

Siberian Whitefish (*Coregonus lavaretus pidschian*, Coregonidae) from the Anabar River: Morphogenetic Structure of the Population

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Abstract—Data on the morphology, biology, and genetics of two ecological forms of *pidschian*-like whitefishes of the genus *Coregonus*, corresponding to the descriptions of East Siberian whitefish, *C. lavaretus pidschian* natio *brachymystax*, and glacial-plain whitefish, *C. lavaretus pidschian* natio *glacialis*, from the Anabar River of western Sakha (Yakutia) Republic (Russia), are presented. According to meristic characters, no differences are found between these ecological forms, while on the basis of plastic traits and occupied ecological niches these whitefishes differ substantially. We demonstrate that, on the basis of the sequences of the *ND1* gene of the mtDNA, the East Siberian whitefishes are only slightly different from the whitefishes from the lower Ob River and Lake Teletskoye (Upper the Ob River basin), and probably have a common origin with them. Glacial-plain whitefishes from the Anabar River have a common origin with whitefishes from the water bodies of the Taimyr Peninsula and represent a complex of forms/species.

Keywords: Siberian whitefish, Sakha (Yakutia), Anabar River, whitefish, *Coregonus lavaretus pidschian*, sympatry, ecological form, secondary intergradation, mtDNA

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INTRODUCTION

Whitefishes (Teleostei: Salmoniformes: Coregonidae) are predominant forms/species in ichthyocenoses of freshwater subarctic ecosystems. Numerous representative of the *Coregonus lavaretus* sensu lato complex are widespread in the Palearctic from alpine lakes to Beringia. Owing to high morpho-ecological plasticity and abundance of allopatric and sympatric forms and populations of unclear status, they are a model group in taxonomic, phylogenetic, and microevolutionary studies [1–5]. According to various data, from 6 to 44 subspecies/species of whitefish were described during long-term studies within the borders of Eurasia [6–8]. In our opinion, such significant discrepancies are foremost associated with a different interpretation of the term “ecological form” of different authors.

Molecular genetic studies demonstrated that, despite significant morphological differences observed between ecological forms/species of sympatric whitefishes from the water bodies of South Siberia, they usually have common or weakly divergent mtDNA haplotypes. And vice versa, despite close

morphological characteristics, sympatric riverine whitefishes often have high mtDNA diversity [9–16].

According to L.S. Berg [4], East Siberian whitefish *C. l. pidschian* natio *brachymystax* Smitt, a polymorphous ecotype of humpback whitefish previously described from the Yenisei River as a separate species *Coregonus polcur* Smitt, is widespread in the Anabar River, similar to other rivers of Yakutia east toward the Lena River. Later, F.N. Kirillov [17] described the glacial-plain whitefish *C. l. pidschian* natio *glacialis* Kirillov from the water bodies of Yakutia and demonstrated that these ecological forms are characterized by noticeable morphological differences and prefer different biotopes. East Siberian whitefish inhabits rivers throughout the whole course in most water bodies (from upper to lower course). Glacial-plain whitefish inhabits lakes and estuary parts of rivers that flow into the sea and also occurs in certain sea gulfs. These two sympatric forms inhabit the lower courses of rivers and, actually, are like biological species [18]. However, in a number of publications from the end of the 20th to the beginning of the 21st century, they are

down to the ecological form level and do not have definitive taxonomic status [7, 19].

The goal of the present study is a comparative morphogenetic analysis of *pidschian*-like whitefishes from the water bodies of the Taymyr Peninsula and Northwestern Yakutia, which will further make it possible to determine the degree of differences between sympatric whitefishes from the Anabar River, phylogenetic affinity, and possible migratory routes of whitefishes in the studied region in postglacial period.

MATERIALS AND METHODS

Characteristics of the studied region. The Anabar River discharges into the Laptev Sea. Its headwaters is located in the northwestern part of Yakutia on the Anabar Plateau, 700 m above sea level. The river length is 939 km (including Bol'shaya Kuonamka River); the basin area is 104461 km [20]. The largest tributaries of the Anabar River are the Malaya Kuonamka, Kharabyl, Ebelyakh, Udia, Zhilinda, Uele, and Suolema rivers [21]. From east and south, the dividing range of the Anabar River borders with that of the Olenek River. From the west, the Anabar River is margined by the basin of the Popigai River, which flows into Khatanga Gulf. The upper course of the Anabar River is rocky, with small rifts and wide stretches. The middle and lower course of the river are calmer and the river has a sandy bed. The tide is well noticeable in the river mouth, and it encompasses a significant portion of the lower course of the river. The ichthyofauna of the Anabar River includes 27 fish species. Among whitefishes (according to their systematics by Yu.S. Reshetnikov), the following occur: *pidschian*-like whitefish *Coregonus lavaretus pidschian* Gmelin, muksun *C. muksun* (Pallas), broad whitefish *C. nasus* Pallas, Arctic cisco *C. autumnalis* Pallas, peled *C. peled* (Gmelin), least cisco *C. sardinella* Valenciennes, tugun *C. tugun* (Pallas), and inconnu *Stenodus leucichthys nelma* (Pallas) Gldenstdt [17, 22].

