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Graylings (Thymallidae) of Water Bodies in Western Mongolia: Morphological and Genetic Diversity

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Abstract—Morphological characters, the pattern on the dorsal fin, some biological parameters, and variations of mtDNA control region were studied in graylings of the upper reaches of the Khovd River (western Mongolia). Obtained results demonstrated that grayling of this part of the river was presented by great (predatory) and small (benthophagous) forms of Mongolian grayling *Thymallus brevirostris.* The last form was erroneously equated to Arctic grayling *Thymallus arcticus.* However, genetic unity of great and small forms, homogeneity by meristic characters, and similarity in varying the color of scales and pattern on the dorsal fin attest their belonging to the same species. Water bodies of the Central Asian basin are also populated with populations of Mongolian grayling with mixed type of feeding and signs of external structure, which are typical for both forms in a different degree.

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Investigation of graylings (Thymallidae) as well as of other fishes of Mongolia is of great scientific and practical interest. The recent riverine-lacustrine system of western Mongolia shows that the residues of the great freshwater water body existed several million years ago.[1] Some authors consider (Svetovidov, 1936; Tugarina and Dashidorzhi, 1972; Tugarina, 1981; Makoedov, 1999) that dispersal of graylings in Pliocene–Pleistocene time occurred from this region.

It was considered until recently that lakes and rivers of the Central Asian basin are populated by Mongolian *Thymallus brevirostris* Kessl. and Siberian *T. arcticus* (Pall.) graylings; Lake Khuvsgul, by kosogol grayling *T. arcticus nigrescens* Dor.[2]; upper reaches of Yenisei and Selenga rivers, by West Arctic grayling *T. arcticus arcticus* (Pall.); and Kerulen and Onon rivers, by Amur grayling *T. grubii* Dyb. (Dulma, 1973; Pivnička and Hensel, 1978; Shatunovskii, 1983, 1985; Baasanzhav et al., 1988; Baasanzhav and TSend-Aiush, 2001; Knizhin et al., 2004). Kottelat (2006) considered, on the basis of analysis of earlier published works about Mongolian fishes, that one more species *Thymallus* sp. additionally to the above mentioned taxi inhabits the Shishkid Gol River (upper reaches of the Yenisei River, Darkhat Depression) and Lake Uvs Nur (personal communication). The upper Ob River basin adjacent to the Khovd River is populated by Upper Ob grayling *T. nikolskyi* Kasch.[3]

The discussion about the taxonomic status of Mongolian grayling *Thymallus brevirostris* has continued since the mid-19th century. One specimen of this species from an unknown water body situated in the southern part of Altai in China is stored in the British Museum of Natural History (BMNH no. 1898.2.17.1). It is this individual that was studied by Boulenger (1898) and served the basis for description of *Phylogephyra altaica.* Benke (1965) studied this specimen's designated great head, long upper jaw, and the number of rays in pelvic fin as the characters differed from the other representatives of genus *Thymallus.* The investigated specimen had 12 rays in pelvic fin, and the author considered that was 1–2 rays greater than in known species and subspecies.[4] The description by Boulenger (1898) largely correspondent to the description of *T. brevirostris* given by Kessler (1879), and because of this *P. altaica* was considered by Berg (1907) as its synonym. However, Benke (1965), Jordan (1923), and Travers (1989) considered *P. altaica* to be an independent taxon. Svetovidov (1936) entertained the possibility of classification of *Phylogephyra* as a specific subgenus of genus *Thymallus.*

[1] The hypotheses considered that the development of hydrological network in the territory of Mongolia in Pliocene–Pleistocene are presented by Tugarina and Dashidorzhi (1972).

[2] Taxonomic status of kosogol grayling requires elaborating (Knizhin and Weiss, 2007; Weiss et al., 2007).

[3] The authors consider the species is the form populating upper reaches of the Ob River (Biya, Katun, and Chuya rivers) described by Kashchenko (1899).

[4] It is not said in cited work if all rays were accounted or only branched rays.

Expedition of Kozlov and Kaznakov brought graylings (nos. 11747 and 12644) collected in the Khovd River[5] to the Museum of the Zoological Institute, Russian Academy of Sciences (St. Petersburg) in the late 19th century. Part of the individuals of this collection Berg (1907) classified as Arctic grayling *T. arcticus.* The fact that this species lives in water bodies of western Mongolia was not doubted for a long time. Svetovidov (1936) and then Berg (1948) assumed probable hybridization of Siberian *T. arcticus* and Mongolian *T. brevirostris* graylings in the Khovd River basin. Svetovidov (1936) found the characters of both species in one specimen from the collection of the Zoological Institute, Russian Academy of Sciences (no. 9666) from this river. Ioganzen (1945) did not exclude that grayling from Lake Teletskoe (upper reaches of the Ob River) "bears the impress of Mongolian grayling or even represents to some degree the hybrid *Th. arcticus* × *Th. brevirostris*" (p. 9). Pivnička and Hensel (1978) noted significant variability of morphological characters in populations of Mongolian grayling and assumed that existence of forms of hybrid origin in water bodies of the Central Asian basin is a probable cause of this phenomenon. Zinov'ev (2005) also mentioned two individuals, which he captured in the Khovd River basin in Tuva, with signs of hybridization of above named taxi in external structure. On the contrary, Gundrizer (1966) denied Arctic grayling completely inhabited the basin of this river. He considered also that specimens from the collection of Kozlov and Kaznakov, classified by Svetovidov (1936) as Arctic grayling, were collected actually, not in the Khovd River, but in the upper Ob River.

Dashdorzh et al. (1968) described the subspecies of Mongolian grayling *T. brevirostris kozovi* by several large individuals from the upper Khovd River. Baasanzhav et al. (1983, 1988) found, in addition to this species, Arctic grayling *T. arcticus* in this part of the river. They came to the conclusion on the basis of comparative study that separating of above named subspecies in Mongolian grayling is invalid.

The results of molecular genetic study (Koskinen et al., 2002; Froufe et al., 2005) demonstrated that Mongolian grayling *T. brevirostris* and graylings from the rivers Shishkid Gol (upper reaches of the Yenisei River) and Biya (upper reaches of the Ob River) classified earlier as nominative subspecies of Arctic grayling (Svetovidov, 1936; Berg, 1948; Severin and Zinov'ev, 1982; Shatunovskii, 1983; Zinov'ev, 2005) are relatively close. The results of the revision of genus *Thymallus* carried out by Pivnička and Hensel (1978) also suggest that graylings from the above mentioned water bodies have some morphological similarity.

Hence, the problems concerning distribution of Arctic grayling in water bodies of the Khovd River basin and probability of its hybridization with Mongolian grayling remain to be seen. The data on morphology and genetics of Eurasian graylings obtained recently (Antonov, 2004; Knizhin et al., 2004, 2006a, 2006b, 2006c; Froufe et al., 2005; Romanov, 2005; Weiss et al., 2006, 2007) allow seeing in a new light taxonomic status and phylogenetic relationships between the forms inhabiting western Mongolia, and this was the aim of our work.

