INTRASPECIFIC STRUCTURE OF THE *COREGONUS LAVARETUS* COMPLEX IN WATER BODIES OF SIBERIA: A CASE OF POSTGLACIAL ALLOPATRIC ORIGIN OF YUKAGIRIAN WHITEFISH

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Abstract The results of morphological and genetic analyses of forms/species of the *Coregonus lavaretus pidschian* complex from the Indigirka and Kolyma river basins are presented in the context of there being recent postglacial speciation events. It has been found that the forms/species of the whitefishes studied belong to the sparsely-rakered and low lateral line forms and have previously been described as *C. l. pidschian* natio *jucagiricus*. Based on these characters *C. l. pidschian* natio *jucagiricus* does not differ from most Arctic whitefish populations (in particular from *C. l. glacialis*). Analysis of variability of the ND1 gene of the mitochondrial DNA showed that whitefishes from the Indigirka and Kolyma basins belong to a distant phylogenetic lineage, which are significantly different from all previously studied whitefish lineages from the Ob, Yenisei, Lena, Anadyr, and Amur river basins. Analysis of variability of the ITS1 fragment of the nuclear DNA showed that all studied forms/species (from Ob River basin to Amur River basin), including *C. l. pidschian* n. *jucagiricus*, have a tandem arrangement of two identical nucleotide fragments and very similar nucleotide composition of the ITS1 region. Based on contemporary data this phylogenetic lineage of the *C. pidschian* complex could be seen as a young postglacial allopatric species.

Introduction

Different representatives of the subfamily Coregoninae are very popular topics for the study of microevolutionary processes in aquatic animals. Within this subfamily the complex of *C. lavaretus* sensu lato (including one of its subspecies *C. l. pidschian*) is most frequently studied (Siwertsson et al. 2010; Öhlund et al. 2020; Thibert-Plante et al. 2020). The whitefishes are widespread geographically from the North Sea basin to the Bering Strait and display a high phenotypic variability. Due to the wide geographical distribution of whitefishes, they are characterized by a large number of taxonomically indefinite forms of intraspecific rank (Pravdin 1954; Kottelat and Freyhof 2007). Some whitefishes have been described earlier as subspecies, whose validity remained controversial, while others were reduced in rank to an ecological form/population during the 20th century (Issatchenko 1925; Kaganovsky 1933; Dulkeit 1949; Gundrizer et al. 1962; Reshetnikov 1980; Gundrizer et al. 1981; Chereshnev 1996; Himberg 1970; Kottelat and Freyhof 2007; Golubtsov and Malkov 2007). As consistent with the latest revision, there are at least 14 species and a number of subspecies within the *C. lavaretus* complex in Eurasia (Bogutskaya and Naseka 2004). The total number of forms/subspecies according to different sources varies from 46 to 48 (Shaposhnikova 1974; Reshetnikov 1980; Kottelat and Freyhof 2007).

Unfortunately, the majority of described forms/subspecies of whitefishes that have been analyzed by different researchers in different times was very subjective. Due to the presence of several opposing points of view, there are no clearly defined criteria for differentiation based on meristic characteristics among forms/species. It is known that such important character as the number of gill rakers on the first brachial arch is complicated to use for taxonomic diagnosis of a number of forms/species of whitefishes, since genetically distant forms/species possess the same number of gill rakers (Bochkarev et al 2018, 2021). Hence, most of the described subspecies/species of whitefishes could be attributed to the population rank (Reshetnikov 1979; Reshetnikov and Lukin 2006). In any case, it is apparent that the morphological diversity of populations/forms/subspecies more depends on a specific point of view of the researcher than on real morphological differences (Reshetnikov 1980; Bogutskaya and Naseka 2004; Kottelat and Freyhof 2007).

The list of whitefishes proposed by M. Kottelat and J. Freyhof (2007) for European Russia comprises the following taxa: (1) ludoga whitefish *C. lutokka* (*C. l. ludoga)*, (2) volkhov whitefish *C. baerii* (or *C. l. baeri*), (3) *C. maraena* and (4) *C. maraenoides* (or *C. l. maraenoides*), etc. In Siberia, there are found only two subspecies *C. l. pidschian* and *C. baunti*. In turn, *C. l. pidschian* contains many intraspecific forms defined by Reshetnikov (1980) as: (1) *C. l. n. pravdinellus* (*C. pravdinellus*) from Teletskoye Lake (the Ob River basin); (2) East Siberian whitefish *C. l. pidschian* natio *brachymystax*, and glacial-plain whitefish *C. l. pidschian* natio *glacialis* (*C. l. glacialis*) from the lakes and estuaries of Eastern Siberia; (3) *C. l. pidschian* natio *taimyrensis* and *C. l. pidschian* natio *logaschevi* from Taimyr Lake (Taimyr Peninsula).

Genetic analysis revealed that *C. l. pidschian* is an artificial taxonomic unit that includes different whitefishes from the population to the species ranks (Bochkarev et al. 2013; Bochkarev et al. 2017). It is known that *C. l. pidschian* forms lacustrine (in lakes) and riverine (in rivers) sympatric pairs of forms/species which are characterized by different levels of genetic divergence within these pairs (Bochkarev et al., 2011; 2019; 2020). For example, the study of riverine whitefish populations from the Yenisei River and the Anadyr River basins (north part of central Siberia) has shown that these whitefishes *C. fluviatilis* and *C. anaulorum*, considered earlier as ecological forms/populations (Shaposhnikova 1974; Reshetnikov et al. 1979; Reshetnikov 1980), are represented as divergent mitochondrial lineages corresponding to the species rank (Bochkarev et al. 2017). In the same time, in spite of significant morphologic differences between some sympatric pairs of lacustrine whitefishes (for example, from the Teletskoye and Baunt lakes) no divergence of the mtDNA between them was found (Skryabin 1977; Bochkarev et al. 2013; 2017). Also it turned out, that the same forms of species of Arctic whitefishes were described by different authors, at different times and under different names that leads to additional biases in determination of diversity of whitefishes in the given area. For *C. l. pidschian* from Siberian arctic areas the problem of correct determinations of the number of forms/species is especially important. In brief, on Taimyr Lake (Taimyr Peninsula) V.S. Mikhin (1955) described two sympatric forms/species of whitefish named as *C. l. pidschian* n. *taimyrensis* and *C. l. pidschian* n. *logaschevi*. In the same time, from water bodies of Yakutia (East Siberia) L.

Berg (1948) and A. Kirillov (1972) described another pair of whitefishes named as *C. l. pidschian* n. *brachymystax* and *C. l. glacialis* respectively. Further studies have shown that *C. l. pidschian* n. *taimyrensis* and *C. l. glacialis* as well as *C. l. pidschian* n. *logaschevi* and *C. l. pidschian* n. *brachymystax*, based on their morphological characteristics, are similar to each other (Romanov et al. 2016). Later, in the Siberian arctic basin of the Anabar River (north part of central Siberia) two whitefishes (Fig. 1) morphologically (body shape) similar to whitefishes from the Taimyr Lake were found (Romanov et al. 2016; Bochkarev et al. 2017). Based on mtDNA sequencing, it has been shown that these two whitefishes are well distinguished from each other (Bochkarev et al. 2020). Hence, to date, the whitefish named as *pidschian*-like includes both real and synonymous taxonomic units.

After it was shown that the number of forms/species of whitefishes is much less than expected, the attempts were made to reveal the phylogenetic relationships among them. Thus, it was shown that the mitochondrial lineage of *C. l. pidschian* n. *brachymystax* from the Anabar River (north part of central Siberia) is phylogenetically close to one of the mitochondrial lineages of whitefishes from the Ob River (West Siberia) (Bochkarev et al. 2018). The phylogenetic relationships of *C. l. glacialis* with other forms/species of Siberian whitefishes were unrevealed. It has been suggested that the *C. l. glacialis* whitefishes are characterized by distant mitochondrial unique haplotypes, which are presumably derived from previously widely distributed pre-glacial forms/species (Bochkarev et al. 2018, 2020).

In more recent studies of the genetic structure of Arctic whitefish forms/species from the water bodies of the Indigirka and Kolyma river basins (East Siberia) it was found there existed a genetically cryptic form/species e.g. *C. l. pidschian* n. *jucagiricus* Drjagin (Berg) 1932. This whitefish was found by P.A. Dryagin in the Kolyma River (East Siberia) in 1948 and then was described by L.S. Berg (1948) based on a morphologic approach. However, this form does not differ clearly from *C. l. glacialis* in terms of the number of gill rakers on the first brachial arch and the number of perforated scales in the lateral line (Novikov 1966).

In previous studies it has been shown that the postglacial distribution of whitefishes originated from the Altai refugia along the Ob River and further along the Arctic coast in both western and eastern directions (Bochkarev et al 2018; 2020; 2021). It is obvious that, besides whitefishes from the Altai refugia, the whitefishes from arctic water bodies of Siberia (*C. l.* n. *glacialis*) also settled the lakes of both Fennoskandia and the eastern coast of the Arctic seas of Siberia (Østbye et al 2005).

In order to understand the future distribution from these origins, and the possible routes of distribution of whitefishes, the glacial events (e.g. their power and frequency) have to be considered. Such events could have differentially affected the fish populations of Siberian river basins. The most extensive glaciations were in the Altai region, but to the eastwards a continuous glacial cover was not likely present (Grosswald 1965; Grosswald and Rudoy 1996; Matz et al. 2001; Vysotsky 2001; Arzhannikov et al. 2010). In the same time, small valley glaciers in the Kolyma and Indigirka River basins existed (Khvorostova and Kashmenskaya, 1962; Rusanov, Borodenkova and Goncharov 1967). As a result, numerous lakes of different size (such as Labynkyr, Ichelyah lakes) were formed in the upper reaches of these river drainages. Perhaps, all these lakes were refugia for different fishes, including whitefishes, during different periods of the Pleistocene. It thus seems likely that the populations of glacial-plain whitefish previously inhabiting these lakes are a base ancestor for *C. l. pidschian* n. *jucagiricus*. Previous studies did not include phylogenetic information about different forms/species of whitefishes from a number of refugia across the greater part of Eurasia. The present study is the first attempt to incorporate the invalid form/species of whitefish in a general phylogeny of whitefishes from Siberian water bodies and, consequently, Holoarctic ones. This attempt will shed light on the origin, distribution, and phylogenetic positions of all known whitefishes from Siberian water bodies. The addition of one more link of this evolutionary chain such as *C. l. pidschian* n. *jucagiricus* is discussed.

The main aim of the present study was to detect the genetic relationships based on ND1 (mtDNA) and ITS1 (nDNA) of the Arctic forms/species of *pidschian*-like whitefishes inhabiting the main river basins from central to East Siberia. A special emphasize has been placed on the origin, genetic structure and distribution of *C. l. pidschian* n. *jucagiricus* as an unstudied whitefish of the Siberian ones. Due to a comprehensive review of this topic being long overdue, this is presented here as necessary for clarification of the aspect of diversity and shaping of some cryptic forms / species of the *pidschian*-like whitefishes.

