ISSN 0032-9452, Journal of Ichthyology, 2006, Vol. 46, No. 1, pp. 34–43. © Pleiades Publishing, Inc., 2006.
Original Russian Text © I.B. Knizhin, S.J. Weiss, B.E. Bogdanov, S.S. Samarina, E. Froufe, 2006, published in Voprosy Ikhtiologii, 2006, Vol. 46, No. 1, pp. 38–47.

# Finding a New Form of the Grayling *Thymallus arcticus* (Thymallidae) in the Basin of Lake Baikal

**I. B. Knizhin*, S. J. Weiss**, B. E. Bogdanov***, S. S. Samarina*, and E. Froufe******

**Irkutsk State University, ul. Karla Marksa 1, Irkutsk, 664003 Russia*
***Institut für Zoologie, Karl-Franzens Universitat Graz, Graz, A-8010 Austria*
****Limnological Institute, Russian Academy of Sciences, ul. Ulan-Batorskaya 3, Irkutsk, Russia*
*****Faculdade de Ciencias, Universidade do Porto, Praca Gomes Teixeira, Porto, 4000-002 Portugal*
*E-mail: knizhin@home.isu.ru*

Received February 10, 2004

**Abstract**—A dwarf form of the Arctic grayling *Thymallus arcticus*, inhabiting a group of small lakes at the origin of the Yakchii stream, which flows into the Verkhnyaya Angara River (basin of Lake Baikal), has been found in the northeastern watershed of the Baikal and Lena basins. The form is similar to upper Lena populations in body coloration and the pattern of dorsal fin. Our comparison by meristic characters indicated that the grayling of the Yakchii Lakes is more similar to the fish from Kutima River (basin of the upper courses of the Lena River) than to the black Baikal grayling *T. arcticus baicalensis*. The presence in Lake Baikal of a population similar to upper Lena graylings may have three causes: (1) possible drainage from Baikal to the pra-Lena via ancient valleys of the Barguzin and the Upper Angara; (2) appearance of transit zones as a result of glacial or tectonic events during the periods of watershed development between the Baikal and Lena basins; (3) the upper Lena grayling could be an endemic of the Baikal basin which was replaced by graylings penetrating from the Yenisei basin and remained in the form of relic populations in the upper courses of certain tributaries of the northern and northeastern parts of Lake Baikal.

**DOI:** 10.1134/S003294520601005X

Populations of fish inhabiting the watershed areas of river basins are extremely interesting. The study of such populations inhabiting adjoining hydrological systems could provide answers to many questions associated with the history of their development and fauna exchange during the glacial and postglacal periods. During the last hundred thousand years, the Baikal region witnessed significant transformations of the earth surface and its hydrological network. These changes were associated with tectonic activity and the movements of glaciers, causing a redistribution of water masses in central Asia (Kozhov, 1972; Florensov, 1978; Grosswald, 1983; Grosswald, 1998; Kuz'min, 2001).

Lake Baikal was previously thought to be inhabited by a subspecies of the Arctic grayling, the Baikal grayling *Thymallus arcticus baicalensis*, represented by two forms, black and white graylings (Svetovidov, 1936; Berg, 1948; Tugarina, 1981; Egorov, 1985; Dorofeeva, 1998, 2002).[1] The taxonomic status of these forms is still uncertain. It has been hypothesized that a population of the Lena grayling may inhabit the upper courses of the Barguzin River, one of the main tributaries of Lake Baikal (Matveev, Knizhin, 1996, Elaev *et al.*, 1998); however, materials supporting the presence of such subspecies in the Baikal basin have not been presented.

In this paper, we present the morphological characteristics and biological characters of graylings observed in the watershed between the Lena River and Lake Baikal, and discuss their relationships and the causes of the modern distribution of different forms of graylings in the Baikal and Lena basins.

## MATERIALS AND METHODS

The material was collected from the end of July to the beginning of August 2001 at the watershed of the rivers Pravaya and Levaya Mama (Vitim River–Lena River), the Kichera River, and the group of lakes near the origin of the Yakchii stream, which flows into the Angara River (Lake Baikal). For comparative analysis, we used our own samples of the Arctic grayling *T. arcticus* from the Kutima River and Lake Kunerma (basin of the Lena's upper reaches, Kirenga River), and the black Baikal grayling *T. a. baicalensis* from the Tompuda River (Northern Baikal) (Fig. 1) and several other water bodies of the following basins: Lena (Olongdo River, Lake Lesha, Lake Chitkanda, basin of the Olekma River); Baikal (Dagar Bay, Lake Sobolinoe, basin of Snezhnaya River); Angara (Taltsinka River, Irkutsk Reservoir); Yenisei (Nizhnyaya Tun-

[1] Lake Chovsgol, a part of the Baikal system, is inhabited by another subspecies of the Arctic grayling, the Kosogol grayling *T. a. nigrescens*.

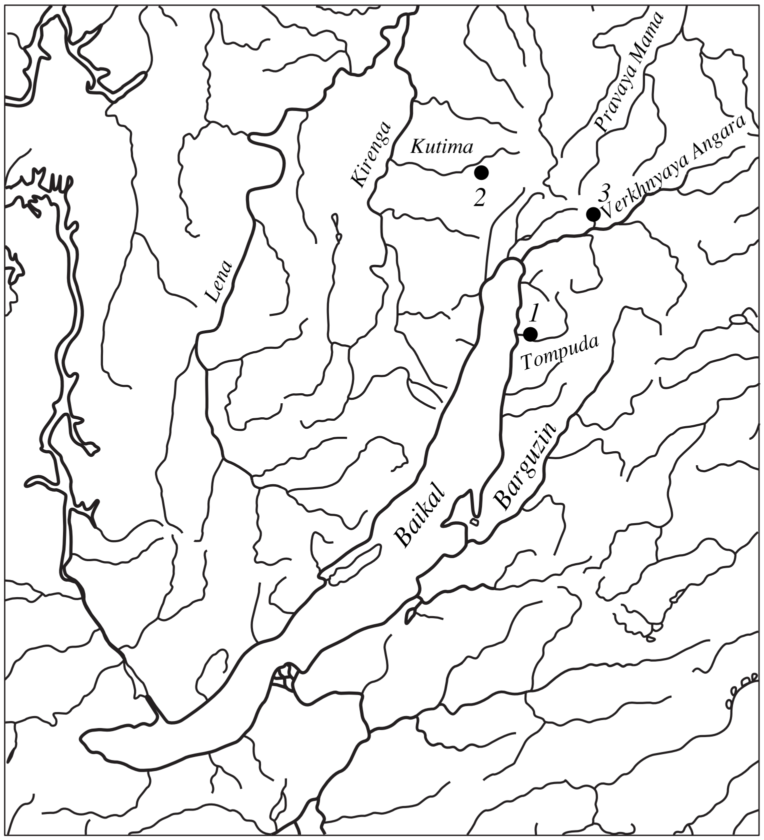



**Fig. 1.** The map of the study area: (*1*) Tompuda River, (*2*) Kutima River; (*3*) Yakchii lakes.

guska River); and the Central Asian basin (Lake Khokh Nur).