MATERIAL AND METHODS

Material of the study was presented by the grayling samples collected in July 1998 in the Terkhin Gol River (upper reaches of the Selenga River, 47°45′ N, 99°20′ E) and lake Khokh Nur[6] (upper reaches of the Dzabkhan River, Shar-Us-Gol, 47°29′ N, 98°33′ E); in July 2006 in the basin of the upper Khovd River, Lake Khoton Nur [48°37′09 N, 88°20′22 E[7], Lake Khurgan Nur[8] (48°33′37 N, 88°42′22 E*), and Lake Tolbo Nur (48°35′01 N, 90°00′16 E*) (Fig. 1). Earlier published data on morphology and genetics of graylings from different water bodies of Siberia referred in the text were used for comparison. The collections of the Zoological Museum, Moscow State University (Moscow), the Zoological Institute, Russian Academy of Sciences (St. Petersburg), and Museum für Naturkunde, Humboldt University (Berlin) were also examined in the course of the work. When studying museum pieces, particular emphasis was placed upon head form, sizes of jaws, body color, and dorsal fin pattern of graylings. Dissection of fishes was not carried out.

In field, individuals were differentiated by external characters, which characterized Mongolian *T. brevirostris* (snout acuminate, upper jaw reaching eye center, developed teeth) and Siberian *T. arcticus* (snout subcircular, upper jaw not reaching eye center, teeth slightly expressed) graylings on the basis of diagnoses presented in the works by Kessler (1879), Boulenger (1898), Svetovidov (1936), and Berg (1948). In this result, we found in the studied water bodies, in addition to typical Mongolian grayling, a sympatric form similar in external characters to Arctic grayling. Because its taxonomic status required verification, it is referred in this text as "Arctic grayling" *T.* cf. *arcticus.* Individuals of both forms (both juveniles and mature) well identified according to the above listed characters were found in lakes Khoton Nur and Khurgan Nur. Graylings from Lake Tolbo Nur had external characters, which were peculiar in different degrees to both of the above named species. Because only Mongolian grayling was noted for this lake in earlier published works (Dulma, 1973;

[5] The Khovd (Mongolian) River.

[6] Other variants of the name of this lake are the following: Khukhe-Nuur, Khukhe Nur, and Khukh Nur in the work by Shatunovskii (1985).

[7] Coordinates were determined with the help of GPS–12 Garmin, and the others were calculated using geographic map 1 : 1 000 000.)

[8] This lake is presented in the work by Shatunovskii (1985) as Khorgon Nur.

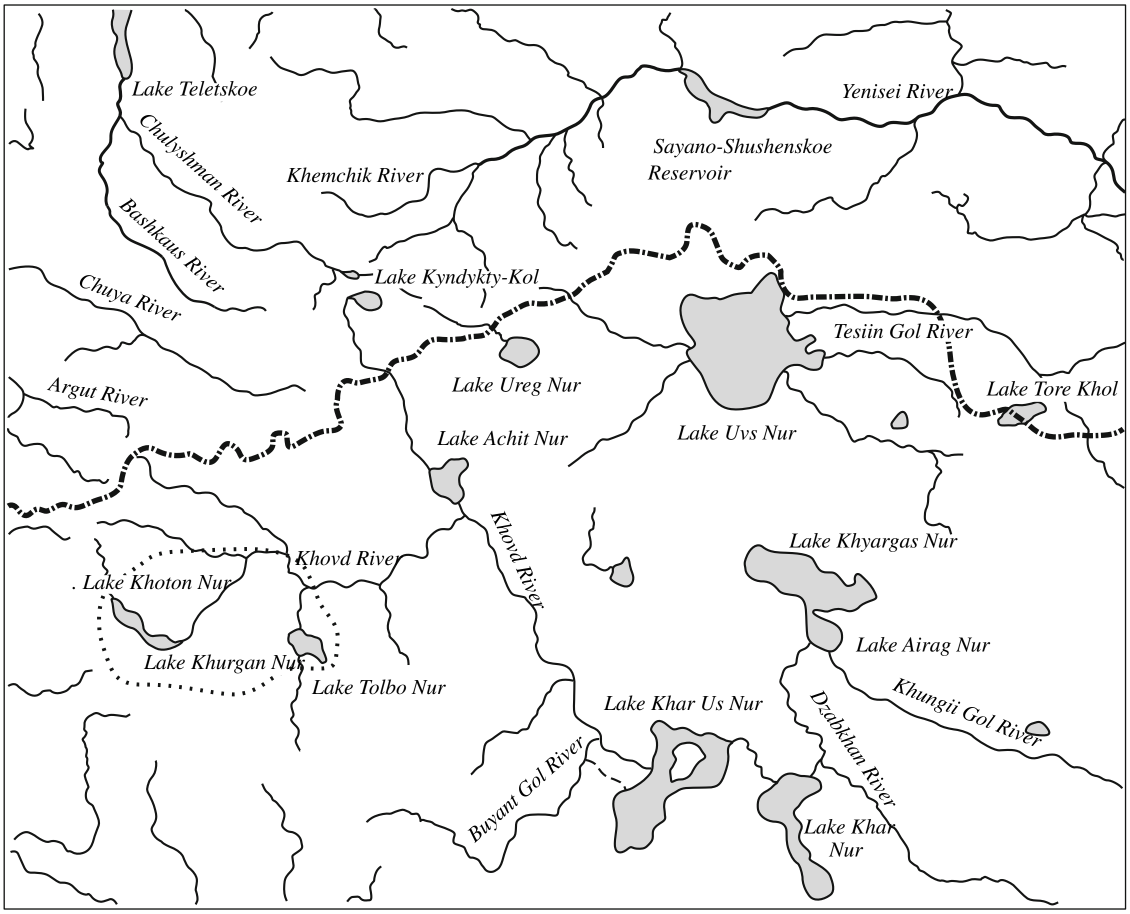

Fig. 1. Schematic map of studied region. Western Mongolia. Dotted line outlined the region of material collecting in 2006.

Shatunovskii, 1983), we classified three fishes from this water body, which we had at our disposal, preliminarily as *T. brevirostris.*

The age was determined by scales according to recommendations by Chugunova (1959). Body length and weight data of grayling individuals of different age from western Mongolia in comparison with earlier published data are presented in Table 1.

Morphometric characters were analyzed according to the method by Pravdin (1966), taking into consideration recommendations by Svetovidov (1936) and Tugarina (1981). All estimates were obtained by one operator. Indices of body measurements were calculated relative fork length (L_{Sm}). Additionally to standard morphometric characteristics, we analyzed the complex of characters suggested earlier for diagnostics of different grayling forms (Knizhin et al., 2004). Descriptions of color and photographs of fishes were performed by mature individuals in fresh material. Statistical analysis of data was carried out using program packages Statistica 5.5A (Borovikov and Borovikov, 1998) and SPSS 8.0. Significance of differences was estimated by *t*-test, taking $p \leq 0.001$, and the size of difference, by CD value (Mayr et al., 1953). Principal components analysis was performed by variance–covariance matrix.