Material and methods

Sampling and morphological analysis

Samples were taken during summer seasons between 2012-2019 from the Indigirka and Kolyma river basins (East Siberia). So, nine whitefish samples from Ichilyakh Lake, one sample from the Kaidusun River and one sample from Labynkyr Lake (all were from the upper reach of Indigirka river, East Siberia) were collected (Fig. 1). Ten whitefish samples from the Moma River mouth (middle reach of Indigirka River, East Siberia) were also collected (Fig. 2). In addition, 16 whitefish samples were taken from the Suturuokha River (the middle reach of the Indigirka River). Twelve whitefish samples were collected from the lower reach of the Kolyma River (East Siberia). Ten whitefish samples were caught from Ilirnei Lake (the Malyi Anyui River basin, right tributary of the Kolyma River, East Siberia). To delineate the distribution area of a new whitefish form/species, the haplotypes from other populations of Siberia were taken (for this see Table 1). The frozen whitefish samples from the most distant areas of Siberia were delivered to the laboratory, where they were identified and photographed. Also, the number of gill rakers (*sp.br.*) and the number of perforated scales along the lateral line (*ll*) were counted.

Meristic data was tested for normality using the Anderson-Darling test. Lateral line scales and the number of gill rakers follow a normal distribution ($p > 0.05$). Since the variances of lateral scale number were equal according to Levene’s F-test ($p > 0.05$), the one-way ANOVA together with the Tukey HSD post-hoc test for unequal sample sizes were used to compare means.

For genetic analysis liver tissue samples were taken from both fresh and frozen whitefishes. The liver samples were fixed in 70% ethanol for storage. Total genomic DNA was extracted in accordance with the method described earlier (Sambrook et al. 1989) and stored at the -20 ˚C. The ND1 gene of the mitochondrial DNA (mtDNA) was amplified in a 25 μl reaction volume (Bochkarev et al., 2011) using the two pairs of primers shown below: 1) ND1 5'-GGCCTAAGCCCTTTTTCTCA-3' Forward; 2) ND1632 5'-GGCTGGAACGAGCAATCAGA-3' Reverse; 3) ND1596 5'-TTCGAGCCGTAGCACAAACT-3' Forward; 4) ND1 5'-GAGGGGACTTGAACCCCTAT-3' Reverse. As a result of complete gene amplification, sequences of 1091 bp length were obtained.

The ITS1 fragment of the nuclear DNA (nDNA) was amplified according to Sajdak and Phillips (1997). A fragment was amplified using the primers MD1-forward 5′- CTTGACTATCTAGAGGAAGT-3′ and 5.8 S-reverse 5′-AGCTTGGTGCGTTCTTCATCGA-3′ in accordance with the protocol proposed (Sajdak and Phillips 1997; Sukhanova et al. 2004). As a result of amplification, sequences of 579-722 bp length were obtained. For the second reaction the following pair of primers was used: KP2-forward 5′-AAAAAGCTTCCGTAGGTGAACCTGCG-3′ и 5.8 S-reverse.

PCR products were purified with BIOSILICA reagents (Novosibirsk, Russia) and sequenced on an automated ABI 3130xl Genetic Analyser (Applied Biosystems) in the Genomics Core Facility SB RAS, Novosibirsk, Russia, http://sequest. niboch.nsc.ru) using BigDye terminator (Applied Biosystems). The sequences were aligned with the ClustalW algorithm (Larkin et al. 2007) and then manually edited. In total, 140 ND1 haplotype gene sequences of 975 bp length were deposited into the GenBank database (for Accession Numbers see Table 1).

Polymorphisms of mtDNA

To analyze the genetic polymorphism of different whitefish populations/forms, several parameters, such as the number of polymorphic (segregating) sites (S), the number of haplotypes (h), haplotype diversity (H_d), nucleotide diversity (π) and the average number of nucleotide differences (k) were estimated. All calculations were performed using DnaSP v. 5.10 (Librado and Rozas 2009).

Phylogeny and haplotype distribution

We determined the best fit models of nucleotide substitution using MEGA v. 5.2 (Tamura et al. 2011). The best model was Kimura two-parameter with gamma distribution (parameter $\alpha = 0.5$) as for the ND1 gene of the mtDNA and the ITS1 fragment of the nDNA. These models were used to reconstruct phylogenetic relationships among the whitefish forms/species studied using the maximum likelihood (ML) algorithm for the mitochondrial and nuclear fragment. Additionally, Bayesian analysis was performed with MrBayes v.3.2 (Ronquist and Huelsenbeck 2003) under the Felsenstein model (F81) for the ITS1 fragment. The evolutionary genetic distances were estimated with the Kimura two-parameter model for both genes. The significance of the phylogenetic reconstructions was assessed by a bootstrap test with 1000 replications (Saitou and Nei 2011). Additionally the haplotypes of 14 whitefish species obtained earlier (Bochkarev et al., 2018) were used for comparative analysis in the phylogenetic reconstruction with the inclusion of *Prosopium cylindraceum* as an outgroup. As a result, 27 nucleotide sequences of the ITS1 fragment of the nuclear genome were obtained for whitefishes for different types and forms, the haplotypes were deposited into the GenBank database under the accession numbers MZ087758 - MZ087787. Moreover, the following ITS1 were taken from NCBI (AJ417728 - AJ417732, MT458442, MT458445, MT458446, MT458407, MT458303, MT458304, MT458287, MT458277, KR376139, KR376138, KP184423, KJ742925, KJ742924, JQ731750, AY125106, KP184422, KP184423) and Sajdak and Phillips (1997).

Neutrality tests and mismatch distribution

To check the samples for selective neutrality, the Tajima's D and Fu's F_S tests were calculated with Arlequin v. 3.5.2.2 (Excoffier and Lischer 2010). The significance of these tests was calculated using the coalescent simulation with 1000 permutations. To assess demographic parameters, a histogram of mismatch distributions (MMD) was constructed using DnaSP v. 5.10. The bootstrap approach (1000 replications) was used to test the observed data with the simulated data under the models of pure demographic expansion and spatial expansion by comparing the sum of squared deviations (SSD) between the observed (SSD_{obs}) and simulated (SSD_{sim}) data. The Harpending's raggedness index (*r*) was used to test for a deviation from unimodality of the mismatch distribution (Rogers and Harpending 1992). The significance of the estimated parameters was also obtained from the corresponding *P* values. The 95%-confidence intervals around τ, M and Theta were calculated with the bootstrap approach (1000 replications) using Arlequin v. 3.5.2.2. The divergence rate of coregonid's mtDNA was assumed as $0.97 \cdot 10^{-8}$ nucleotide substitutions per year as suggested earlier by Koskinen et al. (2002) and Wilson and Turner (2009).

Results

Morphology

According to F.N. Kirillov (1972) and our own data, *pidschian*-like whitefishes from the Indigirka and Kolyma river basins (East Siberia) have some points of similarity with the well-known *C. l. pidschian* n. *glacialis* and whitefishes from the Anabar River (north part of central Siberia) (Kirillov 1972; Sendek and Ivanov 2017; Bochkarev et al. 2017). The abovementioned whitefishes have a tall body with a well-defined hump and a relatively small head with a lower mouth (Fig. 1). Based on the number of gill rakers on the first brachial arch and the number of perforated scales along the lateral line, *C. l. pidschian* n. *jucagiricus* belongs to the sparsely-rakered and low-scaled whitefishes. The whitefishes from the lower reach of the Kolyma River and the Indigirka River basins (East Siberia) are characterized by a similar number of gill rakers and perforated scales on the lateral line. The whitefishes from Ilirnei Lake (the Malyi Anyui River, Kolyma River basin, East Siberia) have a low number of perforated scales on the lateral line. The glacial-plain whitefishes from the Khroma River (East Siberia) are similar to the *C. l. pidschian* n. *brachymystax* from the Buotoma River (the middle reach of the Lena River) based on the main meristic characters (Table 2). The whitefish samples from the Ichilyakh and Ilirnei lakes (the Indigirka and Kolyma river basins) are differed based on the number of perforated scales in the lateral line (*P* > 0.05). The whitefish samples from the Moma-Kolyma,

($P > 0.001$), Moma-Suturuokha ($P > 0.01$), Kolyma-Buotoma ($P > 0.001$) are differed based on the gill raker numbers on the first brachial arch.

Mitochondrial DNA polymorphism

A median-joining (MJ) network was constructed based on the ND1 haplotypes using Network v. 4.6 (Bandelt 1999). While constructing the MJ network, all unique haplotypes, except for *C. l. pidschian* n. *jucagiricus* haplotypes were excluded from analysis for simplification of the MJ network. As a rule, the whitefish populations from water bodies of the Siberian Arctic are characterized by average or high levels of polymorphism of the mtDNA (Bochkarev et al. 2018). A relatively high level of haplotype (H_d) and nucleotide (π) diversity was registered in the majority of the whitefish populations inhabiting the different Arctic river basins, and based on morphological characters belong to the *C. l. pidschian* n. *glacialis* whitefishes. Moreover, these populations are characterized by an average or high value of nucleotide differences (k). The lowest level of genetic polymorphism was found in the *C. l. pidschian* n. *brachymystax* populations inhabiting some water bodies of the Lena River basin (East Siberia) which are distant from the main river channel (for example, the Markha River and Bolshoye Toko Lake (Lena River basin, East Siberia). The whitefish populations from the Lena River channel (the Buotoma River mouth, the upper reach of the Lena River, East Siberia) are characterized by a higher level of genetic polymorphism. Also, a high level of mitochondrial polymorphisms was observed in the whitefish populations from the Khatanga River basin, the Kureyka River and Khantayskoye Lake of the Yenisei River basin (Taymyr Peninsula) compared with other populations. As for the populations from the Ilirnei (lower reach of Kolyma River) and Ichilyakh lakes (upper reach of Indigirka River), the Moma (middle reach of Indigirka River, East Siberia) and Kolyma rivers (East Siberia), the lowest genetic polymorphism was found here. A high level of genetic polymorphism in the coregonid populations from the Kolyma River and the Moma River mouth (middle reach of Indigirka River basin) is due to introgression of some distant phylogenetic lineages of *C. l. pidschian n. glacialis*. After deletion of alien haplotypes from the analysis the level of the genetic polymorphism in *C. l. pidschian* n. *jucagiricus* populations was greatly reduced (Table 3). Only three out of the thirteen *C. l. pidschian* n. *jucagiricus* haplotypes in the populations from the mouth of the Suturuokha River (the Indigirka River basin, East Siberia) analyzed were revealed as *C. l. pidschian* n. *jucagiricus*, while the rest were identified as the *C. l. pidschian n. glacialis* whitefishes. After removal of irrelevant haplotypes the H_d and π values in *C. l. pidschian* n. *jucagiricus* samples from the Suturuokha River (middle reach of Indigirka River, East Siberia) decreased as well.