The origin of the Yakchii stream 56°05′.9 N and 110°46′.7 E) is a mountain multilake system linked by a network of shallow streams, most of which run dry in absence of rains. The total length of the stream is 20 km. The Yakchii Lakes are small, on average 0.5 × 0.5 km, with a depth in the middle part of up to 15 m. The littoral with depth up to 1.5–2 m represents about 5–10% of the total area, then the slope begins. The bottom is covered with mud and sand, and is slimy. The coastline is represented by large stones and pebbles. Pondweeds occur at the warm shores.

The fish were caught at all depths using gill nets with mesh size 14 and 27 mm, as well as by fly-fishing. Overall, 46 specimens were caught. In external morphology, they were similar to the graylings inhabiting the water bodies of the Lena River. The river minnow *Phoxinus phoxinus* also occurred in the lakes.

The fish were preserved in 4% formaldehyde solution and subsequently subjected to complete morphological and biological analysis (Pravdin, 1966). We measured the fork length (the Smitt's length, LSm). We studied 12 meristic and 29 morphometric characters in 32 individuals aged from 3–6 years with gonads at maturity stage III. The methods of morphological analysis have been described in detail previously (Froufe *et al.*, 2003; Knizhin *et al.*, 2004).

Fish age was determined from the scales (Chugunova, 1959). The analysis of feeding was conducted in accordance with the recommendations published in the *Manual of Methods* (1974).

The statistical data analysis was conducted using Statistica 5.5a and SPSS 8.0 packages. The variance-covariance matrix was used for the principal components analysis. The significance of the differences and their value were assessed, respectively, with the *t*-test and the *CD* coefficient (Mayr, 1971; Rokitskii, 1973).

## RESULTS

**Description of graylings of Yakchii lakes** D VII–IX 11–14 (total 19–22), A IV–V 7–10, P I 14–17, V II 8–10, ll 78–96, sp. br. 15–21, r. br. 8–10, vert. 54–57, pc 11–18.

The assessments of morphometric and meristic characters are presented in Tables 1 and 2. Body shape oblong. Snout rounded, eyes large. Upper jaw bone overlaps the anterior margin of eye. Teeth on jaws small, poorly discernible. Forehead wide. Postorbital part is about half of head length. Dorsal fin with small base and deep anterior part. Posterior margin of dorsal

**Table 1.** Morphometric characters of the Arctic grayling *Thymallus arcticus* from the studied water bodies

| Characters | Yakchii Lakes ($n$ = 32) | Kutima River ($n$ = 28) | Tompuda River ($n$ = 50) |
|---|---|---|---|
| $L_{Sm}$, mm | 154.6 / 133.3–185.2 | 211.1 / 184.5–244.0 | 314.0 / 227.4–428.8 |
| In % $L_{Sm}$ | | | |
| l | 94.6 ± 0.11 / 0.61, 93.02–95.78 | 95.1 ± 0.09 / 0.46, 93.99–95.98 | 95.4 ± 0.08 / 0.57, 93.58–97.04 |
| $l_2$ | 76.8 ± 0.16 / 0.91, 75.07–78.35 | 79.2 ± 0.15 / 0.77, 77.24–80.66 | 77.2 ± 0.18 / 1.30, 74.79–79.97 |
| ao | 6.0 ± 0.06 / 0.34, 5.31–6.73 | 5.8 ± 0.05 / 0.25, 5.32–6.3 | 6.2 ± 0.05 / 0.33, 5.46–6.99 |
| o | 5.4 ± 0.04 / 0.24, 4.70–5.85 | 4.4 ± 0.04 / 0.22, 3.93–4.75 | 4.3 ± 0.03 / 0.22, 3.78–4.82 |
| f | 10.1 ± 0.06 / 0.32, 9.60–10.79 | 9.0 ± 0.06 / 0.3, 8.6–9.7 | 9.9 ± 0.06 / 0.41, 9.15–11.22 |
| c | 20.6 ± 0.11 / 0.59, 19.82–21.96 | 18.6 ± 0.08 / 0.42, 17.88–19.89 | 19.5 ± 0.09 / 0.64, 18.25–21.32 |
| $ch_2$ | 14.7 ± 0.10 / 0.54, 13.68–15.93 | 13.8 ± 0.11 / 0.56, 12.84–15.15 | 14.1 ± 0.11 / 0.75, 12.82–16.03 |
| $ch_1$ | 11.0 ± 0.10 / 0.59, 10.09–12.46 | 9.9 ± 0.11 / 0.57, 8.94–11.28 | 10.1 ± 0.07 / 0.52, 9.18–11.87 |
| k | 6.1 ± 0.04 / 0.25, 5.70–6.83 | 6.0 ± 0.05 / 0.27, 5.57–6.56 | 6.0 ± 0.05 / 0.39, 5.17–6.76 |
| lmx | 6.3 ± 0.05 / 0.26, 5.65–6.89 | 5.0 ± 0.04 / 0.2, 4.6–5.42 | 5.8 ± 0.05 / 0.35, 5.28–6.76 |
| i/lmx | 2.0 ± 0.04 / 0.20, 1.65–2.48 | 1.9 ± 0.02 / 0.12, 1.63–2.17 | 1.9 ± 0.03 / 0.18, 1.61–2.36 |
| lmd | 10.5 ± 0.08 / 0.46, 9.69–11.58 | 8.9 ± 0.04 / 0.23, 8.56–9.5 | 9.9 ± 0.06 / 0.44, 8.94–11.11 |
| H | 18.3 ± 0.20 / 1.10, 16.63–21.64 | 19.3 ± 0.17 / 0.9, 17.75–21.37 | 19.6 ± 0.17 / 1.20, 17.16–22.17 |
| h | 6.9 ± 0.04 / 0.25, 6.44–7.43 | 6.6 ± 0.04 / 0.24, 6.07–7.12 | 6.3 ± 0.05 / 0.38, 4.40–7.28 |
| w | 12.0 ± 0.20 / 1.11, 9.34–14.75 | 13.6 ± 0.11 / 0.57, 12.57–14.75 | 11.7 ± 0.12 / 0.88, 9.66–14.15 |
| aD | 34.7 ± 0.16 / 0.91, 31.72–35.95 | 33.1 ± 0.14 / 0.75, 31.7–34.72 | 34.8 ± 0.13 / 0.95, 33.16–36.94 |
| pD | 41.3 ± 0.21 / 1.22, 37.39–43.47 | 42.1 ± 0.27 / 1.41, 39.14–44.95 | 41.8 ± 0.20 / 1.42, 39.17–45.05 |
| aA | 71.3 ± 0.23 / 1.30, 68.42–73.70 | 70.2 ± 0.21 / 1.13, 67.94–73.07 | 71.7 ± 0.17 / 1.18, 69.14–74.48 |
| aV | 45.8 ± 0.23 / 1.29, 42.77–47.79 | 45.1 ± 0.24 / 1.29, 42.45–47.75 | 47.8 ± 0.17 / 1.19, 45.06–50.34 |
| lp | 15.9 ± 0.16 / 0.89, 13.89–18.53 | 16.7 ± 0.14 / 0.72, 15.25–18.07 | 16.9 ± 0.14 / 1.01, 14.51–19.03 |