Adipose fin clips for molecular genetic analysis were taken from every fish and fixed in 96° ethanol. Additionally to own data, we used in this study the materials on graylings from Lake Achit Nur 49°25′32 N 90°39′55 E (*T. brevirostris*) and its tributary the Bokhmoroon Gol River 49°39′35 N 90°16′35 E (*T. arcticus*), kindly presented by M. Kottelat.[9] We used also for comparison the information from available literature (Koskinen et al., 2002; Froufe et al., 2003, 2005; Knizhin et al., 2004; Stamford and Taylor, 2004; Weiss et al., 2006).

The complete mt-DNA control region and partial segments of both flanking genes of t-RNA were amplified in 37 individuals using primers LRBT–25 and LRBT–1195 (Weiss et al., 2002). These individuals included the following: one individual of the Upper Ob grayling *T. nikolskyi*, four individuals of the upper Yenisei grayling *Thymallus* sp. from the Shishkid Gol River basin, 17 individuals of Mongolian grayling

[9] Taxonomic belonging of graylings from these water bodies was determined by M. Kottelat.

Table 1. Average values of body length and weight of graylings *Thymallus* from water bodies of western Mongolia (by observed data)

Taxon, water body (source of information), number of studied fishes	Age, years										
	2+	3+	4+	5+	6+	7+	8+	9+	10+	11+	12+
T. brevirostris, lakes Khoton Nur and Khurgan Nur (own data), $n = 20$	200/67	244/125	343/345	343/455	437/988	496/1300	584/1800	–	612/2650	550/1770	
T. brevirostris, lakes Khoton Nur and Khorgon Nur (Shatunovskii, 1985)											
Males*	–	–	236/145	260/180	300/177	361/450	390/480	440/650	485/980	508/1100	549/1250
Females*	–	202/75	237/135	271/150	315/189	363/455	398/485	431/615	488/100	–	–
T. brevirostris, upper reaches of the Khovd River, males, (Baasanzhav et al., 1988)*	–	–	234/145	260/180	300/177	361/450	390/480	440/650	485/980	580/1100	549/1250
T. brevirostris, Lake Kyndykty-Kol (Gundrizer and Popkov, 1984)*	108/12	118/25	146/46	171/73	194/104	214/149	233/197	250/244	268/293	–	–
T. brevirostris, Lake Sut-Kol (Gundrizer and Popkov, 1984)*	236/185	321/405	–	398/775	–	–	–	–	–	–	–
T. brevirostris, the Bogdoin-Gol River (Tugarina and Dashidorzhi, 1972), $n = 65$	–	217/90	255/153	281/200	326/302	369/438	–	–	–	–	–
T. brevirostris, Lake Khokh Nur (own data), $n = 7$	–	–	297/266	–	325/316	358/449	400/588	419/676	–	–	–
T. brevirostris, Lake Khokh Nur (Shatunovskii, 1985)											
Males*	–	206/75	248/136	265/202	306/234	338/350	373/462	–	–	–	–
Females*	–	216/72	248/98	–	306/268	332/356	376/480	–	–	–	–
T. brevirostris, Lake Tolbo Nur (own data), $n = 3$	–	255/175	295/285	292/270	–	–	–	–	–	–	–
Thymallus cf. *arcticus*, upper reaches of the Khovd River (own data), $n = 34$	185/69	229/127	253/167	290/303	283/262	–	–	–	–	–	–
T. arcticus, upper reaches of the Khovd River (Baasanzhav et al., 1988)											
Males*	166/55	192/83	226/128	250/188	260/195	–	–	–	–	–	–
Females*	165/53	177/73	208/127	220/115	250/180	–	–	–	–	–	–

Note: Above the line, Smitt's length (L_{Sm}), mm; under the line, body weight, g; *number of fishes was not given.