Phylogeny

The reconstruction of the phylogenetic relationships between the whitefish forms from this study based on the ND1 sequences reveals 12 clusters. The haplotypes of *P. cylindraceum* formed a distant outgroup from *S. leucichthys,* and all whitefish haplotypes, with strong support. The *S. leucichthys* haplotypes occupy the basal position relative to other whitefish haplotypes (Fig. 3). All major clusters are well-supported statistically. It seems that inconnu is a very ancient representative among all studied coregonid fishes. The *C. l. pidschian* n. *jucagiricus* haplotypes form a distant well-supported cluster within the *C. lavaretus/C. muksun* complex. However, the genetic distance between the *C. l. pidschian* n. *jucagiricus* haplogroup and *pidschian*-like whitefish groups from West and East Siberian water bodies is less than 1% (Table 3) (Supplementary 1, 2)**.**

Haplotype distribution

Two groups were observed in the structure of the median-joining network based on the ND1 whitefish haplotypes (Fig. 4). Haplogroup (I) represents a very characteristic star-like pattern of haplotypes from the whitefish populations inhabiting the Indigirka and Kolyma river, the Moma and Khroma river basins, and the Ichilyakh and Ilirnei lakes. Its center is occupied by a central haplotype (H7) which occurs in almost all water bodies. Also, the haplogroup comprises a number of minor haplotypes from the same water bodies separated from the central haplotype by 1-4 mutations. The distribution pattern of ND1 haplotypes in haplogroup (II) is remarkably different by comparison with haplogroup (I), and the network structure is much more reticulated and complicated. Several star-like patterns within this haplogroup, derived from populations from the Lena, Omoloi, Khroma, Yenisei and Khatanga river basins are revealed. A number of star-like structures in the haplogroup (II) were depicted by the East Siberian whitefish haplotypes. The majority of the star-like patterns of the haplogroup (II) are joined with each other by a number of hypothesised sequences (median vectors) and cyclic links. Probably, most of the peripheral haplotypes belong to *C. l. pidschian n. glacialis* whitefishes (Bochkarev et al., 2018). There are six substitutions and two rare whitefish haplotypes from the Suturuokha River (H33) and the Kolyma River (H8) between the haplogroups (I) and (II).

Pairwise F_{ST} values calculated between whitefish populations indicated the occurrence of a high degree of genetic differentiation between *C. l. pidschian* n. *jucagiricus* populations (the Ilirnei and Ichilyakh lakes) and populations from the Yenisei, Lena, Yana and Khroma river basins, up to 0.736 (Table 4). For the populations of East Siberian and glacial-plain whitefishes, there were low F_{ST} values under their pairwise comparison, not exceeding 0.402.

Neutrality tests

Most of the whitefish populations studied are characterized by negative (but insignificant) values of Tajima's D and Fu's F_S tests. Positive values (also insignificant) of this test were registered in the whitefish populations from the Khroma, Kureyka and Zakharova Rassokha rivers (Table 5). Negative values of Tajima's D test with low reliability were found in *C. l. pidschian* n. *jucagiricus* populations from the Ichilyakh and Ilirnei lakes. Negative and significant values ($p > 0.0001$) of Fu's F_S test were obtained for the whitefish population from the Suturuokha River and for all whitefish populations studied from the Indigirka River basin. Negative values (with low reliability) of Fu's F_S test were detected for the whitefish populations from Ichilyakh Lake, the Markha River and for all whitefish populations from the Yenisei and Khatanga rivers (Table 5).

Mismatch distribution

Mismatch distribution has an L-shaped pattern for *C. l. pidschian* n. *jucagiricus* (Fig. 5). The MMD values computed for these whitefish populations have shown that assumptions regarding the demographic and spatial expansion of haplotypes cannot be rejected. However, the MMD parameters corresponds better to the spatial expansion model (SSD_{obs} = 0.00069, p = 0.840; r = 0.147, p = 0.800).

Polymorphisms of ITS1

The maximum likelihood (ML) and MrBayes (MB) trees based on ITS1 are presented in Figure 6. It should be noted that the effect of the repeated nucleotide tandems are not represented on both trees. The majority of the whitefish species (genus *Coregonus*) including different *pidschian*-like *nations* and *C. l. pidschian* n. *jucagiricus* were used in analysis of ITS1 polymorphisms. The sequences of all studied specimens belonging to the same form/species of whitefish were identical with each other. The significant part of each ITS1 fragment was presented by a tandem arrangement of three repeated sequence fragments formed by 66 b.p. The shortest length of ITS1 found in *C. automnalis* and *C. sardinella* included only one fragment with 66 b.p. Among pidschian-like whitefish, the same short fragment of ITS1 was found only for whitefish from the Baltic Sea. While, all other forms/species of *C. l. pidschian*, including *C. l. pidschian* n. *jucagiricus,* had two such fragments in their ITS1 rDNA. In the same group (two repeated tandems) there were also included such whitefish species as *C. mucsun, C. nasus, C. anaulorum, C. fluviatilis,* as well as sympatric whitefishes from the Amur River basin. In the group with three repeated tandems there were the *C. clupeaformis*, a sympatric pair of whitefishes from Teletskoye Lake (Ob River basin) and whitefishes from lakes of the Todzha depression (Yenisei River basin). The main nucleotide differences among whitefishes were found in the beginning and in the end of the ITS1 fragment. The pairwise distances within groups ranged from 0.000 to 0.0096, whereas among groups ranged from 0.000 to 0.0480. In some cases, such differences represent significant differentiation (more than 2%). Within Eurasian whitefishes the distances varied from 0.0006 to 0.002.

Discussion

Morphological and ecological properties of *C. l. pidschian* n. *jucagiricus*

The present results have shown that *C. l. pidschian* n. *jucagiricus* occur in both lower and upper reaches of the large fast-flowing rivers (Indigirka, Kolyma, Moma and Kaidusun) and large lakes (Ilirnei, Ichilyakh, and Labynkyr) from East Siberia. In some lakes (Ichilyakh, Ilirnei) they form homogeneous populations, while in others (the Suturuokha River, the Indigirka River basin) they form mixed groups with glacial-plain whitefish *C. l. pidschian* n. *glacialis*. Different ecotopes occupied by *C. l. pidschian* n. *jucagiricus* suggest that this whitefish is capable of forming both lacustrine and riverine populations, in contrast to *C. l. pidschian* n. *glacialis* inhabiting only lakes and estuaries.

C. l. pidschian n. *jucagiricus* belongs to the sparsely-rakered whitefishes based on the number of gill rakers on the first brachial arch. Different authors have reported that whitefishes from the Indigirka and Kolyma river basins having 18.80-20.10 gill rakers (Novikov 1966; Kirillov 1972). According to our data *C. l. pidschian* n. *jucagiricus* from the Kolyma River has more gill rakers (22.60) than reported earlier (19.01) (Novikov 1966). Data from this study and literature concerning the number of perforated scales on the lateral line are consistent. It should be noted that the majority of all populations/forms/species of whitefish from the basin of the Ob River to the basin of the Anabar River are characterized by the low number of perforated scales on the lateral line (78-85) and *C. l. pidschian* n. *jucagiricus* is no exception (78-82). In Siberia, only whitefishes from water bodies situated in the Baikal Rift Zone have a much higher number of scales on the lateral line (88-100) (Kirillov 1972; Skryabin 1977; Reshetnikov 1980). Thus, it is practically impossible to distinguish *C. l. pidschian* n. *jucagiricus* from most of the Siberian whitefish forms/species based on meristic characters.

Phylogeny and haplotype distribution ND1 mtDNA

The analysis of the phylogenetic relationships among different whitefishes clearly shows that haplotypes of *C. l. pidschian* n. *jucagiricus* form a highly supported separate cluster. Genetic distances between whitefish species vary from 2 to 5% (except for inconnu *S. nelma* and round whitefish *P. cylindraceum*); and genetic distance between *C. l. pidschian* n. *jucagiricus* and other species is up to 3%. The lowest distances (0.06 and 0.09%) were obtained under pairwise comparison of *C. l. pidschian* n. *jucagiricus* with other *pidschian*-like whitefishes from Siberian water bodies. This fact, as well as minor morphological differences, from the glacial-plain (*C. l. pidschian* natio *glacialis*) clearly indicates a relatively recent evolutionary divergence of this whitefish form (Bochkarev et at 2018; 2021). However, the threshold at 2% of nucleotide differences is significant for cryptic species (April et al. 2013).

In accordance with the network structure, all haplotypes of whitefishes from Lena Rivers to Kolyma River basins divided into two large groups. The first haplogroup is characterized by a compound structure with a large number of star-like patterns and alternative links having lengths produced by inverse or parallel mutations. Such a structure provides proof of a long-term evolutionary period during which these whitefishes were exposed to changing environmental conditions including altered population size and/or occurrence of adjacent refugia sets (Avise 2000). This structure comprises the East Siberian whitefish (*C. l. pidschian* n. *brachymystax*) haplotypes forming several star-like patterns and unique haplotypes of glacial-plain whitefishes. The haplotypes of *C. l. pidschian* n. *jucagiricus* form the second haplogroup, which is characterized by a star-like form with a central haplotype (H7) including a relatively large number of randomly spaced minor haplotypes (Supplementary 1, 2).

ITS1 nDNA

It should be noted that the structure of the ITS1 fragment of pidschian-like whitefishes from Siberian waterbodies is almost identical, including such distant species as *C. nasus* and *C. mucsun*. We have confirmed the level of polymorphism of the ITS1 rDNA region, obtained in a previous study (Sajdak and Phillips 1997). In the present study, all studied forms/species (from Ob River basin to Anadyr River basin), including *C. l. pidschian* n. *jucagiricus*, have tandem arrangement of two identical nucleotide fragments and very similar nucleotide composition of the ITS1 region. The only forms/species of whitefishes that have differences from our studied pidschian-like whitefishes in ITS1 structure, in terms of insertions and deletions, are those from the basin of Baikal Lake such as *C. fluviatilis*, *C. l. baicalensis*, and *C. migratorius*. Surprisingly, a whitefish from North America is identical to whitefishes from waterbodies of the Altai-Sayan mountainous country (West-Central Siberia), and is different from whitefishes from waterbodies of the Altai region at only one deletion in the beginning, and one insertion in the end of ITS1 fragment (Sajdak and Phillips 1997).

Allozymic analysis

Based on the allozymic analysis it was shown that glacial-plain whitefishes from the Anabar River are closely related to whitefishes from the Kolyma and Indigirka rivers (Sendek and Ivanov 2017). Meanwhile, *C. l. pidschian* n. *brachymystax* from the Lena River is demonstrated to be in a more distant position with reference to *C. l. pidschian* n. *jucagiricus* than to *pidschian*-like whitefish populations from the Ob and Yenisei rivers (Sendek et al. 2013).