Sampling and morphological analysis. Whitefishes in the Anabar River were caught using stake nets and a throw net during a period from July 10 to August 10, 2014, at three points (Fig. 1). The first point was located at the origin of the Anabar River, at the confluence of the Bol'shaya and Malaya Kuonamka rivers (70°46' N, 113°19' E). The second point was located downstream of the Anabar River, close to the mouth of the Udy River (71°45' N, 114°10' E), and the third was 10 km upstream of the mouth of the Suolema River (73°01' N, 113°33' E). Identification of the forms of whitefishes was conducted according to the description of F.N. Kirillov [17]. A total of 60 specimens of East Siberian whitefish and 45 specimens of glacial-plain whitefish were caught and analyzed. Only East Siberian whitefish occurred at points 1 and 2; both forms were registered at point 3, but glacial-plain whitefish were predominant (Fig. 2). Immediately after catching, the fishes were weighed, scales

were collected, the gill raker numbers on the first branchial arch and the number of perforated scales in the lateral line were determined, and tissues were fixed for genetic analysis. Morphological analysis was performed on the basis of digital images according to the previously described method [23]. The fishes were measured in the laboratory according to the standard Pravdin scheme [24] in AxioVision 3.1 (Carl Zeiss Vision GmbH). For morphological analysis, we used 57 specimens of East Siberian (fork length 219–357 mm) and 22 specimens of glacial-plain (263–465 mm) adult whitefishes, for which we used 31 morphometric and 2 meristic features (the number of perforated scales in the lateral line *ll* and the gill raker numbers on the first branchial arch *sp. br.*).

The intergroup morphological variability of whitefishes was evaluated according to conventional set of morphometric features using the principal component method [10, 11, 23]. Since in the case of allometric growth the body shape depends on the size, all morphometric data was adjusted to take the size of the specimens into account before multivariate analysis [25, 26]. The main components obtained in the analysis are linear combinations of the original features and are orthogonal to each other [27]. The statistical confidence for the differences between the two datasets was evaluated using multivariate ANOVA (MANOVA) [28]. The Statistica 5.0 (StatSoft, United States) software package was used for statistical processing of the digital materials.

Age and diet of fishes. The age of the fishes was identified on the basis of the scales [29, 30]. For this purpose, we photographed the scales using Canon Power Shot G7 digital camera with Carl Zeiss Stemi 2000-C binocular microscope. Next, digital images of the scales were processed in Adobe Photoshop CS, and the annual rings were counted. For the analysis of age and growth rate, we used 60 specimens of Eastern Siberian and 45 specimens of glacial-plain whitefish. The statistical significance for the differences between the arithmetic means in the same age groups of both ecological forms was evaluated using Student's *t*-test. To identify the special features of feeding habits of the whitefishes from the Anabar River, the gastrointestinal tracts were fixed in 10% formaldehyde solution. A total of 12 stomachs from fishes of each ecological form were dissected. The contents of stomachs were sorted by taxonomic groups and the percentage composition of prey in each group was calculated [31].

Variability of the NDI gene of the mitochondrial DNA. Total genomic DNA was isolated from the whitefish liver fixed in 96% ethanol using the phenol-chloroform method [32]. The isolated DNA was stored at 4°C. We analyzed the variability of the mitochondrial *NDI* gene, amplified in polymerase chain reaction using our original external primers 5'GGCCTAAGCCCTTTTCTCA3' Forward and 5'GAGGGGACTTGAACCCCTAT3' Reverse. The