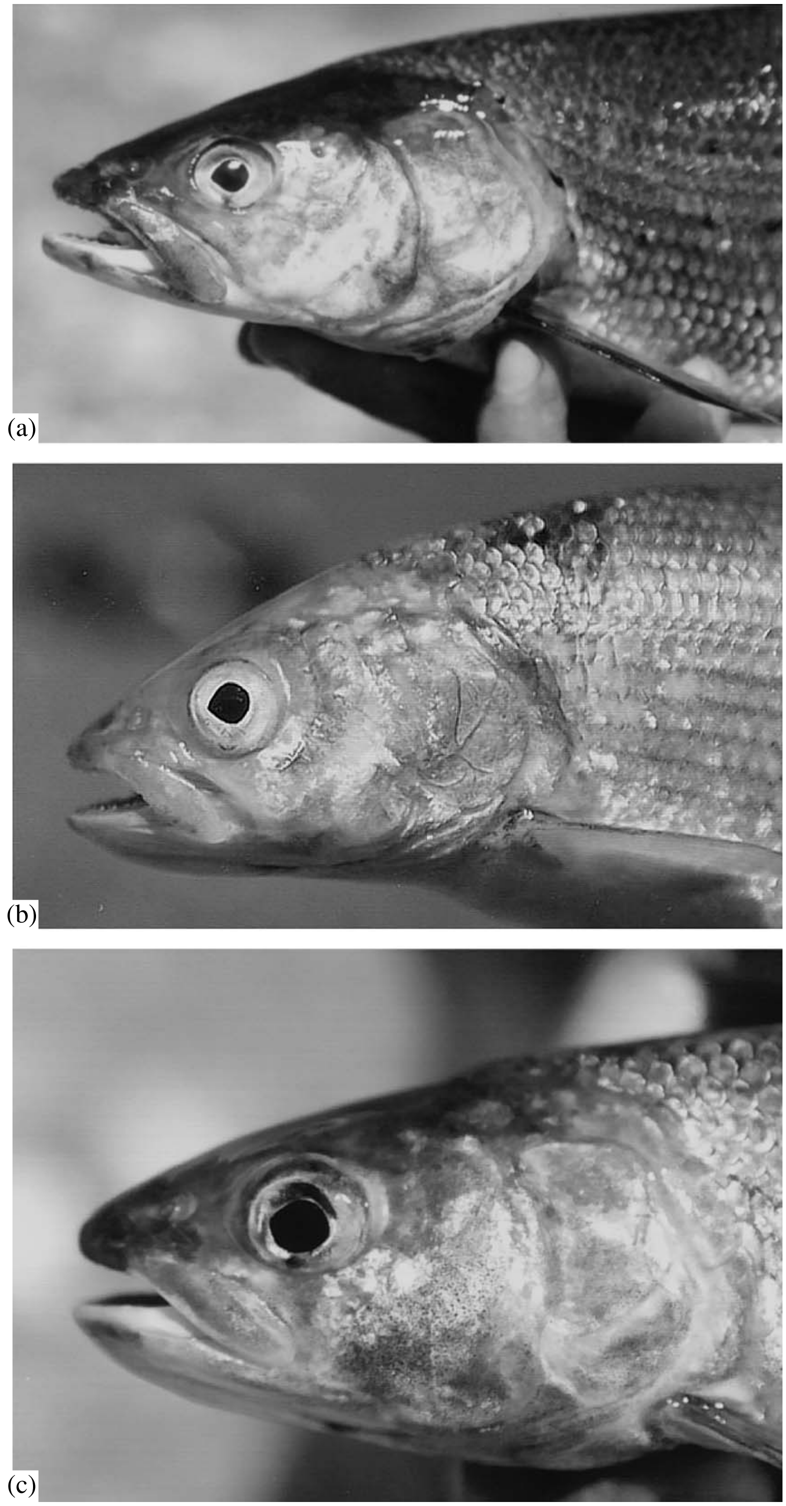

Fig. 2. Heads of graylings *Thymallus* from water bodies of western Mongolia: (a) Mongolian *T. brevirostris*, outlet of the Khovd River from Lake Khurgan Nur; (b) *T. brevirostris*, Lake Tolbo Nur; c, Arctic grayling *T.* cf. *arcticus*, Lake Khoton Nur.

T. brevirostris, and 15 individuals of Arctic grayling *T.* cf. *arcticus* from the basin of the upper Bogdo River, Lake Achit Nur, and the Bokhmoroon Gol River. The conditions of PCR (25 μl of reaction) were the following: every reaction contained 19 μl of H_2O, 2.5 μl of tenfold Promega buffer, 0.5 μl 10 mM of every primer, 1.5 μl 25 mM $MgCl_2$, 0.5 μl 10 mM dNTP, 0.1 μl of *Taq* DNA polymerase Promega, and 0.5 μl of 100 ng/μl

DNA. The cycle of parameters was the following: initial denaturation was carried out under 94°C during 3 min, denaturation under 94°C during 40 s, annealing under 53°C, and synthesis under 72°C during 40 s. A sum total of 30 cycles were carried out. Amplified DNA was purified using a NucleoSpin Extract Kit (Machery–Nagel). About 100 ng of purified product of PCR were used in the cycle of sequencing according the protocol ABI PRISM BigDye Terminator. The sequences were determined in an automatic sequenator ABI–3130. The sequences of mtDNA obtained in the course of the study were placed into GenBank with access codes EU676264–EU676300. Alignment of newly obtained sequences was carried out by hand together with 28 earlier published haplotypes representing the following taxi: *T. brevirostris* ($n = 4$) from Lake Khokh Nur (the Dzabkhan River basin), *T. grubii* ($n = 6$), *T. baicalensis* ($n = 9$), *T. arcticus* ($n = 8$), and *T. nikolskyi* ($n = 1$) (Koskinen et al., 2002; Froufe et al., 2003, 2005). Phylogenetic analysis was performed using the program package PAUP*4.0b10 (Swofford, 2002). Phylogenetic tree was constructed using the Neighbor-Joining (NJ) method based on the calculation of pair genetic distances using the model of nucleotide substitutions Kimura–2. Node support was estimated with 1000 bootstrap replicates. Between-group variation, corrected for within-group variation (*p*-distances), was calculated in the program MEGA ver. 3.1 (Kumar et al., 2001).

RESULTS

Mongolian grayling (Figs. 3a, 3b). Individuals from lakes Khoton Nur and Khurgan Nur have barlike body. Back dark; belly light. Color of scales varies from silvery dull to dark gray with blued tint. Many small black spots on body sides from the head to the posterior edge of dorsal fin; they are absent in some individuals. Snout elongated. Head slightly flattened top down. Mouth large. Posterior edge of upper jaw reaching behind eye center and slightly bended downward (Fig. 2a). Teeth well seen on jaws, tongue, palate, and vomer (Fig. 4). Dorsal fin small and upper part of its posterior edge is slightly pointed in fishes of both sexes. Last rays of dorsal fin are equal or slightly shorter than the longest rays in its anterior part. The spots on interray webs are oval, pale red, or scarlet, and form four incomplete rows parallel to the fin base. The spots are well seen only on last three to four interray webs in fishes from the Khovd River and Lake Khokh Nur (upper reaches of the Dzabkhan River). Some spots of the upper row are often of elongated form with tops forming very narrow border of scarlet color (Figs. 5a, 5b).

Individuals from Lake Tolbo Nur have cylindricale and slightly slender body form. Scales have uniform silvery dull color. Ten to 15 small black spots are situated on body sides from the head to the end of dorsal fin base. Snout slightly acute. There are small teeth on jaws, vomer, and plate. Upper jaw elongated, almost the same form as in fishes from Lakes Khoton Nur and Khurgan Nur, but its posterior edge not reaching behind eye center and is not bended downward (Fig. 2b). The dorsal fin pattern is composed of four to five uneven, slightly ascending toward posterior upper edge of the fin rows of damask, oval, slightly elongated in horizontal direction spots. The spots are greater in the posterior part of the fin than in anterior part. Some spots in the upper row are elongated vertically and their tops join forming slightly expressed scarlet fringe (Fig. 5c).

"Siberian" grayling (Fig. 3c). Body cylindrical, slender. The scales have most often uniform silvery color, back dark, belly light. Some individuals can have very dark color. Black spots on the body are relatively evenly distributed from the head to the end of dorsal fin base or are absent. Snout tip oval. Mouth small. Upper jaw of ellipsoid form; its posterior edge is not bended downward and not reaching behind eye center (Fig. 2c). Teeth on jaws, palate, and vomer poorly developed. Dorsal fin small, its end slightly pointed, posterior rays slightly shorter or have the same length as the rays in anterior part. The pattern on the fin in graylings from the Khovd River and lakes Khoton Nur and Khurgan Nur is similar largely to that in individuals from Lake Tolbo Nur (Figs. 5d, 5e).

Mongolian grayling in lakes Khoton Nur and Khurgan Nur grows more quickly than in main stream of the Khovd River and other water bodies of the Central Asian basin (Table 1). Some individuals of typical form from the studied lakes reached by the age of 7 years weigh 1.6–1.8 kg and L_{Sm} 550–560 mm. One 11-year-old individual had length 665 mm and weight 3.350 kg. In the Khovd River, weight of captured fishes at the age of 6–7 years and L_{Sm} 350 to 400 mm did not exceed 700 g. The graylings with weight more than 5 kg are found in these lakes according the interview data. Individuals of "Siberian" grayling from the basin of the upper Khovd River in our catches dominated by fishes of length 250–280 mm and weight 150–250 g. Maximum length of one 6-year-old individual comprised 365 mm and weight 545 g. Morphometric characters of studied grayling forms are presented in Table 2.

Molecular genetic analysis. Aligned block of 65 sequences included complete control region (CR, 1006 pairs of nucleotides) and adjacent fragment of genes of tRNA proline (68 pairs of nucleotides) and phenylalanine (15 pairs of nucleotides). We revealed 39 haplotypes[10], including 18 haplotypes found first, among 65 sequenced sequences on the base of 115 variable sites, of which 98 were phylogenetically informative.