Demographic history

All whitefish populations discussed (except for *C. l. pidschian* n. *jucagiricus*) are characterized by a high level of genetic polymorphism. It is known that a high level of genetic polymorphisms exists in populations which maintain a high effective number for a long time. In some cases a high level of genetic polymorphism could have formed from populations of several divergent mitochondrial lineages (Avise 2000). As was shown earlier, the majority of Arctic whitefish populations/forms have approximately the same genetic diversity based on ND1 mtDNA (Bochkarev et al. 2017). However, the haplotype and nucleotide diversity of the *C. l. pidschian* n. *jucagiricus* population is twice as low in comparison to Arctic Siberian whitefish populations. Only in the whitefish population from Karakul Lake (the Abakan River basin, central Siberia) were similar levels of genetic polymorphism ($H_d = 0.230$, $\pi = 0.00019$) observed; thus, we conclude that this postglacial lake, located between Kolyma and Indigirka rivers, has recently been colonized by a small number of founders (Bochkarev et al. 2017). Based on the aforementioned conclusion, we argue that *C. l. pidschian* n. *jucagiricus* is a separate allopatric subspecies/species that has been formed relatively recently. Obviously, the high frequency of the central haplotype (H7), which comprises whitefish haplotypes from both the Kolyma and Indigirka rivers, is due to the founder effect rather than the long-term evolution of *C. l. pidschian* n. *jucagiricus* (April et al. 2013). This assumption is also supported by the absence of clear genetic differences between whitefish populations from the Indigirka and Kolyma river basins (East Siberia). Whitefish haplotypes from geographically remote areas such as upstream of Indigirka River (Ichilyakh Lake) and downstream of Kolyma River (Ilirnei Lake) have formed genetically pure populations, suggesting that *C. l. pidschian* n. *jucagiricus* rapidly colonized the Kolyma and Indigirka river basins (East Siberia).

The neutrality tests Tajima’s D and Fu’s Fs are negative and statistically significant for *C. l. pidschian* n. *jucagiricus* population, indicating either the recent demographic expansion or negative (purifying) selection (Avise 2000). However, the value of SSD_{obs} and Harpending’s roughness index are indicative of deviation from this model. The existence of identical phylogenetic lineages of *C. l. pidschian* n. *jucagiricus* in lakes that are very distant from each other and from the main highways of settlement, directly indicates the territorial and demographic expansion of the new form/species. Using the equation $\tau = 2ut$, the mean divergence rate of $0.97 \cdot 10^{-8}$ nucleotide substitutions and assuming one generation per year, we can very roughly estimate the expansion time for *C. l. pidschian* n. *jucagiricus* populations. Thus, the expansion time (with 95% confidence interval) is 9-30.000 years ago based on the ND1 gene of the mtDNA. The upper limit (30.000 years ago, at a minimum) seems more likely.

In regards to the paths of origin of *C. l. pidschian* n. *jucagiricus,* we can propose two hypotheses. The first one is that the Siberian populations have shown that only a small number of *C. l. pidschian* n. *jucagiricus* haplotypes were revealed in other Siberian water bodies. However, *C. l. pidschian* n. *glacialis* haplotypes were found in the Kolyma and Indigirka rivers. It was shown that ND1-haplotypes of *C. l. pidschian* n. *glacialis* from the Anabar River form similar weak links with a number of unique haplotypes (Bochkarev et al. 2018). Similar patterns of haplotype networks were observed for whitefishes from Khantayskoye Lake, Khroma and Yana rivers (Central Siberia). These haplotypes are adjacent to minor whitefish haplotypes from the Indigirka and Kolyma rivers (East Siberia) (Fig. 4). The presence of *C. l. pidschian* n. *glacialis* haplotypes from the Khroma River in the star-like structure of *C. l. pidschian* n. *jucagiricus* network suggests that there are high chances that these whitefish originated from the ancient haplotypes of *C. l. pidschian* n. *glacialis*. The low level of genetic polymorphism in the *C. l. pidschian* n. *jucagiricus* population is indicative of either its recent evolutionary divergence after passing through a “bottleneck” event, or the founder effect (Bernatchez and Wilson 1998). It seems unlikely, that *C. l. pidschian* n. *jucagiricus* could have originated from whitefishes inhabiting the Lena River basin (East-Siberian whitefishes) during a relatively short time period (9 000-30 000 years) (Fig. 4). Much more likely, that *C. l. pidschian* n. *jucagiricus* originated from ancient haplotypes of *C. l. pidschian* n. *glacialis,* and this hypothesis is supported by the structure of the network with a limited number of differently distant minor haplotypes. These haplotypes join with the central haplotype via two or three nucleotide substitutions, and their positions within the network structure could be representative of their more ancient origin. All haplotype networks obtained for whitefishes from other water bodies, having a postglacial origin, are characterized by a more compact structure (Bochkarev et al. 2018). The distant position of *C. l. pidschian* n. *jucagiricus* from a large and ancient group of whitefishes from the Lena River, their relatively young age (according to the haplotype network) and the identity of *C. l. pidschian* n. *jucagiricus* populations from the Kolyma and Indigirka rivers are no longer discordant. We assume that a sudden irruption within a small population of *C. l. pidschian* n. *glacialis* took place at the end one of the last glaciations and lead to the formation of the allopatric form/species *C. l. pidschian* n. *jucagiricus*.

In another scenario, earlier *C. l. pidschian* n. *jucagiricus* was widely distributed across a vast territory, and then this area became drastically restricted due to unspecified catastrophic events. In this case, the subsequent expansion of European and Siberian *pidschian*-like whitefish forms/species would have had to destroy all of its traces in Siberian water bodies. It should be noted, however, that *C. l. pidschian* n. *jucagiricus* haplotypes were not found in the middle reaches of the Anadyr River, nor Lena River basin, which is adjacent to the Kolyma and Indigirka river basins (Bochkarev 2018).

It should be noted that the signs of at least two different glaciations were found in the upper reaches of the Kolyma and Indigirka rivers (Rusanov et al. 1967). It is believed that the first glaciations was relatively stronger than the second one. The centers of glacier formation were located on the highest North-East part of the Suntar-Khayata Range (East Siberian System, 62°36′00″N 140°53′00″E). Due to their huge size and mass during the first glacial period, the glaciers could replace water with ice in those regional waterbodies. Later glaciations were weaker, but persisted for a long time (Khvorostova and Kashmenskaya 1962). It could be expected that *C. l. pidschian* n. *jucagiricus* was formed after the last glacial period (Bernatchez and Wilson 1998).

CONCLUSION

Obviously, the genetic heterogeneity of Arctic whitefishes is associated with the different origins of their modern populations. These populations arose as a result of the dispersal of various earlier widespread evolutionary lineages of whitefishes from geographically distant refugia that existed in the Quaternary. The preliminary genetic analysis has shown that there are a relatively few number of forms/species of whitefishes in arctic waterbodies of Siberia. If we exclude whitefish species from Baikal Lake (*C. fluviatilis*, *C. l. baicalensis*, and *C. migratorius*) and the Anadyr River (*C. anaulorum*), the final number of forms/species of whitefishes inhabiting the area from the Ob River until the Kolyma River will be around three or four forms of pidschian-like whitefishes. But if we include in this number, based on the present study, *C. l. pidschian* n. *jucagiricus* as a new form/species, the final number increases to five. The area of these whitefishes is located in the middle and lower reaches of the Ob, Yenisei, and Lena Rivers. The modern forms of these whitefishes were apparently formed in refugia of the upstream areas of the same rivers. *C. l. pidschian* n. *brachymystax* is a widespread whitefish in the Lena River basin that is likely a descendant (or ancestor) from *C. l. pidschian* inhabiting the Ob River basin. *C. l. pidschian* n. *glacialis* inhabits lakes and estuaries of the entire Siberian arctic region. To date, the origin of this whitefish is impossible to explain by data presented here. Probably, *C. l. pidschian* n. *glacialis* is a relatively ancient form/species and was widespread along the arctic coast until the last period of glaciations. It is believed that the area was not affected by the middle and late Pleistocene glaciations. That is why the most "clean" *C. l. pidschian* n. *jucagiricus* lives in the upper reaches of the rivers. Whereas *C. l. pidschian* n. *glacialis* and *C. l. pidschian* n. *brachymystax* had the greatest influence on the genetic structure of *C. l. pidschian* n. *jucagiricus* in the middle and lower reaches of these rivers. Meanwhile, in the arctic part of the basin of the Kolyma and Indigirka Rivers there are found only haplotypes of the whitefish from the Rassokha River basin (Khatanga River basin). It should be noted, that *C. l. pidschian* n. *jucagiricus* was formed relatively recently, and therefore, is currently confined to the basins of the Indigirka and Kolyma rivers.

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Tamura, K., Peterson, D., Stecher, G., Nei, M., and Kuma, S. 2011. MEGA5: Phylogenetic and molecular evolutionary analyses were conducted using MEGA version 5. Mol. Biol. Evol. **28**: 2731–2739. doi: 10.1093/molbev/msr121.

Titles

Fig. 1 Arctic whitefish heads: a – *C. l. pidschian jucagiricus* from Ilirnei Lake, the Maly Anyui River of the Kolyma River basin; b – *C. lavaretus pidschian* n. *glacialis* from the Anabar River; c – *C. l. pidschian* n. *brachymystax* from the Anabar River (Bochkarev et al., 2018).

Fig. 2 Map of study area. Sampling sites are shown as 1-15.

Fig. 3 Maximum likelihood phylogenetic tree for species of the genus *Coregonus* based on the ND1 nucleotide sequences of the mtDNA. Bootstrap values from ML analysis expressed as a percentage (above 70 %) are indicated. The scale is given in expected substitutions per site. 0 – an outgroup (round whitefish and inconnu); 1 – Arctic cisco; 2 – vendace, peled, *C. subautumnalis;* 3 – *C. nasus*; 4 – *herring*-like whitefish; 5 – Ussuri and chadary whitefishes; 6 – Baikal omul; 7 – *C. fluviatilis*; 8 – haplotypes of *vendace*-like whitefish from Baunt Lake; 9 – tugun; 10 – haplotypes of Anadyr whitefish; 11 – *pidschian*-like whitefish from Ob, Yenisei and Lena rivers; muksun from Ob, Lena and Indigirka rivers. 12 – *C. l. pidschian jucagiricus.* Whitefish haplotypes from the water bodies of the Todzha Depression and distant whitefish haplotypes from Teletskoye Lake are highlighted by grey color. a, b – nodes with an unresolved branching.

Fig. 4 Median-joining ND1 haplotypes network for whitefishes from some Siberian water bodies. The circle sizes correspond to relative haplotype frequencies (circular size scales are shown in the lower left corner); small white squares are median vectors. 1 – Kolyma River; 2 – Suturuokha River; 3 – Ilirnei Lake; 4 – Khroma River, 5 – Kureyka River (Yenisei River basin); 6 – Rassokha River, Khantayskoye Lake; 7 – Ichilyakh Lake; 8 – Moma River; 9 – Omoloi River; 10 – Markha River; 11 – B. Toko Lake (Lena basin); 12 – Buotoma River (Lena basin); 13 – the upper reach of the Lena River; 14 – Yana River.

Fig. 5 Mismatch distribution of *C. l. pidschian jucagiricus* based on the ND1 spatial expansion model. Dashed line and grey dotted lines represent expected distribution and the 95% credible interval under the spatial expansion model.

Fig. 6 The scheme of phylogenetic relationchips among studied species of whitefish (genus Coregonus) based on ITS1 nDNA. Bayesian posterior probabilities BI and bootstrap values from ML analysis are presented at nodes. The asterisk denotes sequences obtained from (Sajdak, Phillips, 1997).