**Table 1.** (Contd.)

| Characters | Yakchii Lakes ($n$ = 32) | Kutima River ($n$ = 28) | Tompuda River ($n$ = 50) |
|---|---|---|---|
| PV | $\frac{26.9 \pm 0.27}{1.53,\ 23.81–29.27}$ | $\frac{27.9 \pm 0.23}{1.23,\ 25.37–30.03}$ | $\frac{29.7 \pm 0.19}{1.33,\ 25.87–32.02}$ |
| VA | $\frac{25.8 \pm 0.17}{0.98,\ 24.12–28.48}$ | $\frac{26.8 \pm 0.16}{0.83,\ 25.35–28.94}$ | $\frac{25.2 \pm 0.17}{1.19,\ 22.74–28.68}$ |
| lD | $\frac{19.8 \pm 0.22}{1.26,\ 17.25–23.04}$ | $\frac{21.9 \pm 0.23}{1.22,\ 19.31–24.83}$ | $\frac{19.4 \pm 0.16}{1.14,\ 16.67–21.58}$ |
| $hD_1$ | $\frac{11.3 \pm 0.19}{1.10,\ 9.48–13.89}$ | $\frac{10.0 \pm 0.12}{0.65,\ 8.55–11.53}$ | $\frac{11.4 \pm 0.12}{0.87,\ 9.75–13.94}$ |
| $hD_2$ | $\frac{10.2 \pm 0.39}{2.21,\ 7.80–16.00}$ | $\frac{12.4 \pm 0.45}{2.39,\ 8.6–17.71}$ | $\frac{10.8 \pm 0.33}{2.33,\ 7.86–16.78}$ |
| lA | $\frac{9.2 \pm 0.16}{0.89,\ 7.99–11.44}$ | $\frac{9.6 \pm 0.09}{0.49,\ 8.72–10.77}$ | $\frac{8.3 \pm 0.06}{0.45,\ 7.47–9.58}$ |
| hA | $\frac{13.8 \pm 0.19}{1.05,\ 11.33–15.29}$ | $\frac{11.9 \pm 0.2}{1.08,\ 9.67–14.63}$ | $\frac{10.7 \pm 0.13}{0.90,\ 9.05–13.29}$ |
| lP | $\frac{16.2 \pm 0.10}{0.58,\ 14.76–17.33}$ | $\frac{14.6 \pm 0.13}{0.7,\ 12.97–15.58}$ | $\frac{16.0 \pm 0.09}{0.67,\ 14.72–17.59}$ |
| lV | $\frac{15.6 \pm 0.18}{1.02,\ 14.12–18.31}$ | $\frac{14.6 \pm 0.13}{0.67,\ 13.51–15.96}$ | $\frac{14.5 \pm 0.11}{0.79,\ 12.67–16.65}$ |

Note: Mran value and its standard error are above the line, standard deviation and range, below the line. $L_{sm}$—Smith's length; l—trunk length; $l_2$—the length to the termination of the scale cover; ao—snout length; o—horizontal orbit diameter; f—postorbital head area; c—head length; $ch_2$, $ch_1$—head depth at the occiput and eye; k—forehead width; lmx, i/lmx—upper jaw length and width; lmd—lower jaw length; H, h—the maximum and the minimum body depth; w—body width; aD—antedorsal distance; pD—postdorsal distance; aA—anteanal distance; aV—anteventral distance; PV—pectoventral distance; VA—ventroanal distance; lp—the length of the caudal peduncle; lD—the length of the dorsal fin base; $hD_1$—the depth of the anterior part of the dorsal fin; $hD_2$—the depth of the posterior part of the dorsal fin; la—the length of the anal fin base; hA—the depth of the anal fin; lP—the length of the pectoral fin; lV—the length of the abdominal fin.

fin does not reach fatty fin. Abdominal fins and anal fin elongated.

Overall coloration background is gray. Oval spots characteristic of juvenile salmonids are well seen on the sides of the body in fish of all age groups.[2] Head and gill covers with vivid violet shine. Short and thin continuous zigzag stripes continue along the rows of scales from the head to the tail. Two longitudinal brown stripes are seen from the bottom part of the body, from head to abdominal fins. Three or four parallel rows of horizontally elongated oval red or maroon spots run along the dorsal fin. Their upper row forms a so-called "sling." The edge continues along the whole margin and has the same color as the spots. Dark vinous oblique stripes are present on the abdominal fins. Caudal fin and the caudal peduncle red or maroon.

**Comparative characteristic.** Graylings of the Yakchii lakes are similar to the upper Lena population of the Kutima River by the pattern of the dorsal fin, by the presence of the characteristic sling and 3–4 parallel rows of spots along the whole fin. Unlike the Yakchii and upper Lena populations, the pattern in the Baikal grayling is characterized by uneven lines and spots of different sizes are located on the posterior part of the fin. In addition, gill covers of the Lena and Yakchii fish have a characteristic violet shine, and short dashed zigzag stripes run along the scales, which is not characteristic of Baikal fish. As in the upper Lena fish, Yakchii graylings are characterized by the absence of copper-red spots above the abdominal fins at the caudal on the body peduncle; such spots are present in Baikal graylings and other populations inhabiting the rivers Angara, Yenisei, Ob', Indigirka, Kolyma, and Amur (Figs 2, 3). On the whole, by the body coloration and the pattern on the dorsal fin, the fish from the Yakchii Lakes are quite similar to the fish inhabiting all of the large tributaries of the Lena (with the exception of the delta areas): the Kirenga, Vitim, Olekma, Aldan, Vilyui, and other rivers.

