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Phylogenetic relationships in vendace and least cisco, and their distribution areas in western Eurasia

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I conducted a population-genetic study of the Eurasian cisco complex in an area extending from the Baltic Sea to the East-Siberian Sea using 30 enzyme loci. The results indicate that the least cisco (*Coregonus sardinella*) populations from most rivers of the Kara, Laptev and East-Siberian sea basins are genetically fairly homogeneous, and that the cluster they form is different from the one for the vendace (*C. albula*) populations from the waterbodies of the Baltic and White seas (Nei's genetic distance (D_N) = 0.076). The least cisco and vendace originated from two major phylogenetic lineages of the species occurring as the purest form in the above regions. As a result of the evolution and complex interactions among local populations within the two phylogenetic lineages of cisco at the various stages of Middle and Late Quaternary glaciations, most extant modern populations are hybrid in origin. For example, the Barents Sea populations and the easternmost population from the East-Siberian Sea basin (Kolyma River) emerged as a result of hybridization during the last colonization wave by the least cisco (East Siberian) along the Arctic coast upon cisco's interaction with local ciscoes in the west and east. The White and Kovzhskoye lake populations from the Caspian Sea basin, which form a joint cluster with them, are the hybrids of the local vendace and the descendants of the first wave of least cisco's (West Siberian) expansion to Europe. In this paper, I also discuss the most probable scenarios of cisco's colonization of the study area using paleolimnological reconstructions.

Introduction

Cisco (a species complex including the vendace, *Coregonus albula*, and the least cisco, *Coregonus sardinella*) together with the European whitefish (*Coregonus lavaretus*), are fish species of the Coregonidae family with the widest circumpolar distribution: their distribution area extends from Great Britain's inland waterbodies in the west through northern Eurasia to Bristol Bay and the Yukon, Colvill and McKenzie river basins in North America (Reshetnikov 1980, Kotellat & Freyhof 2007). In this area, cisco displays a great variety of ecological forms and life histories: lacustrine and semi-anadromous populations, autumn- and spring-spawning fish, and large rapidly growing and common small forms that often occur sympatrically. The geographic distribution of cisco with different life histories shows a distinctive pattern: semi-anadromous

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forms predominate in Siberia, while lacustrine populations prevail in Europe. This ecological difference, together with other features, is commonly used to divide cisco into two species: (1) the vendace, *Coregonus albula*, which occurs from Great Britain to the Urals, and (2) the least cisco, *Coregonus sardinella*, which occurs to the east of the Kara River (Nelson 2006, Reshetnikov 2010). The least cisco and vendace can be distinguished using some morphological characters, such as the number of vertebras, the number of scales in the lateral line and the distance from the tip of the snout to the base of the fins. However, these are not rigorous characters used in species diagnostics due to the absence of a hiatus (Berg 1948, Reshetnikov 1980). Some authors (McPhail & Lindsay 1970, Chereshnev *et al.* 2002) identify ciscoes from northeastern Asia and North America as the least cisco, although both lacustrine and semi-anadromous forms of cisco are encountered there.

The systematic status of both nominal species and many ecological groups within them was addressed in early studies, and remains the subject of debate. In Europe, for example, up to nine cisco species are identified within the so-called *Coregonus albula* group; interestingly, *C. albula* and *C. sardinella* are described as individual species (Kotellat & Freyhof 2007). Other authors concluded that morphological differences between the vendace and least cisco are not species-specific (Pokrovsky 1967, Shaposhnikova 1968: 54–67, 1976, Dryagin *et al.* 1969, Behnke 1972, Ustyugov 1972, Solovkina 1974). Obviously, the method used for systematic subdivision depends on the weight of the diagnostic characters chosen and the author's opinion of the 'dividing' and 'combining' concept. Validity of the taxa identified was earlier based mainly on analysis of biological (morphological and ecological) characters, but in the late 20th–early 21st centuries phylogenetic studies were conducted successfully by means of molecular-genetic analysis. For example, Svärdson (1979) provided arguments in favor of the allopatric origin of ciscoes spawning in spring, and used this character to identify the "good species" *C. trybomi*. More recently, Kotellat and Freyhof (2007) described *C. fontanae* and *C. lucinensis* as two more spring-spawning species. However, genetic analyses showed the independent postglacial origin of spring- and autumn-spawning fish in each of the pairs of sympatrically occurring *C. albula* populations (Vuorinen *et al*. 1981, Schulz *et al*. 2006, Delling *et al*. 2014).

To describe a variety of biological and ecological forms of boreal fish species within one systematic scheme, one should understand the interaction of the discrete phylogenetic lineages of complex species in different colonization periods. The solution to this problem has an important applied aspect, since in cisco fishery management in Russian, the typological concept of the species still dominates; thus, in the exploitation, conservation and restoration of populations, genetic diversity and phylogenetic relationships between populations are rarely taken into account. Molecular-genetic methods for the study of the European vendace populations are used to delineate geographic areas where the vendace and/or its major phylogenetic lineages interact (Perelygin 1988, Bodaly *et al.* 1991, 1994, Sendek 1998, Makhrov *et al*. 2003, Borovikova 2009, Borovikova & Makhrov 2012, Gordeyeva *et al*. 2009, Delling *et al*. 2014, Borovikova & Artamonova 2018), to show the degree of introgressive hybridization between them (Sendek 1998, Schulz *et al*. 2006, Borovikova & Makhrov 2012, Borovikova *et al.* 2013) and to prove that the colonization of continental waterbodies was initiated by several colonization waves during glacial and postglacial periods (Sendek 2000, 2002, Borovikova 2009, Gordeyeva *et al*. 2009, Sendek *et al*. 2012, 2013a, 2013b, Borovikova & Makhrov 2012). The genetic studies of the least cisco show that the Siberian and Beringean least cisco evolved through complex interactions of several phylogenetic lineages of this or related species (Ermolenko 1989, 1992, Sendek 2000, 2002, Sendek *et al*. 2013a, 2013b, Padula *et al*. 2017, Borovikova *et al*. 2018). Therefore, the generally accepted view of the systematics and distribution area of *C. albula* and *C. sardinella* should be revised (Sendek *et al*. 2013b).

The aim of this study was to perform population-genetic analysis of the cisco complex occurring within a large area in Eurasia. Genetic data were combined with the results of paleolimnological reconstructions using available evidence

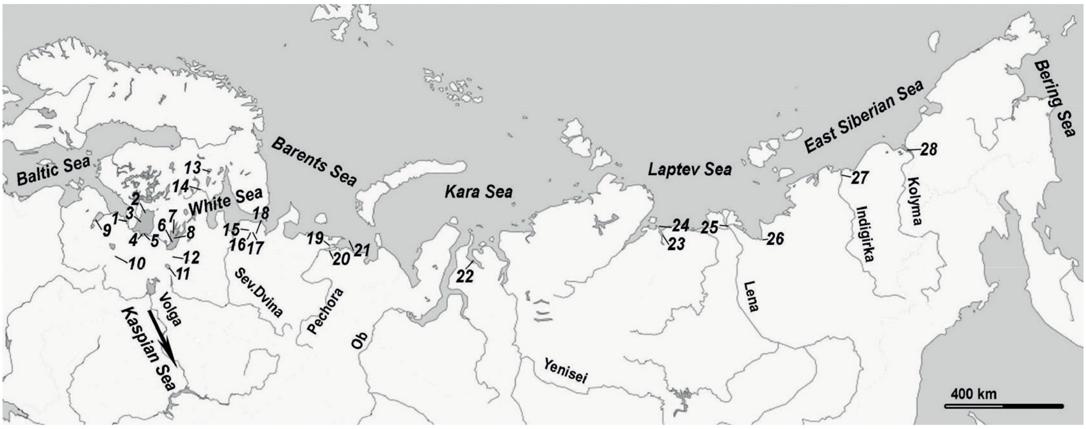

Fig. 1. Sampling sites of the cisco populations. 1 = Neva River mouth (Gulf of Finland of the Baltic Sea); 2 = Skerries (Ladoga Lake); 3 = Konevets Island (Ladoga Lake); 4 = Volkhov Bay (Ladoga Lake); 5 = Volkhov Bay, *ripus* (Ladoga Lake); 6 = Bay of Svir' (Onega Lake); 7 = Trans-Onega Bay (Onega Lake); 8 = Onega proper, *kiletz* (Onega Lake); 9 = Chudskoye Lake; 10 = Vel'ye Lake; 11 = White Lake (Volga River system); 12 = Kovzhskoye Lake (Volga River system); 13 = Pyaozero Lake; 14 = Kuyto Lake; 15 = Volch'ji Lake (Megra River system); 16 = Bolshoye Vostochnoye Lake (Megra River system); 17 = Zapadnye Megorskie Lakes (Megra River system); 18 = Yernozero Lake (Kuloi River system); 19 = Golodnaya Guba Lake, *saurey* (Pechora River system); 20 = Main current, *zeld* (Pechora River system); 21 = Pechora River Bay, *zeld*; 22 = Mongatalyang-yakha mouth; 23 = Suolema River (Anabar River system); 24 = Khorgo Cape; 25 = Lena River; 26 = Omoloy River; 27 = Indigirka River; 28 = Kolyma River. Population numbers correspond to site numbers in Table 1.

for the variability of morphological, ecological and genetic characters in cisco's distribution area. Another aim of this study was to reveal the probable sources of the main phylogenetic lineages of the group and to shed light on major colonization trends and mutual influence (introgressive hybridization) in the past that gave rise to modern populations in western Eurasia.

Materials and methods

I took samples of the north-Eurasian cisco populations ranging from the Baltic Sea drainage basin to the Kolyma River (Fig. 1). A complete list of all sampling sites and sample sizes is given in Table 1. The results also include earlier data (Sendek 2002, 2012, Sendek *et al.* 2012, 2013a, 2013b) on the East-Siberian least cisco population (Kolyma River), East-European vendace populations as well as on various forms of mixed-origin cisco from the Pechora River area. Biochemical data on the allele distribution of several variable loci for the cisco published by other authors (Vuorinen *et al.* 1981, Perelygin 1988, Ermolenko 1989, Bodaly *et al.* 1991, Yakhnenko & Mamontov 2002, Gordeyeva *et al.* 2009, Borovikova & Makhrov 2012) were also used in this analysis.