SUPPLEMENT 1. The ML haplotypes network based on mutational differences among 102 *Coregonus lavaretus* composite mtDNA sequences found in Siberian rivers. The designations A-H corresponds to Fig. 4

SUPPLEMENT 2. Geographical distribution of 15 populations of *Coregonus lavaretus pidschian* complex The designations 1-15 corresponds to Fig. 4, and table 1, 3

FIGURES

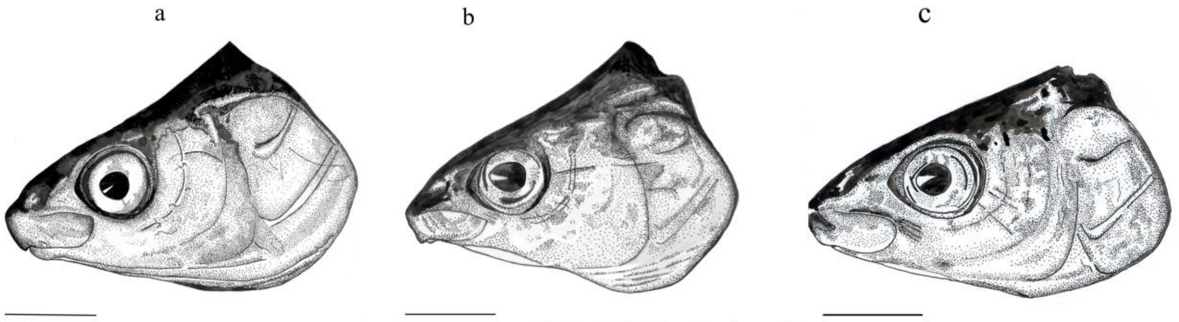


FIGURE 1

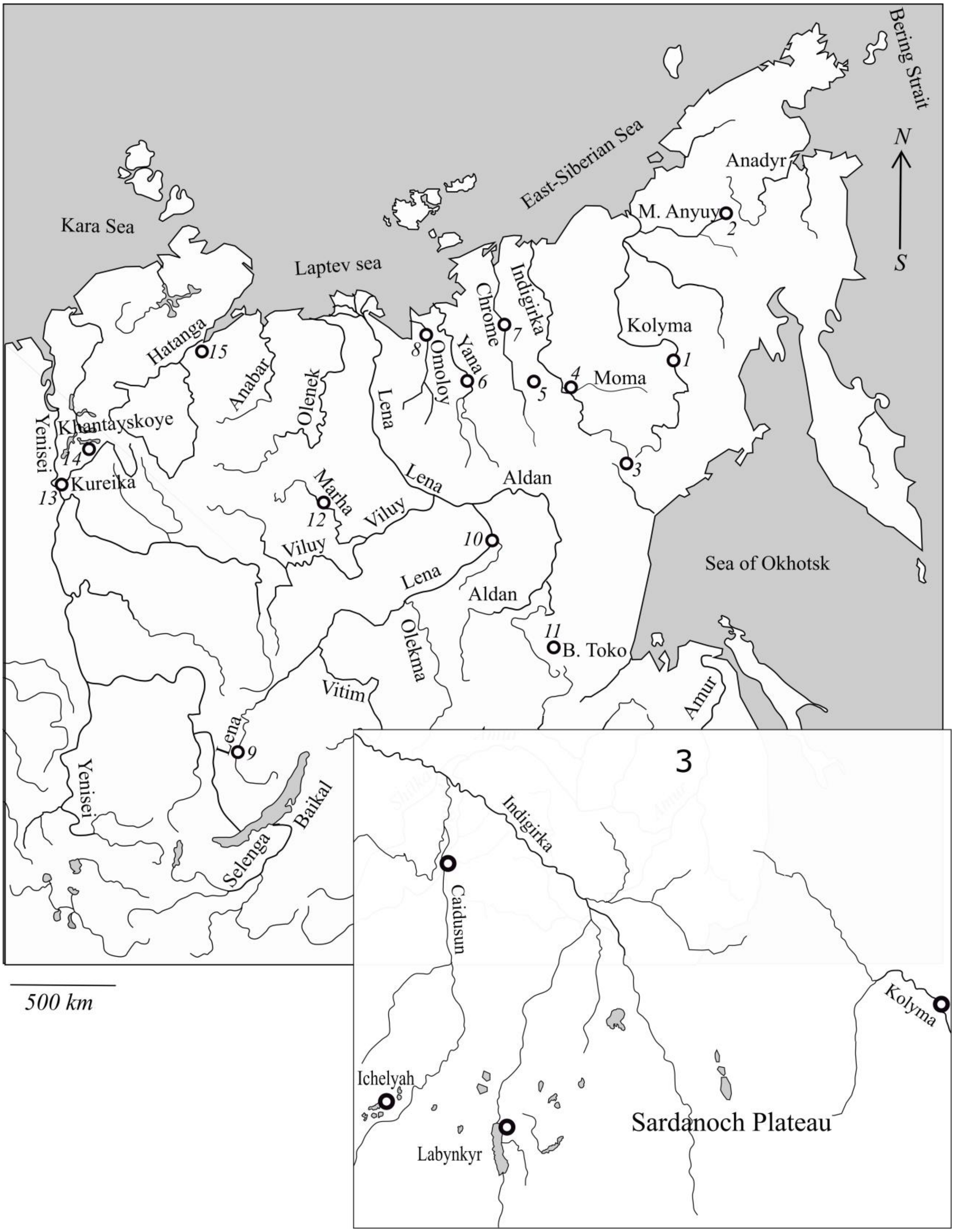

Bering Strait
East-Siberian Sea
Kara Sea
Laptev sea
N
S
Anadyr
M. Anyuy
2
Kolyma
1
Indigirka
Chrome
7
Moma
4
5
Yana
6
Omoloy
8
Lena
Hatanga
15
Anabar
Olenek
Khantayskoye
14
Yenisei
Kureika
13
Marha
12
Viluy
Lena
Aldan
10
3
Sea of Okhotsk
Lena
Aldan
11
B. Toko
Olekma
Vitim
Amur
Lena
9
Yenisei
Baikal
Selenga
500 km
3
Indigirka
Caidusun
Kolyma
Ichelyah
Labynkyr
Sardanoch Plateau

FIGURE 2

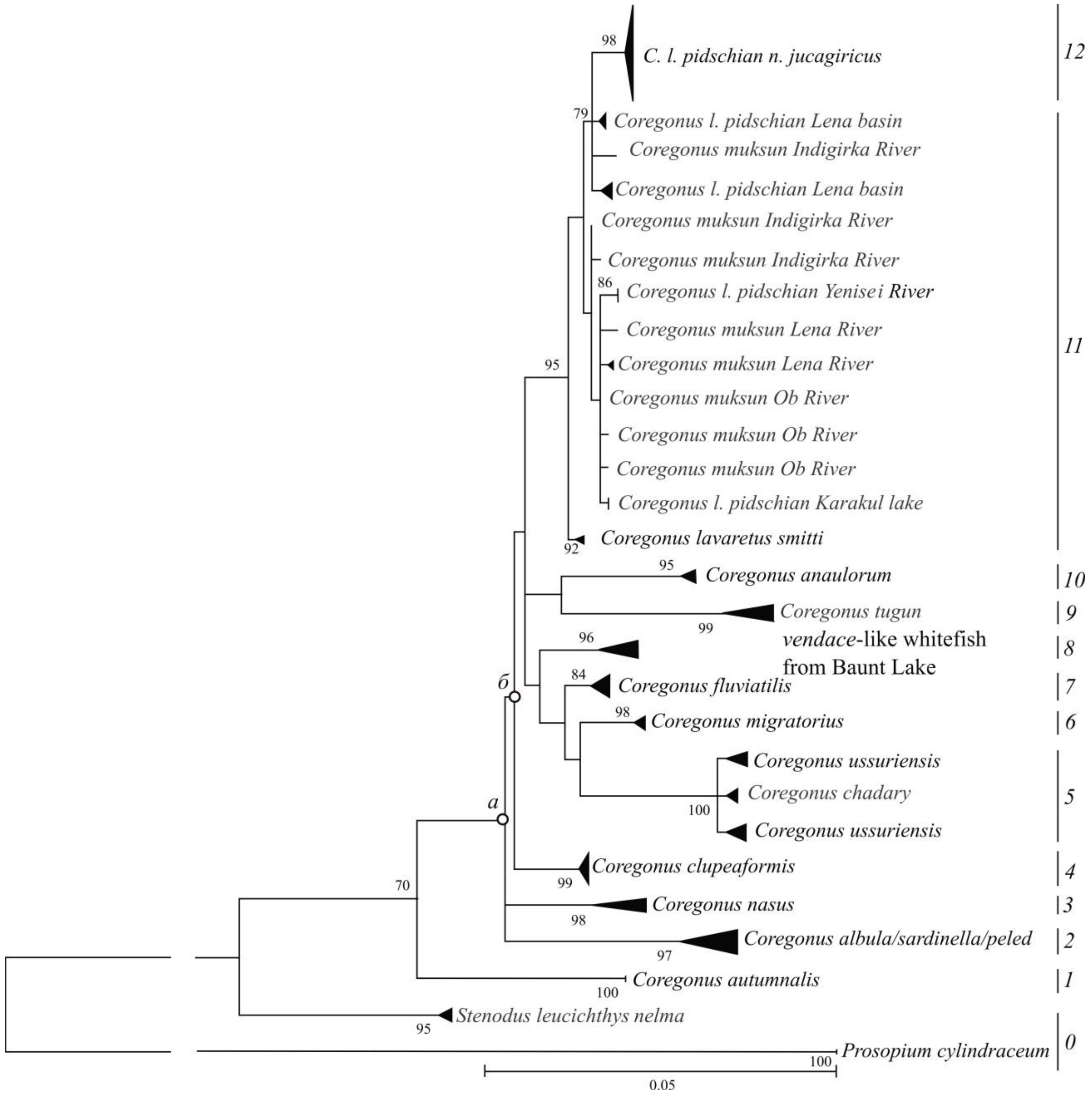
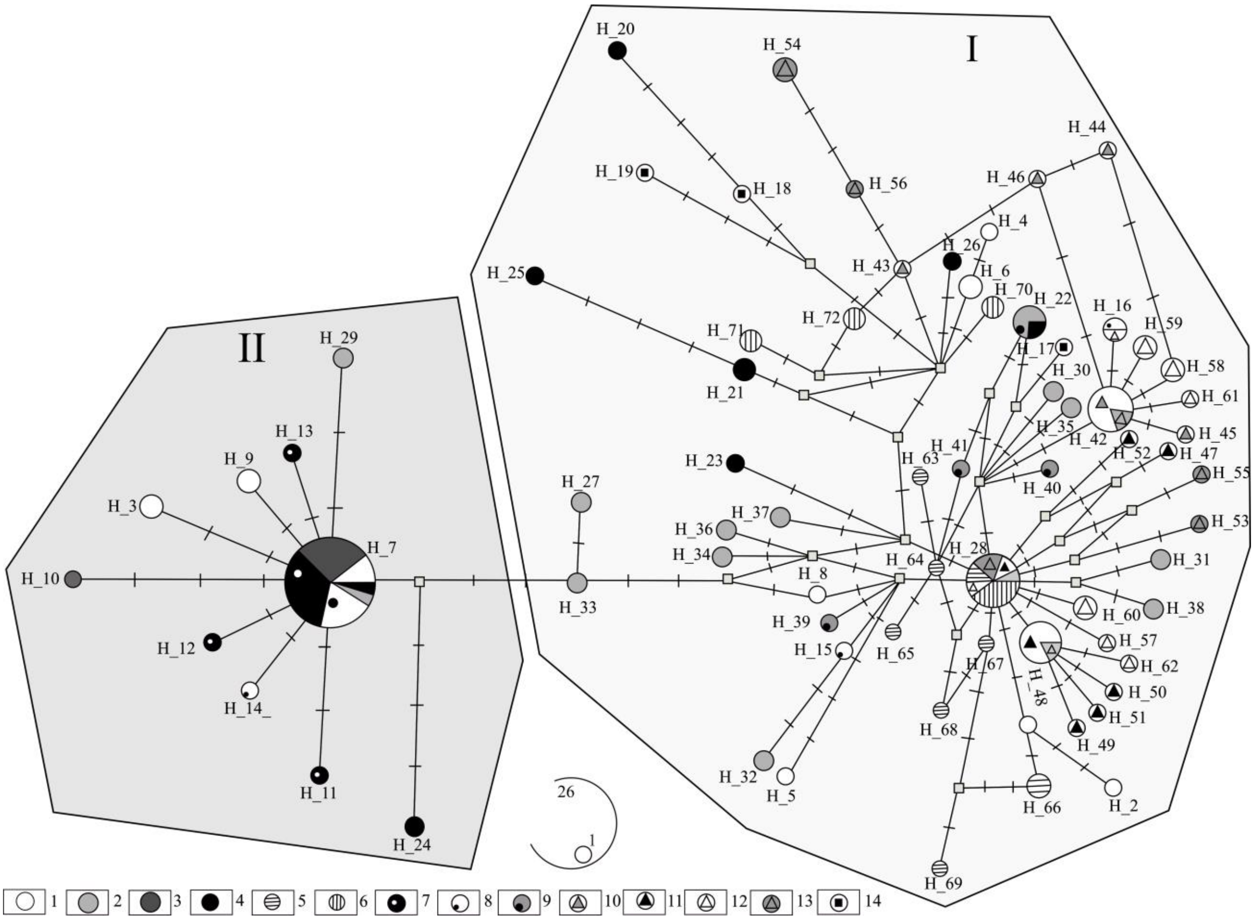