The Yakchii population significantly ($p < 0.001$) differs from the population of the Kutim River by the number of branched rays in the pectoral fin, non-branched and branched rays in the anal fin, and from graylings of Tompuda River, by the number of scales in the lateral line, the number of branched rays in the pec-

[2] After preservation in formaldehyde, the spots become inconspicuous.

**Table 2.** Meristic characters of the Arctic grayling *Thymallus arcticus* from the studied water bodies and their comparison by t-test and the difference coefficient, CD

| Characters | Yakchii Lakes ($n$ = 32) | Kutima River ($n$ = 28) | Tompuda Rive ($n$ = 50) | Comparison $t$/CD | | |
|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 1–2 | 1–3 | 2–3 |
| ll | 89.1 ± 0.71<br>4.04, 78–96 | 91.8 ± 0.73<br>3.88, 86–103 | 99.5 ± 0.68<br>4.79, 88–110 | 2.68<br>0.49 | 10.61<br>1.66 | 7.72<br>1.25 |
| $D_1$ | 7.5 ± 0.12<br>0.65, 7–9 | 7.8 ± 0.1<br>0.54, 7–9 | 7.8 ± 0.10<br>0.71, 7–10 | 1.47<br>0.27 | 1.47<br>0.24 | 0.00<br>0.00 |
| $D_2$ | 12.8 ± 0.11<br>0.65, 11–14 | 12.5 ± 0.19<br>0.98, 11–14 | 12.5 ± 0.12<br>0.88, 11–15 | 1.41<br>0.26 | 1.97<br>0.29 | 0.04<br>0.01 |
| D | 20.4 ± 0.13<br>0.75, 19–22 | 20.3 ± 0.17<br>0.9, 19–22 | 20.3 ± 0.11<br>0.77, 19–22 | 0.56<br>0.10 | 0.35<br>0.06 | 0.30<br>0.05 |
| P | 15.1 ± 0.14<br>0.77, 14–17 | 14.1 ± 0.13<br>0.69, 13–15 | 14.7 ± 0.09<br>0.66, 13–16 | 5.50<br>1.02 | 2.70<br>0.44 | 3.79<br>0.63 |
| V | 9.1 ± 0.09<br>0.53, 8–10 | 8.9 ± 0.04<br>0.19, 8–9 | 9.8 ± 0.06<br>0.45, 9–11 | 2.34<br>0.41 | 6.19<br>0.96 | 12.48<br>1.84 |
| $A_1$ | 4.5 ± 0.09<br>0.50, 4–5 | 3.8 + 0.07<br>0.38, 3–4 | 4.5 ± 0.07<br>0.50, 4–5 | 5.96<br>1.08 | 0.00<br>0.00 | 6.87<br>1.08 |
| $A_2$ | 8.7 ± 0.12<br>0.70, 7–10 | 9.3 ± 0.09<br>0.48, 9–10 | 8.9 ± 0.09<br>0.66, 8–11 | 3.87<br>0.68 | 0.93<br>0.15 | 3.46<br>0.54 |
| sp. br. | 18.3 ± 0.24<br>1.34, 15–21 | 18.6 ± 0.17<br>0.9, 17–20 | 20.7 ± 0.21<br>1.50, 17–23 | 0.92<br>0.17 | 7.46<br>1.18 | 7.81<br>1.21 |
| r. br. | 8.6 ± 0.11<br>0.60, 8–10 | 9.1 ± 0.14<br>0.74, 8–11 | 9.3 ± 0.08<br>0.58, 8–10 | 2.86<br>0.54 | 5.07<br>0.83 | 1.12<br>0.19 |
| vert | 55.6 ± 0.17<br>0.96, 54–57 | 55.3 ± 0.13<br>0.71, 54–57 | 55.9 ± 0.25<br>1.77, 52–59 | 1.59<br>0.28 | 0.99<br>0.15 | 2.27<br>0.34 |
| pc | 15.5 ± 0.35<br>1.95, 11–18 | 15.9 ± 0.37<br>1.96, 12–19 | 15.7 ± 0.29<br>2.06, 10–21 | 0.84<br>0.16 | 0.62<br>0.10 | 0.32<br>0.05 |

Note: ll—the number of perforated rays in the lateral line; $D_1$—the number of nonbranched rays in the dorsal fin; $D_2$—the number of branched rays in the dorsal fin; D—total number of rays in the dorsal fin; P—the number of branched rays in the pectoral fin; V—the number of branched rays in the abdominal fin; $A_1$—the number of nonbranched rays in the anal fin; $A_2$—the number of branched rays in the anal fin; sp. br—the number of gill rakers; r. br—the number of gill rays; vert—vertebral number; pc—the number of pyloric ceca.

toral fin, and the number of gill rakers and gill rays. Graylings of the rivers Kutima and Tompuda revealed differences in the number of scales in the lateral line and the numbers of branched rays in the pectoral and abdominal fins, of nonbranched and branched rays in the anal fin, and of gill rakers (Table 2).

High values of the *CD* coefficient were noted during the comparisons of the Yakchii and upper Lena populations from the Kutim River with Baikal graylings from the Tompuda River by the number of rays in the lateral line, the number of rakers at the first gill arch, and the number of branched rays in the abdominal fin (Table 2).