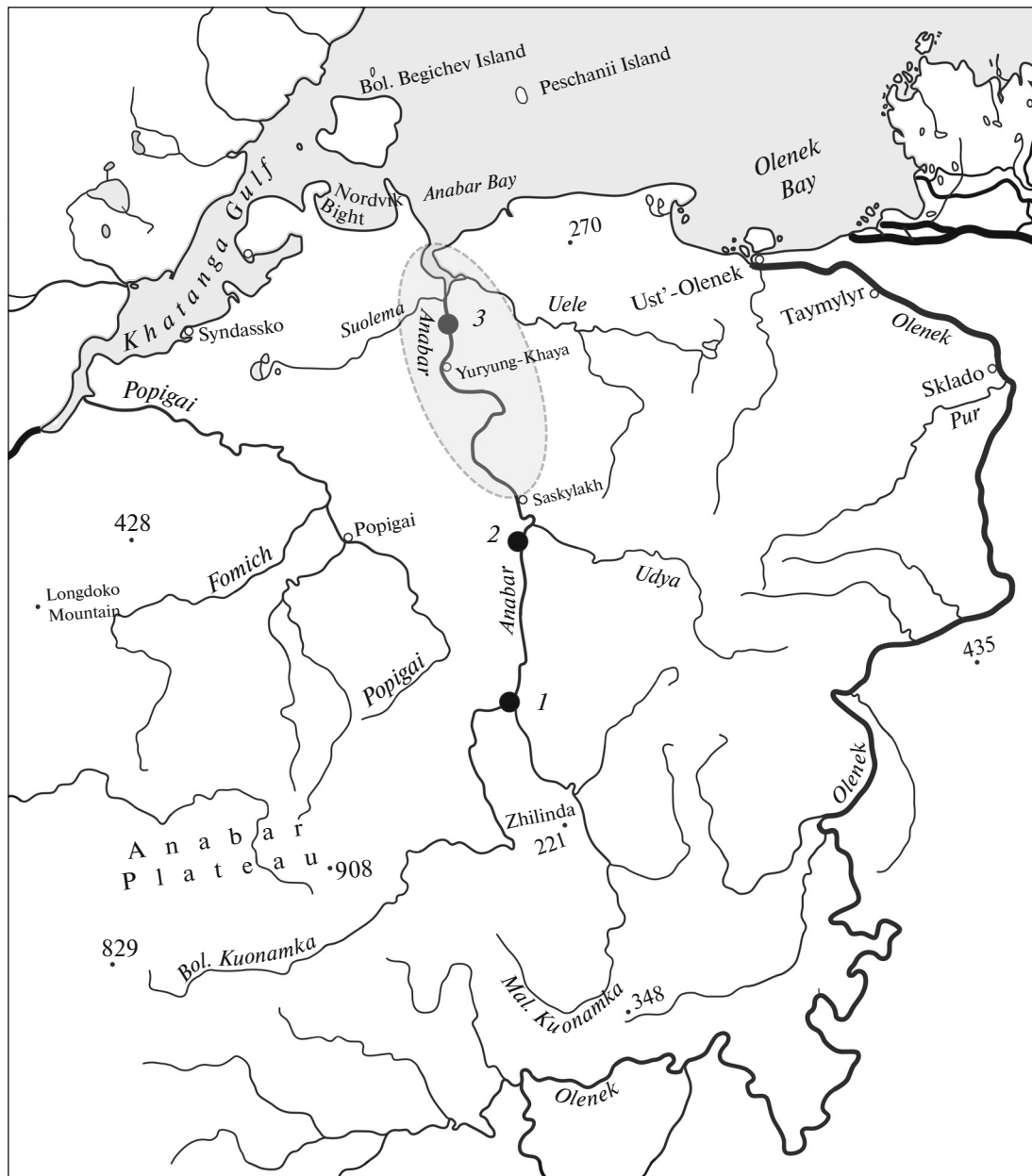


Fig. 1. Schematic map of the Anabar River basin. (1–3) Sites of fish catching. Ellipse notes the locations of glacial-plain whitefish encounters.

fragment was amplified in 20 μ L of reaction mix volume [12]. As a result of amplification of the *ND1* mtDNA gene fragment, 1091 bp sequences were obtained. PCR products were purified using the BIO-SILICA reagent kit (Novosibirsk, Russia) and sequenced in both directions on an automated ABI 3130xl Genetic Analyzer (Applied Biosystems, Inc., United States) at the Genomics Core Facility of the Siberian Branch of the Russian Academy of Sciences (Novosibirsk, Russia, <http://sequest.niboch.nsc.ru>) using the BigDye Terminator Kit (Applied Biosystems). The nucleotide sequences were then aligned

using the ClustalW algorithm and edited manually. The obtained sequences were deposited into the GenBank database (the numbers are listed in Table 1). For analysis of polymorphism of the nucleotide sequences that we obtained in the present study, we calculated the following parameters: the number of polymorphic (segregating) sites (S), the number of haplotypes (h), the haplotype diversity (H_d), the nucleotide diversity (π), and the average number of nucleotide differences (k). All calculations were carried out in DnaSP v. 5.10 [33]. The genetic analysis included, besides whitefishes from the Anabar River, datasets of whitefishes

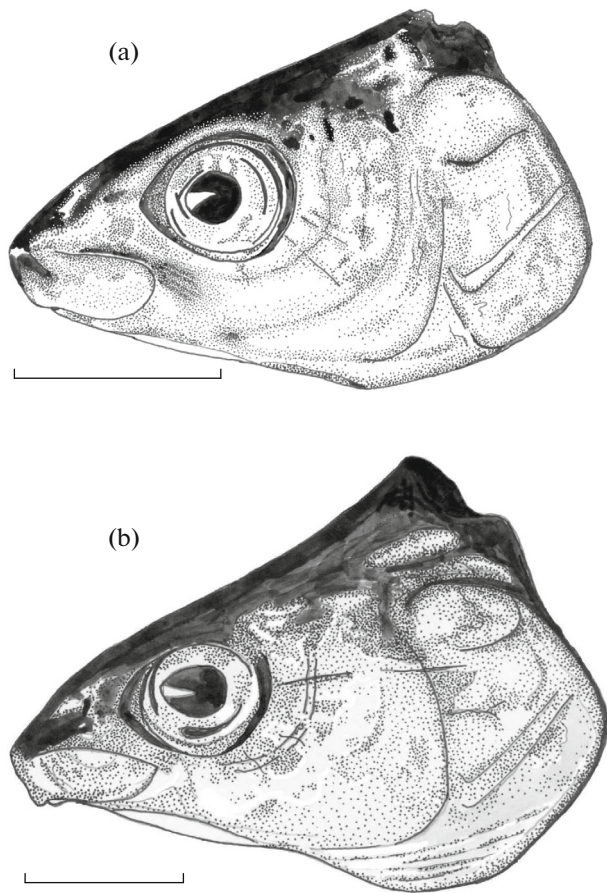


Fig. 2. Heads of riverine *pidschian*-like whitefish of the Anabar River (a) and glacial-plain whitefish from the Sulema River of the Anabar River basin (b). Scale 1 cm (illustration by N.A. Bochkarev).

from Lake Khantayskoe, the Kureika River (the Yenisei River basin), and the Zakharova Rassokha River (the Khatanga River basin) and datasets of whitefishes from the lower Ob River tributaries. Furthermore, the most common haplotypes of whitefishes from Lake Teletskoye were included in the analysis (Table 1). To evaluate the genealogical relationship between the haplotypes of the putative forms/species of whitefish, a median network was constructed in Network v. 4.5 using the median-joining algorithm [34].