98
C. l. pidschian n. jucagiricus
12
79
Coregonus l. pidschian Lena basin
Coregonus muksun Indigirka River
Coregonus l. pidschian Lena basin
Coregonus muksun Indigirka River
Coregonus muksun Indigirka River
86
Coregonus l. pidschian Yenisei River
Coregonus muksun Lena River
Coregonus muksun Lena River
Coregonus muksun Ob River
Coregonus muksun Ob River
Coregonus muksun Ob River
Coregonus l. pidschian Karakul lake
11
95
92
Coregonus lavaretus smitti
95
Coregonus anaulorum
10
Coregonus tugun
9
99
96
vendace-like whitefish from Baunt Lake
8
б
84
Coregonus fluviatilis
7
98
Coregonus migratorius
6
Coregonus ussuriensis
Coregonus chadary
5
100
Coregonus ussuriensis
a
Coregonus clupeaformis
4
99
70
Coregonus nasus
3
98
Coregonus albula/sardinella/peled
2
97
Coregonus autumnalis
1
100
Stenodus leucichthys nelma
95
Prosopium cylindraceum
0
100
0.05

FIGURE 3


I
II
H_20
H_54
H_44
H_19
H_18
H_56
H_46
H_4
H_25
H_43
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H_6
H_70
H_22
H_72
H_16
H_59
H_71
H_17
H_58
H_30
H_21
H_61
H_35
H_45
H_42
H_52
H_47
H_41
H_63
H_23
H_55
H_40
H_27
H_37
H_53
H_36
H_28
H_34
H_31
H_64
H_8
H_33
H_39
H_60
H_38
H_57
H_15
H_65
H_67
H_62
H_48
H_50
H_51
H_68
H_49
H_32
H_5
H_66
H_2
H_69
H_29
H_13
H_9
H_3
H_7
H_10
H_12
H_14_
H_11
H_24
26
1
1
2
3
4
5
6
7
8
9
10
11
12
13
14

FIGURE 4

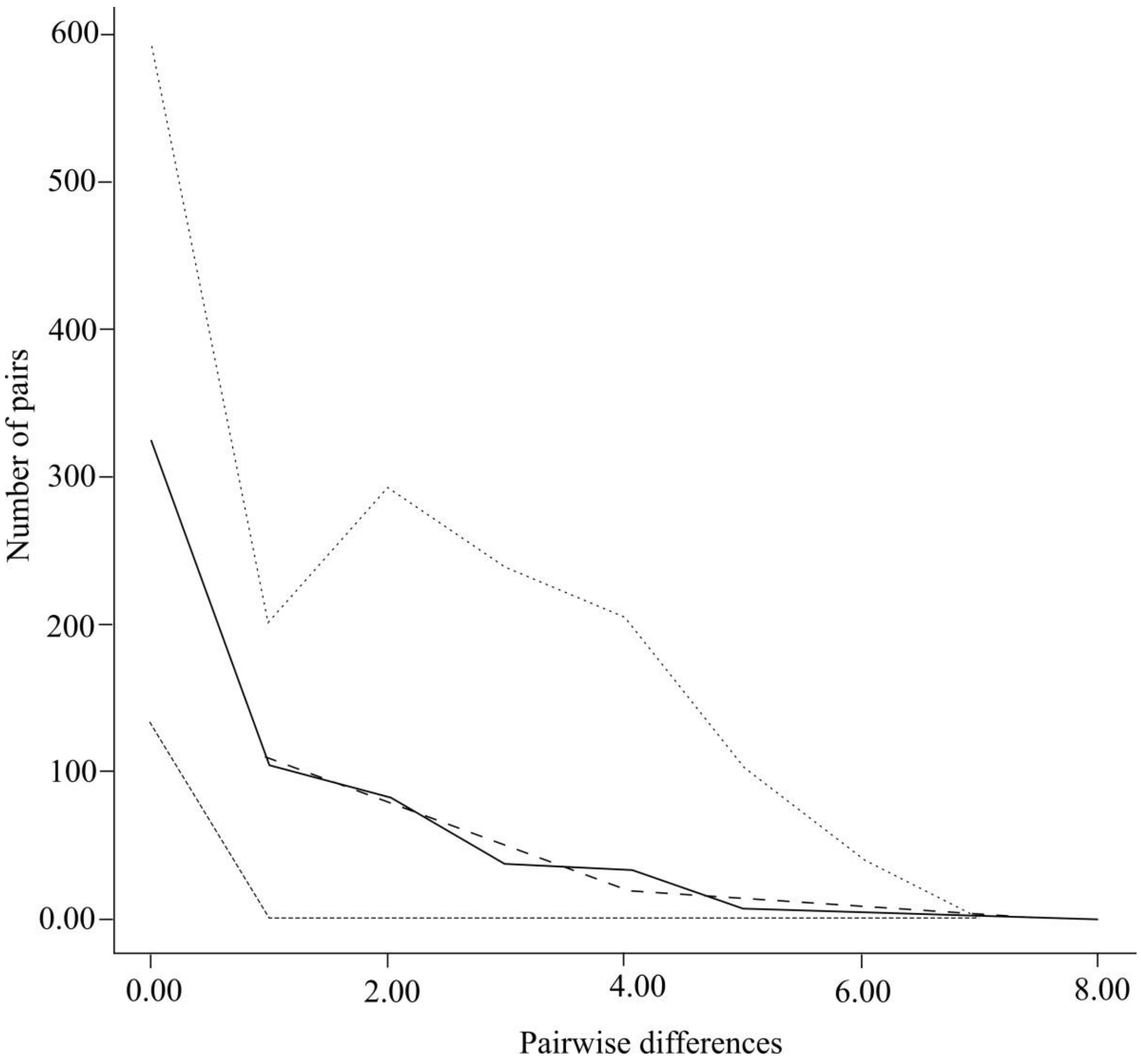

600
500
400
300
200
100
0.00
Number of pairs
0.00
2.00
4.00
6.00
8.00
Pairwise differences

