 123.58 E, ZIN (2);

Republic of Yakutia-Sakha, lower part of Lena River, approximate coordinates 70.828 N, 127 E, ZIN (1);

Republic of Yakutia-Sakha, Verkhoyanskiy District, Yana River 50 km lower Verkhoyansk, 67.565 N, 134.034 E, ZIN (1);

Republic of Yakutia-Sakha, Ust-Mayskiy District, mouth of Chabda River — left tributary of Maya River, 59.776 N, 134.812 E, ZMMU (1);

Republic of Yakutia-Sakha, Verkhoyanskiy District, Adycha River, Ust-Charky, 66.764 N, 136.601 E, ZIN (1);

Khabarovskiy Kray, Ul'banskiy Bay, Itkan River, 53.529 N, 137.644 E, ZMMU (1);

Republic of Yakutia-Sakha, Oymyakon Plateau, 100 km from Tas-Kys-Tabyt Range, 63.29 N, 143.06 E, ZMMU (1);

Republic of Yakutia-Sakha, Allaikhovskiy District, Berelekh River valley, 70.979 N, 148.979 E, ZMMU (1);

Chukot Autonomous Province, vicinities of Anadyr' airport, 64.807 N, 177.584 E, ZMMU (1);

Magadan Region, vicinities of Omsukchan, 62.531 N, 155.848 E, ZIN (1);

Magadan Region, Elikchanskiye Lakes, 60.755 N, 151.786 E, IBPN (1);

Republic of Yakutia-Sakha, Nizhnekolymskiy District, upper part of Stadukhinskaya channel, 68.663 N, 161.152 E, ISEA (1);

Koryakskiy Autonomous District, Shayboveem River, tributary of Pehzhina River, 64.102 N, 164.489 E, ZMMU (1);

Chukot Autonomous Province, Sredniy Kaiemravaam River - the left tributary of Mechkereva River, 66.823 N, 169.556 E, IBPN (2);

Chukot Autonomous Province, vicinities of Pevek, 69.681 N, 170.411 E, ZMMU (1);

Chukot Autonomous Province, Chaunskiy District, upper Keveem River, Mayskiy, 68.966 N, 173.7 E, IBPN (2).

Appendix II. The list of specimens used in genetic analysis. The Genebank/BOLD ID-s are shown.

Label	Museum ID	ID	Locality
Maya	ZMMU S-183385	HM137743/ MEP162-08	Republic of Yakutia-Sakha, Ust-Mayskiy District, mouth of Chabda River — left tributary of Maya River, 59.776 N, 134.812 E
Putorana 1	ZMMU S-181778	HM137750/ SKMZM521-08	Krasnoyarskiy Kray, Putorana Plateau, Kureyka River 68.3 N, 93.6 E
Putorana 2	ZMMU S-181780	HM137749/ SKMZM522-08	Krasnoyarskiy Kray, Putorana Plateau, Kureyka River 68.3 N, 93.6 E
Putorana 3	ZMMU S-181792	HM137748/ SKMZM523-08	Krasnoyarskiy Kray, Putorana Plateau, Kureyka River 68.3 N, 93.6 E
Putorana 4	ZMMU S-181791	HM137747/ SKMZM524-08	Krasnoyarskiy Kray, Putorana Plateau, Kureyka River 68.3 N, 93.6 E
Putorana 5	ZMMU S-181779	HM137746/ SKMZM525-08	Krasnoyarskiy Kray, Putorana Plateau, Kureyka River 68.3 N, 93.6 E
Putorana 6	ZMMU S-181794	HM137745/ SKMZM526-08	Krasnoyarskiy Kray, Putorana Plateau, Kureyka River 68.3 N, 93.6 E
Putorana 7	ZMMU S-181789	HM137744/ SKMZM527-08	Krasnoyarskiy Kray, Putorana Plateau, Kureyka River 68.3 N, 93.6 E
Putorana 8	ZMMU S-181782	HM137751/ SKMZM239-07	Krasnoyarskiy Kray, Putorana Plateau, Kureyka River 68.3 N, 93.6 E

Appendix II (continued).

