ISSN 0032-9452, Journal of Ichthyology, 2006, Vol. 46, No. 6, pp. 418–435. © Pleiades Publishing, Inc., 2006.
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Graylings of Baikal Lake Basin (*Thymallus*, Thymallidae): Diversity of Forms and Their Taxonomic Status

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Received June 29, 2005

Abstract—The morphological characters, molecular-genetic features, and patterns of the dorsal fin in different subspecies and forms of Arctic grayling *Thymallus arcticus* populating Lake Baikal and its tributaries, Irkutsk Reservoir, and Lake Khubsugul have been studied. Three groups are discernable. The first includes the white and black Baikal graylings *T. a. baicalensis*, as well as the western Siberian *T. a. arcticus*; the second group is represented by the Kosogol grayling *T. a. nigrescens*, and the third is composed of *T. arcticus* ssp. from the Yakchii lakes (the Verkhnyaya Angara basin) with a phenotype close to graylings populating the upper reaches of the Lena River. All of them are distinguished by some morphological characters, elements of the dorsal fin pattern, and by body coloration. The populations of black Baikal graylings are genetically uniform, and their distinctions from white Baikal graylings are insignificant, which agrees with the absence of a considerable divergence of these forms by a complex of meristic characters. It is assumed that in the black and white Baikal graylings the exchange by genetic information has either ceased quite recently, or persists, although, insignificantly. Some genetic remoteness of the west Siberian grayling from Irkutsk Reservoir and Nizhnyaya Tunguska, closely related to the Baikal grayling, is recorded. The formation of the Khubsugul subspecies is possibly a result of the contact of grayling populations during the rearrangements of the river system in the last glaciation period in the upper reaches of Yenisei and Selenga in Mongolia. The habitation in the Baikal system of the Upper Lena graylings indicates a connection between the Lena and Baikal basins in the past. The results of a multivariate analysis of meristic characters and the sequences of mitochondrial DNA confirm the conclusion made by Svetovidov (1931, 1936), concerning the absence of grounds to assign a species status to the Baikal forms.

DOI: 10.1134/S0032945206060026

Graylings (Thymallidae) are among the most interesting groups demonstrating a high level of polymorphism. Under different conditions of habitation they manifest diverse adaptive abilities, thereby reflecting a wide range of genotype responses. For this reason issues of their taxonomy have remained for a long time unsolved and are often debatable.

The diversity, taxonomic status, origin, and dispersal routes of graylings from Lake Baikal have been discussed for 230 years, since Georgi (1775) first identified the Baikal grayling as a species *Salmo thymallus*. For a very long period, several opinions regarding the diversity of forms in Baikal and the water bodies of its basin have been expressed (Dybowski, 1874; Dybowski, 1876; Berg, 1900, 1916, 1923, 1932, 1948; Gratsianov, 1902; Dorogostaiskii, 1923; Svetovidov, 1931, 1936; Tugarina, 1958, 1981, 2001, 2002; Skurikhina, 1984; Egorov, 1985; Makoedov, 1999; Koskinen et al., 2002; et al.). Two varieties of graylings, black and white, were usually indicated for Baikal. In addition, in the lake itself and in the rivers connected with it, grey grayling, prival'nyi grayling, marsovik, belyak, ledyanka, borozdovik, etc. are visually discerned (Dorogostaiskii, 1923; Tugarina, 1981; Egorov, 1985). Mostly, the above names reflect seasonal variation in the body coloration or in the spatial distribution of forms. Svetovidov (1936) arrived at the conclusion that Baikal is inhabited by a subspecies of *T. arcticus*, the Baikal grayling *T. arcticus baicalensis*, and its ecological form the white grayling *T. a. baicalensis* infrasubspecies *brevipinnis*. Gratsianov (1902) as well as Pivnička and Hensel (1978) considered that graylings in Baikal are represented by only one species *T. baicalensis*. A conclusion on the species status of both forms was made by Tugarina (1981, 2001). In reviews summarizing data on the freshwater fish of Russia and in a few other works, Baikal graylings are indicated either as subspecies forms of *T. a. baicalensis* (Dorofeeva, 1998, 2002) or as independent species *T. baicalensis* and *T. brevipinnis* (Bogutskaya and Naseka, 2004).

As for the water bodies connected with Baikal, it is known that Irkutsk Reservoir, the Angara River, and the Yenisei (except several tributaries in its lower reaches) are populated by a nominative subspecies of *T. a. arcticus* (Svetovidov, 1931, 1936; Egorov, 1985), which, in the opinion of Romanov (2004), is morphologically and phenotypically close to the black Baikal grayling. In the Angara and the Yenisei basin, white and black graylings that populate sites with different current patterns are also recorded (Svetovidov, 1936; Egorov, 1985; Zadelenov and Gulimov, 2000; Romanov, 2004).

In the upper reaches of a tributary of the Verkhnyaya Angara (northern Baikal), a dwarf form of *T. arcticus* was found, with several close characters to graylings populating the upper, middle, and, in part, the lower reaches of the Lena (Knizhin et al., 2006). There is a supposition that the east Siberian grayling *T. a. pallasii* inhabits the upper reaches of one of the biggest tributaries of the lake, the Barguzin River (Matveev and Knizhin, 1996; Elaev et al., 1998), although there is no direct proof.[1]

Lake Khubsugul connected with Baikal via the Selenga River is populated by an endemic subspecies of *T. arcticus*, the Kosogol grayling *T. a. nigrescens* (Dorogostaiskii, 1923; Shatunovskii, 1983; Dorofeeva, 1998, 2002; Tugarina, 2002), considered in some papers as an independent species *T. nigrescens* (Svetovidov, 1936; Berg, 1948; Pivnička and Hensel, 1978; Scott and Crossman, 1998; Bogutskaya and Naseka, 2004). It is unclear which form of *T. arcticus* populates the upper and middle reaches of the Selenga in Mongolia.

The available results of the molecular-genetic studies of Baikal graylings (Skurikhina, 1984; Knizhin et al., 2000; Knizhin et al., 2001; Koskinen et al., 2002) are difficult to compare mainly due to the differences in the methods and the interpretation of the data obtained. The studies of Skurikhina (1984) performed with a DNA-hybridization method permitted the conclusion that black and white graylings are independent species, and the grayling that populates Angara is apparently a hybrid form of the black Baikal and "arctic" graylings. An analysis of the sequences of mitochondrial and nuclear DNA in Baikal graylings and of the adjacent basins, carried out by Koskinen et al. (2002), oppositely revealed no noticeable differentiation in the Baikal forms.

It follows that no unambiguous conclusion regarding the taxonomic status and phylogenetic relations of graylings of the Baikal drainage system has been made as of yet. This paper provides additional materials on the morphology and genetics of Baikal forms of graylings, as well as specific features of their dorsal fin pattern. The purpose of this paper, in regard to the new data, is to assess the genetic and phenetic diversity of graylings, their taxonomic status, to establish their origin, and the routes of their dispersal in Baikal and the water bodies connected with it.

MATERIAL AND METHODS

The present study is based on grayling samples taken from 1998 to 2004 from water bodies of the Baikal basin. Graylings were caught using gill nets with 20- to 40-mm of mesh, during the spawning period in the mouths of the following rivers: Molokon, Frolikha, Shegnanda, Tompuda, Selenga, and Taltsinka (Irkutsk Reservoir), as well as off Cape Ukhan; graylings were also caught during the feeding period in the following locations: off Cape Khoboi (Olkhon Island), Cape Elokhin, B. Ushkanii Island, in Dagar Bay (Dagary), Lake Sobolinoe (the Snezhnaya River basin, southern Baikal), Yakchii lakes (the Verkhnyaya Angara basin), and Lake Khubsugul (Mongolian People's Republic) (Fig. 1). For a comparison the analysis included the authors' materials on the morphology and genetics of the grayling population from the Nizhnyaya Tunguska River (the Yenisei basin).

During an analysis of morphometric and meristic characters, we followed Pravdin's recommendations (1966); all estimates were obtained by one operator. The indices of the measurements were calculated with respect to the fork length (L_{Sm}). Additional data on the methods of morphological analysis are provided in the previously published paper of Knizhin et al. (2004).

The description of the external characters was made on new material. Particular attention was paid to the pattern and form of the dorsal fin, since it was demonstrated that these characters can be successfully used for taxa differentiation of a species rank (Makoedov, 1983, 1999; Antonov, 2004; Knizhin et al., 2004). Dried fins of fish and photographs of this were used for making illustrations.

A total of 436 grayling individuals were collected and treated, including 265 individuals of the black grayling, 66 individuals of the white grayling, 38 individuals of the west Siberian grayling, 35 individuals of the Kosogol grayling, and 32 individuals of the Upper Lena grayling.[2]

Statistic analysis and comparison of the samples were made by conventional methods (Plokhinskii, 1970; Rokitskii, 1973) using Statistica software 5.5A (Borovikov and Borovikov, 1998) and SPSS version 8.0. For an analysis of morphological characters by the principal component method (PCA) the variation–covariation matrix was used. The significance of differences and their value were determined by *t*-test at the level of $p \leq 0.001$ and by the CD coefficient (Mayr et al., 1956), respectively.

Total DNA was isolated by a standard method of high-salt extraction (Sambrook et al., 1989). The mito-

[1] The taxonomic status of a grayling discovered in the upper reaches of the Barguzin River has not been established as of yet and mentioning it as a subspecies, east Siberian grayling *T. a. pallasii*, is not justified.

[2] The taxonomic status of the form has not yet been established; therefore, its preliminary name is used.