RESULTS

Morphological Analysis

According to the results of the analysis of meristic features, no differences between the two forms of whitefishes are discovered. The number of perforated scales in the lateral line of East Siberian whitefish (82.14 ± 0.44) is somewhat higher than in glacial-plain whitefish (80.97 ± 0.58). The number of gill rakers on the first branchial arch is approximately the same in both forms: 19.11 ± 0.18 and 19.67 ± 0.30 . The differ-

ences are statistically insignificant in both cases. Ordination by morphometric features of the whitefish specimens from the Anabar River using the principal component method showed that distributions of the two datasets have insignificant overlap (Fig. 3). The main positive and negative loadings to the first principal component were from body proportion indices (*CC*, *aA*, *aV*, *aD*, *aP*, *DC*, *VC*). Glacial-plain whitefish has a relatively higher body and tail stem (*H*, *h*) than East Siberian whitefish and relatively smaller head (*C*) and, therefore, lower values of the head measurements. This ecological form is characterized by relatively longer dorsal and anal fins compared to East Siberian whitefish (*ID*, *IA*). The zone of overlapping consists of four specimens of glacial-plain whitefish and six specimens of East Siberian whitefish, which is 13% of the total dataset size. Distribution analysis based on the individual features identified no hiatus between the forms/species of whitefish. Nevertheless, the visual identification of the forms/species of whitefish corresponds well to the results of statistical analysis. Multivariate analysis of variance (MANOVA) based on morphometric features showed that all datasets were well differentiated (Wilk's $\Lambda = 0.2558$, $F = 4.65$, $df1 = 30$, $df2 = 48$) and differed from each other significantly ($P < 0.001$). The significance level after Bonferroni correction was also high (Pillai trace = 0.7442 , $F = 52.49$, $df1 = 62$, $df2 = 358$, $P < 0.001$).

Ecological Characteristics of the Sympatric Forms of Whitefishes

East Siberian whitefish inhabits the entire river: from the upper course to the Anabar Gulf estuary, mainly on sand and pebble shoals of the river. The largest aggregations of fish are found near the mouths of rivers and streams. On the basis of the survey data, spawning migration has not been noted for East Siberian whitefish. Apparently, this whitefish species spawns near the feeding area. Glacial-plain whitefish is absent from the middle and upper course of the river during the summer; it is common from the village of Yuryung-Khai to the bay. In the lower course of the river, where there are significant tidal currents, both forms of whitefish are encountered, although the population of East Siberian whitefish is far smaller than the glacial-plain whitefish population. For whitefishes inhabiting the tidal zone, the locals note spawn migration. During the period of spawning, the fish migrate up the Anabar River toward the village of Saskylakh. According to the data obtained, the population of East Siberian *pidschian*-like whitefish from the Anabar River includes at least ten age groups and is characterized by a fairly low rate of linear growth. Glacial-plain whitefish grows slightly faster than East Siberian whitefish, and eleven age groups were registered for this form (Fig. 4). Differences in growth rate between the two ecological forms of whitefishes are statistically significant ($P \leq 0.01$).

Table 1. Species/forms/populations of whitefishes, sampling sites, water basin, and GenBank accession numbers

No.	Form/species	Sample collection sites	Basin	Number of fishes	GenBank accession numbers
1	<i>C. l. pidschian natio brachymystax</i>	Anabar River	Anabar River	19	KU948937–KU948950
2	<i>C. l. pidschian natio glacialis</i>	Anabar River	Anabar River	18	KU948951–KU948962
3	<i>C. l. pidschian</i>	Lake Khantayskoe	Yenisei River	4	KU948967–KU948970
4	<i>C. l. pidschian</i>	Zakharova Rassokha River	Khatanga River	5	KU948963–KU948966
5	<i>C. l. pidschian</i>	Kureika River	Yenisei River	7	KU948985–KU948988
6	<i>C. l. pidschian</i>	N. Tunguska River	Yenisei River	1	KU948984
7	<i>C. l. pidschian</i>	Sob River	Ob River lower course	4	KU948971, KU948972
8	<i>C. l. pidschian</i>	Sosva River	Ob River lower course	4	KU948973, KU948974
9	<i>C. l. pidschian</i>	Lake Vorchato	Ob River lower course	5	KU948978, KU948979
10	<i>C. l. pidschian</i>	Voikar River	Ob River lower course	4	KU948976, KU948977
11	<i>C. l. pidschian</i>	Lake Langtibeito	Gulf of Ob	4	KU948980–KU948983
12	<i>C. l. pidschian</i>	Taz River	Gulf of Ob	2	KU948975
13	<i>C. l. pidschian</i> + <i>C. l. pravdinellus</i>	Lake Teletskoye	Ob River upper course	15	HM535618, HM535621

All stomachs of the whitefishes from the upper and middle course of the river had medium filling (2, 3). In the lower course of the river, the stomachs of both whitefish forms were slightly more filled (3, 4). The basis of East Siberian whitefish diet in the Anabar River during the summer consisted of Gastropoda and Bivalvia mollusks (74.4%); a smaller portion was composed of *Gammarus* sp. (Amphipoda) (14.6%), *Saduria entomon* (Isopoda) (5.7%), and young fishes (5.3%). In the diet of glacial-plain whitefish, isopods were predominant (64.7%); gastropod and bivalve mollusks (20.3%) and gammarus (15.0%) were noted.