Muscle and liver samples from each fish were kept frozen before biochemical analysis. Twelve enzyme systems encoded by 30 loci were analysed by polyacrylamide gel electrophoresis. The list of the loci scored, their tissue expression and the buffer systems employed correspond to those reported by Sendek (2002), except for the loci *G3PDH-3** and *mMEP-1,2**. Percentage of polymorphic loci (P, 99% criterion), mean expected heterozygosity (H_{exp}), Nei's (1978) genetic distance (D_{N}) and a chi-square test for comparison of the populations studied by the frequencies of polymorphic loci (homogeneity test) were calculated. The rate of gene flow between pairs of populations was estimated using the fixation index F (Wright 1978). Hierarchical analyses of population differentiation were calculated using the Wright (1978) method. All the calculations were made using the BIOSYS software (Swofford & Selander 1981) and its modified version BIOSYS-2 (Black 1997). The procedures NEIGHBOR and CONSENSE of the PHYLIP3.5C software package (Felsenstein

1993) were used to assess the confidence of the tree topologies constructed from 100 UPGMA trees based on bootstrapped distance matrices. The Waples (1988) method was used to estimate allele frequencies at each of the loci for polymorphic isoloci.

Available literature was used to compile a review of the variability of ciscoes in Eurasia in terms of morphological and genetic characteristics, and the results of the most significant studies are cited below.

Morphological variability in vendace and least cisco

The Siberian least cisco differs from the European vendace by having a greater number of scales in the lateral line (L.l.), and a greater number of vertebrae (Vert.) (Reshetnikov 2010). The number of branched rays in the dorsal (D) and anal (A) fins in the Siberian least cisco is greater than that in European vendace (Pokrovsky 1967). The dorsal and ventral fins in the European vendace are closer to the anterior end of the body than in the European vendace. Therefore, the antedorsal (aD) and anteventral (aV) distances relative to body length (%L) are smaller, and the ventroanal (VA) distance in the Siberian least cisco is greater than that in the European vendace.

Comparative analysis of the morphological characters of the vendace from the lakes of the White–Caspian–Baltic sea watershed shows that these populations are of hybrid origin and are thus similar to the hybrid forms of cisco from the Pechora River basin. The cisco from the studied populations were found to be more similar in

Table 1. Cisco populations surveyed with the number of specimens sampled. The site numbers correspond to population numbers in Fig. 1.

Drainage basin	Gulf/lake/river	Locality (ecological form)	Number of sampled specimens
Baltic Sea	Gulf of Finland	1. Neva River mouth	34
	Lake Ladoga	2. Skerries	50
		3. Konevets Island	50
		4. Volkhov Bay	50
		5. Volkhov Bay (*ripus*)	50
	Lake Onega	6. Bay of Svir’	29
		7. Trans-Onega Bay	29
		8. Onega proper (*kiletz*)	52
	Lake Chudskoye	9. Lake Chudskoye	52
	Lake Ilmen’	10. Lake Vel’ye	39
Kaspian Sea	Volga River	11. Lake White	45
		12. Lake Kovzhskoye	22
White Sea	Kovda River	13. Pyaozero	9
	Kem’ River	14. Lake Kuyto	13
	Megra River	15. Lake Volch’ji	37
		16. Lake Bolshoye Vostochnoye	55
		17. Zapadnye Megorskie lakes	20
	Kuloi River	18. Yernozero	10
Barents Sea	Pechora River	19. Lake Golodnaya Guba (*saurey*)	44
		20. Main current (*zeld*)	216
	Pechora Bay	21. Pechora Bay (*zeld*)	5
Kara Sea	Gydana Bay	22. Mongatalyang-yakha River mouth	12
Laptev Sea	Anabar River	23. Suolema River	14
	Anabar Bay	24. Khorgo Cape	20
	Lena River	25. Lena River	21
	Omoloy River	26. Omoloy River	50
East Siberian Sea	Indigirka River	27. Indigirka River	50
	Kolyma River	28. Kolyma River	50

selected morphological characters to *C. sardinella* which in terms of diagnostic characters (number of vertebrate, antedorsal and ventroanal distances) was similar to *C. albula* (Konovalov & Bolotova 2014). Some scholars assume that geographic variability of cisco morphology from east to west (from the Kolyma River to Sweden's lakes) is due to the fact that the European vendace originated from a Siberian species (Pokrovsky 1967, Konovalov & Bolotova 2014).

According to Kirillov (1972), western populations of the Siberian least cisco from the rivers of the Kara Sea basin differ from the eastern populations (in the area between the Khatanga River and the Kolyma River) by a smaller number of elements in meristic characters, earlier maturation, a shorter life cycle and a smaller size. Therefore, Kirillov (1972) identified two subspecies: typical West-Siberian *C. sardinella sardinella* Valenciennes and East-Siberian *C. sardinella orientalis* Kirillov.

The Yenisei River basin of the Kara Sea is inhabited by two anadromous forms of the Siberian least cisco. Interestingly, the more freshwater Turukhan cisco does not occur in Yenisei Bay whose salinity exceeds 4‰–5‰, while the East-Siberian (Kara) cisco tolerates salinity of up to 27‰. According to Ustyugov (1976), the co-existence of two forms of anadromous cisco in the Yenisei River system means that the Kara Sea basin was colonized by the East-Siberian cisco from the rivers of the Laptev Sea basin and that it was a two-stage process.

Reshetnikov (1975, 1980, 1995) argued that the Siberian least cisco has no well-defined subspecies and that the least cisco from the Amguema River and Chukotka's waterbodies is more similar to North American ciscoes. Later, Chereshnev *et al*. (2002) concluded that the variability pattern of the taxonomic characters of the Siberian least cisco from northeastern Eurasia is fairly high, covering practically the entire spectrum of extreme values known for the species within its distribution area. The Siberian least cisco of some populations (e.g. Chukotka dwarf cisco and some lake cisco populations from the Bering shore and the Anadyr River) deviates towards the European vendace. Chereshnev *et al*. (2002) assumed that some characters of the Chukotka dwarf cisco are similar to those of the European vendace due to convergent similarity caused by slow growth and a lacustrine mode of life.

Cisco's genetic variability

The European vendace from Swedish, Finnish and German waterbodies in the Baltic Sea basin was genetically studied together with the Siberian least cisco from North America and Siberia (Yamal Peninsula) using published data on the latter species. The results showed that cisco populations of various ecological forms occurring in Europe belong to two mitochondrial clades and two microsatellite assemblages being the descendants of the ciscoes from at least two periglacial refugia (Delling *et al*. 2014). The results support the earlier conclusion that mtDNA of the Baltic cisco is paraphyletic relative to the Siberian least cisco from North America (Schulz *et al*. 2006). The Siberian least cisco from Yamal was more similar to two major clades of the European vendace, but was clearly different from the Siberian least cisco from North America. Analysis of AFLP polymorphism, attempted earlier by Mehner *et al*. (2010), suggests that the ecological diversity of vendace in Europe is based on the interaction of its several phylogenetic lineages.

Molecular-genetic studies of the vendace populations from the Baltic, White and Caspian sea watershed revealed some molecular marker characters typical to the Siberian least cisco (Sendek 1998, 2002, Konovalov *et al*. 2002, Makhrov *et al.* 2003, Borovikova *et al*. 2006) that are due to the introgressive hybridization of two nominal species: *Coregonus albula* and *Coregonus sardinella* (Sendek *et al*. 2012, 2013b), although there is another hypothesis regarding their formation (*see* below).

The mtDNA haplotypes characteristic of the European vendace were found by Borovikova (2009) in the Siberian least cisco from Yamal. In a recent study of ciscoes from Sobachye Lake, which is part of the Putoran Plateau in western Siberia, Borovikova *et al*. (2018) showed that this population is very similar in the morphology and polymorphism of mitochondrial DNA to the European vendace from European Russia's waterbodies. They concluded that such phylogenetic relations of the ciscoes are due to the eastward spreading of the European vendace during the last glaciation.

The results of primary sequences of the *nd1* gene analysis revealed the existence of three mtDNA phylogenetic lineages in the European and Siberian cisco populations (Borovikova & Artamonova 2019). If the lineage *ALBP2* has a local distribution in Lake Pleshcheyevo of the Volga river basin, then the other two lineages are wider: the carriers of lineage *S* are found in the largest Siberian rivers, in the Pechora river, in the White Sea basin, and in the Volga river basin; and the haplotypes of lineage *E* are found in the waterbodies of the Kara Sea basin and in numerous European lakes. Borovikova and Artamonova (2019) concluded that *C. albula* and *C. sardinella* are not an independent monophyletic species, and that both nominal species are conspecific. Thus, *C. sardinella* should be considered a regional (Siberian) form of a single Eurasian species *C. albula*, or a subspecies *C. albula sardinella* (Borovikova & Artamonova 2019).

Recent studies on the Siberian least cisco from Alaska show that a great variety of life cycles and ecological characteristics of the species in this region is due to a great genetic diversity (68 mitochondrial haplotypes were identified in 305 fishes collected from nine localities in three areas), but this variation is not distributed in a uniform manner across all regions and all haplotype groups (Padula *et al*. 2017). North American *C. sardinella* displays a more homogeneous younger radiation than European *C. albula* (Schulz *et al*. 2006, Delling *et al.* 2014). Curiously, the European vendace — not differing clearly from the analyzed Siberian least cisco populations — was used as an out-group for constructing an ML tree on a dendrogram.