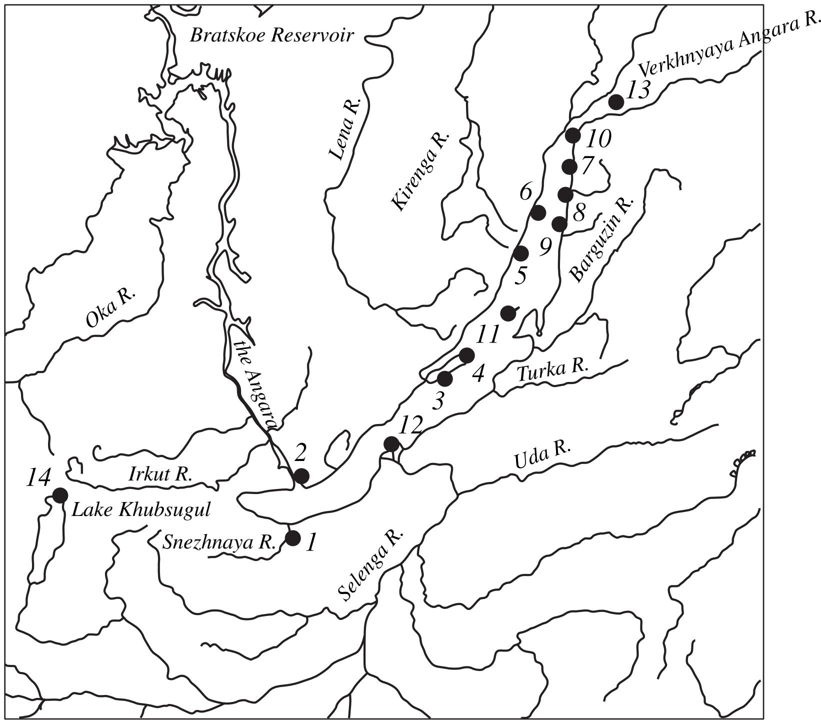

Fig. 1. Map-scheme of the study area: (*1*) Lake Sobolinoe; (*2*) the Taltsinka River; (*3*) Cape Ukhan; (*4*) Cape Khoboi; (*5*) Cape Elokhin; (*6*) the Molokon River; (*7*) the Frolikha River; (*8*) the Tompuda River; (*9*) the Shegnanda River; (*10*) Dagar Bay (Dagary); (*11*) Ushkan'i Islands; (*12*) the Selenga River; (*13*) Yakchii lakes; (*14*) Lake Khubsugul.

chondrial gene ATP VI was amplified by a polymerase chain reaction (PCR), using primers L8558 and H9208 cited in the paper of Giuffra et al. (1994). The PCR conditions (25 μl of reaction) were as follows: each reaction involved 19 μl of H_2O, 2.5 μl of tenfold buffer of Promega Co., 0.5 μl of 10 mM of each primer, 1.5 μl of 25 mM $MgCl_2$, 0.5 μl of 10 mM of dNTP, 0.1 μl of Taq DNA of polymerase of Promega Co., and 0.5 μl of 100 ng/μl of DNA. The cycle of the parameters was as follows: initial denaturation at 94°C for 3 min, denaturation at 94°C for 40 s, annealing at 53°C, and synthesis at 72°C for 40 s. A total of 30 cycles were performed. The amplificated DNAs were purified using a NucleoSpin Extract Kit (Machery-Nagel). About 100 ng of the purified product of PCR were used in the sequenation reaction cycles according to the ABI PRISM BigDye Terminator protocol. Sequences were determined by the ABI-3100 automatic sequenator.

DNA sequences were analyzed in 65 grayling individuals from nine populations: the Molokon River, the Tompuda River, the Shegnanda River, the Selenga River, Ukhan Cape, Sobolinoe Lake, the Taltsinka River, the Nizhnyaya Tunguska River, and Lake Khubsugul.[3] The genetic relation between them was assessed from the Reynolds distances (Reynolds et al., 1983) calculated on the basis of the paired values of the F_{st} test, using the Arlequin program (Schneider et al., 2000), according to the following formula:

$$D = -\ln(1 - F_{st}).$$

The obtained matrix of distances was analyzed by the nearest neighbors method, and the construction of the tree (NEIGHBOUR) used PHYLIP 3.62 software (Felsenstein, 1992).

RESULTS

Pattern and Form of Dorsal Fin

Previous papers provided a detailed description of the body coloration of graylings inhabiting Lake Baikal and its tributaries (Dorogostaiskii, 1923; Svetovidov, 1931, 1936; Tugarina, 1981, 2001, 2002), whereas the pattern of the dorsal fin was considered less comprehensively. The characters cited below can be used for differentiating the forms studied.

West Siberian grayling. Dorsal fin of medium sizes. Its posterior edge in males deep and broad. In the lowered position, only in large individuals, it can almost extend to the adipose fin. Fin insertion small. Along the upper edge, from the middle to the last rays, there runs a red claret gradually widening fringe. Spots are mainly concentrated in the posterior part. Here the fringe fuses with the upper row of spots forming broad and short bands with uneven outline. Rows incomplete,

[3] The molecular-genetic studies of graylings from the Yakchii lakes are not discussed in this paper because the study has not been completed.

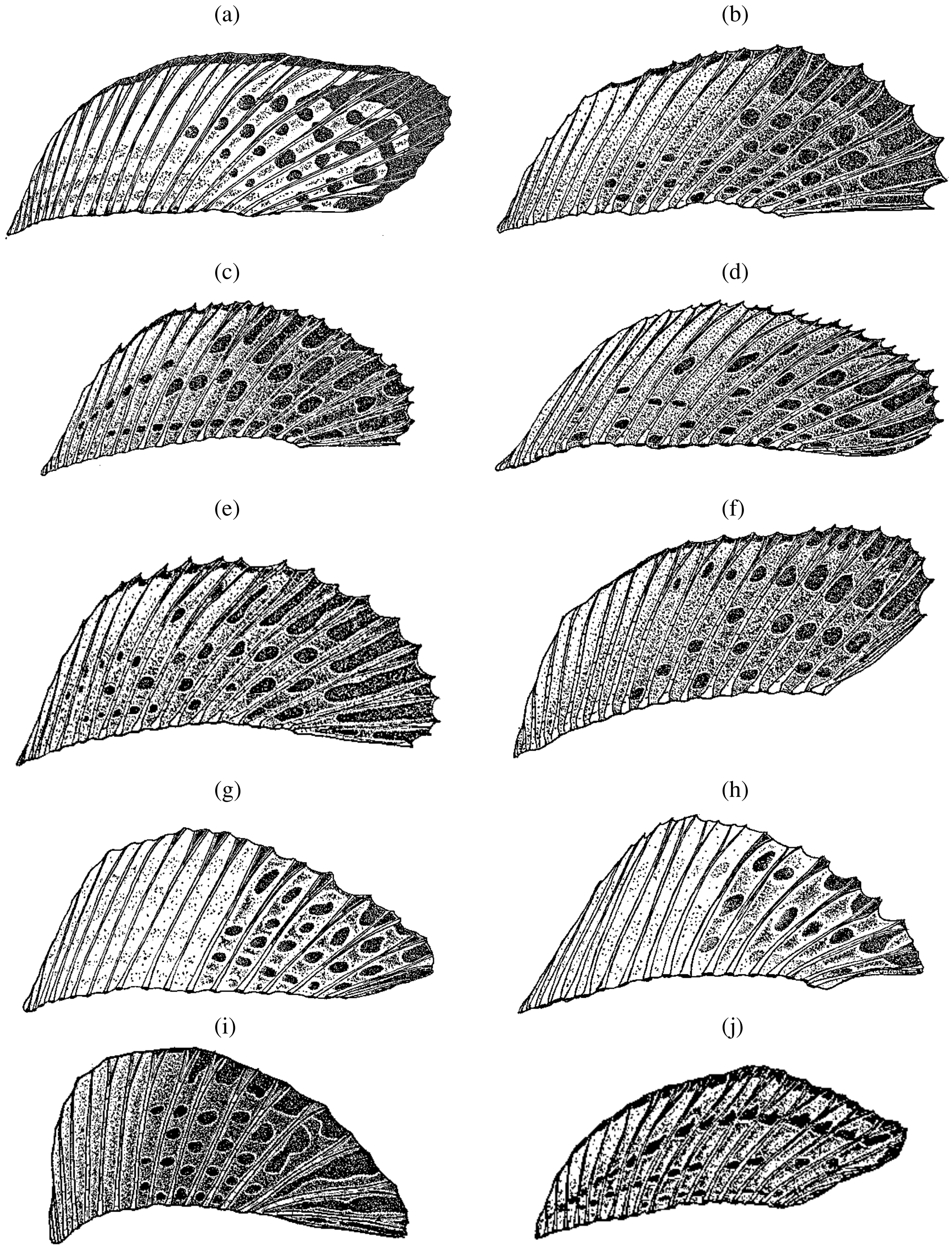

Fig. 2. Variants of dorsal fin patterns in *Thymallus* graylings of the studied subspecies and forms of the Baikal basin. The west Siberian grayling *T. a. arcicus*: (a) the Nizhnyaya Tunguska River, (b) the Taltsinka River; the black Baikal grayling *T. a. baicalensis*: (c) the Frolikha River, (d) Cape Elokhin, (e) Lake Sobolinoe, (f) Dagar Bay; white Baikal grayling *T. a. baicalensis* infrasubspecies *brevipinnis*: (g) Dagar Bay, (h) the Selenga River; the Kosogol grayling *T. a. nigrescens*: (i) Lake Khubsugul; the Upper Lena grayling; (j) Yakchii lakes.

no more than four. Outside water, spots on the fin have an intense turquoise-violet shade. General background dark (Figs. 2a and 2b).

Black Baikal grayling. The form and pattern of dorsal fin almost the same as in the west Siberian grayling. In many individuals in the anterior part of the fin an ascending row of small oval spots almost extending to its middle can be clearly discerned. The Angara–Yenisei graylings differ only in having a smaller fin depth in its posterior part (Figs. 2c, 2d, 2e, and 2f).

White Baikal grayling. Dorsal fin small, in a lowered state does not extend to the adipose fin. Its posterior edge is not deeper than the anterior part. Insertion small. The anterior part of the fin has no pattern; in the posterior part there are generally three to four rows of pale-red claret color, often with uneven outline. From the middle of the fin, along its upper edge, passes a narrow crimson fringe. The entire space between the branched ends of rays of its posterior part has the same coloration. Background light grey (Figs. 2g and 2h).

Kosogol grayling. Dorsal fin small. Its posterior edge generally not deeper than the anterior and does not extend to the adipose fin. Spots located in the posterior part, red claret, oval with uneven edges. Number of rows three or four. The fringe fusing with upper spots forms broad protrusions continuing inward, the fin up to the middle of rays and lower. Background dark (Fig. 2i).

The Upper Lena grayling. Dorsal fin small, its posterior edge in males deeper than the anterior. Along the insertion there are three to four complete rows of small, oval, red, claret spots. The fringe of the same color gradually widening extends to the end of last rays and never fuses with spots of the underlying row. The upper row of spots forms a complete band and is slightly separated from other rows. Background dark grey (Fig. 2j).

Comparative remarks. The black Baikal grayling, similarly to the populations of west Siberian subspecies from the Taltsinka and Nizhnyaya Tunguska rivers, is characterized by similarity not only in the dorsal fin pattern, but also in the body coloration. The closeness of these forms by the aforementioned characters is noted in papers by Svetovidov (1931, 1936), Tugarina (1981), and Romanov (2004).

The white grayling has common features with the black and west Siberian graylings, although to a smaller extent, in the dorsal fin pattern. It is mainly manifested in the location of spots and the number of their rows. However, there are characters typical of this form only. Spots on the dorsal fin of mature individuals of white graylings are pale without the turquoise-violet shade typical of black and west Siberian graylings. A specific feature of the white graylings is the red crimson coloration of the entire space between the branched ends of rays in the posterior end of the fin.

The Kosogol grayling, having a relatively small dorsal fin, in the location and form of spots, resembles the black, white, and west Siberian graylings.

Graylings from the Yakchii lakes have another pattern typical of the fish inhabiting the upper, middle, and most of the lower reaches of the Lena (Knizhin et al., 2006).

Concerning the depth of the posterior part of the dorsal fin, there are differences between male white and black graylings, but none between the females (Svetovidov, 1931, 1936; Tugarina, 1981). Maximum fin sizes among all the analyzed populations are recorded in the west Siberian grayling from the Taltsinka River.