In the mouth of the Anabar River, the diet structure of both forms of whitefishes was identical.

Variability of the Mitochondrial DNA

Haplotypes of whitefishes from the Anabar River were sorted into two groups by correspondence with different ecological forms/species. The first group included the dataset of East Siberian whitefish; the second group included the dataset of glacial-plain whitefish. In addition to whitefishes from the Anabar River, three more groups were formed, which included

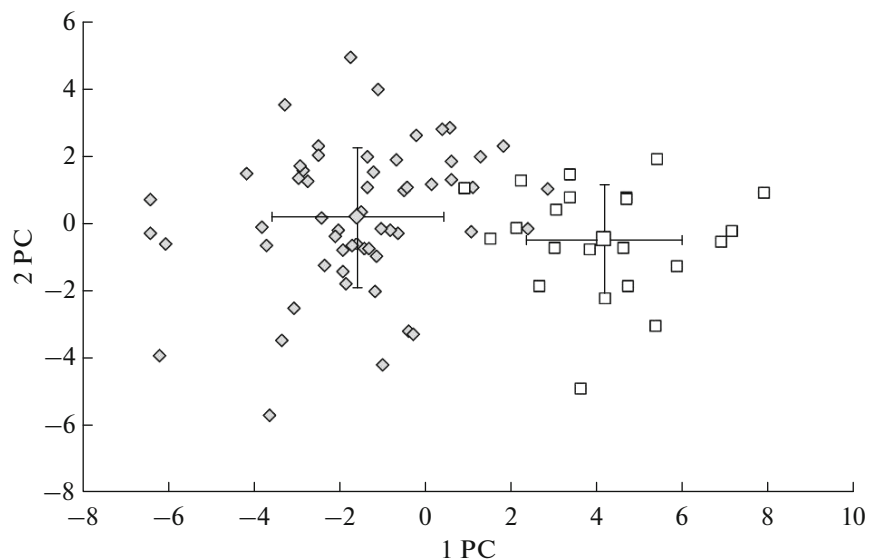


Fig. 3. Ordination of two sympatric forms of *pidschian*-like whitefishes from the Anabar River by morphometric features in space of first and second principal components: (diamonds) East Siberian whitefish; (squares) glacial-plain whitefish. \pm mean square deviation. Length of eigenvector is 1.

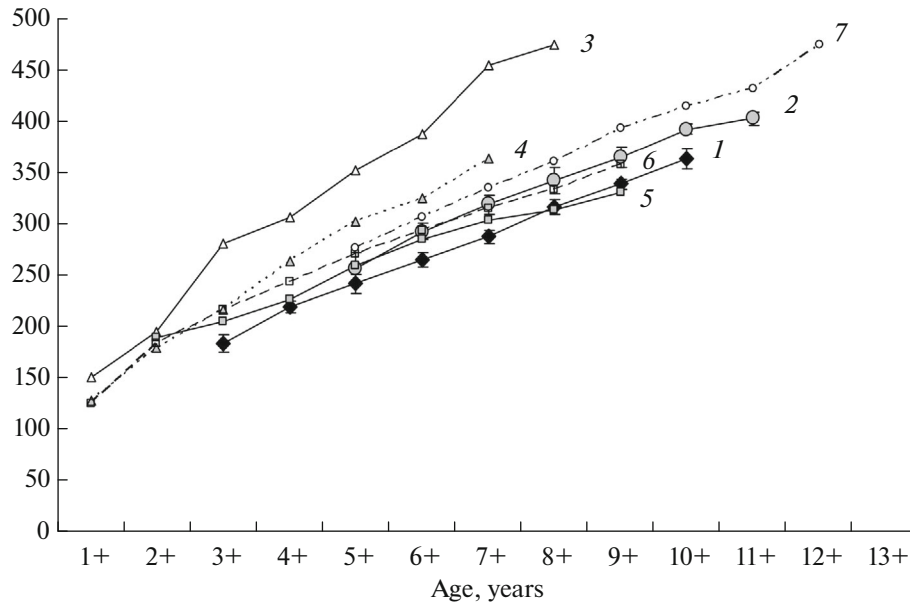


Fig. 4. Rate of linear growth of East Siberian and glacial-plain whitefishes from different basins of rivers of Yakutia. (1) East Siberian whitefish from the Anabar River; (2) glacial-plain whitefish from the Anabar River; (3) East Siberian whitefish from the Verkhny Vilyuy River; (4) East Siberian whitefish from the Nizhny Vilyuy River; (5) East Siberian whitefish from the Indigirka River; (6) East Siberian whitefish from the Kolyma River; (7) glacial-plain whitefish from the Khroma River ((1, 2) our own data; (3–7) sensu Kirillov, 1972 [17]).

haplotypes of the whitefishes from water bodies of the Taymyr Peninsula (group 3), from the lower course of the Ob River (group 4), and from Lake Teletskoye (group 5). The number of the studied specimens in the groups varied from 15 (Lake Teletskoye) to 22 (basin of the lower course of the Ob River). The number of haplotypes in the groups varied from 12 to 14 (Table 2). All the studied populations were characterized by high haplotype diversity, with the highest values of nucleotide diversity observed in both whitefish populations from the Anabar River and the lowest values in the whitefish populations from the lower course of the Ob

River (4). The greatest mean number of nucleotide differences was also noted in the whitefish populations from the Anabar River (Table 2).