The population-genetic study of ciscoes from a large area shows their considerable genetic heterogeneity in allozyme markers. The variability pattern of the marker alleles of diagnostic loci shows a minimum difference from the farthest eastern European population (Pechora River), and the outermost eastern population of eastern Siberia (Kolyma River). The results obtained suggest that in the central part of North Eurasia's old, typically freshwater cisco fauna — still existing in the purest form in the sub-Arctic along the margins of its distribution area — was more recently largely replaced by *C. sardinella* colonizers from southern and central Siberia (Sendek *et al.* 2013b).

Comparison of the so-called Baunt cisco from Trans-Baikal Lake Baunt with the closest Siberian least cisco population from the Lena River shows that genetic distances between them in allozyme loci are consistent with the differentiation of the subspecies level in other fishes of the Coregonidae family (Yakhnenko & Mamontov 2002). Phylogenetic analysis of the Baunt cisco revealed that in spite of relative morphological homogeneity, the genotypes of the population exhibit two phylogenetic lineages of mtDNA; interestingly, both belong to whitefish rather than cisco lineages (Bochkarev *et al*. 2013). One of the main hypothesis for the formation of the Baunt cisco is hybridization of Siberian whitefish, pidschian, with an unknown ancestor, probably ancient cisco.

Results

The following eight loci in studied material were monomorphic: *GPI-B2**, *sIDHP-3**, *LDH-A2**, *LDH-B1**, *MDH-A2**, *MDH-B2**, *sMEP-3**, *PGDH**. Ciscoes in the study area are characterized by a high proportion of polymorphic loci demonstrating significant ($p < 0.001$ unless indicated differently) differences in the allele frequencies (20 of 22): *AAT-1**, *AAT-2**, *CK-A1**, *CK-A2**, *ESTD**, *G3PDH-1**, *G3PDH-2**, *GPI-A1**, *GPI-A2** ($p < 0.05$), *GPI-B1**, *IDDH-1**, *IDDH-2**, *sIDHP-4**, *LDH-B1** ($p < 0.05$), *MDH-A1**, *MDH-B1** ($p < 0.05$), *sMEP-4**, *PGM-3**, *PGM-4**, *mSOD**, *sSOD**.

I found the highest genetic variability of all the cisco samples for a Siberian least cisco population from the Kolyma River ($P = 53.3$, $H_e = 0.140$), and a vendace population from Kovzhskoye Lake ($P = 43.3$, $H_e = 0.168$). Also the values for the population of the Siberian least cisco from the Lena River ($P = 50.0$, $H_e = 0.115$), and two ecological forms of ciscoes from the Pechora River (*saurey*: $P = 43.3$, $H_e = 0.156$; *zeld*: $P = 50.0$, $H_e = 0.123$) were high (*see* Appendix). A considerable portion of inter-population gene diversity within the total gene diversity in the ciscoes was due to differences among populations from different marine basins (21.0%), and the intra-specific component (72.1%) (Table 2).

Interpopulation comparisons made for the European vendace showed small genetic differences among populations in the Baltic Sea (mean D_N = 0.005) and White Sea basins (mean D_N = 0.013), and substantial among populations in the Caspian Sea basin (D_N = 0.037) (Table 3). Genetic differences among six out of seven Siberian least cisco samples from the Kara, Laptev and East-Siberian sea basins were small: $0 < D_N < 0.015$. The easternmost Siberian least cisco sample from the Kolyma River was genetically most similar to three cisco samples from the Barents Sea basin ($0.008 < D_N < 0.011$). On an UPGMA dendrogram, they all lie between typical European vendace and Siberian least cisco clusters. The European vendace samples from White and Kovzhskoye lakes (Caspian Sea basin) were similar to those from the Barents Sea basin but were different from other samples in the cluster (Fig. 2). However, the position of the branches was not supported by high bootstrap values.

The allele *CK-A1.2*d* was revealed in one of two duplicated loci in the semi-diadromous Siberian least cisco populations from the largest Siberian rivers Ob, Yenisei, Lena and Indigirka, but it did not occur in most lacustrine landlocked European vendace populations from the Baltic and White sea basins. However, a marker allele was widespread in the hybrid forms of two cisco species from the Pechora River basin and in some other populations occurring as far as the Baltic, White, Caspian sea watershed (Sendek 1998, Konovalov *et al*. 2002, Makhrov *et al*. 2003, Borovikova *et al*. 2006). The gen-

Table 2. Distribution of gene diversity among the studied cisco populations.

Levels of hierarchy	Relative gene diversity (%)
Among sea basins*	21.0
Among large waterbodies within sea basins	3.5
Among localities within large waterbodies (or within sympatric populations**)	3.4
Within samples	72.1

* Sea basins (number of populations studied): Baltic (10), Caspian (2), White (6), Barents (3), Kara (1), Laptev (4), East Siberian (2).
** Sympatric pairs of populations were scored for Lake Ladoga, Lake Onega, Pechora River, Anabar River.

Table 3. Nei's genetic distance (D_N, range in parentheses) among the cisco populations from different basins.

Sea basin	Population number	Baltic	Caspian	White	Barents	Kara	Laptev	East Siberian
Baltic	10	0.005 (0.000–0.012)						
Caspian	2	0.058 (0.034–0.085)	0.037 (0.037–0.037)					
White	6	0.012 (0.000–0.038)	0.062 (0.028–0.103)	0.013 (0.001–0.030)				
Barents	3	0.052 (0.040–0.062)	0.024 (0.017–0.034)	0.053 (0.038–0.078)	0.004 (0.000–0.007)			
Kara	1	0.107 (0.099–0.118)	0.069 (0.065–0.073)	0.100 (0.088–0.117)	0.032 (0.030–0.034)	–		
Laptev	4	0.098 (0.081–0.119)	0.065 (0.053–0.071)	0.095 (0.077–0.117)	0.030 (0.023–0.041)	0.011 (0.007–0.015)	0.007 (0.000–0.012)	
East Siberian	2	0.072 (0.057–0.093)	0.048 (0.035–0.063)	0.071 (0.049–0.096)	0.017 (0.008–0.026)	0.021 (0.010–0.033)	0.015 (0.001–0.030)	0.015 (0.015–0.015)

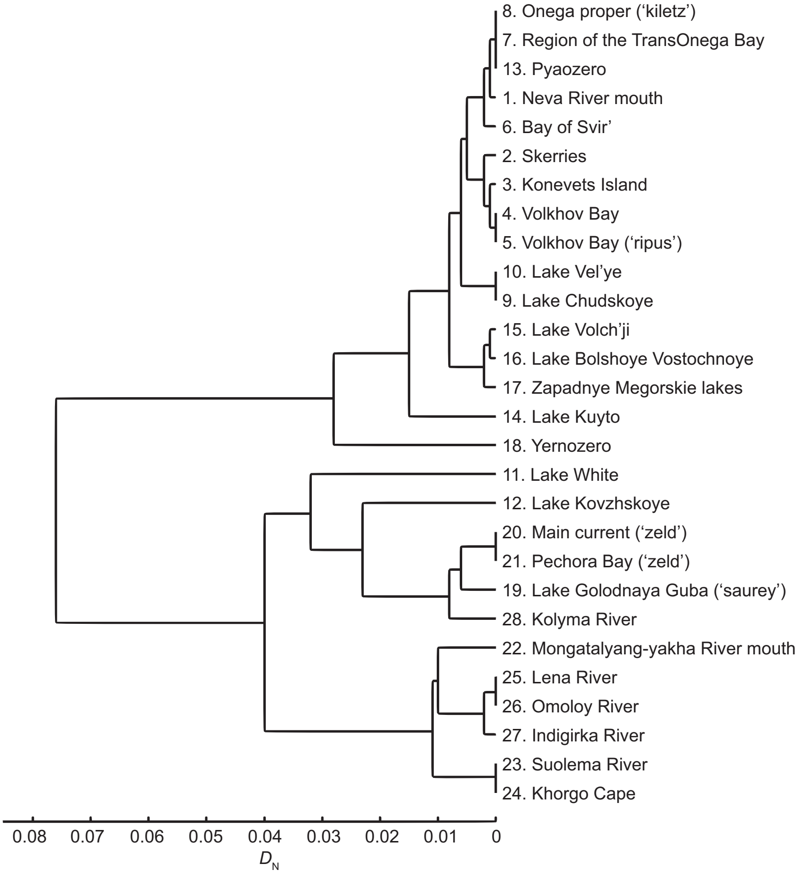

Fig. 2. UPGMA dendrogram of unbiased genetic distances for the studied cisco populations. All bootstrap values < 50%. D_N = Nei's genetic distance.

otypes of cisco from Lake Kovzhskoye with a high frequency ($p = 0.41$) contained the allele *CK-A1.2*c*, widespread in some of Siberia's fishes of the Coregonus family and reported earlier as a minor allele in a few European vendace populations from the Baltic Sea basin (Vuorinen *et al*. 1981, Perelygin 1988).

The population variability in both cisco species for the duplicated loci of iditol dehydrogenase *IDDH-1.2** was due to the presence of three major alleles: *a**, *c** and *d** in their genotypes. Geographically, three alleles with relatively high frequencies (commonly $p > 0.1$) were present in all the studied cisco populations of both nominal species except in the three European vendace populations from the White Sea-Kuloi Plateau, which is part of the Megra River basin (Volch'ji Lake, Bolshoye Vostochnoye Lake, Zapadnye Megorskie Lake). These populations contain only two alleles: *a** and *c** (Sendek *et al*. 2012) which were fixed for alternative alleles (Appendix).

Discussion

Comparison of the European vendace from the Baltic and White sea basins with most of the Siberian least cisco populations from the Kara, Laptev and East-Siberian sea basins shows genetic differentiation, $D_N = 0.076$. Large-sized forms of the European vendace from Ladoga (*ripus*) and Onega (*kiletz*) lakes showed no signs of genetic isolation from the European vendace of normal size. The genetic divergence revealed by inter-basin comparison increased to 21.0% since more populations of the least cisco from the Kara, Laptev and East-Siberian sea basins were assessed, as compared with 11.2%, when the only Siberian least cisco sample from the Kolyma River was analyzed (Sendek *et al*. 2013b). Ciscoes from the Caspian and Barents sea basins form a loose branch on the dendrogram which lies between two major clusters formed by *C. albula* and *C. sardinella*. Both cisco species have similar allele variants in most of the loci analyzed. The distribution of individual marker genes may become most informative when reconstructing cisco colonization events.