Morphological Analysis

Assessments of morphometric and meristic characters of grayling populations from water bodies of the Lake Baikal basin are listed in Tables 1 and 2.

At the first stage, 14 samples of graylings relating to the aforementioned forms were studied by 12 meristic characters using the principal component method (PCA). The first two main components explain 74.9% of the total dispersion. The loadings of eigenvectors are shown in Table 3. The highest load on the first main component is made by the number of scales in the lateral line, and the highest load on the second component is made by the number of pyloric caeca and the number of gill rakers (Table 3). The scatter plot (Fig. 3a) shows the separation of all individuals into three groups. The first is formed of samples of the black and white Baikal graylings, as well as of graylings from the Taltsinka River (Irkutsk Reservoir); the second is formed of the Kosogol grayling from Lake Khubsugul; and the third is formed of the Upper Lena grayling from the Yakchii lakes.

Having excluded from analysis the Khubsugul and Upper Lena graylings, one can see the absence of a noticeable divergence between the samples of the black, white, and west Siberian graylings comprising of a single group (Fig. 3b). In this case the first two principal components explain 68.0% of the total dispersion. The greatest loadings of eigenvectors on the first principal component, as during the analysis of 14 populations, are made by the number of scales in the lateral line, and on the second component are made by the number of pyloric caeca and the number of vertebrae (Table 3).

A comparison of graylings forms from the Baikal system by the CD coefficient confirms the difference between white and black Baikal graylings and the Khubsugul and Upper Lena graylings in several characters (Table 4). According to meristic characters, the size of the CD coefficient for the black Baikal grayling with respect to all the studied forms, except the Upper Lena form, exceeds the formal subspecies level by the number of gill rakers. From the graylings of the Yakchii lakes, the black Baikal grayling differs in the number of scales in the lateral line and from the Kosogol grayling, in addition to the number of gill rakers, and in the number of pyloric caeca. Between the Upper Lena grayling and the white grayling, considerable differences are recorded in the number of scales and branchiostegal rays. From the black and Kosogol graylings, the Upper Lena grayling differs only in the number of gill rakers.

From the morphometric characters, the black and white graylings differ in the depth of the dorsal fin and the length of paired fins, which agrees with the data previously obtained by Tugarina (1981, 2001) and

Table 1. Morphometric and meristic characters of populations of the black grayling *Thymallus arcticus baicalensis* from the Lake Baikal basin

Characters	Water body (sample size, individuals)						
	Frolikha River ($n = 32$)	Tompuda River ($n = 50$)	Shegnanda River ($n = 30$)	Molokon River ($n = 31$)	Cape Ukhan ($n = 36$)	Cape Elokhin ($n = 18$)	Lake Sobolinoe ($n = 48$)
L_{Sm}, mm	339 / 298–405	314 / 227–428	354 / 292–417	346 / 293–443	339 / 303–386	300 / 260–333	271 / 221–321
In % of L_{Sm}							
l_1	95.6 ± 0.07 / 0.39, 94.4–96.4	95.4 ± 0.08 / 0.57, 93.5–97.0	95.5 ± 0.11 / 0.61, 94.3–97.0	95.6 ± 0.09 / 0.49, 94.5–96.8	95.5 ± 0.09 / 0.53, 93.9–96.7	95.2 ± 0.11 / 0.45, 94.3–96.0	95.2 ± 0.10 / 0.68, 91.6–96.3
l_2	77.8 ± 0.25 / 1.41, 75.0–80.0	77.3 ± 0.18 / 1.30, 74.8–79.9	77.6 ± 0.23 / 1.26, 75.4–80.3	78.2 ± 0.17 / 0.97, 75.9–79.7	78.3 ± 0.16 / 0.97, 75.9–80.4	77.1 ± 0.21 / 0.89, 74.7–78.2	78.7 ± 0.15 / 1.05, 75.2–80.8
ao	6.2 ± 0.07 / 0.37, 5.4–7.1	6.2 ± 0.05 / 0.33, 5.4–6.9	6.2 ± 0.08 / 0.42, 5.5–7.2	6.1 ± 0.07 / 0.39, 4.8–6.9	6.0 ± 0.06 / 0.34, 5.4–6.6	6.0 ± 0.06 / 0.27, 5.5–6.7	5.9 ± 0.05 / 0.35, 5.3–6.5
o	4.3 ± 0.03 / 0.18, 4.0–4.8	4.3 ± 0.03 / 0.22, 3.8–4.8	4.2 ± 0.04 / 0.22, 3.9–4.8	4.1 ± 0.04 / 0.22, 3.2–4.5	4.2 ± 0.07 / 0.41, 3.7–6.3	4.2 ± 0.06 / 0.26, 3.7–4.9	4.2 ± 0.03 / 0.18, 3.7–4.5
f	10.0 ± 0.07 / 0.42, 9.3–11.0	9.9 ± 0.06 / 0.41, 9.1–11.2	9.9 ± 0.06 / 0.35, 9.3–10.7	9.9 ± 0.09 / 0.49, 7.7–10.5	9.7 ± 0.05 / 0.31, 9.2–10.3	9.9 ± 0.11 / 0.48, 9.3–11.7	9.3 ± 0.06 / 0.38, 8.6–10.1
c	19.5 ± 0.09 / 0.49, 18.5–20.8	19.5 ± 0.09 / 0.64, 18.2–21.3	19.5 ± 0.08 / 0.46, 18.6–20.4	19.2 ± 0.16 / 0.88, 15.2–20.2	19.0 ± 0.09 / 0.57, 17.7–20.2	19.3 ± 0.16 / 0.69, 18.6–21.9	18.9 ± 0.07 / 0.48, 18.1–19.9
cH	14.3 ± 0.09 / 0.52, 13.4–15.6	14.1 ± 0.11 / 0.75, 12.8–16.0	14.3 ± 0.08 / 0.46, 13.5–15.3	13.9 ± 0.14 / 0.79, 10.7–15.2	13.8 ± 0.08 / 0.48, 12.9–15.0	13.9 ± 0.17 / 0.70, 13.2–16.2	13.9 ± 0.07 / 0.49, 13.2–16.0
ch	10.1 ± 0.08 / 0.48, 9.2–11.3	10.1 ± 0.07 / 0.52, 9.2–11.8	10.3 ± 0.08 / 0.43, 9.4–11.2	9.9 ± 0.11 / 0.60, 7.9–11.2	9.8 ± 0.09 / 0.52, 8.9–11.1	10.0 ± 0.13 / 0.55, 9.5–11.9	10.1 ± 0.06 / 0.39, 9.4–11.2
k	5.9 ± 0.08 / 0.44, 4.9–6.7	6.1 ± 0.05 / 0.39, 5.1–6.7	5.9 ± 0.09 / 0.51, 5.0–6.7	5.8 ± 0.08 / 0.44, 4.8–6.6	5.7 ± 0.07 / 0.41, 4.7–6.5	6.2 ± 0.08 / 0.32, 5.8–7.1	5.8 ± 0.06 / 0.45, 5.0–6.9
lmx	5.9 ± 0.05 / 0.30, 5.2–6.6	5.8 ± 0.05 / 0.35, 5.3–6.7	6.0 ± 0.06 / 0.33, 5.5–7.0	5.7 ± 0.06 / 0.31, 4.5–6.2	5.7 ± 0.04 / 0.23, 5.2–6.2	5.7 ± 0.06 / 0.26, 5.3–6.4	5.4 ± 0.03 / 0.23, 4.9–5.9
i/lmx	1.9 ± 0.03 / 0.19, 1.5–2.3	1.9 ± 0.03 / 0.18, 1.6–2.3	1.9 ± 0.03 / 0.19, 1.5–2.2	1.9 ± 0.03 / 0.19, 1.4–2.3	1.9 ± 0.03 / 0.19, 1.5–2.2	1.9 ± 0.04 / 0.17, 1.7–2.4	1.8 ± 0.03 / 0.17, 1.5–2.2
lmd	9.9 ± 0.08 / 0.47, 8.9–10.7	9.9 ± 0.06 / 0.44, 8.9–11.1	10.0 ± 0.07 / 0.40, 9.2–10.8	9.8 ± 0.09 / 0.52, 7.8–10.4	9.6 ± 0.07 / 0.44, 8.6–10.5	9.8 ± 0.08 / 0.36, 9.2–10.8	9.3 ± 0.07 / 0.49, 8.4–10.6
H	20.1 ± 0.22 / 1.27, 18.1–22.8	19.6 ± 0.17 / 1.20, 17.1–22.1	20.1 ± 0.17 / 0.91, 18.6–22.5	19.9 ± 0.22 / 1.20, 17.8–22.7	20.1 ± 0.22 / 1.33, 18.07–23.0	19.7 ± 0.28 / 1.17, 18.2–23.7	20.6 ± 0.15 / 1.04, 18.4–22.8
h	6.3 ± 0.04 / 0.20, 6.0–6.6	6.3 ± 0.05 / 0.38, 4.4–7.3	6.3 ± 0.05 / 0.29, 5.8–7.1	6.3 ± 0.06 / 0.33, 5.1–6.8	6.1 ± 0.05 / 0.29, 5.7–6.7	6.2 ± 0.06 / 0.24, 5.7–6.8	6.7 ± 0.04 / 0.25, 5.9–7.0

Table 1. (Contd.)