FIGURE 5

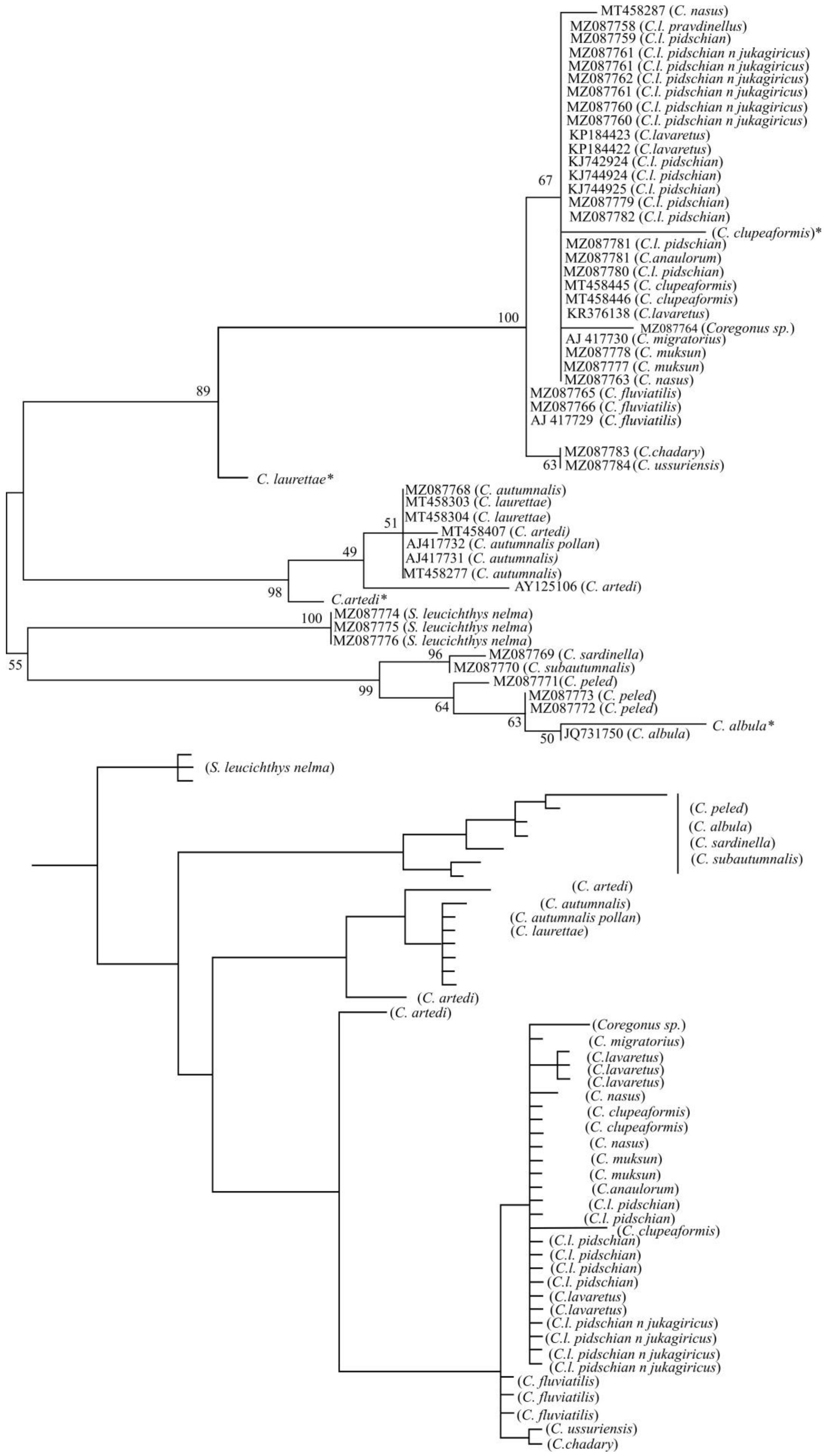

MT458287 (C. nasus)
MZ087758 (C.l. pravdinellus)
MZ087759 (C.l. pidschian)
MZ087761 (C.l. pidschian n jukagiricus)
MZ087761 (C.l. pidschian n jukagiricus)
MZ087762 (C.l. pidschian n jukagiricus)
MZ087761 (C.l. pidschian n jukagiricus)
MZ087760 (C.l. pidschian n jukagiricus)
MZ087760 (C.l. pidschian n jukagiricus)
KP184423 (C.lavaretus)
KP184422 (C.lavaretus)
KJ742924 (C.l. pidschian)
67
KJ744924 (C.l. pidschian)
KJ744925 (C.l. pidschian)
MZ087779 (C.l. pidschian)
MZ087782 (C.l. pidschian)
(C. clupeaformis)*
MZ087781 (C.l. pidschian)
MZ087781 (C.anaulorum)
MZ087780 (C.l. pidschian)
MT458445 (C. clupeaformis)
MT458446 (C. clupeaformis)
KR376138 (C.lavaretus)
100
MZ087764 (Coregonus sp.)
AJ 417730 (C. migratorius)
MZ087778 (C. muksun)
MZ087777 (C. muksun)
MZ087763 (C. nasus)
89
MZ087765 (C. fluviatilis)
MZ087766 (C. fluviatilis)
AJ 417729 (C. fluviatilis)
MZ087783 (C.chadary)
63
MZ087784 (C. ussuriensis)
C. laurettae*
MZ087768 (C. autumnalis)
MT458303 (C. laurettae)
51
MT458304 (C. laurettae)
MT458407 (C. artedi)
49
AJ417732 (C. autumnalis pollan)
AJ417731 (C. autumnalis)
MT458277 (C. autumnalis)
AY125106 (C. artedi)
98
C.artedi*
100
MZ087774 (S. leucichthys nelma)
MZ087775 (S. leucichthys nelma)
MZ087776 (S. leucichthys nelma)
55
96
MZ087769 (C. sardinella)
MZ087770 (C. subautumnalis)
MZ087771(C. peled)
99
MZ087773 (C. peled)
64
MZ087772 (C. peled)
63
C. albula*
50
JQ731750 (C. albula)
(S. leucichthys nelma)
(C. peled)
(C. albula)
(C. sardinella)
(C. subautumnalis)
(C. artedi)
(C. autumnalis)
(C. autumnalis pollan)
(C. laurettae)
(C. artedi)
(C. artedi)
(Coregonus sp.)
(C. migratorius)
(C.lavaretus)
(C.lavaretus)
(C.lavaretus)
(C. nasus)
(C. clupeaformis)
(C. clupeaformis)
(C. nasus)
(C. muksun)
(C. muksun)
(C.anaulorum)
(C.l. pidschian)
(C.l. pidschian)
(C. clupeaformis)
(C.l. pidschian)
(C.l. pidschian)
(C.l. pidschian)
(C.l. pidschian)
(C.lavaretus)
(C.lavaretus)
(C.l. pidschian n jukagiricus)
(C.l. pidschian n jukagiricus)
(C.l. pidschian n jukagiricus)
(C.l. pidschian n jukagiricus)
(C. fluviatilis)
(C. fluviatilis)
(C. fluviatilis)
(C. ussuriensis)
(C.chadary)

FIGURE 6

TABLES

TABLE 1 Water bodies, whitefish form, sample size, collection coordinates, and the GenBank Accession numbers of haplotypes of whitefishes of the *Coregonus lavaretus pidschian* complex

Species/forms	*n*	Latitude	Longitude	Accession numbers
1. *C. l. pidschian jucagiricus*, Kolyma River	12	68°86′N	156°19′E	MT862480, MT862481, MT862499-MT862503, MT862495,
2. *C. l. pidschian jucagiricus*, Ilirneir Lake (M. Anyui River)	8	67°36′N	168°34′E	MT862482, MT862496 MT862479, MT862479
3. *C. l. pidschian jucagiricus*, Ichilyakh Lake (Indigirka River)	12	62°60′N	142°78′E	MT862483, MT862484 MT862493, MT862494
4. C. l. pidschian jucagiricus, Moma River (Indigirka River)	8	66°44′N	143°17′E	MT862485, MT862486 MT862497, MT862504
5. Suturuokha River (Indigirka River)	16	68°54′N	146°17′E	MT862488- MT862492 MT862517- MT862524
6. *C. lavaretus pidschian* n. *glacialis* Yana River	3	70°79′N	136°21′E	MT862505- MT862507
7. *C. lavaretus pidschian* n. *glacialis* Khroma River	9	70°84′N	143°59′E	MT862487, MT862498 MT862508- MT862513
8. *C. l. pidschian* natio *brachymystax* Omoloi River	6	70°81′N	133°49′E	MT862514- MT862516 MT862536
9. *C. l. pidschian* natio *brachymystax* Upper Lena River	10	59.39′N	112°5′E	KM013418-KM013424 MT862526, MT862535
10. *C. l. pidschian* natio *brachymystax* Buotoma River (Lena River basin)	10	61°26′N	128°77′E	MT862527- MT862533

11. *C. l. pidschian* natio *brachymystax* B. Toko Lake (Lena River basin)	11	56°07′N	130°82′E	KM013410-KM013417 MT862534
12. *C. l. pidschian* natio *brachymystax* Markha River (Lena River basin)	9	65°06′N	116°42′E	KM013405-KM013409 MT862525
13. *C. l. pidschian* Kureyka River (Yenisei River basin)	7	68°30′N	96°00′E	KU948984–KU948988
14. Khantayskoye Lake (Yenisei River basin)	4	68°24′N	91°28′E	KU948967–KU948970
15. Rassokha River (Khatanga River basin)	15	72°07′N	101°08′E	KU948963–KU948966
16. Yenisei River *C. autumnalis*	2	66°29′N	87°15′E	KJ767526, KJ767527
17. Yenisei River *C. peled, C. sardinella*	4	66° 29′N	87° 15′E	KX151779-KX151781, JN629025-JN629029
18. Penzhina *C. subautumnalis*	1	64° 54′N	163° 31′E	KX151778
19 Lena River. *C. tugun*	4	61°14′N	128° 36′E	KX151786-KX151789
20. Anadyr river *C. anaulorum*	8	64° 68′N	170°41′E	KX151812-KX151819
21. Teletskoye lake *C. l. pidschian*	2	51° 59′N	87° 65′E	KX171168, KX171169
22. Ob river C. *muksun*	3	-	-	KX151801-KX151803
23.Lena River *C. muksun*	2	-	-	KX151794, KX151795
24. Yenisei River *C. muksun*	1	-	-	KX151796
25. Indigirka River *C. muksun*	3	-	-	KX151798-KX151800
26. Ob river *S. l. nelma*	3	-	-	KX151782-KX151784
27. Anadyr river *S. l. nelma*	1	64° 68′N	170°41′E	KX151785
28. *P. cylindraceum*	1	-	-	NC020764

TABLE 2 Morphological characteristics of *C. l. pidschian jucagiricus* whitefishes from the Indigirka and Kolyma river basins and glacial-plain and East Siberian whitefishes (*C. l. pidschian* n. *brachymystax*) from the Khroma and Lena rivers.

Character	Ichilyakh (*n* = 9)a	Ilirnei (*n* = 10)b	Moma (*n* = 10)c	Kolyma (*n* = 10)d	Suturuokha (*n* = 15)e	Khroma (*n* = 9)f	Buotoma (*n* = 25)g
1	2	3	4	5	6	7	8
ll	82.56±0.78	78.70±0.73	80.20±0.68	80.30±0.70	80.60±0.81	81.11±0.73	80.96±0.78
sp.br.	20.78±0.79	19.03±0.63	18.30±0.40	22.60±0.84	21.13±0.86	20.55±0.47	19.16±0.23

Ichilyakh lakes-Indigirka river basin, river mouth Moma Suturuokha - Indigirka river basin, Ilirnei lake - Kolyma river basin, river mouth Buotoma Lena river basin

TABLE 3 Evolutionary distances between the different populations/forms/species whitefishes of genus *Coregonus* based on Kimura two-parametric model

Whitefishes	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1. *P. cylindraceum*	0															
2.*C. peled*	0.199	0														
3.*C. tugun*	0.205	0.048	0													
4. *C. nasus*	0.197	0.040	0.050	0												
5.*C. muksun*	0.198	0.035	0.040	0.027	0											
6. *C. autumnalis*	0.214	0.052	0.065	0.049	0.044	0										
7. *C. clupeaformis*	0.201	0.033	0.036	0.026	0.019	0.040	0									
8. *S. leucichthys*	0.205	0.062	0.067	0.066	0.053	0.064	0.057	0								
9. C. fluviatilis	0.190	0.035	0.041	0.028	0.016	0.041	0.019	0.049	0							
10. *Coregonus sp.*	0.202	0.038	0.042	0.031	0.025	0.045	0.022	0.057	0.020	0						
11. *C. l. p.* n. *brachymystax*	0.199	0.033	0.040	0.026	0.006	0.044	0.018	0.053	0.016	0.024	0					
12. *C. l. pidschian*	0.197	0.036	0.040	0.026	0.004	0.044	0.019	0.054	0.017	0.025	0.007	0				
13. *C. migratorius*	0.204	0.038	0.039	0.032	0.020	0.044	0.020	0.050	0.014	0.022	0.020	0.021	0			
14. *C. ussuriensis*	0.199	0.050	0.047	0.042	0.031	0.056	0.029	0.065	0.026	0.036	0.031	0.032	0.028	0		
15. *C. chadary*	0.197	0.048	0.046	0.040	0.029	0.056	0.028	0.065	0.025	0.034	0.028	0.030	0.026	0.005	0	
16. *C. anaulorum*	0.189	0.041	0.041	0.037	0.030	0.049	0.028	0.065	0.024	0.034	0.030	0.030	0.030	0.036	0.035	0
17. *C. l. p.* n. *jucagiricus*	0.200	0.038	0.041	0.030	0.008	0.046	0.019	0.054	0.019	0.028	0.006	0.009	0.023	0.032	0.029	0.031

TABLE 4 Pairwise F_{ST} values between the whitefish populations studied based on ND1 gene of mtDNA.