The clinal variability in the distribution of the locus alleles *CK-A1.2** revealed in this study also occurs in northeastern Eurasia: allele *CK-A1,2*d* frequency decreases gradually from west to east from the Lena River to the Indigirka River (Sendek *et al.* 2013a); in the Kolyma and Chaun river populations, it becomes practically equal to the frequency of the same allele in the Pechora River, and in the easternmost cisco population from the Anadyr River, and in Alaska only the alleles *CK-A1.2*a* and *CK-A1.2*b*, characteristic of the European vendace, occur (Sendek *et al.* 2013b). The genotypes of practically all European vendace populations from the Baltic and White sea basins are dominated by the allele *CK-A1.2*a*, but the populations studied from the Barents and Caspian sea are dominated by the allele *CK-A1.2*b*, which is widespread in the Siberian least cisco populations.

It should be noted that the homozygous condition of the loci *IDDH-1.2** with alleles *a** and *c** revealed in cisco populations of the waterbodies of the Megra River basin predominates (or is the only one) for most *Coregonus* species. In other words, it seems to be an ancestral (basal) variant in the Coregonidae family. In addition, these three cisco populations typically display the lowest genetic variability values of all the cisco populations analyzed, as indicated by their polymorphism and the average expected heterozygosity index.

In view of the latest paleolimnological reconstructions (Mangerud *et al.* 1998, 2004, Svendsen *et al.* 1999, 2004, Astakhov 2004, Hughes *et al.* 2016, Panin *et al.* 2020), the most probable sequence of events in cisco colonization is as follows. Eurasian glacial shields reached a maximum distribution during the Late Saalian glaciation (160–130 thousand years ago). At that time some of the glacier petals in Europe reached 50°N, while the ice margin in western Siberia extended about 1400 km south of the Arctic shoreline. The glaciation boundaries nearly coincided with the approximate maximum boundaries of earlier Quaternary glaciations. The glacier destroyed the entire freshwater fauna that existed in the periarctic regions of Europe and western Siberia prior to its advance. After the Late Saalian glacier retreat, ice-free areas were flooded by sea water during the Eemian Interglacial (Svendsen *et al.* 2004), thus preventing recolonization by freshwater fauna. Thus, cisco and other fish could survive only along the margin of the Late Saalian glaciations and later in inland freshwater bodies located at the periphery of marine transgression waters. Geological maps of those glaciations show that such a waterbody in Europe could exist to the south of the British Isles, i.e. to the west of the European vendace's main distribution area. In eastern Europe, unaffected by Saalian glaciation, only areas in the upper reaches of the Pechora River near the Pechora–Kama watershed and Volga River (both Caspian Sea basin) could remain (Fig. 3A).

After the Late Saalian glaciations and the Eemian Interglacial transgression, typical lake vendace occurring in eastern Europe since pre-Late Quaternary glaciations could survive in local populations near the Barents–Caspian sea watershed. During the Early Weichselian glaciation (90–80 ka), this vendace migrated through the Pechora and Severnaya Dvina rivers into large periglacial lakes that existed in the Pechora Lowland and into the White Sea basin. There was a common runoff from Lake Komi and its extension into the White Sea hollow and the Baltic Sea basin through which vendace migrated to western Europe. This colonization could be the first wave of the westward spreading of the species, unless the autochthonous lineage of vendace continued to exist at that time in western Europe (Fig. 3A).

The populations of this phylogenetic lineage and/or its derivatives could survive in local waterbodies after the emptying of the periglacial lake followed by glacier retreat and the formation of runoff into the ocean. Modeling suggests that huge periglacial lakes were emptied within several months to two years (Mangerud *et al.* 2004). Radical changes in the volumes of periglacial lakes during a short time span contributed to the rapid evolution of the populations that survived due to a considerable decrease in their abundance and changes in their habitat.

At the time of the Early Weichselian glaciations, there was a large periglacial water-

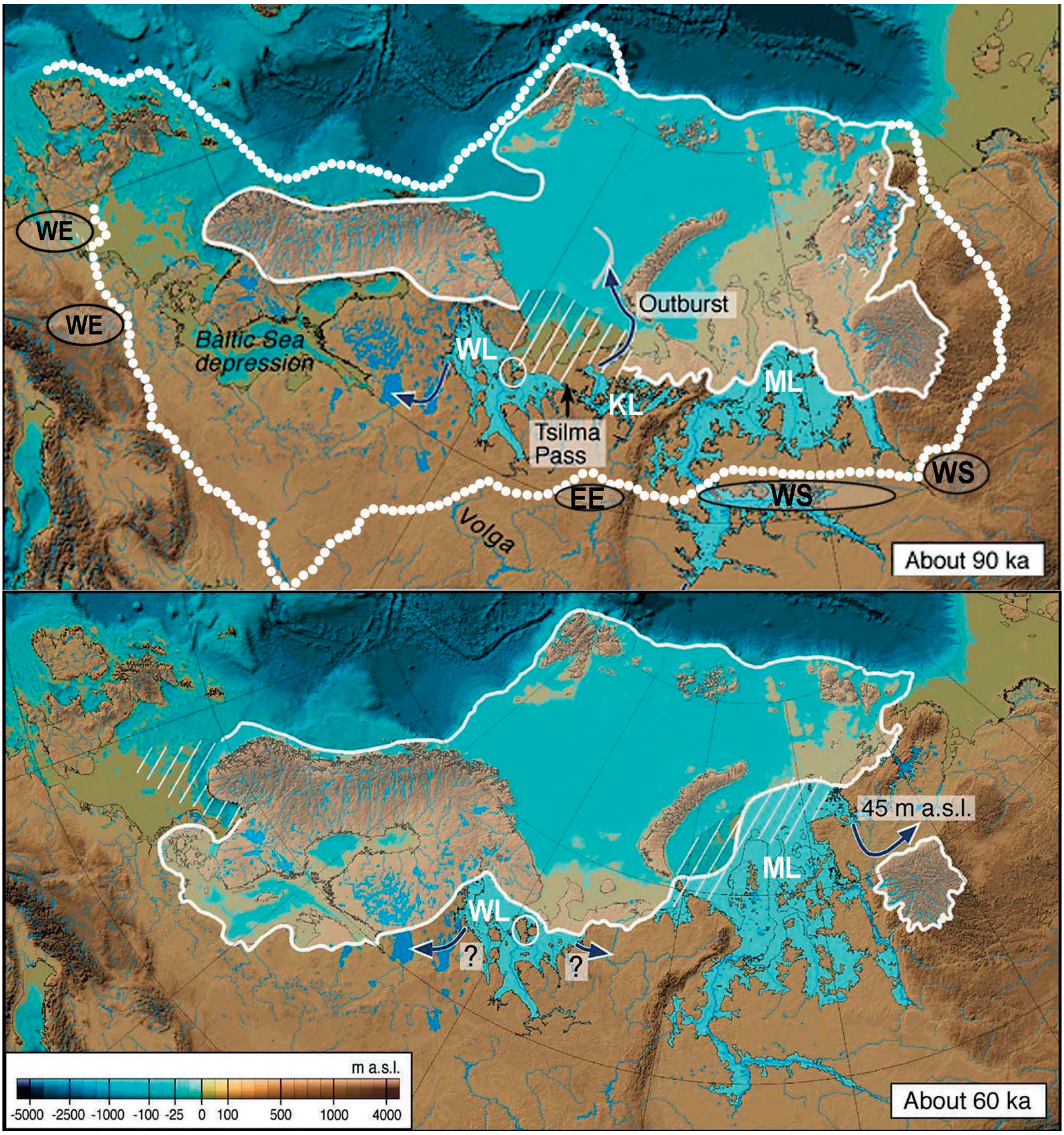

Fig. 3. Reconstructions of ice-dammed lakes and rerouting of rivers during (**A**) the Early Weichselian and (**B**) the Middle Weichselian (after Mangerud *et al*. 2004). Ice margins are shown with solid white lines. In the hatched areas, positions of ice margins are unknown. Arrows show assumed outlet paths. Sea level was lower by 50 m during the Early Weichselian, and 60 m during the Middle Weichselian (from Mangerud *et al*. 2004). The dotted white line shows the Late Saalian glaciation (> 140 ka) (from Svendsen *et al*. 2004). The abbreviations WE, EE, WS indicate the assumed position of freshwater refugia during the Saalian glaciation in western Europe, eastern Europe and Western Siberia, respectively. Abbreviations: ML = West Siberian Mansi Lake, KL = Komi Lake of Pechora lowland, WL = White Sea Lake. The white oval shows the area of the lakes of the Megra river system, not affected by the Lower Pleistocene glaciation. Reproduced with permission from the copyright owner.

body in western Siberia (Mansi Lake). Its water flowed southwards into the Aral and Caspian seas. West-Siberian glacial lake and Komi glacial lakes were separated from each other by the Uralian Ridge, so that there was no direct contact between their aquatic faunas at that time (Fig. 3B). The cisco of hybrid origin was widespread in the West-Siberian periglacial lake. The hybrid cisco resulted from the first westward migration wave of the typical East-Siberian least cisco in pre-Lower Quaternary time (Ustyugov 1976). Recurrent Middle Quaternary glaciations and marine transgressions (probably even earlier transgressions, as indicated by the occurrence of marine deposits in the middle reaches of the Yenisei River (Svendsen *et al*. 2004)) made the cisco migrate upstream along West Siberia's river valleys. As a result, its spawning grounds in the Yenisei River and current feeding and growing grounds were spaced 1550–1970 km apart (Podlesny & Sesyagin 1966). This form, known now as 'Turukhan cisco', combines the characters of both the European vendace and Siberian least cisco. The West-Siberian periglacial lake was probably inhabited sympatrically with Turukhan cisco by a local lacustrine form of European vendace, because extensive areas in the southern West-Siberian Plain with potential water refugia for cisco were not affected by Quaternary glaciations and marine transgressions (Fig. 3A). The West-Siberian least cisco populations with the morphological and genetic characters of the European vendace in some waterbodies on the Putoran Plateau (Borovikova *et al*. 2018) and the Norilsk–Pyasina lake-river system (Nikulina & Borovikova 2018) probably originated from the autochthonous form of cisco that existed before the Saalian glaciations. The old origin of the West-Siberian lake cisco populations is indirectly indicated by the presence of an unusual European whitefish, *C. lavaretus*, which occurred together with cisco and was identified earlier as a form/natio. For example, described for the Norilo-Pyasina lake system were *mogchegor* whitefish *C. lavaretus pidschian* n. *mokschegor*, *khenyu* whitefish *C. lavaretus pidschian* n. *ajakliensis* and lacustrine Norilsk whitefish *C. lavaretus pidschian* n. *norilensis* (Ostroumov 1937, Mikhin 1955). Such a great variety of whitefish forms is characteristic of European waterbodies but is not typical of Siberia, where Siberian pidschian predominates over a larger area (Reshetnikov 1980).