By all 11 meristic characters, the lowest overlap in the space of the first two principal components, accounting for 86.5% of the total variance, is observed between the populations of Yakchii lakes and the Tompuda River—19.5%. The values of the loadings are presented in Table 3. On the first principal components, the maximum loadings include the number of scales in the lateral line, the number of branched rays in the abdominal fin, and the number of gill rakers. On the second principal component, they include the number of pyloric ceca. Individuals from the Kutima River significantly overlap with graylings of the Yakchii Lakes—

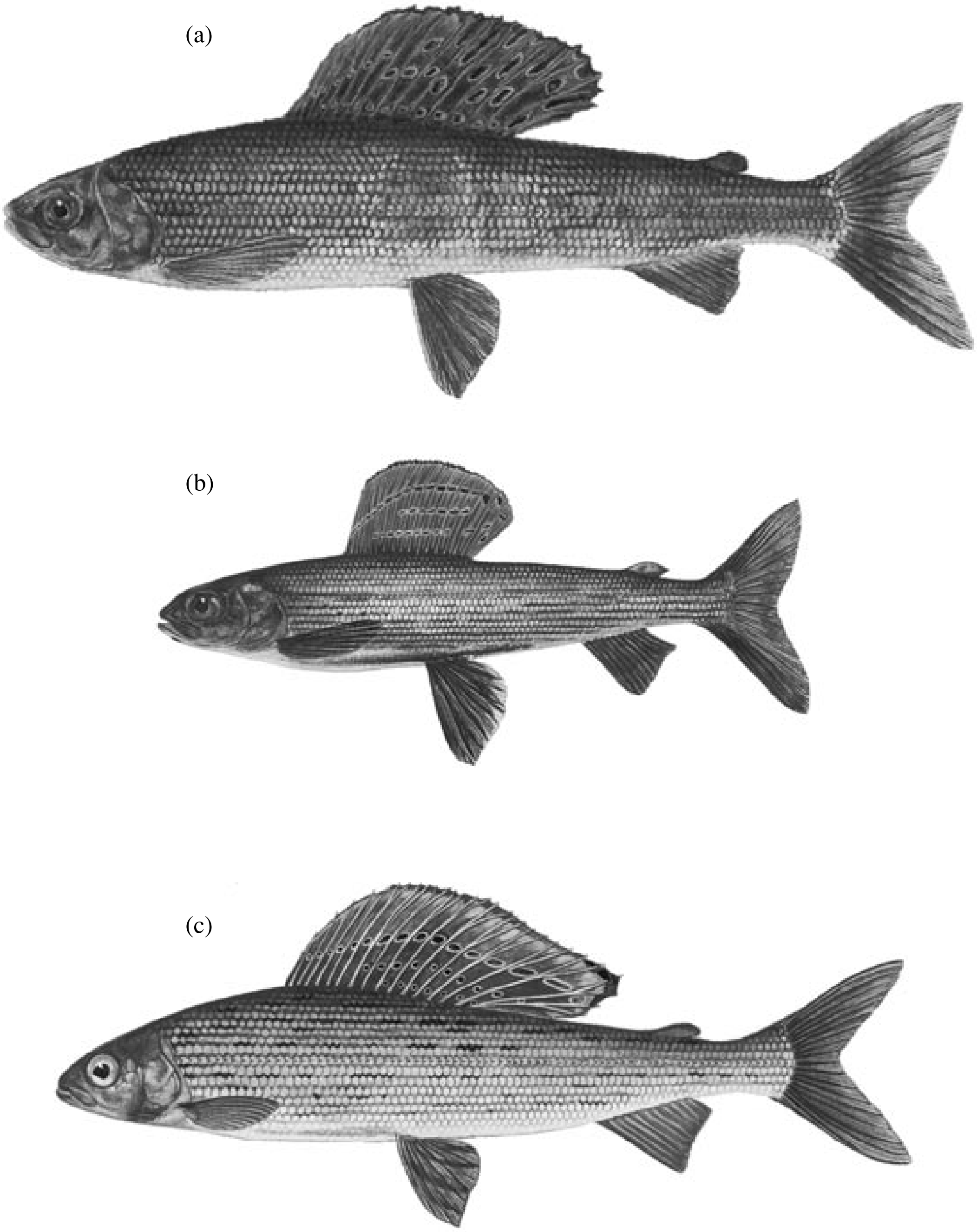


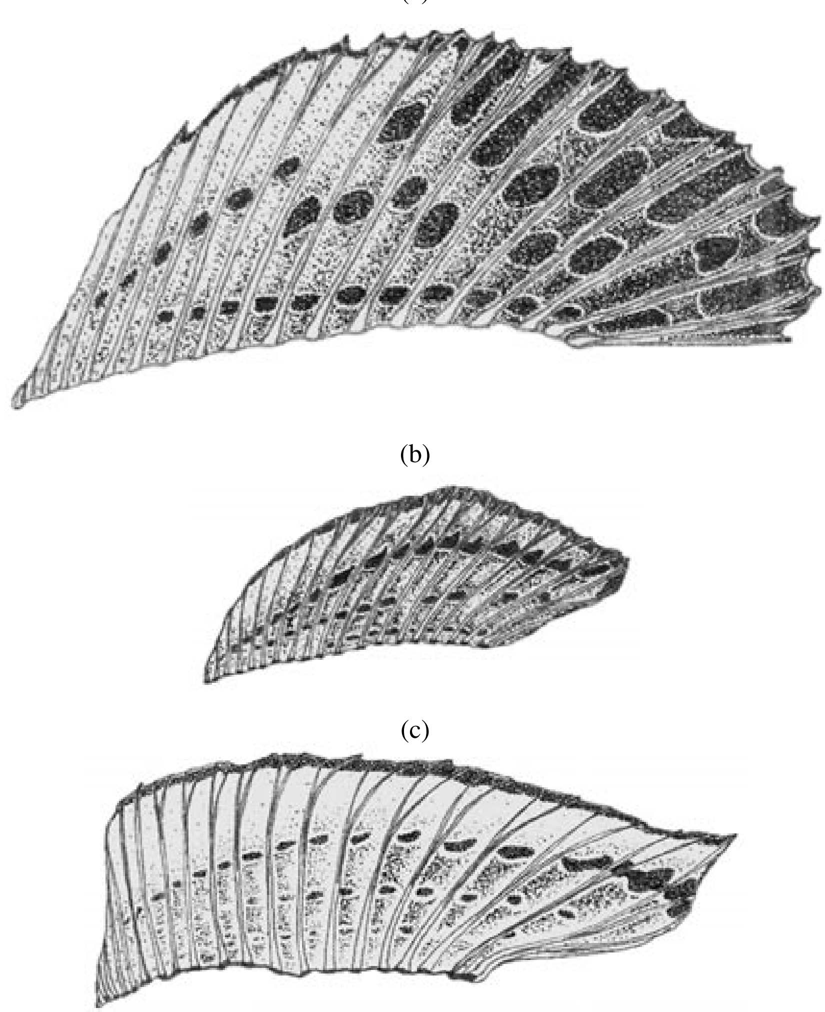

**Fig. 2.** Graylings *Thymallus arcticus* of the Baikal Basin (a—Tompuda River; b—Yakchii Lakes) and the basin of the upper courses of the Lena River (c—Kutima River).