Phylogenetic Relationships

The reconstruction of phylogenetic relationships between whitefish populations from the Anabar River showed that they can be divided into two haplogroups: haplogroup I, composed mainly of East Siberian whitefish haplotypes, and haplogroup II, composed mainly of glacial-plain whitefish (Fig. 5). In the com-

Table 2. Polymorphism of the *ND1* gene of the mtDNA in sequence datasets of *pidschian*-like whitefishes of some water bodies of the Siberian Arctic

Population	<i>n</i>	<i>S</i>	<i>h</i>	H_d	π	<i>k</i>
1. Anabar <i>C. l. p. natio brachymystax</i>	20	20	13	0.953	0.00562	5.478
2. Anabar <i>C. l. p. natio glacialis</i>	17	22	14	0.971	0.00495	4.823
3. Taymyr and Yenisei River	17	17	12	0.919	0.00415	4.044
4. Ob River (lower course)	22	20	13	0.922	0.00382	3.727
5. Ob River (Lake Teletskoye)	15	—	—	—	—	—

n, number of samples; *S*, number of polymorphic (segregating sites); *h*, number of haplotypes; H_d , haplotype diversity; π , nucleotide diversity; *k*, average number of nucleotide differences (per site). 1, East Siberian whitefish of the Anabar River; 2, glacial-plain whitefish from the Anabar River; 3, the Taymyr Peninsula: the Zakharova Rassokha, the Khatanga River basin, Lake Khantayskoe (the Yenisei River basin), the Kureika River (the Yenisei River basin); 4, the Ob River and Gulf of Ob basin (haplotypes of whitefishes from the S. Sosva, Sob, and the Voikar rivers, Lake Varchato, the Taz River, Lake Langtibeito (the Yamal Peninsula); 5, Lake Teletskoye whitefish *C. l. smitti*.

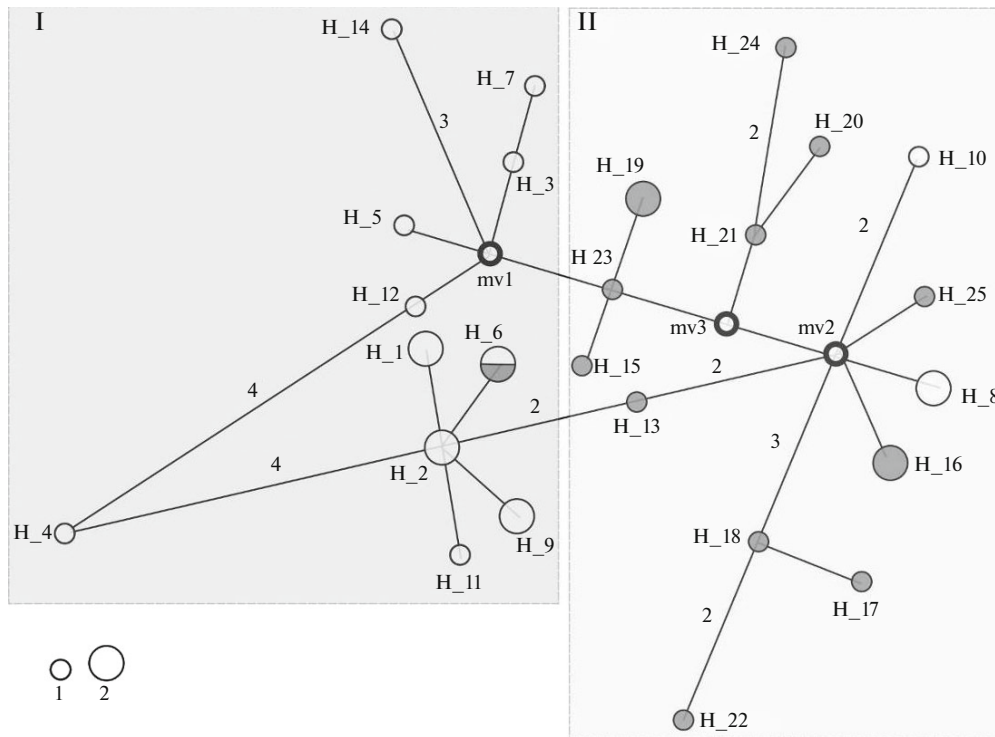


Fig. 5. Median networks of haplotypes of whitefish from the Anabar River (white circles denote haplotypes of East Siberian whitefish; light gray circles denote haplotypes of glacial-plain whitefish); mv1–mv3, undetected or extinct hypothesized haplotypes. Numbers above connections designate number of substitution. I and II, designated haplogroups. Diameter of circles is proportional to haplotype frequency.

position of the median network, star-shaped structures were formed with several central haplotypes: mv1, mv2, H_2, H_21. East Siberian whitefish (mainly) correspond to the two distant (7–8 substitutions) and rather compact structures with central haplotypes mv1 and H_2, respectively. Glacial-plain whitefish were structured significantly more weakly. The H_21 star-shaped structure, with the hypothesized mv3 haplotype and the adjacent H_15, H_19, and H_23 haplotypes, is completely formed by glacial-plain whitefish. It is most probable that the H_21 structure, same as H_23, represents the remainders of the ancestral mtDNA of the previously more common phylogenetic lineages, most of which was lost as a result of introgressive hybridization. In the structure of the hypothetical haplotype mv2, there are haplotypes of both glacial-plain and East Siberian whitefish.