Phylogenetic NJ tree (Fig. 6) was depicted on the base of obtained distances of Kimura–2 parameter

[10] Total number of haplotypes was 46, taking into account insertions/deletions, but the data on indels were not included in this analysis.

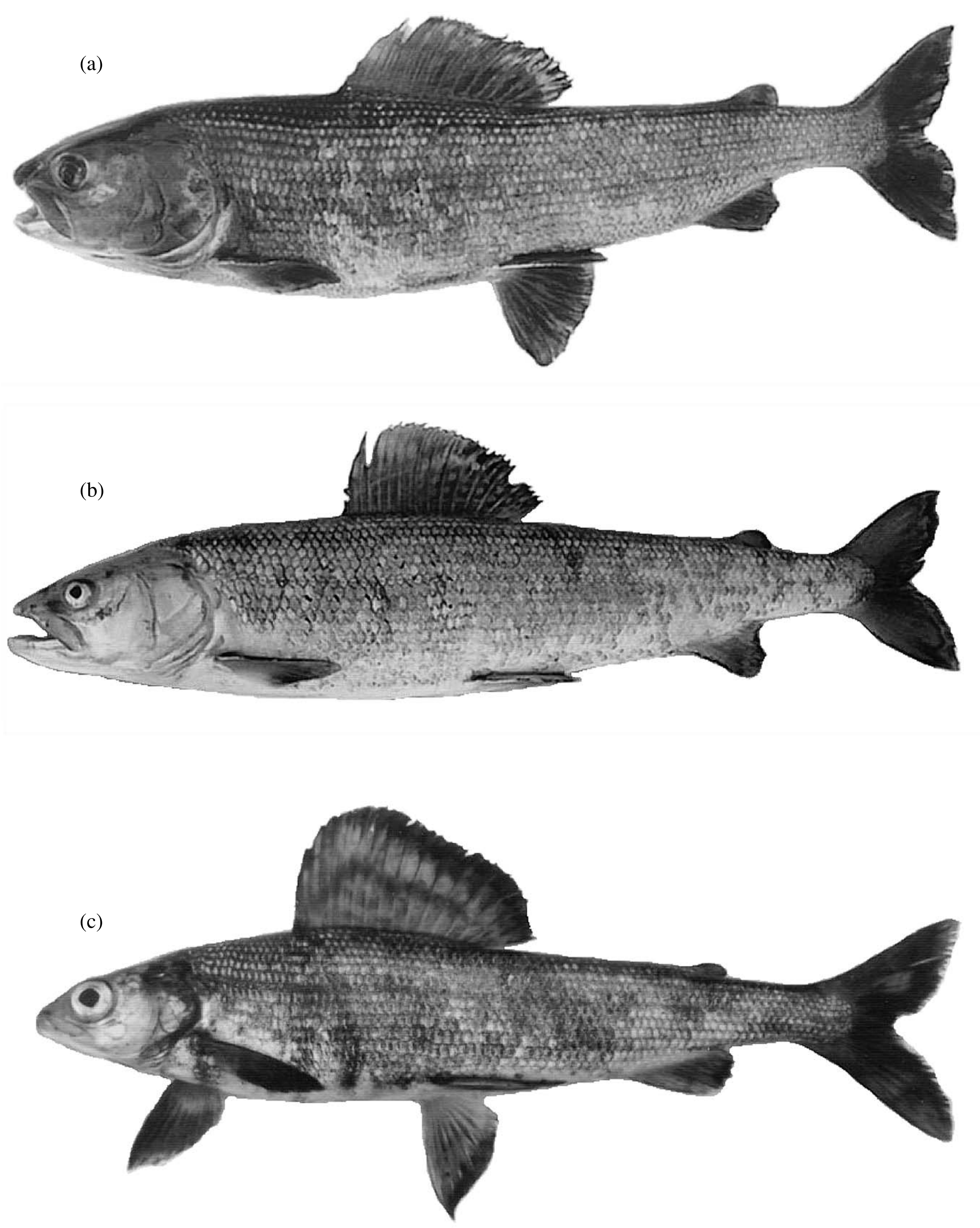

Fig. 3. Graylings *Thymallus* from water bodies of the upper Khovd River (western Mongolia): (a, b) *T. brevirostris*, upper Khovd River; (a) male L_{Sm} 665 mm, weight 3350 g, age 10+; (b) female L_{Sm} 558 mm, weight 1850 g, age 6+; (c) Arctic grayling *T.* cf. *arcticus*, male L_{Sm} 265 mm, weight 187 g, age 4+.

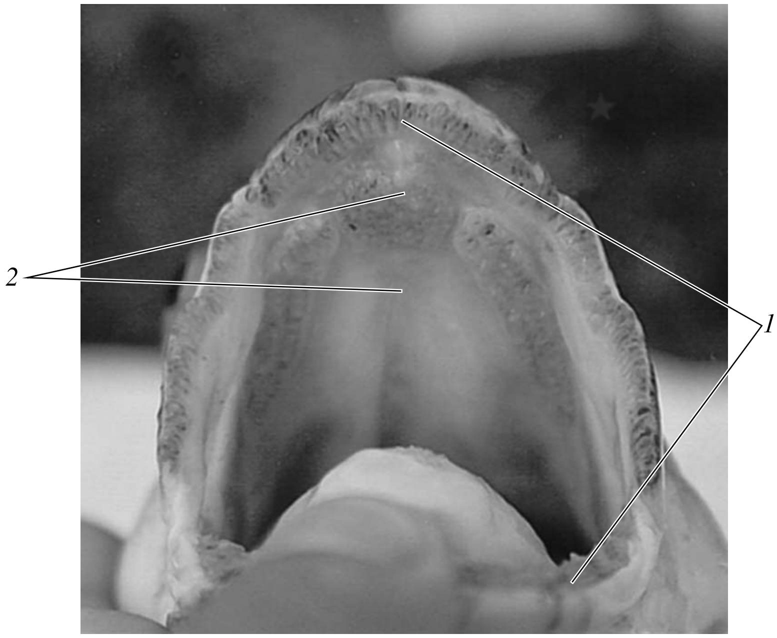

Fig. 4. Teeth on jaws (*1*) and vomer (*2*) in Mongolian grayling *Thymallus brevirostris* from Lake Khoton Nur.

(K2P), where the sequences of Amur grayling *T. grubii*[11] were used as external enrooting group. We can see in it separate branches with high values of bootstrap support of nodes, representing different taxi. It should be noted that all samples from water bodies of the Central Asian basin including earlier obtained haplotypes of four individuals of Mongolian grayling (Cas01–04), first published in the work by Koskinen et al. (2002), formed one branch. It included 36 sequences, which contained only 13 polymorphic sites, representing 18 haplotypes, of which 14 were found firstly (Table 3). Any structuring of haplotypes within this branch was not observed. For example, one haplotype Cas2, first described in Mongolian grayling from Lake Khokh Nur (the Dzabkhan River basin), was found in ten individuals from different localities in the basin of the upper Khovd River, which had phenotypes peculiar to both discussed forms.