Waterbodies	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1. Kolyma River	0													
2. Ilirnei Lake (M. Anyui River, Kolyma River basin)	0.299	0												
3. Ichilyakh Lake (Indigirka River)	0.300	0.000	0											
4. Moma River (Indigirka River)	0.085	0.067	0.675	0										
5. Suturuokha River (Indigirka River)	0.176	0.549	0.550	0.377	0									
6.Yana River	0.104	0.483	0.484	0.280	0.011	0								
7. Khroma River	0.325	0.747	0.749	0.512	0.263	0.190	0							
8. Omoloi River	0.030	0.429	0.430	0.167	0.185	0.119	0.282	0						
9. Upper Lena River	0.176	0.643	0.644	0.398	0.159	0.154	0.254	0.185	0					
10. Buotoma River (Lena River basin)	0.249	0.703	0.704	0.437	0.254	0.217	0.211	0.211	0.133	0				
11. B. Toko Lake (Aldan River)	0.268	0.764	0.766	0.504	0.298	0.281	0.253	0.254	0.202	0.267	0			
12. Markha River (Vilyuy River)	0.270	0.812	0.814	0.573	0.278	0.274	0.377	0.376	0.254	0.154	0.534	0		
13 .Kureyka River (Yenisei River basin)	0.152	0.719	0.720	0.721	0.089	0.111	0.180	0.180	0.245	0.245	0.279	0.402	0	
14. Khantayskoye Lake (Yenisei River basin)	0.243	0.734	0.736	0.480	0.292	0.275	0.238	0.238	0.217	0.264	0.311	0.503	0.18	0
15. Rassokha River (Khatanga River basin)	0.225	0.664	0.665	0.425	0.262	0.225	0.224	0.223	0.198	0.199	0.328	0.353	0.20	0.10

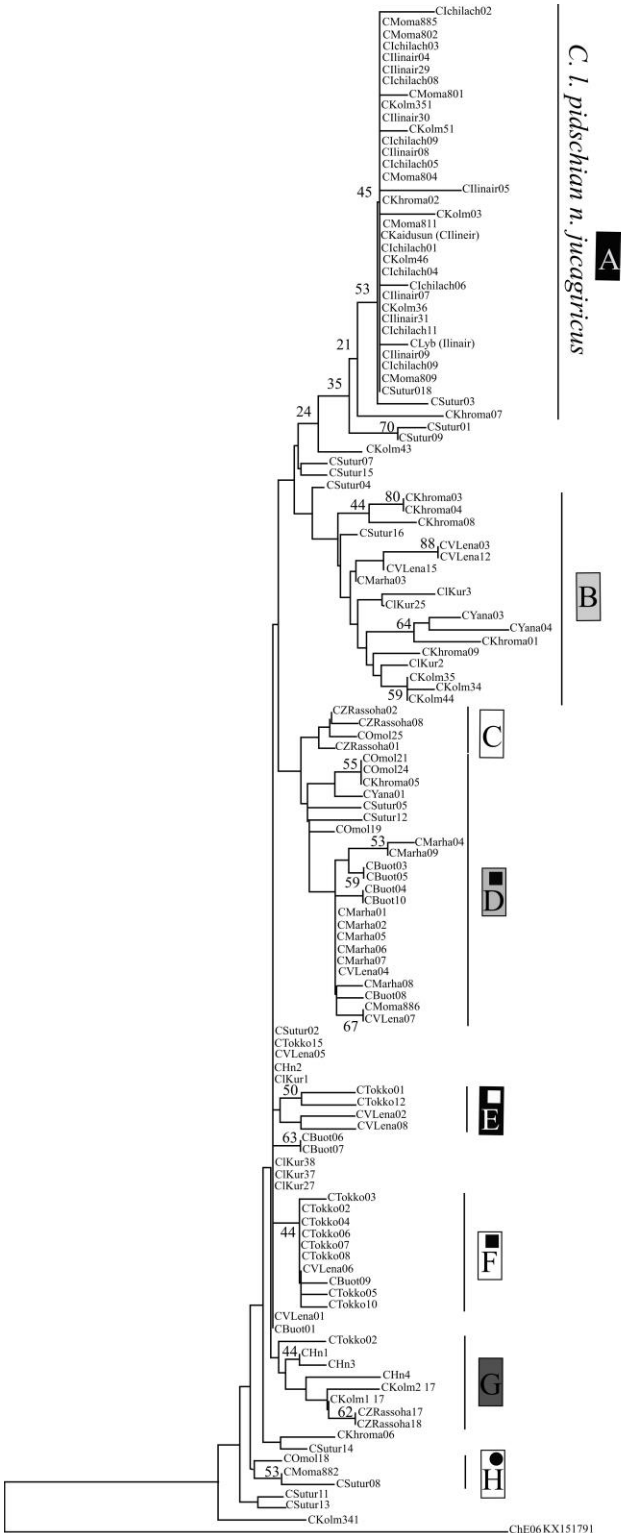
Note*:* 1-5 – *C. l. pidschian n. jucagiricus*; 6-8, 14, 15 – *C. lavaretus pidschian* n. *glacialis*; 9-13 – *C. lavaretus pidschian* n. *brachymystax*

TABLE 5 Neutrality tests for the whitefish populations studied.

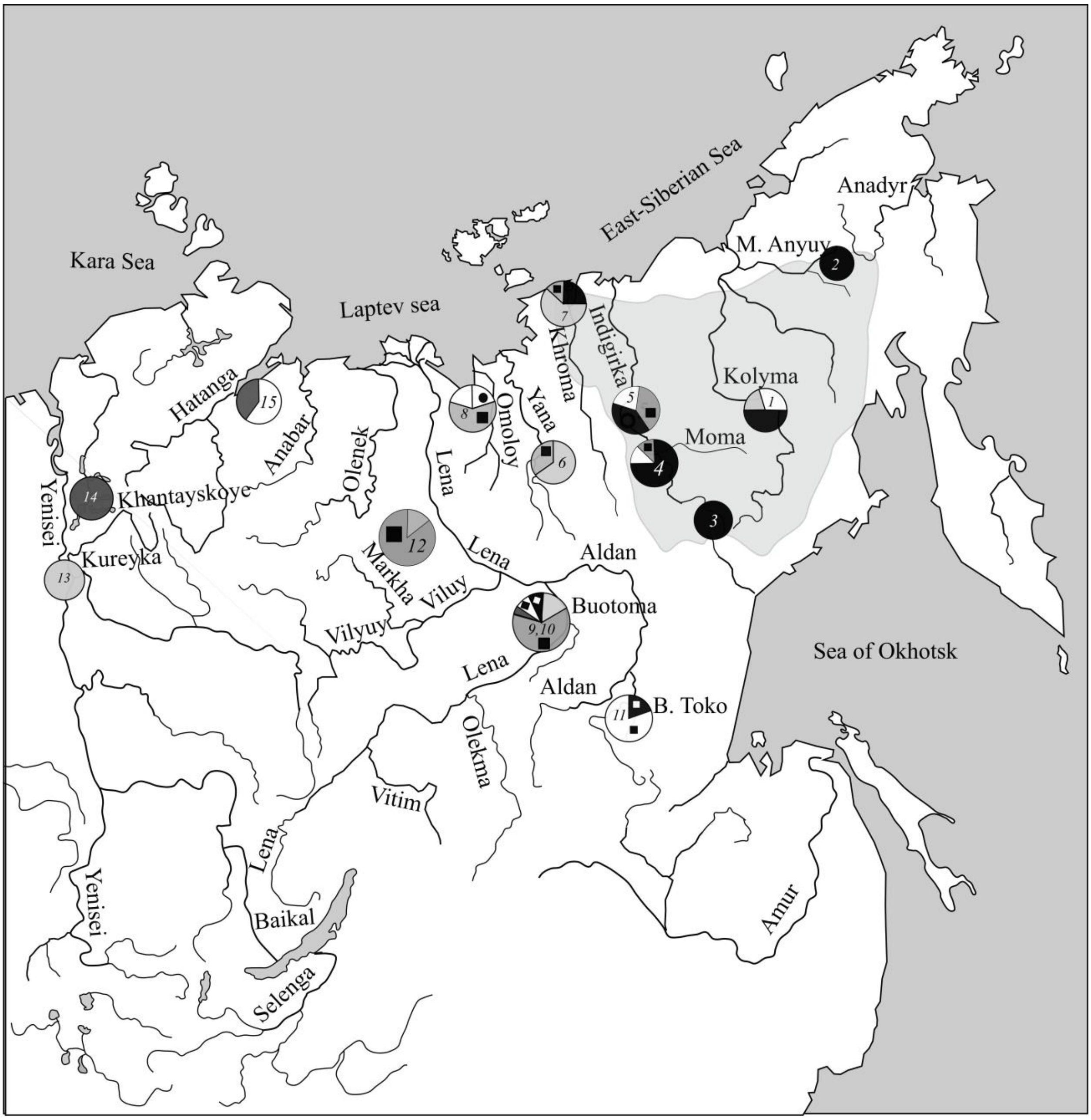
Species/populations/catching areas	*n*	Tajima's *D*	Fu's F_S
1. Kolyma River	12	-0.066	-1.572*
2. Ilirnei Lake (M. Anyui River, Kolyma River basin)	8	-1.447*	1.415
3. Ichilyakh Lake (Indigirka River)	12	-1.746*	-1.489*
4. Moma River (Indigirka River)	8	-0.824	1.153
5. Suturuokha River (Indigirka River)	16	-0.269	-13.309*
6.Yana River	3	–	–
7. Khroma River	9	0.012	-1.974
8. Omoloi River	6	-0.504	0.110
9. Upper Lena River	10	-0.092	-2.515*
10. Buotoma River (Lena basin)	10	-0.127	-1.969
11. B. Toko Lake (Aldan River, Lena River basin)	11	-1.417	-2.818*
12. Markha River (Vilyuy River, Lena River basin)	9	-0.630	-0.976
13. Kureyka River (Yenisei River basin)	7	0.451	0.426
14. Khantayskoye Lake (Yenisei River basin)	4	-0.796	-1.514
15. Rassokha River (Khatanga River basin)	5	0.912	0.051
16. Kolyma River	20	-0.885	0.103
17. Indigirka River	32	-1.065	-9.383*
18.Yenisei River	16	-0.372	-4.227*
19. Only *C. l. pidschian jucagiricus*	35	-2.534*	-6.584*

Note: 1-5 – *C. l. pidschian n. jucagiricus*, 6-8, 14, 15 – *C. l. pidschian* n. *glacialis.* 9-13 – *C. lavaretus pidschian* n. *brachymystax.* 16 – all whitefish haplotypes from the Kolyma River basin; 17 – all whitefish haplotypes from the Indigirka River basin; 18 – all whitefish haplotypes from the Yenisei River basin.

Supplementary



SUPPLEMENT 1 The ML haplotypes network based on mutational differences among 102 *Coregonus lavaretus* composite mtDNA sequences found in Siberian rivers. The designations A-H corresponds to Fig. 4



SUPPLEMENT 2 Geographical distribution of 15 populations of *Coregonus lavaretus pidschian* complex The designations 1-15 corresponds to Fig. 4., and table 1, 3