Characters	Water body (sample size, individuals)						
	Frolikha River (*n* = 32)	Tompuda River (*n* = 50)	Shegnanda River (*n* = 30)	Molokon River (*n* = 31)	Cape Ukhan (*n* = 36)	Cape Elokhin (*n* = 18)	Lake Sobolinoe (*n* = 48)
w	11.6 ± 0.16 / 0.90, 9.5–13.5	11.7 ± 0.12 / 0.88, 9.6–14.1	11.6 ± 0.23 / 1.24, 9.2–13.6	11.7 ± 0.18 / 0.98, 9.6–13.7	11.6 ± 0.17 / 1.02, 10.1–13.9	12.1 ± 0.15 / 0.62, 11.0–13.6	12.6 ± 0.15 / 1.07, 10.8–15.1
aD	35.0 ± 0.18 / 1.00, 32.9–36.9	34.8 ± 0.13 / 0.95, 33.1–36.9	35.1 ± 0.18 / 0.98, 32.7–37.4	34.8 ± 0.21 / 1.18, 31.9–38.2	34.3 ± 0.14 / 0.82, 32.5–36.4	34.7 ± 0.19 / 0.79, 33.6–37.1	34.4 ± 0.15 / 1.07, 31.9–38.9
pD	42.8 ± 0.28 / 1.60, 39.8–45.5	41.8 ± 0.20 / 1.42, 39.1–45.0	42.0 ± 0.27 / 1.46, 39.5–45.4	42.8 ± 0.24 / 1.31, 40.0–45.2	43.2 ± 0.17 / 1.04, 41.1–45.1	42.4 ± 0.36 / 1.53, 39.6–44.8	42.9 ± 0.16 / 1.14, 40.0–46.6
aA	72.1 ± 0.23 / 1.33, 68.7–74.4	71.7 ± 0.17 / 1.18, 69.1–74.5	72.1 ± 0.22 / 1.23, 69.2–74.7	71.7 ± 0.19 / 1.06, 69.7–74.0	71.6 ± 0.19 / 1.16, 68.8–75.2	70.9 ± 0.29 / 1.22, 68.5–73.0	71.3 ± 0.13 / 0.92, 67.9–73.8
aV	47.8 ± 0.21 / 1.19, 45.2–50.6	47.8 ± 0.17 / 1.19, 45.0–50.3	47.7 ± 0.19 / 1.05, 45.2–49.8	47.0 ± 0.20 / 1.09, 44.7–49.0	46.9 ± 0.20 / 1.21, 44.8–50.0	46.5 ± 0.28 / 1.18, 44.9–49.5	46.9 ± 0.14 / 0.96, 43.9–48.9
lp	16.5 ± 0.13 / 0.73, 14.5–17.6	16.9 ± 0.14 / 1.01, 14.5–19.0	16.4 ± 0.16 / 0.89, 14.5–18.2	16.2 ± 0.14 / 0.79, 13.5–17.2	16.6 ± 0.11 / 0.66, 15.2–17.9	17.3 ± 0.12 / 0.51, 15.7–17.9	16.8 ± 0.12 / 0.85, 13.0–19.1
PV	30.0 ± 0.23 / 1.28, 27.5–32.8	29.7 ± 0.19 / 1.33, 25.8–32.0	29.8 ± 0.21 / 1.12, 27.0–31.9	29.6 ± 0.22 / 1.25, 26.3–32.0	29.9 ± 0.15 / 0.88, 27.5–31.6	28.8 ± 0.31 / 1.31, 25.8–31.4	29.7 ± 0.15 / 1.05, 27.0–31.7
VA	25.2 ± 0.23 / 1.28, 22.3–27.6	25.3 ± 0.17 / 1.19, 22.7–28.7	25.3 ± 0.23 / 1.25, 23.2–27.9	25.5 ± 0.17 / 0.96, 24.0–27.8	25.5 ± 0.19 / 1.17, 23.5–28.4	25.2 ± 0.38 / 1.60, 22.6–28.2	25.3 ± 0.18 / 1.22, 21.4–27.2
lD	19.3 ± 0.21 / 1.18, 17.2–23.3	19.4 ± 0.16 / 1.14, 16.6–21.6	19.5 ± 0.22 / 1.20, 17.1–21.6	19.1 ± 0.17 / 0.95, 17.1–21.1	19.3 ± 0.15 / 0.90, 17.3–20.9	18.9 ± 0.22 / 0.95, 17.3–21.2	19.6 ± 0.19 / 1.29, 16.6–23.9
hD_1	11.1 ± 0.14 / 0.77, 9.4–13.4	11.4 ± 0.12 / 0.87, 9.7–13.9	11.5 ± 0.17 / 0.92, 9.2–13.8	11.2 ± 0.17 / 0.91, 8.9–13.8	10.8 ± 0.17 / 1.00, 8.8–13.0	11.2 ± 0.24 / 1.01, 9.1–12.8	11.5 ± 0.19 / 1.34, 8.8–14.4
hD_2	10.2 ± 0.54 / 3.07, 5.9–18.6	10.9 ± 0.33 / 2.33, 7.8–16.7	11.9 ± 0.49 / 2.66, 7.8–16.6	10.8 ± 0.44 / 2.47, 7.4–16.4	9.2 ± 0.31 / 1.86, 6.6–14.8	9.7 ± 0.46 / 1.93, 6.6–13.6	10.1 ± 0.26 / 1.82, 6.1–14.1
lA	8.5 ± 0.10 / 0.57, 7.4–10.3	8.3 ± 0.06 / 0.45, 7.4–9.6	8.7 ± 0.10 / 0.54, 7.6–9.8	8.5 ± 0.12 / 0.66, 6.1–9.7	8.4 ± 0.11 / 0.66, 6.9–9.9	8.1 ± 0.10 / 0.44, 7.2–8.9	8.3 ± 0.07 / 0.52, 7.2–9.3
hA	10.9 ± 0.19 / 1.09, 9.0–12.6	10.7 ± 0.13 / 0.90, 9.0–13.3	10.9 ± 0.21 / 1.13, 8.8–13.1	11.0 ± 0.17 / 0.97, 9.33–13.0	10.8 ± 0.18 / 1.06, 8.9–12.7	10.6 ± 0.20 / 0.86, 9.5–12.4	11.1 ± 0.13 / 0.89, 8.6–13.1
lP	15.7 ± 0.18 / 1.03, 13.3–17.5	16.0 ± 0.09 / 0.67, 14.7–17.6	16.4 ± 0.12 / 0.67, 14.8–17.9	15.9 ± 0.14 / 0.80, 14.6–17.8	15.6 ± 0.17 / 1.01, 12.8–17.5	15.5 ± 0.26 / 1.10, 13.4–17.2	15.0 ± 0.10 / 0.71, 13.3–16.3
lV	13.9 ± 0.17 / 0.97, 11.9–15.8	14.5 ± 0.11 / 0.79, 12.6–16.6	14.4 ± 0.15 / 0.80, 12.6–16.4	14.1 ± 0.16 / 0.87, 12.3–16.0	13.2 ± 0.14 / 0.85, 11.21–15.0	13.8 ± 0.22 / 0.93, 12.3–15.2	14.5 ± 0.12 / 0.86, 12.9–17.1

Table 1. (Contd.)

Characters	Water body (sample size, individuals)						
	Frolikha River (n = 32)	Tompuda River (n = 50)	Shegnanda River (n = 30)	Molokon River (n = 31)	Cape Ukhan (n = 36)	Cape Elokhin (n = 18)	Lake Sobolinoe (n = 48)
	Meristic characters						
ll	$\frac{99.7 \pm 0.66}{3.72, 94–108}$	$\frac{99.5 \pm 0.68}{4.79, 88–110}$	$\frac{100.9 \pm 0.56}{3.05, 93–106}$	$\frac{99.3 \pm 0.70}{3.91, 91–108}$	$\frac{99.2 \pm 0.57}{3.39, 92–105}$	$\frac{98.9 \pm 0.86}{3.73, 94–108}$	$\frac{98.9 \pm 0.56}{3.89, 91–107}$
D_1	$\frac{7.5 \pm 0.14}{0.79, 6–10}$	$\frac{7.8 \pm 0.10}{0.71, 7–10}$	$\frac{7.2 \pm 0.11}{0.63, 6–9}$	$\frac{7.5 \pm 0.15}{0.84, 6–10}$	$\frac{7.5 \pm 0.11}{0.64, 6–9}$	$\frac{7.8 \pm 0.18}{0.77, 7–9}$	$\frac{7.6 \pm 0.10}{0.73, 6–9}$
D_2	$\frac{12.1 \pm 0.14}{0.78, 10–13}$	$\frac{12.5 \pm 0.12}{0.88, 11–15}$	$\frac{12.6 \pm 0.17}{0.95, 10–14}$	$\frac{12.5 \pm 0.14}{0.80, 11–14}$	$\frac{12.6 \pm 0.15}{0.91, 11–14}$	$\frac{12.7 \pm 0.19}{0.85, 11–14}$	$\frac{12.6 \pm 0.12}{0.84, 10–14}$
D	$\frac{19.7 \pm 0.17}{0.98, 18–23}$	$\frac{20.4 \pm 0.11}{0.77, 19–22}$	$\frac{19.9 \pm 0.17}{0.91, 18–22}$	$\frac{20.0 \pm 0.14}{0.80, 19–22}$	$\frac{20.2 \pm 0.16}{0.94, 19–22}$	$\frac{20.5 \pm 0.19}{0.82, 19–22}$	$\frac{20.2 \pm 0.12}{0.85, 19–23}$
P	$\frac{14.9 \pm 0.15}{0.84, 14–17}$	$\frac{14.7 \pm 0.09}{0.66, 13–16}$	$\frac{14.6 \pm 0.10}{0.54, 14–16}$	$\frac{14.8 \pm 0.11}{0.61, 14–16}$	$\frac{15.0 \pm 0.12}{0.74, 14–17}$	$\frac{14.8 \pm 0.17}{0.74, 14–16}$	$\frac{14.6 \pm 0.08}{0.57, 13–16}$
V	$\frac{9.9 \pm 0.10}{0.54, 8–11}$	$\frac{9.8 \pm 0.06}{0.45, 9–11}$	$\frac{9.7 \pm 0.11}{0.62, 8–11}$	$\frac{9.7 \pm 0.11}{0.62, 8–11}$	$\frac{9.7 \pm 0.07}{0.43, 9–10}$	$\frac{9.8 \pm 0.09}{0.41, 9–10}$	$\frac{9.7 \pm 0.06}{0.42, 9–10}$
A_1	$\frac{4.3 \pm 0.10}{0.59, 3–5}$	$\frac{4.5 \pm 0.07}{0.50, 4–5}$	$\frac{4.3 \pm 0.10}{0.53, 3–5}$	$\frac{4.4 \pm 0.09}{0.49, 4–5}$	$\frac{4.4 \pm 0.08}{0.49, 4–5}$	$\frac{4.4 \pm 0.11}{0.50, 4–5}$	$\frac{3.9 \pm 0.02}{0.14, 3–4}$
A_2	$\frac{8.7 \pm 0.11}{0.61, 7–10}$	$\frac{8.9 \pm 0.09}{0.66, 8–11}$	$\frac{9.1 \pm 0.09}{0.50, 8–10}$	$\frac{8.9 \pm 0.12}{0.69, 8–11}$	$\frac{9.1 \pm 0.12}{0.70, 8–11}$	$\frac{9.0 \pm 0.13}{0.56, 8–10}$	$\frac{8.7 \pm 0.09}{0.62, 8–10}$
sb	$\frac{20.2 \pm 0.19}{1.09, 18–23}$	$\frac{20.7 \pm 0.21}{1.50, 17–23}$	$\frac{20.5 \pm 0.25}{1.36, 18–23}$	$\frac{20.5 \pm 0.21}{1.16, 18–23}$	$\frac{20.6 \pm 0.19}{1.14, 18–23}$	$\frac{20.4 \pm 0.37}{1.63, 16–23}$	$\frac{20.6 \pm 0.15}{1.07, 19–23}$
rb	$\frac{9.3 \pm 0.12}{0.69, 8–11}$	$\frac{9.3 \pm 0.08}{0.58, 8–10}$	$\frac{9.3 \pm 0.10}{0.54, 8–10}$	$\frac{9.1 \pm 0.11}{0.61, 8–10}$	$\frac{9.5 \pm 0.08}{0.50, 9–10}$	$\frac{9.3 \pm 0.13}{0.58, 8–10}$	$\frac{9.4 \pm 0.08}{0.53, 8–10}$
vert.	$\frac{53.0 \pm 0.17}{0.90, 52–55}$	$\frac{55.9 \pm 0.25}{1.77, 52–59}$	$\frac{53.0 \pm 0.13}{0.73, 52–54}$	$\frac{53.3 \pm 0.14}{0.78, 52–55}$	$\frac{53.1 \pm 0.18}{1.07, 52–56}$	$\frac{55.5 \pm 0.25}{1.09, 54–58}$	$\frac{57.8 \pm 0.17}{1.04, 56–60}$
pc	$\frac{15.9 \pm 0.36}{1.92, 12–20}$	$\frac{15.8 \pm 0.29}{2.06, 10–21}$	$\frac{15.3 \pm 0.41}{1.58, 13–18}$	$\frac{15.0 \pm 0.27}{1.52, 12–18}$	$\frac{14.6 \pm 0.41}{2.15, 11–20}$	$\frac{15.7 \pm 0.48}{2.10, 11–19}$	$\frac{14.1 \pm 0.27}{1.69, 12–19}$