Exchange of the phylogenetic lineages of ciscoes on both sides of the Ural Mountains took place later during the Middle Weichselian glaciation 60–50 ka. There was a periglacial lake in the White Sea basin at that time. Its water flowed most probably to the Pechora Lowland via the Timan Pass. The area between the Pechora River mouth and the strait which separates the Barents Sea from the Kara Sea at some stage was a bay of the West-Siberian periglacial lake into which European lake vendace migrated with water runoff from the White Sea basin, while the anadromous Turukhan least cisco migrated in the opposite direction (Fig. 3B). I assume that the colonization of eastern Europe by the West-Siberian (Turukhan) cisco can be traced using morphological and genetic markers in some lake populations near the White–Baltic–Caspian sea watershed. Both evolutionary lineages present at that time in the White Sea basin (the descendants of local European vendace and new colonizers (Turukhan cisco) which came from the east) could later spread to Europe as far as the western boundary of the modern European vendace's distribution area.

My data suggest that as the lake level during the Middle Weichselian glaciations was lower than that during the Early Weichselian glaciations (Mangerud *et al*. 2004), some of the populations from the first wave of expansion survived in pure form in landlocked waterbodies located at the highest altitudes above sea level. I assume that the cisco populations from the lakes of the Megra River basin — located at an altitude of over 70 m a.s.l. and unaffected by the most vigorous Late Weichselian sheeted glaciation of Europe — are the descendants of (one of the lineages and probably the first lineage) colonizers of this species in Europe. My assumption is supported by low genetic variability indices in the populations from this river system and the aforementioned homozygous condition for the loci *IDDH-1.2**, which is fairly variable in other cisco populations. An indirect argument in favor of the historical isolation of the lakes in the Megra River system located high above sea level is provided by the fact that two of the lakes are inhabited by a whitefish form with a large number of gill rakers (grn > 51) very uncommon in whitefish from this region (Sendek *et al*. 2012).

The East-Siberian least cisco could migrate again to western Siberia through the Khatanga River or along the Arctic coast at the late stages of the Middle Weichselian glaciation. The current distribution of the East-Siberian cisco in Western Siberia is limited by the sea coast (the Shchuchya River in the Ob River basin, the Messo River in Tazov Bay and the Yuribei River in Gydana Bay). I assume, therefore, that the East-Siberian cisco colonized the region during emptying of the West-Siberian periglacial lake during the stage of marine regression. Presently flooded West-Siberian (Pyasina, Yenisei, Pur and Ob) and East-Siberian (Pechora) river valleys were close to each other during the marine regression stage, thus contributing to freshwater faunal exchange on both sides of the Ural Mountains. At later transgression stages, generatively freshwater fishes had to migrate upstream along river channels seeking suitable spawning grounds. For example, the spawning grounds of most Pechora River fishes of the Coregonidae family are now located in the Usa River, which flowed independently into the sea prior to the isostatic land uplift. The spawning grounds are at a distance of about 300 km from the present sea coast, which corresponds roughly to the distribution altitude of the zone affected by the Middle Weichselian marine transgression 40–20 ka (Svendsen *et al*. 2004). I believe that it is at that time that stable originally Siberian fish (peled *C. peled* Gmelin, broad whitefish *C. nasus* Pallas, Arctic cisco *C. autumnalis* Pallas and inconnu *Stenodus leucichthys* Güldenstadt) populations in the Pechora River formed. The East-Siberian cisco and pidschian migrated together with typical Siberian fish of the Coregonidae family as far as the Trans-Ural region and were hybridized with the evolutionary lineages of both species established earlier in eastern Europe. As a result, two anadromous forms of cisco formed in the Pechora River (Sendek 2002). It seems that the origin of local populations of least cisco in western Siberia is also related to the Middle Weichselian boreal transgression, because the feeding and growing grounds, as well as breeding areas, of East-Siberian least cisco in the rivers of the Kara Sea basin are spaced 30–400 km apart.

It appears that the East-Siberian least cisco in Europe could not spread or spread to a limited degree westwards of the Pechora, while the morphological and genetic signs of West-Siberian least cisco's westward spreading occur as far as the Baltic–White–Caspian sea watershed. To the west of the watershed, modern populations of this species were dominated by the local lineages of the European vendace that evolved in the Baltic Sea basin. Hence, the influence of the West-Siberian least cisco in western Europe was not practically seen at the morphological level, but may be indicated by the presence of characteristic mtDNA markers in genotypes (Schulz *et al*. 2006).

Thus, the interaction of the various evolutionary lineages of cisco upon the colonization of Europe is complex. The main stages of colonization are related to the Late Quaternary glaciations stages, and I can trace them approximately based on the occurrence of morphological, ecological and genetic characters in recent populations. The Siberian least cisco spread to Europe in two waves at the different stages of the Middle Weichselian glaciations. The first wave was related to the colonization of the West-Siberian (Turukhan) cisco, and the second one to the widening of East-Siberian cisco's distribution area. Anadromous Turukhan cisco from the Yenisei River resulted from hybridization of the first wave of East-Siberian cisco's expanding into the Kara Sea basin and cisco from western Siberia, which is equivalent to the phylogenetic lineage of the European vandace. European vendace's distribution area in Europe expanded owing to the contribution of the local lineage of cisco after the Saalian glaciation, when periglacial lakes produced by Early Weichselian glaciations existed. This lineage spread westwards, where it could contact European vendace from the West European refugium. The same lineage could penetrate into the Kara Sea basin with runoff from a periglacial lake that formed during the Middle Weichselian glaciation. Environmental conditions and fish abundances in different glaciations phases varied considerably, and the colonization stages of discrete cisco lineages were separated by long periods of time. This evidence suggests that the formation of modern cisco populations is based on the introgressive hybridization of several phylogenetic lineages; the main lineages are consistent with the nominal species *Coregonus albula* and *Coregonus sardinella*. European vendace may display up to three large internal lineages consistent with ancestral populations from western Europe, eastern Europe and western Siberia prior to the Saalian glaciation. The evolution of the Turukhan cisco is based on the old hybridization of two nominal cisco species that gave rise to new biological qualities. This suggests that the phylogenetic lineage of least cisco exists as two internal lineages equivalent to the East-Siberian and West-Siberian ciscoes.

I assume that interspecific hybridization in the formation and evolution of individual phylogenetic lineages of cisco, as well as geographic isolation, could play an important role. For example, the genetic differentiation of *S* and *E* haplotype clusters of two widespread phylogenetic lineages of cisco was up to 1.1%, however, the differentiation between the *ALBP2* lineage haplotypes and the variants of *E* lineage was 2.8%, while the genetic distance between cluster *E* haplotypes and the haplotypes of *C. lavaretus* was 3.5% (Borovikova & Artamonova 2019). It can thus be suggested that the *ALBP2* lineage of cisco in the Volga basin was produced by the hybridization of a local cisco population with an ancient form of whitefish. This scenario seems probable because in southern Siberia there exists a so-called Baunt cisco with mtDNA represented by two lineages of whitefish mtDNA (Bochkarev *et al*. 2013), which indirectly implies that the phylogenetic lineages of the least cisco were probably formed by the introgressive hybridization of ancient lacustrine cisco with semi-anadromous whitefish.

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References

Astakhov, V. I. 2004: Middle Pleistocene glaciation of the Russian north. — *Quaternary Science Reviews* 23: 1285–1311.

Behnke, R. J. 1972: The systematics of salmonid fishes of recently glaciated lakes. — *Journal of the Fisheries Research Board of Canada* 29: 639–671.

Berg, L. S. [Берг, Л. С.] 1948: [*Freshwater fishes of the USSR and the contiguous land*]. — Zool. Inst., Acad. Nauk SSSR, Moscow. [In Russian].

Black, W. C. VI 1997: *BIOSYS-2. A computer program for the analysis of allelic variation in genetics*. — Department of Microbiology, Colorado State University.

Bochkarev, N. A., Zuykova, E. I., Abramov, S. A., Katokhin, A. V., Matveev, A. N., Samusenok, V. P., Baldina, S. N., Gordon, N. Yu. & Politov, D. V. 2013: Morphological, ecological and mtDNA sequence variation in coregonid fish from the Baunt Lake system (the Vitim River basin). — *Advances in Limnology* 64: 257–277.

Bodaly, R. A., Vuorinen, J., Ward, M., Luczynski, M. & Reist, J. D. 1991: Genetic comparisons of New and Old World coregonid fishes. — *Journal of Fish Biology* 38: 37–51.

Bodaly, R. A., Vuorinen, J. A., Reshetnikov, Yu. S. & Reist, J. D. 1994: Genetic relationships between five species of coregonid species from Siberia. — *Journal of Ichthyology* 34: 117–130.

Borovikova, E. A. 2009: Phylogeography of the ciscoes *Coregonus albula* (L.) and *C. sardinella* Valenciennes in European North of Russia. — Ph.D. thesis, RUDN University, Moscow. [In Russian with English summary].