Including into analysis of haplotypes of whitefishes from the water bodies of the Taymyr Peninsula and from the lower course of the Ob River and the two most common haplotypes from Lake Teletskoye made the median network much more complicated. All populations were found to be highly mixed. Nevertheless, the median network can also be divided into two haplogroups (Fig. 6). In haplogroup I, a star-shaped structure of mixed composition remains for East Siberian whitefish (H_2). Divided by a single substitution, it is joined by a new (relative to Fig. 5) star-shaped

structure with a central haplotype (H_37) representing whitefishes from Lake Teletskoye. It includes haplotypes of the whitefish from Lake Teletskoye (H_48) and a portion of the whitefish haplotypes from the Lower Ob River and water bodies of the Taymyr Peninsula (H_31, 33, 34). The second haplogroup (II) includes part of the whitefish haplotypes from the rivers of the Lower Ob River, forming the second star-shaped structure with the central haplotype H_38, directly linked to the central haplotype H_28, consisting of the haplotypes of whitefish from the water bodies of the Taymyr Peninsula. This structure is adjoined by haplotypes of glacial-plain whitefish from the Anabar River (H_16, H_20, H_21, H_25) and haplotypes of the whitefishes from the water bodies of the Taymyr Peninsula (H_23, H_24, H_27, H_29, H_30).

DISCUSSION

According to meristic features, both forms of whitefishes from the Anabar River belong to low-scaled and sparsely-rakered whitefishes. Despite the absence of differences in the meristic features, whitefishes are well distinguished by the morphometric features, which suggest their significant isolation. Sympatric whitefish from the Anabar River are characterized by different rates of linear growth. This fact can be partly explained by their dispersion among the habi-

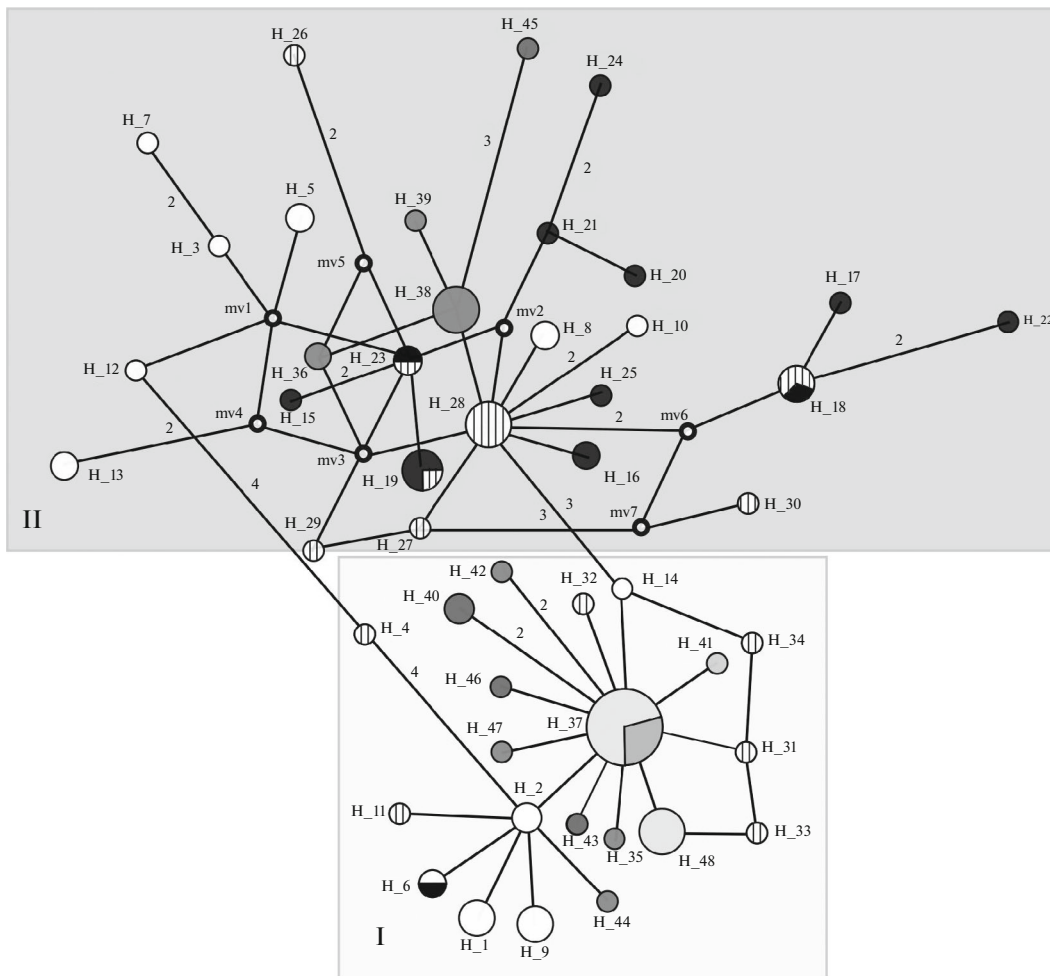


Fig. 6. Median networks of haplotypes of whitefishes from the Anabar River, the Ob River basin, and the water bodies of the Taymyr Peninsula. White circles, haplotypes of East Siberian whitefish; black circles, haplotypes of glacial-plain whitefish; gray circles, Lake Teletskoye; dark gray circles, Lower Ob; vertically hatched circles, haplotypes of whitefish from reservoirs of Taymyr Peninsula. I and II, designated haplogroups. mv1–mv7, undetected or extinct hypothesized haplotypes. Diameter of circles is proportional to haplotype frequency.