Note: L_{Sm}—fork length; l_1—body length; l_2—length to the end of scale cover; ao—snout length; o—horizontal eye diameter; f—postorbital head region; c—head length; cH—head depth at occiput; ch—head depth at eye; k—forehead width; lmx—length of upper jaw; i/lmx—width of upper jaw; lmd—length of lower jaw; H—maximum body depth; h—minimal body depth; w—body thickness; aD—antedorsal distance; pD—postdorsal distance; aA—anteanal distance; aV—anteventral distance; lp—length of caudal peduncle; PV—pectoventral distance; VA—ventroanal distance; lD—length of dorsal fin insertion; hD_1—depth of anterior part of dorsal fin; hD_2—depth of posterior part of dorsal fin; lA—length of anal fin insertion; hA—anal fin depth; lP—length of pectoral fin; lV—length of ventral fin; ll—number of perforated scales in lateral line; D_1—total number of rays in dorsal fin; P—number of branched rays in pectoral fin; V—number of branched rays in ventral fin; A_1—number of nonbranched rays in anal fin; A_2—number of branched rays in anal fin; sb—number of gill rakers; rb—number of branchiostegal rays; vert.—number of vertebrae; pc—number of pyloric caeca. Above the line is the mean value of the character and its error; under the line is the root-mean-square deviation and limits of character variation.

Table 2. Morphometric and meristic characters of populations of *Thymallus* graylings from water bodies of the Baikal basin

Characters	Black grayling	White grayling			West Siberian grayling	Kosogol grayling	Upper Lena grayling
	Cape Khoboi (*n* = 20)	Dagar Bay (*n* = 10)	Ushkanii Island (*n* = 9)	Selenga River (*n* = 47)	Taltsinka River (*n* = 38)	Lake Khubsugul (*n* = 35)	Yakchii lakes (*n* = 32)
L_{Sm}, mm	294 / 228–342	318 / 252–431	300 / 273–369	351 / 242–425	292 / 225–387	275 / 233–333	154 / 133–185
in % of L_{Sm}							
l_1	95.5 ± 0.10 / 0.43, 94.5–96.2	95.4 ± 0.28 / 0.87, 93.9–97.0	95.5 ± 0.25 / 0.75, 93.7–96.4	95.5 ± 0.07 / 0.45, 94.2–96.5	94.6 ± 0.08 / 0.49, 93.4–96.1	95.0 ± 0.08 / 0.45, 94.1–96.2	94.6 ± 0.11 / 0.61, 93.0–95.8
l_2	78.2 ± 0.22 / 0.97, 76.1–79.7	78.5 ± 0.19 / 0.60, 77.8–79.6	78.5 ± 0.31 / 0.94, 77.2–79.9	78.5 ± 0.12 / 0.85, 76.9–80.6	77.3 ± 0.17 / 1.06, 75.8–79.9	78.6 ± 0.19 / 1.15, 75.8–81.7	76.8 ± 0.16 / 0.91, 75.0–78.3
ao	6.3 ± 0.06 / 0.25, 5.8–6.7	5.5 ± 0.08 / 0.27, 5.1–6.1	6.1 ± 0.07 / 0.20, 5.7–6.3	6.1 ± 0.08 / 0.52, 5.3–8.8	6.4 ± 0.04 / 0.24, 5.8–6.8	6.2 ± 0.04 / 0.26, 5.6–6.9	6.0 ± 0.06 / 0.34, 5.3–6.7
o	4.0 ± 0.05 / 0.20, 3.7–4.4	3.9 ± 0.09 / 0.27, 3.5–4.5	3.8 ± 0.06 / 0.18, 3.5–4.1	3.9 ± 0.05 / 0.36, 3.4–5.3	4.5 ± 0.04 / 0.26, 3.9–5.1	3.8 ± 0.05 / 0.27, 3.0–4.6	5.4 ± 0.04 / 0.24, 4.7–5.8
f	10.0 ± 0.06 / 0.27, 9.5–10.4	9.6 ± 0.09 / 0.29, 9.2–10.1	10.0 ± 0.10 / 0.30, 9.7–10.6	10.4 ± 0.12 / 0.80, 9.6–15.1	9.5 ± 0.06 / 0.34, 9.0–10.2	10.5 ± 0.06 / 0.37, 9.8–11.3	10.1 ± 0.06 / 0.32, 9.6–10.8
c	19.4 ± 0.08 / 0.35, 18.7–20.0	18.9 ± 0.16 / 0.49, 17.8–19.5	19.0 ± 0.13 / 0.39, 18.4–19.9	19.3 ± 0.09 / 0.64, 18.1–21.5	19.9 ± 0.08 / 0.49, 18.8–20.8	19.6 ± 0.10 / 0.59, 18.5–21.2	20.6 ± 0.11 / 0.59, 19.8–21.9
cH	13.7 ± 0.12 / 0.53, 12.7–14.6	13.5 ± 0.22 / 0.71, 12.5–14.7	13.0 ± 0.12 / 0.37, 12.5–13.5	14.4 ± 0.07 / 0.46, 13.5–15.3	14.3 ± 0.10 / 0.63, 13.4–16.4	13.9 ± 0.13 / 0.78, 12.5–17.0	14.7 ± 0.10 / 0.54, 13.7–15.9
ch	9.8 ± 0.11 / 0.48, 8.8–10.7	9.5 ± 0.17 / 0.54, 8.8–10.7	9.2 ± 0.12 / 0.37, 8.6–10.0	9.9 ± 0.08 / 0.54, 8.5–11.0	10.1 ± 0.09 / 0.59, 8.7–11.9	9.7 ± 0.09 / 0.53, 8.9–11.3	11.0 ± 0.10 / 0.59, 10.1–12.4
k	6.2 ± 0.06 / 0.26, 5.6–6.6	5.4 ± 0.07 / 0.23, 5.0–5.8	6.0 ± 0.08 / 0.23, 5.7–6.5	6.1 ± 0.05 / 0.34, 5.3–6.8	6.1 ± 0.05 / 0.31, 5.3–6.8	6.0 ± 0.07 / 0.43, 5.5–7.7	6.1 ± 0.04 / 0.25, 5.7–6.8
lmx	5.7 ± 0.06 / 0.25, 5.1–6.1	5.4 ± 0.16 / 0.50, 4.2–6.3	5.5 ± 0.07 / 0.20, 5.3–5.9	5.9 ± 0.05 / 0.31, 5.3–6.7	5.4 ± 0.05 / 0.30, 4.8–6.1	5.5 ± 0.05 / 0.27, 5.0–6.0	6.3 ± 0.05 / 0.26, 5.6–6.9
i/lmx	2.0 ± 0.03 / 0.12, 1.7–2.3	1.7 ± 0.03 / 0.11, 1.6–1.9	1.8 ± 0.03 / 0.10, 1.7–2.0	1.9 ± 0.03 / 0.20, 1.5–2.3	2.0 ± 0.03 / 0.17, 1.4–2.4	2.2 ± 0.02 / 0.14, 1.9–2.5	2.0 ± 0.04 / 0.20, 1.6–2.5
lmd	9.7 ± 0.08 / 0.34, 8.9–10.3	9.2 ± 0.09 / 0.27, 8.7–9.7	9.6 ± 0.09 / 0.27, 9.3–10.1	9.7 ± 0.06 / 0.44, 8.9–10.8	9.8 ± 0.06 / 0.39, 8.9–10.5	9.8 ± 0.07 / 0.39, 9.2–10.7	10.5 ± 0.08 / 0.46, 9.7–11.6
H	20.0 ± 0.26 / 1.15, 17.7–22.1	21.3 ± 0.62 / 1.96, 18.9–24.3	20.1 ± 0.27 / 0.81, 19.0–21.2	21.6 ± 0.21 / 1.44, 17.6–24.5	19.5 ± 0.31 / 1.91, 16.6–24.6	18.2 ± 0.14 / 0.84, 16.2–19.7	18.3 ± 0.20 / 1.10, 16.6–21.6

Table 2. (Contd.)