75%. It should be noted that graylings of the Rivers Kutima and Tompuda, inhabiting different basins and representing (according to modern views) different subspecies of the Arctic grayling, are similar by meristic characters and are characterized by an overlap of about 60% (Fig. 4).

Cluster analysis of meristic characters conducted using the Unweighted Pair-Group Average Method (UPGMA) revealed the division of the populations into four branches. The first branch is formed by graylings of the Baikal and Yenisei basins, the second by graylings of the Lena basin including the sample from the Yakchii Lakes, the third by the Chovsgol grayling *T. nigrescens* from Lake Chovsgol, and the fourth by the Mongolian grayling *T. brevirostris* from Lake Khokh Nur (Fig. 5).

**Biological characteristics and food composition.** The length and the weight of different age groups of graylings from the Yakchii Lakes are presented in Table 4. The fish length did not exceed 200 mm and the weight,

(a)



(b)

(c)

**Fig. 3.** Drawings of the dorsal fins of graylings *Thymallus arcticus*: (a) Tompuda River; (b) Yakchii Lakes; (c) Kutima River.

100 g. Yearly increments are small, pointing to an extremely low growth rate.

All graylings from Yakchii lakes, beginning from the age of three years, during the study had gonads at the III ripeness stage. On the whole, the ratio of the number of females and males in the sample was 3 : 1.

At the end of July, grayling feeds basically on adult-stage amphibiotic insects, represented by caddis flies, stone flies, mayflies, chironomids, beetles, and bugs, which is characteristic of most populations of *T. arcticus*.

**Habitat distribution.** In the main channel of the Yakchii stream, from the origin to the place where it falls into the Verkhnyaya Angara, the grayling is not noted. The fish were found only in small upper lakes, from which they practically do not leave. Most of the time, they keep in shallow places, in the areas of drainage from the lakes, where the current becomes significant. At depths, graylings occur rarely. At the shoreline there are many fingerlings, which do not mix with the numerous shoals of river minnows. The presence of large abundances of juvenile graylings in lakes suggest that spawning occurs not in the channel of the stream, but in streams between the lakes or at the places where small streams fall into the lakes.

## DISCUSSION

Comparison of the meristic characters in graylings from basins of the upper courses of Lena and Baikal revealed significant overlap in many characters. Nonetheless, the number of scales in the lateral line, the number of gill rakers, and the number of branched rays in the abdominal fin in different populations of the Kutim River (ll 91.8, sp. br. 18.6, V 8.9) and the system of lakes of the Yakchii Stream (ll 89.1, sp. br. 18.3, V 9.1) is on average less than in the Baikal grayling from the Tompuda River (ll 99.5, sp. br. 20.7, V 9.8). By the complex of other meristic characters, graylings from the Kutim River and Yakchii Lakes are clearly closer to each other than to the Baikal grayling *T. a. baicalensis* from the Tompuda River. If we exclude the fish from the Lena basin from the scatterplot, the overlap between the Yakchii and Baikal graylings is significantly smaller, suggesting that these groups do not belong to a common unity (Fig. 4). This is also well seen during the cluster analysis of the populations of the water bodies of these three basins of Siberia by meristic characters (Fig. 5). At the dendrogram, the graylings of the Yakchii Lakes are included onto one branch, formed by the Lena populations, which also indicates that they belong to this line. The graylings of the Tompuda River are classified in the group including fish from Baikal and the Angara–Yenisei basins.

The largest differences between all analyzed forms are pronounced when the body coloration and patterns on the dorsal fin, reliable diagnostic characters used for identification of the forms (Makoedov, 1985, 1999; Knizhin *et al.*, 2004), are compared. By these characters, the Yakchii grayling is similar to the populations of the Lena basin and differs from graylings of the Baikal and Angara–Yenisei basins.

The close relatedness and the unity of the origin of the graylings of Baikal and the Lena and their morphological similarity has been noted in many works. These views mostly were based on the data obtained in molecular-genetic studies (Skurikhina, 1984; Knizhin, 1985; Tugarina and Knizhin, 1986; Knizhin *et al.*, 2000; Koskinen *et al.*, 2002; Froufe *et al.*, 2003, 2005; Knizhin *et al.*, 2004). From the viewpoint of molecular genetics, the upper Lena graylings are much closer to the Baikal and Angara-Yenisei populations than to the fish inhabiting the Central Asian and Amur basins (Knizhin *et al.*, 2000; Koskinen *et al.*, 2002; Froufe *et al.*, 2003, 2005; Knizhin *et al.*, 2004). All this suggests that in the recent past there was a link between the Lena and Baikal, and contact was possible during this period between the graylings inhabiting the rivers of the Lena basin, surrounding Baikal from the west, north, and east, and the graylings which had entered Baikal from the Yenisei via the Angara. However, this question is not clear because up to the recent time there was no

**Table 3.** Loadings on the first two principal components for the meristic characters

| Characters | Principal components | |
|---|---|---|
| | 1 | 2 |
| ll | 0.999 | −0.004 |
| $D_1$ | 0.026 | −0.081 |
| $D_2$ | −0.105 | 0.026 |
| P | 0.124 | −0.036 |
| V | 0.475 | 0.046 |
| $A_1$ | 0.095 | −0.122 |
| $A_2$ | −0.053 | 0.232 |
| sp. br. | 0.538 | −0.073 |
| r. br. | 0.312 | 0.043 |
| vert | 0.050 | −0.185 |
| pc | 0.076 | 0.991 |

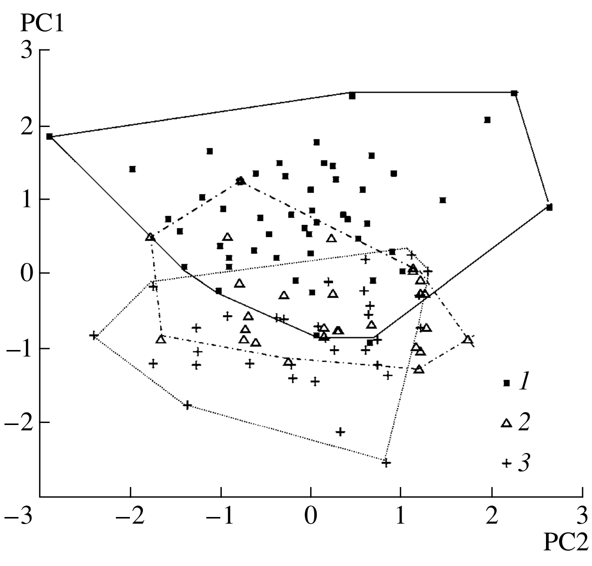



**Fig. 4.** Distribution of the graylings populations *Thymallus arcticus* in the first two principal components (PC) by meristic characters: (*1*) Tompuda River; (*2*) Kutima River; (*3*) Yakchii Lakes.