tats. It is known that sandy habitats, which are predominant in the Anabar River, have low productivity, and East Siberian whitefish inhabiting the mountain rivers is forced to switch to eating fish, which is generally atypical food for true whitefishes, under low abundance of benthos [7, 35]. We observed a similar feeding behavior in lacustrine-riverine whitefish from Lake Taymyr [18]. Glacial-plain whitefish inhabits the tidal zone, rich with isopods. The same East Siberian whitefish inhabiting the liman grows to rather large size (403 mm), although not as large as glacial-plain whitefish (465 mm). The presence of spawning migration in whitefish found in the mouth of the Anabar River is most probably forced. This fact may be explained by the whitefish inhabiting brackish water unsuitable for breeding.

Both studied haplogroups of whitefishes are characterized by a complex structure of the median network and by the presence of a large number of star-

shaped structures (which is more typical of East Siberian whitefish) and the alternative connections of varying length, which typically appear as a result of reverse or parallel mutations. This structure suggests either prolonged evolution of the whitefish populations included in it under sufficiently variable conditions and with frequent changes in the population number or the presence of several neighbour refugia existing simultaneously on a limited territory, which is more probable. All the populations of Arctic whitefish that we have studied are characterized by high haplotype diversity. Maximum values of h were noted in whitefish populations from the Anabar River, suggesting either the ancientness of populations, which is highly improbable owing to periodic glaciers previously existing in these regions [36, 37], or the opposing distribution and secondary intergradation of the previously isolated forms. The highest nucleotide (π) and haplotype diversity, as well as the average number of

nucleotide differences (k), are found in both ecological forms/species of whitefishes from the Anabar River. In populations of *pidschian*-like whitefish of the Lower Ob and inland water bodies of the Taymyr Peninsula, the values of the intrapopulation diversity of the mtDNA are somewhat lower. This fact probably indicates a significant haplotype exchange between different whitefish haplogroups in the last postglacial period rather than ancientness of the studied populations.

It is obvious that the origin of East Siberian whitefish (haplogroup I, Fig. 6) is closely related to one of two phylogenetic lineages of the whitefishes found in the Ob River basin. The origin of this form/species can be associated with two hypothetical refugia. It is considered that one of them existed in the basin of the Pechora River. It is probable that several neighbour refugia also existed in the basin of the Upper Ob [38, 39]. The median network unambiguously indicates a close connection of the haplotypes of whitefishes from Lake Teletskoye, the whitefishes of the Lower Ob, and East Siberian whitefish from the Anabar River. These populations/forms are derived from a common genetic lineage.

Glacial-plain whitefish (haplogroup II, Fig. 6) has considerably more complex origins and is closely related to several phylogenetic lineages of the whitefish from water bodies of the Taymyr Peninsula: the second Ob refugium and, possibly, the refugium associated with the periglacial Lake Komi. In any case, on the basis of the constructed median network haplotypes we can postulate that the modern glacial-plain whitefish is the result of hybridization between the several phylogenetic lineage/forms/species that inhabit (and preserved) periglacial water bodies of the Arctic during the last glaciation and dispersed along the Arctic Coast [40–42], which eventually led to an increase in its genetic diversity.

Sympatric whitefishes that were morphologically similar to whitefishes from the Anabar River were also found in Lake Taymyr; however, they are known there by different names: *C. l. pidschian natio logaschevi* (morphological analog of East Siberian whitefish) and *C. l. pidschian natio taimyrensis* (morphological analog of glacial-plain whitefish) [43, 44]. Whitefishes from Lake Taymyr somewhat differ in the basic meristic features from the whitefishes from the Anabar River, but these differences can be considered interpopulational [18]. The morphologically similar forms/species of whitefish apparently also inhabit the water bodies located east of the Anabar River. Glacial-plain whitefish or forms/species morphologically close to it were noted in the lower course of the Kolyma River. F.N. Kirillov [17] notes glacial-plain whitefish in the Khroma River, in the lakes of the Yana-Indigirka interfluvial area, and in the lakes of the Sordonnokh Plateau (the upper course of the Indigirka River). *Pidschian*-like whitefish, which is morphologically close to East Siberian whitefish, inhabits the area from the

lower course of the Ob River to the Kolyma River inclusively. It was noted in the Lena River basin from the upper course to the delta and in the Yana, Indigirka, and Kolyma rivers [17]. These facts indicate that, in most of the water bodies of the Siberian Arctic, the two aforementioned forms of whitefish are widespread.

The results of our study demonstrate that the modern systematics of the *C. lavaretus* s. l. complex in no way reflect its natural structure. Study of whitefishes from the Anabar River demonstrated that the sympatric East Siberian and glacial-plain whitefishes, are isolated from each other both at the morpho-ecological and genetic levels. Both ecological forms/species are presently a complex of forms/species that have a complex polyphyletic origin with large participation of reticular microevolutionary scenarios. Definition of the status and phylogenetic relationship of “ecological forms” of the whitefishes from the Anabar River using a complex morphogenetic approach is effective and promotes organizing measures of cataloging and conserving biodiversity and regulation of local fishing in this remote area, where ichthyologic and population genetic researches were not paid enough attention up to day.

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