Characters	Black grayling	White grayling			West Siberian grayling	Kosogol grayling	Upper Lena grayling
	Cape Khoboi (*n* = 20)	Dagar Bay (*n* = 10)	Ushkanii Island (*n* = 9)	Selenga River (*n* = 47)	Taltsinka River (*n* = 38)	Lake Khubsugul (*n* = 35)	Yakchii lakes (*n* = 32)
h	6.1 ± 0.07 0.32, 5.4–6.7	6.1 ± 0.09 0.29, 5.5–6.5	5.9 ± 0.08 0.23, 5.6–6.3	6.3 ± 0.03 0.22, 5.8–7.0	6.6 ± 0.06 0.38, 6.1–7.8	6.5 ± 0.05 0.27, 5.9–7.1	6.9 ± 0.04 0.25, 6.4–7.4
w	11.8 ± 0.15 0.68, 10.6–13.6	11.3 ± 0.28 0.88, 10.1–12.4	12.2 ± 0.21 0.62, 11.1–13.1	13.1 ± 0.15 1.00, 11.3–15.5	12.2 ± 0.10 0.62, 10.6–13.4	11.8 ± 0.16 0.92, 9.0–13.3	12.0 ± 0.20 1.11, 9.3–14.7
aD	35.2 ± 0.23 1.04, 32.6–36.7	34.8 ± 0.18 0.56, 33.9–35.5	35.2 ± 0.38 1.14, 32.8–37.3	35.2 ± 0.14 0.98, 33.0–37.6	34.8 ± 0.14 0.89, 33.0–37.0	34.1 ± 0.18 1.04, 31.5–36.3	34.7 ± 0.16 0.91, 31.7–35.9
pD	42.9 ± 0.30 1.35, 40.7–44.9	43.8 ± 0.32 1.00, 42.1–46.0	43.5 ± 0.53 1.58, 41.5–46.4	43.0 ± 0.18 1.25, 39.9–45.6	42.1 ± 0.19 1.18, 39.2–44.8	44.7 ± 0.23 1.33, 42.4–48.0	41.3 ± 0.21 1.22, 37.4–43.4
aA	71.5 ± 0.27 1.21, 68.2–73.3	71.8 ± 0.19 0.60, 70.7–72.8	71.4 ± 0.42 1.26, 69.0–72.8	71.4 ± 0.17 1.16, 68.6–73.4	69.7 ± 0.18 1.14, 67.4–72.9	70.8 ± 0.21 1.22, 68.5–75.1	71.3 ± 0.23 1.30, 68.4–73.7
aV	47.2 ± 0.31 1.39, 43.6–49.3	48.2 ± 0.21 0.66, 46.9–49.3	47.1 ± 0.34 1.03, 44.8–48.7	47.7 ± 0.14 0.99, 45.3–49.6	45.5 ± 0.17 1.06, 43.5–48.2	46.0 ± 0.17 1.02, 43.4–48.3	45.8 ± 0.23 1.29, 42.7–47.8
lp	17.7 ± 0.21 0.94, 15.3–19.3	16.8 ± 0.14 0.46, 15.9–17.6	17.2 ± 0.18 0.55, 16.0–18.0	16.8 ± 0.11 0.77, 15.4–18.2	18.0 ± 0.13 0.79, 15.5–19.9	17.4 ± 0.15 0.90, 15.5–19.1	15.9 ± 0.16 0.89, 13.9–18.5
PV	30.1 ± 0.30 1.36, 27.3–32.9	29.3 ± 0.38 1.20, 28.1–32.2	28.6 ± 0.36 1.07, 26.4–30.2	30.5 ± 0.22 1.52, 26.7–34.0	27.5 ± 0.20 1.24, 24.6–30.2	27.4 ± 0.20 1.16, 25.3–30.3	26.9 ± 0.27 1.53, 23.8–29.2
VA	26.0 ± 0.35 1.56, 23.7–28.5	25.1 ± 0.19 0.61, 23.8–25.9	25.4 ± 0.27 0.81, 24.1–26.9	24.8 ± 0.16 1.10, 22.2–27.8	25.1 ± 0.13 0.80, 23.5–26.5	25.3 ± 0.21 1.22, 22.5–27.8	25.8 ± 0.17 0.98, 24.1–28.5
lD	18.6 ± 0.33 1.46, 15.5–21.6	18.4 ± 0.40 1.26, 16.6–20.6	18.5 ± 0.27 0.80, 16.7–19.3	19.1 ± 0.15 0.99, 17.2–21.2	19.9 ± 0.23 1.44, 16.8–23.5	18.8 ± 0.22 1.28, 16.2–22.2	19.8 ± 0.22 1.26, 17.2–23.0
hD_1	10.4 ± 0.11 0.50, 9.1–11.3	10.8 ± 0.17 0.54, 9.9–11.6	10.1 ± 0.30 0.91, 9.2–11.9	10.9 ± 0.14 0.97, 8.9–12.8	11.6 ± 0.11 0.67, 10.4–12.9	11.4 ± 0.15 0.86, 9.7–13.4	11.3 ± 0.19 1.10, 9.5–13.9
hD_2	7.9 ± 0.48 2.15, 5.8–11.9	6.3 ± 0.31 0.98, 5.2–7.8	5.9 ± 0.14 0.43, 5.1–6.6	7.1 ± 0.12 0.82, 5.7–9.6	11.0 ± 0.47 2.88, 7.4–22.6	9.4 ± 0.24 1.43, 6.9–12.2	10.2 ± 0.39 2.21, 7.8–16.0
lA	8.1 ± 0.14 0.62, 7.1–9.3	8.2 ± 0.19 0.59, 7.2–9.5	7.9 ± 0.21 0.62, 6.8–8.9	8.2 ± 0.09 0.59, 7.0–9.5	8.9 ± 0.10 0.61, 7.5–10.5	8.6 ± 0.18 1.09, 3.6–9.8	9.2 ± 0.16 0.89, 7.9–11.4
hA	9.9 ± 0.18 0.79, 8.7–11.8	9.5 ± 0.23 0.74, 8.1–10.6	8.9 ± 0.24 0.72, 7.9–10.0	10.2 ± 0.12 0.86, 8.4–12.2	11.7 ± 0.14 0.83, 10.3–14.1	10.7 ± 0.21 1.23, 7.5–12.9	13.8 ± 0.19 1.05, 11.3–15.3
lP	14.3 ± 0.37 1.66, 12.7–17.5	13.3 ± 0.12 0.38, 12.5–14.0	13.0 ± 0.20 0.61, 12.2–14.1	13.7 ± 0.08 0.52, 12.8–14.8	15.3 ± 0.11 0.66, 14.2–17.0	15.5 ± 0.13 0.75, 13.6–16.9	16.2 ± 0.10 0.58, 14.7–17.3
lV	12.8 ± 0.25 1.10, 11.2–14.7	12.1 ± 0.16 0.51, 11.3–13.0	11.9 ± 0.13 0.38, 11.2–12.4	12.6 ± 0.10 0.69, 10.2–14.1	14.6 ± 0.15 0.93, 12.8–17.7	14.6 ± 0.15 0.87, 12.9–16.3	15.6 ± 0.18 1.02, 14.1–18.3

Table 2. (Contd.)

Characters	Black grayling	White grayling			West Siberian grayling	Kosogol grayling	Upper Lena grayling
	Cape Khoboi ($n = 20$)	Dagar Bay ($n = 10$)	Ushkanii Island ($n = 9$)	Selenga River ($n = 47$)	Taltsinka River ($n = 38$)	Lake Khubsugul ($n = 35$)	Yakchii lakes ($n = 32$)
Meristic characters							
ll	99.4 ± 0.88 / 3.93, 92–108	95.3 ± 0.76 / 2.41, 90–99	100.9 ± 1.19 / 3.57, 93–105	98.9 ± 0.60 / 4.10, 90–109	97.4 ± 0.55 / 3.39, 89–104	94.2 ± 0.50 / 2.97, 87–100	89.1 ± 0.71 / 4.04, 78–96
D_1	7.9 ± 0.21 / 0.92, 7–10	7.6 ± 0.21 / 0.66, 7–9	7.4 ± 0.17 / 0.50, 7–8	7.9 ± 0.11 / 0.75, 6–9	7.3 ± 0.08 / 0.51, 6–8	7.9 ± 0.13 / 0.77, 7–9	7.5 ± 0.12 / 0.65, 7–9
D_2	12.3 ± 0.23 / 1.01, 10–14	12.2 ± 0.24 / 0.75, 11–13	12.3 ± 0.16 / 0.47, 12–13	12.3 ± 0.14 / 0.91, 11–14	13.1 ± 0.15 / 0.90, 11–15	11.3 ± 0.14 / 0.85, 10–13	12.8 ± 0.11 / 0.65, 11–14
D	20.3 ± 0.20 / 0.90, 19–22	19.8 ± 0.19 / 0.60, 19–21	19.8 ± 0.21 / 0.63, 19–21	20.2 ± 0.13 / 0.86, 18–22	20.3 ± 0.16 / 0.96, 19–23	19.3 ± 0.14 / 0.85, 18–22	20.4 ± 0.13 / 0.75, 19–22
P	15.2 ± 0.14 / 0.62, 14–16	14.7 ± 0.25 / 0.78, 13–16	14.8 ± 0.21 / 0.63, 14–16	14.7 ± 0.12 / 0.80, 13–16	14.2 ± 0.15 / 0.43, 14–15	14.5 ± 0.10 / 0.60, 13–16	15.1 ± 0.14 / 0.77, 14–17
V	9.8 ± 0.15 / 0.65, 8–11	9.7 ± 0.14 / 0.46, 9–10	9.9 ± 0.10 / 0.31, 9–10	9.9 ± 0.06 / 0.44, 9–11	9.9 ± 0.06 / 0.38, 9–11	9.5 ± 0.09 / 0.55, 9–11	9.1 ± 0.09 / 0.53, 8–10
A_1	4.5 ± 0.17 / 0.74, 3–6	4.2 ± 0.13 / 0.40, 4–5	4.0 ± 0.16 / 0.47, 3–5	4.5 ± 0.08 / 0.54, 3–5	4.2 ± 0.07 / 0.41, 4–5	4.7 ± 0.10 / 0.57, 4–6	4.5 ± 0.09 / 0.50, 4–5
A_2	9.0 ± 0.13 / 0.59, 8–10	8.9 ± 0.17 / 0.54, 8–10	9.4 ± 0.17 / 0.50, 9–10	8.7 ± 0.08 / 0.52, 8–10	9.2 ± 0.10 / 0.64, 8–10	8.9 ± 0.13 / 0.77, 8–11	8.7 ± 0.12 / 0.70, 7–10
sb	19.3 ± 0.44 / 1.95, 16–22	17.9 ± 0.26 / 0.83, 17–19	18.3 ± 0.31 / 0.94, 17–20	17.7 ± 0.18 / 1.26, 16–22	18.3 ± 0.17 / 1.07, 16–21	25.9 ± 0.33 / 1.96, 21–30	18.3 ± 0.24 / 1.34, 15–21
rb	9.9 ± 0.17 / 0.77, 8–11	10.2 ± 0.19 / 0.60, 9–11	10 / –	10.2 ± 0.12 / 0.79, 8–12	10.1 ± 0.11 / 0.68, 9–12	9.3 ± 0.11 / 0.66, 8–10	8.6 ± 0.11 / 0.60, 8–10
vert.	57.3 ± 0.16 / 0.71, 56–58	56.1 ± 0.25 / 0.74, 55–57	57.2 ± 0.31 / 0.92, 56–58	55.1 ± 0.28 / 1.92, 52–58	56.2 ± 0.13 / 0.83, 55–58	55.2 ± 0.17 / 1.00, 54–57	55.6 ± 0.17 / 0.96, 54–57
pc	16.3 ± 0.41 / 1.85, 13–19	17.5 ± 0.84 / 2.06, 15–21	18.8 ± 0.72 / 2.15, 16–22	17.6 ± 0.41 / 2.64, 12–23	16.2 ± 0.34 / 1.86, 12–20	23.6 ± 0.55 / 3.23, 16–29	15.5 ± 0.35 / 1.95, 11–18

Note: Note as for Table 1.