Borovikova, E. A., Alekseeva, Ya. I., Schreider, M. J., Artamonova, V. S. & Makhrov, A. A. 2013: Morphology and genetics of the ciscoes (Actinopterygii: Salmoniformes: Salmonidae: Coregoninae: *Coregonus*) from the Solovetsky Archipelago (White Sea) as a key to determination of the taxonomic position of ciscoes in Northeastern Europe. — *Acta Ichthyologica et Piscatoria* 43: 183–194.

Borovikova, E. A. & Artamonova, V. S. 2018: Morphological specificities of vendace (Salmoniformes: Salmonidae: Coregoninae: *Coregonus albula*) population in Lake Pleshcheyevo (the Volga River basin): relationships of two phylogenetic lineages in a new zone of secondary contact. — *Organism Diversity and Evolution* 18: 355–366.

Borovikova, E. A. & Artamonova, V. S. 2019: *Vendace (Coregonus albula) and least cisco (Coregonus sardinella) are conspecific according to data of mitochondrial and nuclear DNA polymorphism*. — Front. Mar. Sci. Conference Abstract: XVI European Congress of Ichthyology, https://doi.org/10.3389/conf.fmars.2019.07.00101.

Borovikova, E. A., Baldina, S. N., Gordon, N. Yu., Makhrov, A. A. & Politov, D. V. [Боровикова, Е. А., Балдина С. Н., Гордон, Н. Ю., Махров, А. А. & Политов, Д. В.] 2006: [Genetic diversity, morphological features and origin of vendace (*Coregonus*) of Vodlozero]. — *Vodlozerskie Chteniya*: 69–74. [In Russian].

Borovikova, E. A. & Makhrov, A. A. 2012: Study of the populations of the transition zone between European and Siberian cisco (*Coregonus*): the role of habitat in speciation. — *Printsipy Ekologii* 1, 4(4): 5–20. [In Russian with English abstract].

Borovikova, E. A., Romanov, V. I. & Nikulina, J. S. 2018: Morphological and genetic features of cisco (Coregonidae: *Coregonus* sp.) from Lake Sobachye (Putorana Plateau). — *Russian Journal of Genetics: Applied Research* 1: 37–43.

Chereshnev, I. A., Volobuev, V. V., Shestakov, A. V. & Frolov, S. V. [Черешнев, И. А., Волобуев, В. В., Шестаков, А. В. & Фролов, С. В.] 2002: [*Salmonid fishes in Russian North-East*]. — Dalnauka, Vladivostok. [In Russian].

Delling, B., Palm, S., Palkopoulou, E. & Prestegaard, T. 2014: Genetic signs of multiple colonization events in Baltic ciscoes with radiation into sympatric spring- and autumn-spawners confined to early postglacial arrival. — *Ecology and Evolution* 4: 4346–4360.

Dryagin, P. A., Pirozhnikov, P. L. & Pokrovsky, V. V. [Дрягин, П. А., Пирожников, П. Л. & Покровский, В. В.] 1969: [Polymorphism of coregonid fish (Coregonidae) and its biological and fishery significance]. — *Voprosy Ikhtiologii* 9: 14–25. [In Russian].

Ermolenko, L. N. [Ермоленко, Л. Н.] 1989: [*Genetic variability of some enzymatic and non-enzymatic proteins of coregonid fishes of Northeast Asia*]. — Ph.D. thesis, University of Leningrad. [In Russian].

Ermolenko, L. N. 1992: Genetic divergence in the family Coregonidae. — *Polish Archives of Hydrobiology* 39: 533–539.

Felsenstein, J. 1997: *PHYLIP (Phylogeny Inference Package) version 3.5c.* — Department of Genetics, University of Washington, Seattle, WA.

Gordeeva, N. V., Kholod, O. N., Dvoryankin, G. A., Sendek, D. S. & Sterligova, O. P. 2009: On the origin of Solovetskaya vendace *Coregonus albula* and of the Syamozero smelt *Osmerus eperlanus*. — *Journal of Ichthyology* 49, 23, https://doi.org/10.1134/S0032945209010032.

Hughes, A. L. C., Gyllencreutz, R., Lohne, Ø. S., Mangerud, J. & Svendsen J. I. 2016: The last Eurasian ice sheets — a chronological database and time-slice reconstruction, DATED-1. — *Boreas* 45: 1–45.

Kirillov, F.N. [Кириллов Ф.Н.] 1972: [*Fishes of Yakutia*] — Nauka, Moscow. [In Russian].

Konovalov, A. F. & Bolotova, N. L. [Коновалов, А. Ф. & Болотова, Н. Л.] 2014: [Morphological peculiarities of hybrid populations of vendace in the reservoirs of watershed White, Caspian and Baltic seas]. — *Vestnik AGTU. Seriya: Rybnoye Khozyaystvo* 1: 7–17. [In Russian].

Konovalov, A. F., Politov, D. V., Gordon, N. Yu., Makhrov, A. A. & Bolotova, N. L. 2002: Genetic and morphological study of *Coregonus* species from lakes in the Vologda region of north European Russia. — In: *Abstract Book of the 8th International Symposium on the Biology and Management of Coregonid Fishes, 26–29 August 2002, Rovaniemi, Finland*: 25.

Kotellat, M. & Freyhof, J. 2007: *Handbook of European freshwater fishes*. — Publications Kottelat, Cornol and Freyhof, Berlin.

Makhrov, A. A., Politov, D. V., Konovalov, A. F., Bolotova, N. L. & Dumnich, N. V. [Махров, А. А, Политов, Д. В., Коновалов, А. Ф., Болотова, Н. Л. & Думнич, Н. В.] 2003: [Hybrid population of European and Siberian cisco in the upper stream of the Volga River]. — In: Zakharov, A. B., Loskutova, O. A., Ponomarev, V. I., Sidorov, G. P., Shubina, V. N. & Patova, E. N. [Захаров, А. Б., Лоскутова, О. А., Пономарев, В. И., Сидоров, Г. П., Шубина, В. Н. & Патова, Е. Н.] (eds.), [*Biological resources of the White sea and inland water bodies of the European North*]: 56–57. Komi Nauchny Tsentr Ural'skogo Otdeleniya Rossiyskoy Akademii Nauk, Syktyvkar. [In Russian].

Mangerud, J., Dokken, T., Hebbeln, D., Heggen, B., Ingólfsson, Ó., Landvik, J. Y., Mejdahl, V., Svendsen, J. I. & Vorren, T. O. 1998: Fluctuations of the Svalbard Barents Sea IceSheet during the last 150 000 years. — *Quaternary Science Reviews* 17: 11–42.

Mangerud, J., Jakobsson, M., Alexanderson, H., Astakhov, V., Clarke, G. K. C., Henriksen, M., Hjort, C., Krinner, G., Lunkka, J.-P., Moller, P., Murray, A., Nikolskaya, O., Saarnistoj, M. & Svendsen, J. I. 2004: Ice-dammed lakes and rerouting of the drainage of northern Eurasia during the Last Glaciation. — *Quaternary Science Reviews* 23: 1313–1332.

McPhail, J. D. & Lindsey, C. C. 1970: Freshwater fishes of northwestern Canada and Alaska. — *Fisheries Research Board Canada Bulletin* 173: 1–381.

Mehner, T., Pohlmann, K., Elkin, C., Monaghan, M. T., Nitz, B. & Freyhof, J. 2010: Genetic population structure of sympatric and allopatric populations of Baltic ciscoes (*Coregonus albula* complex, Teleostei, Coregonidae) — *BMC Evolutionary Biology* 10, 85, https://doi.org/10.1186/1471-2148-10-85.

Mikhin, V. S. [Михин, В. С.] 1955: [Fishes of Lake Taimyr and Taimyr Bay]. — *Izvestiya VNIORKH* 35: 5–43. [In Russian].

Nikulina, Y. S., Borovikova, E. A. & Budin, Y. V. [Никулина, Ю. С., Боровикова, Е. А. & Будин, Ю. В.] 2018: [Morphological differentiation of river and lake populations of cisco (*Coregonus* spp.) from the basins of the Kara and Laptev seas]. — *Uchenye Zapiski RGGMU* 51: 162–175. [In Russian].

Nei, M. 1978: Estimation of average heterozygosity and genetic distance from a small number of individuals. — *Genetics* 89: 583–590.

Nelson, J. S. 2006: *Fishes of the world*, 4th ed. — Wiley & Sons, New Jersey.

Ostroumov, N. A. [Остроумов, Н. А.] 1937: [Fishes and fishery of the Pyasina River]. — *Trudy Polyarnoy komissii* 30: 7–114.

Padula, V. M., Causey, D. & López, J. A. 2017: Mitochondrial DNA phylogeography of least cisco *Coregonus sardinella* in Alaska. — *Journal of Fish Biology* 90: 1001–1020.

Panin, A. V., Astakhov, V. I., Lotsari, E., Komatsu, G., Lang, J. & Winsemann, J. 2020: Middle and Late Quaternary glacial lake-outburst floods, drainage diversions and reorganization of fluvial systems in northwestern Eurasia. — *Earth-Science Reviews* 201, 103069, https://doi.org/10.1016/j.earscirev.2019.103069.

Perelygin, A. A. [Перелыгин, А. А.] 1988: [*Population genetic analysis of albumins of European (Coregonus albula) and Siberian (Coregonus sardinella) cisco*]. — Ph.D. thesis, University of Novosibirsk. [In Russian].

Podlesny, A. V. & Sesyagin, S. M. [Подлесный, А. В. & Сесягин, С. М.] 1966: [Yenisei cisco *Coregonus sardinella* Val.]. — *Voprosy Ikhtiologii* 6, 1(38): 165–168. [In Russian].

Pokrovsky, V. V. [Покровский, В. В.] 1967: [About morphological features, origin and geographical distribution of *Coregonus sardinella maris-albi* Berg.]. — *Izvestiya GosNOIRKH* 62: 10–114. [In Russian].