Label	Museum ID	ID	Locality
Yamal 1	–	HM137742/ SKMZM873-09	Yamal-Nenets Autonomous Province, Yamal Peninsula, right bank of the Yerkata-Yakha river, 68.2 N, 68.8 E
Yamal 2	–	HM137740/ SKMZM875-09	Yamal-Nenets Autonomous Province, Yamal Peninsula, right bank of the Yerkata-Yakha river, 68.2 N, 68.8 E
Yamal 3	–	HM137739/ SKMZM876-09	Yamal-Nenets Autonomous Province, Yamal Peninsula, right bank of the Yerkata-Yakha river, 68.2 N, 68.8 E
Yamal 4	–	HM137738/ SKMZM877-09	Yamal-Nenets Autonomous Province, Yamal Peninsula, right bank of the Yerkata-Yakha river, 68.2 N, 68.8 E
Chukotka 1	IBPN 6034	HM137731/ NAZIM446-08	Chukot Autonomous Province, Sredniy Kaiemravaam River - the left tributary of Mechkereva River, 66.9 N, 169.6 E
Chukotka 2	IBPN 6033	HM137732/ NAZIM445-08	Chukot Autonomous Province, Sredniy Kaiemravaam River - the left tributary of Mechkereva River, 66.9 N, 169.6 E
Chukotka 3	IBPN 6032	HM137733/ NAZIM444-08	Chukot Autonomous Province, Sredniy Kaiemravaam River - the left tributary of Mechkereva River, 66.9 N, 169.6 E
Chukotka 4	IBPN 6031	HM137734/ NAZIM443-08	Chukot Autonomous Province, Sredniy Kaiemravaam River - the left tributary of Mechkereva River, 66.9 N, 169.6 E
Chukotka 5	IBPN 6030	HM137735/ NAZIM442-08	Chukot Autonomous Province, Sredniy Kaiemravaam River - the left tributary of Mechkereva River, 66.9 N, 169.6 E
Olekma	–	HM137736/ NAZIM287-08	Republic of Yakutia-Sakha, Olekminskiy District, vicinities of Torgo village, 58.5 N, 119.5 E
Ural	ZIN 98040	HM137752/ NAZIM738-08	Yamal-Nenets Autonomous Province, Labytnangi City Council, Krasniy Kamen railway station, 66.9 N, 65.7 E
Adycha 1	ZIN 99689	JF723544/-	Republic of Yakutia-Sakha, Verkhoyanskiy District, near the mouth of Tuostakh River, 67.9 N, 135.5 E
Adycha 2	ZIN 99691	JF723545/-	Republic of Yakutia-Sakha, Verkhoyanskiy District, vicinities of Tomtor village, 67.1 N, 134.6 E
Adycha 3	ZIN 99707	JF723546/-	Republic of Yakutia-Sakha, Verkhoyanskiy District, vicinities of Tomtor village, 67.2 N, 134.9 E
M. gromovi 1	ZMMU S-187568	JF723547/-	Khabarovskiy Kray, Tuguro-Chumikanskiy District, Dzhangin River, 55.5 N, 134.4 E
M. gromovi 2	ZMMU S-187569	JF723548/-	Khabarovskiy Kray, Tuguro-Chumikanskiy District, Dzhangin River, 55.5 N, 134.4 E
M. gromovi 3	ZMMU S-187545	JF723549/-	Khabarovskiy Kray, Ayano-Mayskiy District, Eldomu-Makit River, 55.8 N, 134.2 E
M. gromovi 4	ZMMU S-187546	JF723550/-	Khabarovskiy Kray, Ayano-Mayskiy District, Eldomu-Makit River, 55.8 N, 134.2 E
M. mongolicus 1	ZMMU S-180448	HM137754/ SKMZM213-07	Chita Region, Krasnokamenskiy District, 6 km S of Kuytun, 50.1 N, 118.7 E
M. mongolicus 2	ZMMU S-180449	HM137753/ SKMZM215-07	Chita Region, Krasnokamenskiy District, 6 km S of Kuytun, 50.1 N, 118.7 E
M. maximowiczii	ZMMU S-178597	HM137737/ SKMZM179-07	Chita Region, Kalganskiy District, vicinities of Kozlovo village, 51.2 N, 118.9 E
M. fortis	ZMMU S-178587	HM137730/ SKMZM185-07	Chita Region, Aleksandrovo-Zavodskiy District, upper Kher-Khira River, 50.4 N, 118.1 E