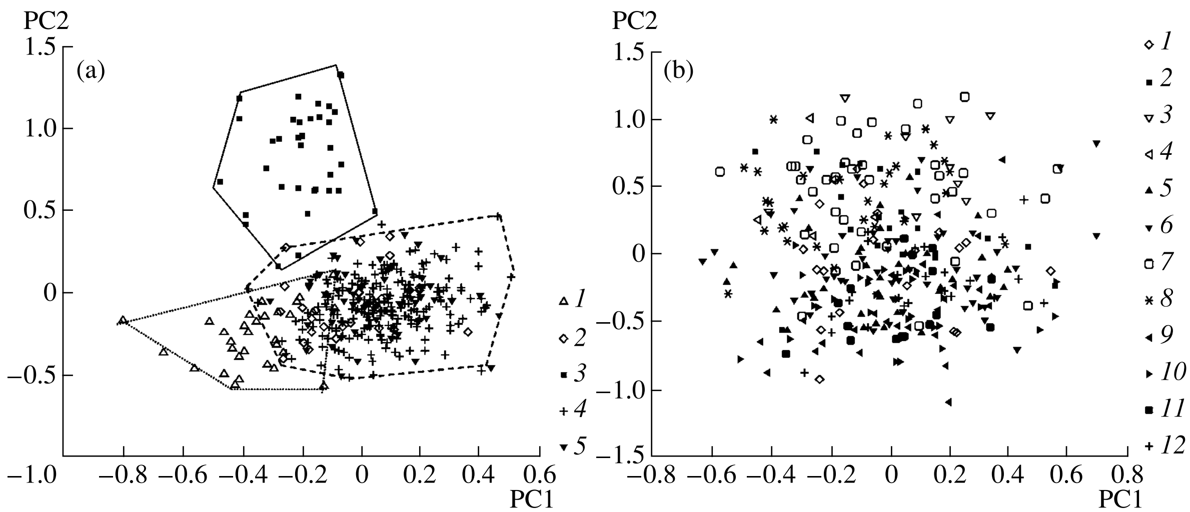

Fig. 3. Diagram of the dispersal of *Thymallus* graylings of the Lake Baikal system in the space of two first principal components (PC) by 12 meristic characters: (a) all studied forms, (*1*) the Upper Lena grayling *T. arcticus* spp. (Yakchii lakes); (*2*) the west Siberian grayling *T. a. arcticus* (the Taltsinka River); (*3*) the Kosogol grayling *T. a. nigrescens* (Lake Khubsugul); (*4*) the black Baikal grayling *T. a. baicalensis*; (*5*) the white Baikal grayling *T. a. baicalensis* infrasubspecies *brevipinnis*; (b) the black, white, and west Siberian graylings from different habitats; (*1*) Cape Elokhin; (*2*) Cape Khoboi; (*3*) Bol'shoi Ushkanii Island; (*4*) Dagar Bay; (*5*) Lake Sobolinoe; (*6*) the Tompuda River; (*7*) the Selenga River; (*8*) the Taltsinka River; (*9*) Cape Ukhan; (*10*) the Molokon River; (11) the Shegnanda River; (12) the Frolikha River.

Svetovidov (1931, 1936). Both forms differ from the Kosogol grayling in the maximum body depth and size of the pectoventral distance, and differ from the west Siberian grayling from the Taltsinka River by the postorbital distance, head length, as well as lengths of the upper and lower jaws, and with the Upper Lena grayling differing in the eye diameter, head and upper jaw lengths, minimal body depth, as well as the size of pectoventral distance and the anal fin depth.

Thus, between the white and black graylings there are significant differences in the number of gill rakers, length of paired fins, and the depth of the posterior part of the dorsal fin. According to the other characters, including those previously suggested by Svetovidov (1931) and Tugarina (1981) as diagnostic (H, pc), the established differences did not exceed the formal subspecies level. The Kosogol grayling differs from all the other studied forms by the number of gill rakers and pyloric caeca, and the Upper Lena grayling differs by the number of scales in the lateral line.

Clusterization of all Baikal populations by the method of unweighted paired group averages (UPGMA) demonstrates an isolated position of the Khubsugul and Upper Lena graylings in relation to the remaining graylings, which, in turn, form two clusters; one is formed of samples of the white grayling and the population from the Taltsinka River, while the other is formed of samples of the black grayling (Fig. 4).

Molecular-Genetic Analysis

The final length of the aligned sequences was 644 base pairs. Twenty three sites were polymorphic; of them 17 parsimonions were informative (six sites were variable in one individual only). The distribution of haplotypes in the studied samples is represented in Table 5.

Baikal populations had a multitude of common haplotypes. One of them (T99) was found in all the popu-

Table 3. Loadings of eigenvectors on the first two principal components for 12 meristic characters

Characters	Principal components			
	14 populations		12 populations	
	1	2	1	2
ll	0.997	0.072	0.999	0.002
D_1	0.007	0.062	0.065	0.107
D_2	0.050	−0.325	0.001	−0.038
D	0.061	−0.271	0.057	0.057
P	0.127	−0.082	0.245	−0.059
V	0.264	−0.024	0.066	0.080
A_1	−0.079	0.144	0.025	0.038
A_2	0.104	0.124	0.089	0.125
sb	−0.010	0.677	0.198	−0.546
rb	0.184	0.021	0.016	0.226
vert.	−0.042	−0.029	−0.055	0.438
pc	−0.166	0.935	0.081	0.903

Table 4. Characters of *Thymallus* graylings from the Baikal basin for which the value of CD coefficient exceeded 1.28

Samples	Samples					
	1	2	3	4	5	6
1		hD_2, lP, lV	PV	f, c, lmx, lmd	o, c, lmx, h, PV, hA	H, PV
2	sb		o, aV, hD_2, hA, lP, lV	f, c, k, lmx, lmd, H, w	l_2, o, c, ch, lmd, H, h, PV, hD_2, hA, lP, lV	H, PV, hD_2, lP, lV
3	sb	–		ao, f, c, cH, k, lmd, w	o, f, lmx, lp, hA, ao/c, o/c, lmx/c	o, f, pD
4	sb	–	–		l_2, o, f, c, ch_2, ch, k, lmx, lmd, h, PV, hA, lP	ao, f, k, i/lmx, lmd
5	ll	ll, rb	ll, rb	ll		l_2, o, ch, lmx, pD, hA
6	sb, pc	sb	D_2, sb, pc	D_2, sb, pc	D_2, sb, pc	

Note: (1) the black Baikal grayling; (2) the white Baikal grayling; (3) the west Siberian grayling (the Nizhnyaya Tunguska River); (4) the west Siberian grayling (the Taltsinka River); (5) Upper Lena grayling (Yakchii lakes, Verkhnyaya Angara River); (6) the Kosogol grayling (Lake Khubsugul). Above the diagonal are plastic characters, and under the diagonal are meristic characters. The designations of characters as for Table 1.

lations from Lake Baikal. The above haplotype was also detected in five of the six sequences of the white grayling from the Selenga River considered. In the Kosogol grayling from Lake Khubsugul, the black Baikal grayling from Lake Sobolinoe, and individuals from the Nizhnyaya Tunguska River, private haplotypes occurred.

A neighbor-joining (NJ) diagram constructed with the Reynolds distances (Table 6) reflects the relationships between the populations based on the frequencies of their haplotypes (Fig. 5). It shows that graylings from the Nizhnyaya Tunguska and Taltsinka rivers do not belong to the clade comprising all other populations. Graylings from the lakes Sobolinoe and Khubsugul form a pair characterized by some differences from all Baikal populations. The white Baikal grayling from the Selenga River does not exhibit considerable genetic distinctions from the black grayling populations.

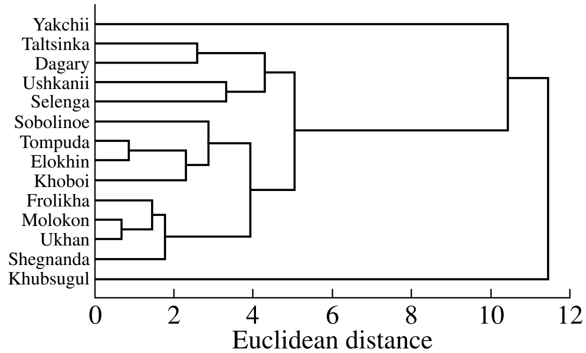

Fig. 4. Dendrogram of the differences between populations of *Thymallus* graylings from the Baikal Lake basin by 12 meristic characters.

DISCUSSION

A long-term study of Baikal graylings, as was already mentioned, did not lead researchers to a consensus on their taxonomic status (Dorogostaiskii, 1923; Svetovidov, 1931, 1936; Berg, 1948; Pivnička and Hensel, 1978; Tugarina, 1981, 2001, 2002; Bogutskaya and Naseka, 2004). Up to now it is unclear whether or not the black and white graylings are independent species or if they are only forms of the Baikal subspecies of *T. arcticus*. The same question also arises with respect to the Kosogol grayling. The previously made conclusions on the status of Baikal forms were mainly based on studies of morphological characters, biological indices (Svetovidov, 1936; Pivnička and Hensel, 1978: Tugarina, 1981, 2002), and, in part, on the data of molecular-genetic analysis (Skurikhina, 1984). The taxonomic conclusions made by Bogutskaya and Naseka (2004) with respect to white, black, Khubsugul, and several other forms that were considered subspecies do not have sufficient grounds.

The morphological characters cited in the papers of Tugarina (1981, 2001, 2002), in her opinion, permit a distinct differentiation of the Baikal groups, considering them as an independent taxa of a species rank. However, such a conclusion mainly resulted from establishing the difference significance based on the paired comparison of characters using the M_{diff} index. Our studies performed by multivariate analysis methods, indicate the opposite, an absence of difference in the white and black Baikal graylings, as well as in Angara graylings that would indicate a species status. This was noted by other researchers as well. Dorogostaiskii (1923), who was among the pioneers in the study of graylings from Baikal and adjacent water bodies, pointed to an external similarity and a morphological relation of the Baikal and Angara graylings. It mostly concerned immature individuals that are almost

Table 5. Distribution of haplotypes in the studied samples of populations of *Thymallus* graylings of the Baikal system

Water body	*n*	Haplotypes																			
		1	2	3	4	5	6	9	10	11	12	13	14	15	16	17	18	19	20	21	22
		Kh7	Kh1	Kh9	Tm99	Tm86	SR13	LS2	U14	U24	U17	Tm102	Tm103	Tl8	Tl10	Tl4	Tl12	LT1	Tl1	Tl7e	Kh3e
Cape Ukhan	6				1				2	1	2										
Molokon River	7				6				1												
Selenga River	7				5	1						1									
Tompuda River	8				2		1		2		1	1	1								
Shegnanda River	6				4				1				1								
Taltsinka River	10				2									2	1	1	1		1	2	
Lake Sobolinoe	6							6													
Lake Khubsugul	9	1	3	3																	2
Lower Tunguska River	6																	6			

Note: Designations of haplotypes include a conventional name of a population and the number of an individual in which this haplotype occurred. Kh is Lake Khubsugul; Tm, the Tompuda River; SR, the Selenga River; LS, Lake Sobolinoe; U, Cape Ukhan; Tl, the Taltsinka River; LT, the Nizhnyaya Tunguska River; *n*, number of analyzed sequences of mtDNA.

Table 6. Paired values of F_{st} criterion (Reynolds distances) for nine studied populations of *Thymallus* graylings of the Baikal basin

Populations	Populations								
	Cape Ukhan	the Molokon River	the Selenga River	the Tompuda River	the Shegnanda River	the Taltsinka River	Lake Sobolinoe	Lake Khubsugul	the Nizhnyaya Tunguska River
Cape Ukhan	–	+	+				+	+	+
Molokon River	0.30465	–				+	+	+	+
Selenga River	0.21863	–0.04386	–			+	+	+	+
Tompuda River	–0.07847	0.17784	0.09014	–			+	+	+
Shegnanda River	0.12000	–0.08621	–0.07117	–0.00110	–		+	+	+
Taltsinka River	0.06601	0.23248	0.13414	0.01998	0.09763	–	+	+	+
Lake Sobolinoe	0.56667	0.84559	0.71906	0.48726	0.70000	0.45455	–	+	+
Lake Khubsugul	0.25908	0.52167	0.41410	0.22007	0.37814	0.21070	0.62719	–	+
Lower Tunguska River	0.56667	0.84559	0.71906	0.48726	0.70000	0.45455	1.00000	0.62719	–

Note: Sign "+" above the diagonal denotes values differing from the zero.

identical in body shape and coloration. It should be noted that, in the mentioned paper the author did not differentiate the Baikal grayling into black and white. Dorogostaiskii also noted a close relation of the Kosogol grayling to the Baikal grayling. The morphological similarity and a considerable overlapping in most characters including diagnostic, in the white, black, and west Siberian graylings are reported in the known papers of Svetovidov (1931, 1936). An analogous conclusion can be made based on the results of studies performed by Tugarina (1981, 2001) and Egorov (1985), as well as from our data (Tables 1 and 2).