Reshetnikov, Yu. S. [Решетников, Ю. С.] 1975: [On the systematic position of coregonids]. — *Zoologicheskiy Zhurnal* 54(11): 1656–1671. [In Russian].

Reshetnikov, Yu. S. [Решетников, Ю. С.] 1980: [*Ecology and systematics of whitefishes*]. — Nauka, Moscow. [In Russian].

Reshetnikov, Yu. S. [Решетников, Ю. С.] 1995: [Modern problems of the study of coregonids]. — *Voprosy Ikhtiologii* 35(2): 156–174. [In Russian].

Reshetnikov, Yu. S. [Решетников, Ю. С.] (ed.) 2010: [*Fishes in the reserves of Russia*, vol. 1]. — T-vo Nauchnykh Izdanii KMK. [In Russian].

Schulz, M., Freyhof, J., Saint-Laurent, R., Østbye, K., Mehner, T. & Bernatchez, L. 2006: Independent evolution of two spring-spawning ciscoes of the *Coregonus albula* (L.) species group, (Salmoniformes: Coregonidae) in Germany. — *Journal of Fish Biology* 68: 1–17.

Sendek, D. S. [Сендек, Д. С.] 1998: [On the species belonging to the ryapushka, living in the Pechora River]. — *Sbornik Nauchnykh trudov GosNIORKh* 323: 191–198. [In Russian].

Sendek, D. S. [Сендек, Д. С.] 2000: [*Phylogenetic analysis of Coregonid fishes by means of allozyme electrophoresis method*]. — Ph.D. thesis, State Research Institute on Lake and River Fisheries (GosNIORKh), Saint-Petersburg. [In Russian].

Sendek, D. S. 2002: Electrophoretic studies of Coregonid fishes from across Russia. — *Advances in Limnology* 57: 35–55.

Sendek, D. S. 2012: Intra-species alliance of the European whitefish *Coregonus lavaretus* L. and vendace *Coregonus albula* L. from the Russian part of the Gulf of Finland and the largest lakes of the eastern Baltic basin. — *Oceanology* 52: 790–796.

Sendek, D. S., Ivanov, E. V. & Fedorova, E. A. [Сендек, Д. С., Иванов, Е. В. & Федорова, Е. А.] 2013a: Genetic differentiation of least cisco from four large rivers of Yakutia. — *Mezhdunarodnyy Zhurnal Prikladnykh i Fundamental'nykh Issledovaniy* 8: 165–168.

Sendek, D. S., Ivanov, E. V., Khodulov, V. V., Novoselov, A. P., Matkovsky, A. K. & Ljutikov, A. A. 2013b: Genetic differentiation of coregonids populations in Subarctic areas. — *Advances in Limnology* 64: 223–246.

Sendek, D. S., Novoselov, A. P., Studenov, I. I. & Gurichev, P. A. 2012: The origin of coregonid fishes of the White Sea Kuloi Plateau. — *Advances in Limnology* 63: 209–227.

Shaposhnikova, G. Kh. [Шапошникова, Г. Х.] 1968: [Comparative morphological analysis of whitefishes of the Soviet Union]. — *Trudy Zoologicheskogo Instituta AN SSSR* 46: 207–256. [In Russian].

Shaposhnikova, G. Kh. [Шапошникова, Г. Х.] 1976: [The story of distribution of whitefishes (genus Coregonus)]. — In: Scarlato, O. A. [Скарлато, О. А.] (ed.), [*Zoogeography and systematics of fish*]: 54–67. Zoologicheskii Institut Akademii Nauk SSSR, Leningrad. [In Russian].

Solovkina, L. N. [Соловкина, Л. Н.] 1974: [Cisco *Coregonus albula sardinella* (Val.) in the basin of the Pechora]. — *Journal of Ichthyology* 14(5): 769–781. [In Russian].

Svärdson, G. 1979: Speciation of Scandinavian *Coregonus*. — *Reports from the Institute for Freshwater Research Drottningholm* 57: 1–95.

Svendsen, J. I., Alexanderson, H., Astakhov, V. I., Demidov, I., Dowdeswell, J. A., Funder, S., Gataullin, V., Henriksen, M., Hjort, C., Houmark-Nielsen, M., Hubberten, H., Ingólfson, Ó., Jakobsson, M., Kjær, K., Larsen, E., Lokrantz, H., Lunkka, J., Lyså, A., Mangerud, J., Matiouchkov, A., Murray, A., M. oller, P., Niessen, F., Nikolskaya, O., Polyak, P., Saarnisto, M., Siegert, C., Siegert, M., Spielhagen, R. & Stein, R. 2004: Late Quaternary ice sheet history of northern Eurasia. — *Quaternary Science Reviews* 23: 1229–1271.

Svendsen, J. I., Astakhov, V. I., Bolshiyanov, D. Y., Demidov, I., Dowdeswell, J. A., Gataullin, V., Hjort, C., Hubberten, H. W., Larsen, E., Mangerud, J., Melles, M., Moller, P., Saarnisto, M. & Siegert, M. J. 1999: Maximum extent of the Eurasian ice sheets in the Barents and Kara Sea region during the Weichselian. — *Boreas* 28: 234–242.

Swofford, D. L. & Selander, R. B. 1981: BIOSYS-1: a FORTRAN program for the comprehensive analysis of electrophoretic data in population genetics and systematics. — *Journal of Heredity* 72: 281–283.

Ustyugov, A. F. [Устюгов, А. Ф.] 1972: [Ecological and morphological characteristics of the Siberian cisco *Coregonus albula sardinella* (Valenciennes) in the Yenisei River basin]. — *Voprosy Ikhtiologii* 12, 5(76): 811–825. [In Russian].

Ustyugov, A. F. [Устюгов, А. Ф.] 1976: [On the origin of two ecological forms of Siberian cisco *Coregonus albula sardinella* (Val.) in the Yenisei river basin]. — *Voprosy Ikhtiologii* 16, 5(100): 773–783. [In Russian].

Vuorinen, J., Himberg, M. K.-J. & Lankinen, P. 1981: Genetic differentiation in *Coregonus albula* (L.) (*Salmonidae*) populations in Finland. — *Hereditas* 94(1): 113–121.

Waples, R. S. 1988: Estimation of allele frequencies at isoloci. — *Genetics* 118(2): 371–384.

Wright, S. 1978: *Evolution and the genetics of populations*, vol. 4: *Variability within and among populations*. — University of Chicago Press, Chicago.

Yakhnenko, V. M. & Mamontov, A. M. 2002: The genetic differentiation of the least cisco (*Coregonus sardinella* Valenciennes, 1848) from Lake Baunt and the Lena River. — *Advances in Limnology* 57: 57–64.

Appendix. Allele frequencies of polymorphic loci, percentage of polymorphic loci (P, 99% criterion) and mean expected heterozygosity (H_{exp}) in the studied populations of cisco. Alleles with mean frequencies $p \geq 0.1$ and $p < 0.1$ are indicated with upper- and lowercase letters, respectively. Sources: *Sendek (2002), Sendek *et al.* (**2012, ***2013a, ****2013b).

Loci	1. Neva R.	2. Skerries (Ladoga L.)*	3. Konevets Island (Ladoga L.)*	4. Volkhov Bay (Ladoga L.)*	5. Volkhov Bay, *ripus* (Ladoga L.)*	6. Bay of Svir' (Onega L.)**	7. Trans-Onega Bay (Onega L.)**	8. Onega proper, *kiletz* (Onega L.)	9. Chudskoye L.	10. Vel'ye L.
*AAT-1**	A(0.94)bd	A(0.96)b	A(0.88)B	A(0.95)b	A(0.97)b	A(0.85)B	A(0.86)B	A(0.77)B	A(0.98)b	A
*AAT-2**	A(0.95)b	A(0.96)b	A(0.88)B	A(0.95)b	A(0.97)b	A(0.85)B	A(0.86)B	A(0.77)B	A(0.97)b	A
*CK-A1**	A(0.98)b	A(0.99)b	A(0.99)b	A(0.98)b	A(0.97)b	A	A(0.98)b	A(0.99)b	A(0.98)b	A(0.97)b
*CK-A2**	A(0.97)b	A	A	A(0.98)b	A(0.98)b	A	A	A(0.99)b	A(0.98)b	A(0.96)b
*ESTD**	A(0.91)b	A(0.87)B	A(0.86)B	A(0.75)B	A(0.69)B	A	A	A(0.98)b	A(0.93)b	A(0.95)b
*G3PDH-1**	A	A	A	A	A	A	A(0.98)d	A	A	A
*G3PDH-2**	A(0.91)de	A(0.89)de	A(0.83)De	A(0.90)de	A(0.95)e	A	A(0.97)de	A	A(0.89)bde	A(0.99)e
*GPI-A1**	A(0.97)c	A(0.98)b	A(0.94)bc	A(0.96)bc	A(0.98)bc	A	A(0.96)c	A(0.99)c	A	A(0.92)b
*GPI-A2**	A	A	A	A	A	A	A	A	A	A
*GPI-B1**	A	A	A	A	A	A	A	A	A	A
*IDDH-1**	AC(0.46)d	AC(0.58)d	AC(0.67)D	AC(0.55)d	AC(0.53)D	A(0.50)CD	AC(0.50)D	AC(0.46)D	A(0.57)Cd	A(0.52)Cd
*IDDH-2**	AC(0.46)d	AC(0.58)d	AC(0.67)D	AC(0.55)d	AC(0.53)D	A(0.50)CD	AC(0.50)D	AC(0.46)D	A(0.57)Cd	A(0.52)Cd
*sIDHP-4**	A	A	A(0.98)bf	A	A(0.98)df	A(0.93)b	A(0.91)bf	A(0.91)bc	A(0.99)c	A
*LDH-A1**	A	A	A	A	A	A	A	A	A	A
*LDH-A2**	A	A	A	A	A	A	A	A	A	A
*LDH-B2**	A	A	A(0.98)de	A	A	A	A	A	A	A
*MDH-A1**	A	A(0.98)d	A(0.97)d	A	A	A	A	A(0.97)d	A	A
*MDH-B1**	A	A	A(0.99)b	A	A(0.98)e	A	A	A	A	A(0.97)b
*sMEP-4**	A(0.82)B	A(0.55)B	A(0.84)B	A(0.71)B	A(0.73)B	A(0.66)Bc	A(0.85)B	A(0.96)b	A(0.50)B	A(0.61)B
*PGDH**	A	A	A	A	A	A	A	A	A	A
*PGM-3**	A(0.85)B	A	A	A	A	A	A(0.91)b	A(0.97)b	A(0.93)b	A(0.96)b
*PGM-4**	A(0.99)b	A(0.98)b	A(0.99)b	A(0.99)b	A(0.98)b	A(0.97)b	A(0.91)b	A(0.94)b	A(0.97)b	A(0.97)b
*mSOD**	A(0.94)b	A(0.99)b	A(0.95)b	A(0.99)b	A(0.98)bc	A	A	A(0.99)c	A	A
*sSOD**	A(0.85)B	A(0.71)B	A(0.88)B	A(0.81)B	A(0.74)B	A(0.60)B	A(0.74)Bd	A(0.90)B	A(0.89)B	A(0.74)B
P (0.99)	50.0	46.7	50.0	43.3	50.0	26.7	43.3	50.0	43.3	40.0
H_{exp} (SE)	0.096 (0.030)	0.093 (0.032)	0.094 (0.026)	0.094 (0.031)	0.096 (0.033)	0.096 (0.035)	0.102 (0.031)	0.090 (0.031)	0.084 (0.030)	0.087 (0.031)