Two individuals of the upper Ob grayling *T. nikolskyi* from the Biya River formed sister branch to Mongolian grayling *T. brevirostris* with divergence level 1.5% (Table 4). The upper Ob grayling in turn was genetically close to grayling from the upper reaches of the Yenisei River in Mongolia. The branch, representing Arctic grayling *T. arcticus*, is essentially distant from the clade, combining above mentioned taxi (3.1–3.7% of divergence). Mongolian, upper Ob, and upper Yenisei graylings are actually the monophyletic group (bootstrap support 99%) relatively close to Baikal grayling *T. baicalensis,* the level of divergence with nearly half the divergence (1.6 to 2.0%) compared to *T. arcticus.*

[11] Topology of NJ and MP trees did not differ significantly.

Comparative remarks. Analysis of variations in mtDNA of Mongolian and "Siberian" graylings from the upper Khovd River suggests their genetic identity. The comparison of these forms by body color and the dorsal fin pattern demonstrated the absence of pronounced difference. Moreover, obtained data allow concluding that the dorsal fin pattern of Mongolian grayling or its description (Svetovidov, 1936; Gundrizer, 1966; Tugarina and Dashidorzhi, 1972; Shatunovskii, 1983) are much similar to that in form, preliminary classified as "Siberian" grayling.

It was considered that scale cover in Mongolian grayling had level silvery dull color (Svetovidov, 1936; Berg, 1948; Gundrizer, 1966; Tugarina and Dashidorzhi, 1972; Baasanzhav et al., 1983; Shatunovskii, 1983; Dorofeeva, 2002). Our observations suggest that this is peculiar mostly to fishes with relatively low growth rate from the Khovd River. Body color in graylings from Lakes Khoton Nur and Khorgon Nur with weight exceeding 1 kg varied in wide range: from silvery dull to dark gray with turquoise tint. The color of scale cover in so-called Arctic grayling is also relatively variable. Two individuals of this form of almost black color were captured in Lake Khoton Nur at the depth 10 m, whereas fishes with only silvery color were found in littoral and main stream of the Khovd River.

When comparing some parameters of the head, one can see that its form and the size of the upper jaw (Fig. 7, Table 5) in populations of graylings from water bodies of western Mongolia are not similar (Gundrizer, 1966; Tugarina and Dashidorzhi, 1972; Shatunovskii,

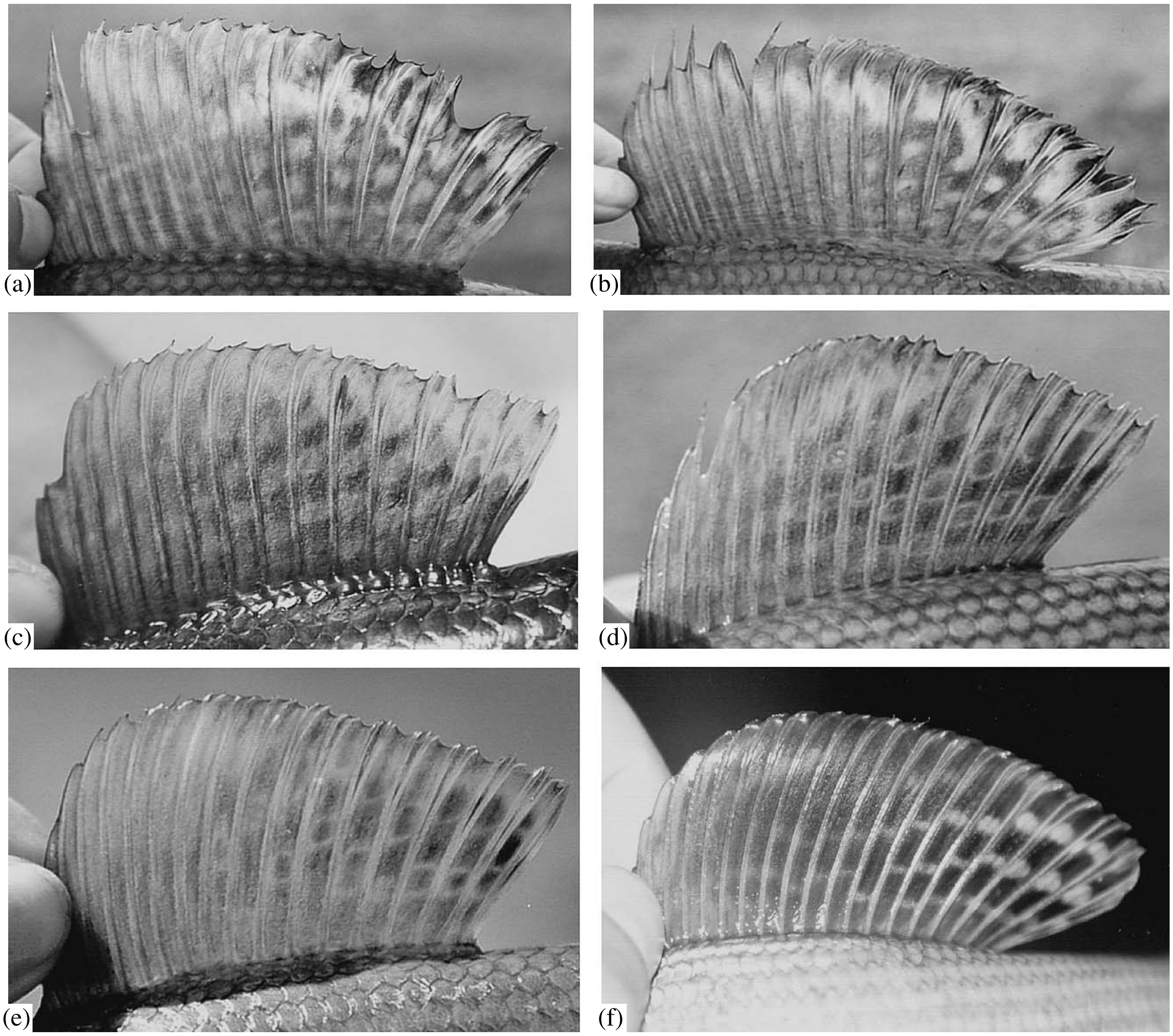

Fig. 5. Dorsal fins of graylings *Thymallus* of Altai and western Mongolia. Upper reaches of the Khovd River: (a, b) Mongolian grayling *T. brevirostris*; (c, d, e) Arctic grayling *T.* cf. *arcticus.* Upper reaches of the Ob River: (f) upper Ob grayling *T. nikolskyi.*

1983; Baasanzhav et al., 1988). The length of maxilla in Mongolian grayling from lakes Khoton Nur and Khurgan Nur was significantly greater in comparison with Arctic grayling. The fact of finding in the studied lakes of well-identified juveniles of both forms suggests that these differences are not connected with size variations. Of 12 examined individuals of Mongolian grayling from Lake Chulug-Kol (the Khovd River basin, Tuva) of L_{Sm} 187–276 mm, stored in the Zoological Museum, Moscow State University (R–20898)[12], two fishes had relatively short rounded snout with maxilla, the end of which almost reaching middle of the eye. The data presented in Table 5 suggest that graylings from different parts of the Khovd River basin, classified earlier like different species, could differ significantly from one another in these characters or are characterized by intermediate values of these characters. Both discussed forms differed from other known taxi of genus *Thymallus*, including those inhabiting adjacent to the Khovd River upper reaches of Ob and Yenisei rivers in the presence of teeth on jaws and vomer and in articulation of mandible with cranium behind the vertical of posterior eye edge.