Several papers demonstrated the possibility of using for the differentiation of different taxa of qualitative characters such as the dorsal fin pattern, form, and body coloration (Makoedov, 1983, 1985, 1999; Chereshnev et al., 2002; Antonov, 2004; Knizhin et al., 2004). An analysis of specific features of the dorsal fin pattern in most of the studied populations indicated an absence of considerable differences between them. The white, black, west Siberian, and Kosogol graylings have much

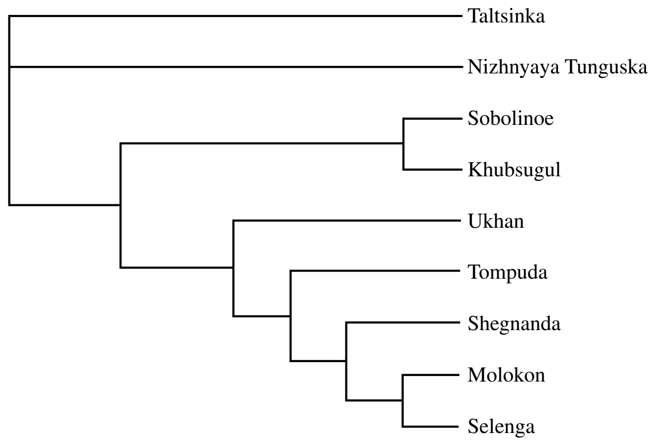

Fig. 5. Dendrogram of the genetic relation between populations of the arctic grayling *Thymallus arcticus* from the Baikal basin constructed by the method of nearest neighbors (NJ) by Reynolds distances (based on data of frequencies of their haplotypes).

in common considering this character. However, the graylings from the Yakchii lakes are undoubtedly closely related to populations from the Lena basin.

Comparing our estimates of the external characters of the Baikal graylings with descriptions cited in the previously published papers (Dorogostaiskii, 1923; Svetovidov, 1936; Tugarina, 1981), one can notice that between the white and black graylings there are considerable differences in the breeding season only, and towards fall, during the winter, and in early spring they disappear. According to our observations, in individuals of the black grayling, outside of the spawning season, body coloration lacks dark colors typical of them in the reproduction period. Tugarina (1981) who studied the morphological characters of graylings, and who conventionally divided the grey and black graylings, proved that there are no morphological differences between them.

Koskinen et al. (2002) demonstrated that genetic differentiation in the Baikal graylings by mitochondrial DNA is insignificant. Proceeding from the mutation rate determined for Salmoniformes as 1–2% per one million years, and considering our results of the molecular-genetic study of white and black Baikal graylings, there are no grounds to expect a considerable divergence in them, since the morphogenesis process still continues. This is evidence that the diagnostics of Baikal graylings from mitochondrial DNA is possible only after a considerable evolutionarily period. It is noted that in populations to some extent isolated, but still geographically connected with the Baikal basin, there may be the same haplotypes as in graylings inhabiting water bodies considerably remote from the lake itself and apparently originating from the Baikal graylings (Lake Khubsugul). Thus, the data obtained do not suggest a complete isolation of white and black graylings. Most probably, an insignificant amount of gene exchange between them either continues or has ceased quite recently.

The white and black graylings differ in several biological indices: the rate of linear and weight growth, fecundity, fatness, biotopic distribution, spawning grounds, and the migration scheme (Tugarina, 1981, 2002; Egorov, 1985). All this indicates successful adaptation of white graylings to life under lacustrine conditions and in large rivers with diverse hydrological characteristics (for instance in the Selenga or the Yenisei). The black grayling mainly retains a mode of life adapted to river conditions, concentrating throughout the year in the near river mouths littoral zone of Baikal or the numerous swift-flowing tributaries where it spawns and in part feeds. Competition for food between these forms was not recorded (Tugarina, 1981).

The absence in the black and white graylings of sufficient morphological and genetic differences does not allow us to agree with the conclusion concerning a species status of these forms. Lack of species–support is also seen in the similarity of the dorsal fin pattern in Baikal, the Angara-Yenisei, and Kosogol graylings—a character that has been demonstrated to differ strongly in sympatric species of the Amur basin (Antonov, 2004; Knizhin et al., 2004). In addition, the parasitological analysis revealed no narrow specific parasites in either of these forms (Pronin and Tugarina, 1971; Tugarina, 1981).

Based on our data and results of the studies performed (Dorogostaiskii, 1923; Svetovidov, 1931, 1936; Tugarina, 1981, 2001, 2002; Egorov, 1985), we may state that in water bodies of the Baikal drainage system there are three relatively isolated groups. The first includes the white and black graylings, as well as the grayling from the Irkutsk Reservoir, the second includes the Kosogol grayling, and the third includes the Upper Lena grayling. In our opinion, the conclusion made by Svetovidov (1931, 1936) on the status of the white grayling as an ecological form of the Baikal subspecies is correct. This repeatedly supports the opinion of a high ecological flexibility of graylings and their adaptive abilities. The existence of the biologically and morphologically diverse populations of Baikal graylings that over a relatively brief evolutionary time have formed several forms in water bodies of the Baikal basin is reported in papers by Tugarina (1981) and Egorov (1985). As for the Kosogol grayling from Lake Khubsugul, its separation as an independent species, in our opinion, is also unjustified due to an absence of sufficient differences in it from all the analyzed forms, which was already previously noted (Dorogostaiskii, 1923; Shatunovskii, 1983; Koskinen et al., 2002; Froufe et al., 2005).

Several hypotheses were advanced concerning the origin of the Baikal graylings that reflected the previously existing concepts of geological processes, glacial periods, and rearrangements of the drainage system that took place over the last several hundred thousands years in the region (Dorogostaiskii, 1923; Svetovidov, 1936; Tugarina, 1981, 2002), as well as were based on the results of molecular-genetic studies (Skurikhina, 1984; Koskinen et al., 2002).

Having considered these hypotheses in the light of modern concepts of the paleoclimate and paleogeography of the Baikal region, we can state our viewpoint concerning the origin of graylings in Baikal, their morphogenesis, and distribution. Both our results and the scenario of grayling penetration into Baikal from the Yenisei via the Angara suggested by Koskinen et al. (2002) do not contradict the conclusions previously made by Svetovidov (1936) on a probable center of origin and possible routes of grayling dispersal over the Eurasian continent. The ancestral form of the Baikal graylings might have inhabited water bodies of the Altai-Sayan Mountains, including the northern and western parts of Mongolia, rather than the Selenga River as suggested by Tugarina (1981, 2002). The dispersal of graylings proceeded in different directions, which resulted from the considerable rearrangements of the drainage system in periglacial water bodies, as well as from processes related to mountain folding in the Pleistocene (Florensov, 1978; Arkhipov et al., 1982; Grosswald, 1983; Borisov and Minina, 1989; Osadchii, 1995; Grosswald, 1998; Kuz'min, 2001). Watersheds that later formed and the resulting isolation barriers led to the formation of different forms of graylings in the basins of the upper reaches of the Ob, Yenisei, and Angara rivers, as well as in lakes Baikal and Khubsugul. The populations inhabiting the Angara and Irkutsk Reservoir can be considered as a buffer group between the Baikal and Yenisei graylings, which agrees with our data and conclusions by Skurikhina (1984) and Koskinen et al. (2002). The absence in them of not only a reproductive isolation, but also of considerable morphological differences, as well as the presence of common features in the body coloration and an almost identical pattern of the dorsal fin cast doubt on the consideration of these forms as different subspecies of *T. arcticus* and indicate that a revision of their taxonomic status is needed.

The Upper Lena grayling found in one of the tributaries of the Verkhnyaya Angara (the basin of the Yakchii Spring) and quite possibly inhabiting the upper reaches of the Barguzin River either penetrated to there from water bodies of the Upper Lena during the rearrangements of the drainage system at the watershed sites of basins that occurred during the Pleistocene (Lamakin, 1950, 1952; Kozhov, 1972; Florensov, 1978; Grosswald, 1983, 1998; Kuz'min, 2001) or previously existed in these rivers (Knizhin et al., 2006).

The external appearance and morphological and genetic specific features of the Kosogol grayling, despite the presence in it of characters common to all forms of the Baikal basin indicate a greater period of its isolation in Lake Khubsugul. This especially manifested itself with the formation of differences in body coloration and the number of pyloric caeca and gill rakers.

To ultimately solve as to what extent our viewpoint is correct is possible only after a more detailed study of the morphological and genetic diversity of graylings in Siberia is performed.

CONCLUSIONS

Summing up the published and original results of studies, it may be concluded that the size of phenetic and genetic differences between the white and black graylings does not permit assigning them a species status. This agrees with the previously stated opinion of Svetovidov (1936) on the existence in Baikal of two forms of Baikal subspecies of *T. arcticus*, which are closely related to populations inhabiting the Angara and Yenisei rivers. The formation of the Kosogol grayling, besides specific habitat conditions, at a certain stage was possibly affected by contacts with the Baikal graylings and with graylings that inhabited the upper reaches of the Yenisei during the rearrangements of the drainage system in the Pleistocene. The Upper Lena graylings are characterized by the presence of several diagnostic characters indicating their considerable divergence in relation to Baikal groups.

ACKNOWLEDGMENTS

The authors are grateful to M.V. Mina (IBR RAN, Moscow), B.E. Bogdanov and L.V. Sukhanova (LIN SO RAN, Irkutsk) for valuable advice and remarks made during the preparation of the manuscript; to S.G. Afanas'ev and O.I. Zhuravlev (Vostsibrybtsentr, Ulan Ude) for their aid in the work and for the kindly provided materials on the white grayling from the Selenga River; to B.E. Bogdanov (LIN SO RAN, Irkutsk), A.N. Zaitseva, A.N. Matveev, S.S. Samarina, V.P. Samusenok, A.L. Yur'ev (Irkutsk University), S.N. Safronov (NII Biologii at ISU), S.N. Veshchev, and the team of the motor ship Professor M.M. Kozhov for help and participation in expedition works.

The study is supported in part by the Federal Target Program *Integration* (grant K0788), Global Ecological Foundation (grant IV 0049-01), the RF Ministry of Education (grant A03-2.12-265, program *Russia's Universities* (grant UR.07.01.009), program RFFI-Baikal (grant 05-04-97214), as well as the Portuguese Ministry of Science (FCT POCT1/33364/BSE/2000).

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Translated by I. A. Pogosyants