Loci	11. White L.	12. Kovzhskoye L.	13. Pyaozero L.	14. Kuyto L.	15. Volch'ji L.**	16. Bol'shoye Vostochnoye L.**	17. Zapadnye Megorskie L.**	18 Ernozero L.**	19. Golodnaya Guba L., *saurey* (Pechora R.)*	20. Main current, *zeld* (Pechora R.)*
*AAT-1**	A	A(0.77)B	A(0.69)B	A(0.88)B	A	A	A	A	A(0.96)b	A(0.99)bc
*AAT-2**	A	A(0.77)B	A(0.69)B	A(0.88)B	A	A	A	A	A(0.96)b	A(0.99)bc
*CK-A1**	aB(0.98)	ABC(0.41)	A(0.94)b	A(0.96)b	A(0.92)b	A(0.90)B	A(0.95)b	A	AB(0.56)D	AB(0.58)D

continued

Appendix. Continued

Loci	11. White L.	12. Kovzhskoye L.	13. Pyaozero L.	14. Kuyto L.	15. Volch'ji L.**	16. Bol'shoye Vostochnoye L.**	17. Zapadnye Megorskie L.**	18 Ernozero L.**	19. Golodnaya Guba L., *saurey* (Pechora R.)*	20. Main current, *zeld* (Pechora R.)*
*CK-A2**	aB(0.99)	ABC(0.41)	A(0.94)b	A(0.96)b	A(0.92)b	A(0.90)B	A(0.95)b	A	AB(0.56)D	AB(0.58)D
*ESTD**	A(0.98)b	A	A	A	A	A	A	A	A	A
*G3PDH-1**	A(0.99)e	A	A	A	A	A	A	A	A	A(0.99)d
*G3PDH-2**	A(0.97)d	A(0.86)Df	A	A(0.96)d	A(0.91)e	A	A	A(0.94)e	A(0.73)dE	A(0.91)de
*GPI-A1**	A(0.97)c	A(0.76)C	A(0.94)c	A(0.96)c	A	A(0.98)b	A	A	A(0.88)C	A(0.96)bc
*GPI-A2**	A	A	A	A	A	A	A	A	A	A
*GPI-B1**	A(0.69)B	A	A	A	A	A	A	A	A	A(0.99)b
*IDDH-1**	AC(0.49)D	AC(0.53)D	AC(0.50)D	A(0.67)CD	A(0.50)C	A(0.50)C	A(0.50)C	A(0.50)cD	AC(0.52)D	AC(0.60)D
*IDDH-2**	AC(0.49)D	AC(0.53)D	AC(0.50)D	A(0.67)CD	A(0.50)C	A(0.50)C	A(0.50)C	A(0.50)cD	AC(0.52)D	AC(0.60)D
*sIDHP-4**	A	A(0.93)bd	A	A(0.83)bcf	A	A	A	A	A(0.97)b	A(0.99)bf
*LDH-A1**	A(0.99)b	A	A	A	A	A(0.99)d	A	A	A	A
*LDH-A2**	A	A	A	A	A	A	A	A	A	A
*LDH-B2**	A	A(0.98)b	A	A	A	A	A	A	A	A
*MDH-A1**	A	A	A(0.89)D	A(0.62)D	A	A	A	A	A	A
*MDH-B1**	A(0.99)c	A	A	A	A	A(0.99)c	A	A	A	A
*sMEP-4**	A(0.94)d	A(0.59)B	A(0.67)BD	A(0.92)d	A(0.79)D	A(0.79)D	A(0.77)D	A	A(0.41)BD	A(0.74)Bd
*PGDH**	A	A	A	A	A	A	A	A	A	A
*PGM-3**	A(0.96)b	A	A	A	A	A	A	A	A(0.89)B	A(0.90)B
*PGM-4**	A(0.97)b	A(0.98)c	A	A	A(0.95)b	A(0.90)B	A(0.65)B	A	A(0.97)b	A(0.97)b
*mSOD**	A	A	A	A	A	A(0.97)c	A	A(0.50)C	A	A
*sSOD**	A(0.87)B	A(0.75)B	A(0.78)B	A(0.63)B	A(0.74)B	A(0.55)B	A(0.73)B	AB(0.70)	AB(0.59)	AB(0.60)
P (0.99)	50.0	43.3	33.3	40.0	26.7	36.7	23.3	16.7	43.3	50.0
H_{exp}	0.082 (0.031)	0.168 (0.044)	0.121 (0.039)	0.113 (0.035)	0.078 (0.028)	0.084 (0.030)	0.082 (0.031)	0.081 (0.037)	0.156 (0.044)	0.123 (0.038)

Loci	21. Pechora Bay, *zeld***	22. Mongatalyang-yakha R.	23. Suolema R.	24. Khorgo Cape	25. Lena R.***	26. Omoloy R.***	27. Indigirka R.***	28. Kolyma R.****
*AAT-1**	A	A	A	A	A(0.99)c	A(0.96)c	A	A(0.99)b
*AAT-2**	A	A	A	A	A(0.99)c	A	A	A
*CK-A1**	AB(0.50)D	D	aD(0.90)	aD(0.95)	AD(0.81)	AD(0.80)	AD(0.64)	AB(0.58)D
*CK-A2**	AB(0.50)D	B	B	B	B	B	B	AB(0.58)D
*ESTD**	A	A	A	A	A	A(0.98)b	A	A
*G3PDH-1**	A	A(0.92)bd	A	A(0.90)C	A(0.88)C	A(0.86)cd	A(0.80)Cd	A(0.79)Cd
*G3PDH-2**	A	A(0.96)d	A(0.50)D	A(0.60)D	A(0.69)C	A(0.87)Ce	A(0.87)C	A(0.90)dg
*GPI-A1**	A(0.80)C	A(0.94)c	A	A(0.98)c	A(0.98)c	A(0.98)c	A	A(0.98)bc

continued

Appendix. Continued

Loci	21. Pechora Bay, *zeld***	22. Mongatalyang-yakha R.	23. Suolema R.	24. Khorgo Cape	25. Lena R.***	26. Omoloy R.***	27. Indigirka R.***	28. Kolyma R.****
*AAGPI-A2**	A	A	A	A	A(0.98)c	A	A	A
*GPI-B1**	A	A	A	A	A	A(0.98)b	A	A
*IDDH-1**	AC(0.75)D	ACD(0.50)	AC(0.50)D	AC(0.50)D	AC(0.61)D	AC(0.56)D	AC(0.51)D	AC(0.55)D
*IDDH-2**	AC(0.75)D	ACD(0.50)	AC(0.50)D	AC(0.50)D	AC(0.61)D	AC(0.56)D	AC(0.51)D	AC(0.55)D
*sIDHP-4**	A(0.90)b	A(0.96)b	A(0.90)b	A(0.93)bcf	A(0.93)bd	A(0.92)bc	A(0.97)bcf	A
*LDH-A1**	A	A	A	A	A	A	A	A
*LDH-A2**	A	A(0.96)b	A	A	A	A	A	A(0.88)Bc
*LDH-B2**	A	A	A	A	A	A	A	A
*MDH-A1**	A	A	A	A(0.98)b	A(0.98)c	A(0.98)b	A(0.98)bd	A(0.95)d
*MDH-B1**	A	A(0.96)b	A(0.90)B	A	A	A	A	A(0.97)b
*sMEP-4**	A(0.60)BD	A(0.42)BD	A(0.90)B	A(0.93)bd	A(0.48)BD	AB(0.48)d	A(0.58)Bd	A(0.56)Bd
*PGDH**	A	A(0.96)b	A	A	A	A	A	A
*PGM-3**	A	A	A	A(0.98)b	A(0.91)b	A	A	A(0.95)b
*PGM-4**	A	A(0.79)B	A	A(0.95)b	A(0.98)b	A(0.99)b	A(0.97)b	A(0.99)b
*mSOD**	A	A	A	A	A	A	A	A
*sSOD**	AB(0.50)	AB(0.83)	B	aB(0.98)	aB(0.93)	aB(0.92)	aB(0.94)	aB(0.94)
P (0.99)	26.7	40.0	23.3	40.0	50.0	46.7	36.7	53.3
H_{exp}	0.131 (0.043)	0.111 (0.038)	0.092 (0.037)	0.088 (0.033)	0.115 (0.035)	0.105 (0.034)	0.105 (0.037)	0.140 (0.039)