The comparison of analyzed forms by *CD* coefficient did not reveal significant difference by meristic characters, whereas such difference was observed by morphometric characters (Table 2). Mongolian grayling from lakes Khoton Nur and Khurgan Nur was characterized by less number of vertebrae (*vert.*) in comparison with individuals of this form from Lake Khokh Nur (49–54 against 56–57). Significant difference of all west Mongolian graylings according to *CD* from other

[12]: Collections of A.S. Golubtsov and A.A. Tsessarskii, 12–13 July, 1999. It is noted in original label: *Thymallus* cf. *brevirostris.*)

Table 2. Morphometric and meristic characters of graylings *Thymallus* from water bodies of the upper reaches of the Khovd River

Character	Lakes Khoton Nur and Khurgan Nur, outlet of the Khovd River		Lake Tolbo	CD/t_{st}		
	T. brevirostris (*n* = 21)*	*T.* cf. *arcticus* (*n* = 31)*	*T. brevirostris* (*n* = 3)			
	1	2	3	1–2	1–3	2–3
L_{Sm}, mm	468.0	260.7	280.4			
	298.0–665.0	212.5–365.8	255.0–294.5			
Morphometric characters, in % L_{Sm}						
l	95.9 ± 0.09	95.5 ± 0.10	95.2 ± 0.35	0.61	0.98	0.37
	0.37, 95.2–96.4	0.54, 94.5–97.2	0.61, 94.7–96.0	2.97	1.94	0.82
l_2	74.6 ± 0.38	78.6 ± 0.14	76.7 ± 0.31	2.34	1.29	2.02
	1.53, 72.6–78.8	0.77, 76.6–80.1	0.54, 76.1–77.4	**9.88**	**4.28**	**5.59**
ao	7.3 ± 0.13	5.9 ± 0.09	6.6 ± 0.18	1.98	1.18	1.18
	0.50, 6.5–8.3	0.50, 5.0–6.9	0.32, 6.2–7.0	**8.85**	3.15	**3.48**
o	3.8 ± 0.10	4.6 ± 0.05	4.1 ± 0.02	1.66	0.75	1.83
	0.40, 3.3–4.7	0.27, 4.1–5.3	0.04, 4.0–4.1	**7.16**	2.94	**9.28**
f	12.0 ± 0.13	10.2 ± 0.13	11.3 ± 0.26	2.05	1.04	1.30
	0.50, 10.8–13.1	0.72, 9.0–11.4	0.45, 10.7–11.7	**9.79**	2.41	**3.78**
Ò	22.0 ± 0.23	19.6 ± 0.16	20.8 ± 0.29	1.94	1.16	1.21
	0.90, 20.6–23.5	0.85, 18.0–21.2	0.51, 20.1–21.2	**8.57**	3.24	**3.62**
cH	14.4 ± 0.16	13.7 ± 0.14	13.9 ± 0.15	0.72	0.72	0.25
	0.64, 13.3–16.1	0.74, 12.1–15.1	0.27, 13.6–14.2	**3.29**	2.28	0.97
ch	9.9 ± 0.14	9.2 ± 0.11	9.5 ± 0.11	0.83	0.67	0.46
	0.57, 8.6–11.4	0.62, 8.2–10.5	0.19, 9.3–9.8	**3.93**	2.25	1.93
io	6.1 ± 0.18	5.6 ± 0.08	6.0 ± 0.07	0.61	0.14	0.94
	0.71, 3.8–6.9	0.41, 4.7–6.2	0.12, 5.9–6.2	2.54	0.52	**3.76**
lmx	7.4 ± 0.13	5.4 ± 0.08	6.4 ± 0.14	3.02	1.73	2.08
	0.52, 6.5–8.3	0.41, 4.7–6.4	0.25, 6.1–6.7	**13.10**	**5.23**	**6.20**
i/lmx	1.8 ± 0.05	1.7 ± 0.04	1.9 ± 0.09	0.35	0.43	0.75
	0.18, 1.4–2.1	0.22, 1.3–2.1	0.15, 1.7–2.1	1.56	0.97	2.03
lmd	13.1 ± 0.18	10.3 ± 0.10	11.5 ± 0.22	3.11	1.95	1.80
	0.72, 11.2–14.3	0.54, 9.2–11.2	0.39, 11.2 ± 12.1	**13.60**	**5.63**	**4.97**
H	20.3 + 0.44	19.9 ± 0.23	19.3 ± 0.79	0.19	0.45	0.32
	1.75, 16.4–23.5	1.26, 17.4–22.3	1.36, 17.8–21.1	0.81	1.11	0.73
h	6.2 ± 0.13	6.9 ± 0.09	6.7 ± 0.07	0.99	0.95	0.40
	0.51, 5.5–7.4	0.49, 6.1–7.7	0.12, 6.5–6.8	**4.43**	3.39	1.75
w	10.5 ± 0.21	11.4 ± 0.15	12.8 ± 0.37	0.77	2.15	1.35
	0.85, 8.9–11.9	0.81, 10.3–13.1	0.65, 12.0–13.6	**3.49**	**5.41**	**3.51**
aD	35.3 ± 0.26	33.0 ± 0.26	34.3 ± 0.29	1.33	0.86	0.88
	1.05, 33.5–37.1	1.38, 29.9–36.5	0.51, 33.6–34.8	**6.26**	2.57	3.34
pD	43.3 ± 0.25	46.3 ± 0.24	45.3 ± 0.28	1.82	1.79	0.72
	1.01, 41.9–45.7	1.30, 43.7–48.7	0.48, 44.8–45.9	**8.66**	**5.33**	2.71
aA	72.2 ± 0.35	70.0 ± 0.27	70.7 ± 0.24	1.09	1.03	0.46
	1.40, 70.4–75.6	1.46, 66.5–72.9	0.41, 70.4–71.3	**4.98**	3.53	1.94
aV	48.7 ± 0.57	44.9 ± 0.23	46.9 ± 0.61	1.47	0.72	1.23
	2.28, 44.9–53.3	1.23, 42.6–48.5	1.06, 46.1–48.4	**6.18**	2.16	3.07
lp	16.3 ± 0.26	17.4 ± 0.14	17.8 ± 0.47	0.86	1.14	0.36
	1.03, 14.4–18.5	0.76, 15.9–20.0	0.81, 16.6–18.5	**3.73**	2.79	0.82
PV	27.0 ± 0.35	27.3 ± 0.21	27.7 ± 0.41	0.17	0.45	0.30
	1.40, 24.7–30.6	1.14, 25.7–30.8	0.71, 26.8–28.4	0.73	1.30	0.87
VA	23.6 ± 0.34	25.2 ± 0.23	25.2 ± 0.69	0.87	0.89	–
	1.35, 20.8–25.8	1.24, 22.3–27.2	1.19, 23.8–26.7	**3.90**	2.08	
lD	17.8 ± 0.25	19.0 ± 0.29	17.5 ± 0.28	0.65	0.27	0.92
	1.01, 15.9–20.1	1.55, 16.3–22.5	0.48, 16.9–17.9	3.13	0.80	**3.72**