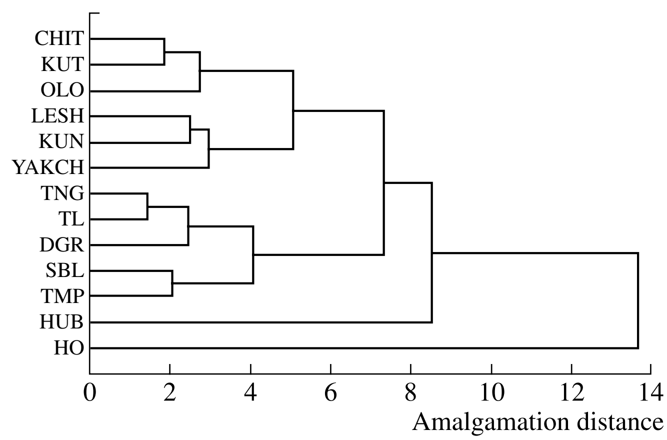



**Fig. 5.** Dendrogram of the differences between the graylings populations in certain water bodies of Eastern Siberia by 11 meristic characters, built using the UPGMA cluster analysis (Euclidean distance). Western Arctic grayling *Thymallus arcticus arcticus*, Angara–Yenisei basin: TNG—Nizhnyaya Tunguska River; TL—Irkutsk Reservoir; Baikal grayling *T. a. baikalensis*, Baikal basin: DGR—Dagar Bay, SBL—Lake Sobolinoye; TMP—Tompuda River; *T. arcticus ssp.*: YAKCH—Yakchii lakes; Kosogol grayling *T. nigrescens*: HUB—Lake Chovsgol; *T. arcticus* ssp.; Lena Basin: KUT—Kutima River; KUN—Lake Kunerma, CHIT—Lake Chitkanda; LESH—Lake Lesha; OLO—Olongdo River; Central Asian Basin, Mongolian grayling *T. brevirostris*: HO—Lake Khokh Nur. All obtained meristic characters except the total number of rays in the dorsal fin (D) were used in the analysis.

**Table 4.** Assessments of the body length and weight of grayling *Thymallus arcticus* from Yakchii lakes (by the observed values)

| Parameter | Age, years | | | | |
|---|---|---|---|---|---|
| | 1+ | 2+ | 3+ | 4+ | 5+ |
| $L_{Sm}$, mm | 72.0 / 95.3–106.6 | 148.4 / 133.3–161.5 | 145.7 / 140.3–150.0 | 158.0 / 141.0–185.2 | 171.0 / 158.4–183.8 |
| Weight, g | 9.0 / 3.9–12.1 | 31.1 / 24.2–48.0 | 36.8 / 29.4–47.2 | 43.6 / 33.1–59.5 | 63.5 / 45.7–96.5 |
| Number of fish, specimens | 14 | 4 | 9 | 16 | 3 |

finding of populations with the typical Lena phenotype in Lake Baikal and the water bodies of its basin. It is difficult to determine how long such contact may have lasted and the extent to which it is reflected in the morphological structures of various groups.

The following scenarios are hypothetical reconstructions of the events occurring after the formation of water drainage from Baikal to the Yenisei via the Angara. In the first case, Lena graylings never inhabited Baikal and lived only in upper courses of certain tributaries, where they sometimes penetrated from the Lena River because of active tectonic processes. In the second case, they may have been displaced by Yenisei graylings, which found favorable conditions in the lake but could not penetrate highland areas, allowing the Lena populations to remain only there.

Currently, geomorphologists consider only one way of the drainage of Baikal waters to Lena River, which occurred via an ancient channel of the Buguldeika River (Southern Baikal) in the Northwestern direction through the valley of pra-Manzurka, which in the past was a part of the Lena basin (Kozhov, 1972; Florensov, 1978; Kuzmin, 2001). The finding of upper Lena graylings in the northern part of Lake Baikal, in a tributary of the Verkhnyaya Angara River, points to the possibility of another geological scenario.

In our opinion, the fact that upper Lena graylings (or populations similar to them) live in the eastern and northeastern tributaries of Lake Baikal at the watershed with Lena may have three causes: (1) drainage from Baikal to pra-Lena via the ancient valleys of the Barguzin or the Verkhnyaya Angara in the past; (2) transit zones, developing as a result of glacial or tectonic events during the development of the watershed between the Baikal and Lena basins; (3) the upper Lena grayling could be a native inhabitant of the Baikal basin but after the drainage direction changed, it was displaced by graylings penetrating from the Yenisei basin, and is currently retained only in relic populations in certain tributaries of Baikal.

On the whole, based on the data obtained, we conclude that a population of the Arctic grayling *T. arcticus* lives in the Yakchii Lakes, which belong to the Baikal basin. The graylings of this population are similar in several characters to graylings inhabiting the Lena River from its upper courses almost to the delta. The main characters linking this population with the Lena graylings include: body coloration, the pattern on the dorsal fin, the number of scales in the lateral line, and the number of gill rakers. The taxonomic status of the Yakchii and Lena forms may be determined after the molecular genetic studies are conducted.

The results obtained in this work are the first to support the hypothesis that Lena graylings inhabit the north part of the Baikal basin, which is evidence of fauna exchange between the Lena and Baikal.

## ACKNOWLEDGMENTS

The authors are deeply indebted to S.S. Alekseev and *P.Ya. Tugarina* for valuable advice on the manuscript; S.G. Afanasiev, S.D. Bezdubnyi, V.V. Buldygerov, V.V. Vanin, E.A. Vasil'eva, V.I. Grishchenko, A.N. Matveev, V.P. Samusenok, R.V. Khalikov, A.L. Yur'ev for significant help during the collection and analysis of the materials and expedition works, D.V. Kuznetsova, for help in the preparation of fish pictures.

The study was supported by the Federal Program Integratsiya, grant K0788, the Ministry of Education of the Russian Federation, grant A03-2.12-265, the program "Universities of Russia," grant UR.07.01.009, the program of the Russian Foundation for Basic research-Baikal, grant 05-04-97214, and the Ministry of Sciences of Portugal (FCT POCT1/33364/BSE/2000).

## REFERENCES

1. L. S. Berg, *Freshwater Fish of the USSR and Adjacent Countries*, 4th ed. (Akad. Nauk SSSR, Moscow, 1948), Part 1 [in Russian].
2. N. I. Chugunova, *Guide on Study of the Age and Growth of Fish* (Sov. Nauka, Moscow, 1959) [in Russian].
3. E. A. Dorofeeva, "The Genus *Thymallus*, in *Annotated Catalog of Cyclostomata and Fish of Continental Waters of Russia*," Ed. by Yu. S. Reshetnikov (Nauka, Moscow, 1998) [in Russian].
4. E. A. Dorofeeva, "The Genus *Thymallus*, in *Atlas of Freshwater Fish of Russia*," Ed. by Yu. S. Reshetnikov (Nauka, Moscow, 2002), Vol. 1 [in Russian].

5. A. G. Egorov, *Fish of Water Bodies of the South of Eastern Siberia (Petromyzonidae, Acipenseridae, Salmonidae, Coregonidae, Thymallidae, and Esocidae)* (Irkutsk. Knizhn. Izd., Irkutsk, 1985) [in Russian].
6. E. N. Elaev, Ts. Z. Dorzhiev, A. B. Imetkhenov, *et al.*, *Nature of Reserve "Dzherginskii" (Baikal Region)* (BGU, Ulan-Ude, 1998) [in Russian].
7. N. A. Florensov, "History of the Lake," in *Problems of Baikal* (Nauka, Novosibirsk, 1978), pp. 9–17 [in Russian].
8. E. Froufe, I. Knizhin, M. T. Koskinen, *et al.*, "Identification of Reproductively Isolated Lineages of Amur Grayling (*Thymallus grubii* Dybowski 1869): Concordance Between Phenotypic and Genetic Variation," Mol. Ecol. **12**, 2345–2355 (2003).
9. E. Froufe, I. Knizhin, and S. Weiss, "Phylogenetic Analysis of the Genus *Thymallus* (Grayling) Based on MtDNA Control Region and ATPase 6 Genes, with Inferences on Control Region Constrains and Broad-Scale Eurasian Phylogeography," Mol. Phylogen. Evol. **34**, 106–117 (2005).
10. M. G. Grosswald, *Ice Caps of Continental Shelves* (Nauka, Moscow, 1983) [in Russian].
11. M. G. Grosswald, "New Approach to the Ice Age Paleohydrology of Northern Eurasia," in *Paleohydrology and Environmental Change*, Ed. by G. Benito, V. R. Baker, and K. J. Gregory (Wiley and Sons, Chichester, 1998), pp. 199–214.
12. I. B. Knizhin, "Structure of Grayling *Thymallus* Populations in the Lena River Basin," in *Proceedings of All-Union Limnological Conference on Matter and Energy Cycle* (Irkutsk, 1985), No. 4, pp. 84–85 [in Russian].
13. I. B. Knizhin, S. J. Weiss, A. L. Antonov, and E. Froufe, "Morphological and Genetic Diversity of Amur Graylings (Thymallus, Thymallidae)," Vopr. Ikhtiol. **44** (1), 59–76 (2004) [J. Ichthyol. **44** (1), 52–69 (2004)].
14. I. B. Knizhin, S. J. Weiss, and S. V. Kirilchik, "MtDNA Sequence Diversity Across the Genus *Thymallus* Both Within and Surrounding the Lake Baikal Basin," in *BDENE*, Novosibirsk, Russia, 2000 ($IC_G$, Novosibirsk, 2000), Vol. 5, Part 2, pp. 21–26.
15. M. T. Koskinen, I. Knizhin, C. R. Primmer, *et al.*, "Mitochondrial and Nuclear DNA Phylogeography of *Thymallus* spp. (Grayling) Provides Evidence of Ice-Age Mediated Environmental Perturbations in the World's Oldest Body of Freshwater, Lake Baikal," Mol. Ecol. **11**, 2599–2611 (2002).
16. M. M. Kozhov, *Essay of Baikal Study* (Vost.-Sib. Knizhn. Izd., Irkutsk, 1972) [in Russian].
17. M. I. Kuz'min, *In the Ice of Baikal* (Geo, Novosibirsk, 2001) [in Russian].
18. A. N. Makoedov, "Phenetic Studies of Thymallidae," in *Proceedings of the 3rd All-Union Conference, Saratov, 1985* (Saratov, 1985), p. 158.
19. A. N. Makoedov, *Relations of Graylings of Siberia and Far East* (UMK Psikhologiya, Moscow, 1999) [in Russian].
20. A. N. Matveev and I. B. Knizhin, "Problems of Systematics of Thymallidae from Lake Baikal Basin," in *Proceedings of the Conference on Study of Water Bodies of Siberia. Tasks and Problems of Development of Fish Industry in Inland Water Bodies of Siberia* (Tomsk, 1996), pp. 93–94.
21. E. Mayr, *Principles of Systematic Zoology* (McGraw-Hill, New York, 1969; Mir, Moscow, 1971).
22. *Methodical Guide on Study of Feeding and Feeding Relationships of Fish in Nature* (Nauka, Moscow, 1974) [in Russian].
23. I. F. Pravdin, *Guide on Study of Fish* (Pishch. Prom-st', Moscow, 1966) [in Russian].
24. P. F. Rokitskii, *Biological Statistics* (Vysheishaya Shkola, Minsk, 1973) [in Russian].
25. A. N. Svetovidov, "European–Asiatic Graylings (Genus *Thymallus* Cuvier)," Tr. Zool. Inst. Akad. Nauk SSSR **3**, 183–301 (1936).
26. L. A. Skurikhina, Candidate's Dissertation in Biology (MGU, Moscow, 1984).
27. P. Ya. Tugarina, *Graylings of Baikal* (Nauka, Novosibirsk, 1981) [in Russian].
28. P. Ya. Tugarina and I. B. Knizhin, "On Morphological Nonuniformity of Fish of the Genus *Thymallus* in Water Bodies of Yakutia," in *Proceedings of XI All-Union Symposium on Biological Problems of the North. Ichthyology, Hydrobiology, Hydrochemistry, Entomology, and Parasitology* (YaF SO AN SSSR, Yakutsk, 1986), No. 4, pp. 64–65.

*Translated by S. V. Budaev*