Table 2. (Contd.)

Character	Lakes Khoton Nur and Khurgan Nur, outlet of the Khovd River		Lake Tolbo	CD/t_{st}		
	T. brevirostris (*n* = 21)*	*T.* cf. *arcticus* (*n* = 31)*	*T. brevirostris* (*n* = 3)			
	1	2	3	1–2	1–3	2–3
hD_1	10.8 ± 0.15 0.59, 9.9–11.9	12.3 ± 0.16 0.86, 10.7–14.7	10.9 ± 0.21 0.36, 10.5–11.3	1.44 **6.84**	0.14 0.39	1.50 **5.30**
hD_2	7.7 ± 0.18 0.71, 6.1–8.9	8.9 ± 0.13 0.70, 7.7–10.6	8.1 ± 0.32 0.55, 7.3–8.7	1.20 **5.40**	0.45 1.09	0.90 2.32
lA	8.2 ± 0.17 0.68, 6.8–9.7	8.6 ± 0.13 0.72, 7.4–10.5	8.6 ± 0.14 0.25, 8.2–8.8	0.40 1.87	0.55 1.82	–
hA	9.7 ± 0.34 1.35, 7.4–12.5	12.1 ± 0.19 1.04, 10.4–14.0	12.5 ± 0.33 0.57, 11.7–13.0	1.41 **6.16**	1.91 **5.91**	0.34 1.05
lP	13.8 ± 0.23 0.91, 12.5–16.3	15.2 ± 0.10 0.56, 14.2–16.0	14.7 ± 0.37 0.64, 13.9–15.5	1.31 **5.58**	0.81 2.07	0.59 1.30
lV	13.0 ± 0.20 0.78, 11.9–14.8	14.4 ± 0.13 0.68, 12.7–16.4	13.8 ± 0.27 0.46, 13.4–14.4	1.35 **5.87**	0.58 2.38	1.18 2.00
Meristic characters						
ll	81.6 ± 0.83 3.71, 75–87	78.8 ± 0.60 3.34, 73–88	77.0 ± 0.47 0.82, 76–78	0.56 2.73	1.21 **4.82**	0.52 2.36
D_1	6.7 ± 0.14 0.64, 6–8	7.0 ± 0.06 0.31, 6–8	6.3 ± 0.27 0.47, 6–7	0.42 1.97	0.50 1.32	1.24 2.53
D_2	12.7 ± 0.12 0.56, 12–14	12.0 ± 0.13 0.74, 10–13	12.3 ± 0.27 0.47, 12–13	0.75 **3.96**	0.55 1.35	0.34 1.00
D	19.4 ± 0.15 0.66, 18–21	19.0 ± 0.14 0.76, 17–20	19.0 ± 0.47 0.82, 18–20	0.40 1.95	0.38 0.81	–
P	14.7 ± 0.13 0.57, 14–16	14.4 ± 0.12 0.66, 13–16	14.0 –	0.34 1.70	1.23 **5.38**	0.61 **3.33**
V	9.4 ± 0.11 0.49, 9–10	9.3 ± 0.10 0.58, 8–10	9.7 ± 0.27 0.47, 9–10	0.13 0.67	0.44 1.03	0.54 1.39
A_1	3.9 ± 0.11 0.48, 3–5	3.9 ± 0.05 0.30, 3–4	4.0 –	–	0.21 0.91	0.33 2.00
A_2	9.0 ± 0.17 0.74, 7–10	8.9 ± 0.11 0.62, 8–10	9.0 –	0.10 0.49	–	0.16 0.91
sb.	18.3 ± 0.25 1.13, 16–20	19.1 ± 0.26 1.47, 15–22	17.7 ± 0.54 0.94, 17–19	0.43 2.22	0.41 1.01	0.80 2.34
rb.	10.2 ± 0.13 0.60, 9–11	9.8 ± 0.09 0.51, 9–11	9.3 ± 0.27 0.47, 9–10	0.51 2.53	1.18 3.00	0.72 1.76
vert.	51.2 ± 0.29 1.31, 49–54	49.9 ± 0.12 0.64, 49–51	50.3 ± 0.27 0.47, 50–51	0.89 **4.14**	0.65 2.27	0.50 1.35
pc	27.5 ± 0.77 3.43, 21–33	26.7 ± 0.69 3.84, 20–35	24.3 ± 0.98 1.70, 22–26	0.16 0.77	0.84 2.57	0.57 2.00

Note: L_{Sm}, fork length; *l*, length to the end of scale cover; l_2, body length; *ao*, snout length; *o*, horizontal diameter of an orbit; *f*, length of postorbital section of a head; *c*, head length; *cH*, head depth near the occiput; *ch*, head depth near the orbit; *io*, forehead width; *lmx*, maxilla length; *i/lmx*, maxilla width; *lmd*, mandible length; *H*, maximum body depth; *h*, minimum body depth; *w*, body thickness; *aD*, antedorsal distance; *pD*, postdorsal distance; *aA*, anteanal distance; *aV*, anteventral distance; *lp*, caudal peduncle length; *PV*, pectoventral distance; *VA*, ventroanal distance; *lD*, length of dorsal fin base; hD_1, depth of anterior part of dorsal fin; hD_2, depth of posterior part of dorsal fin; *lA*, length of anal fin base; *hA*, depth of anal fin; *lP*, length of pectoral fin; *lV*, length of ventral fin; *ll*, number of perforated scales in lateral line; D_1, number of unbranched rays in dorsal fin; D_2, number of branched rays in dorsal fin; *D*, 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 unbranched rays in anal fin; A_2, number of branched rays in anal fin; *sb.*, number of gill rakers; *rb.*, number of gill rays; *vert.*, number of vertebrae without urostyle; *pc*, number of pyloric caeca, above the line, average value and its error, under the line, range and standard deviation.

* Morphometric characters were studied in 16 specimens of Mongolian and 28 specimens of Arctic grayling. Significant values of t_{st} are given in boldface.

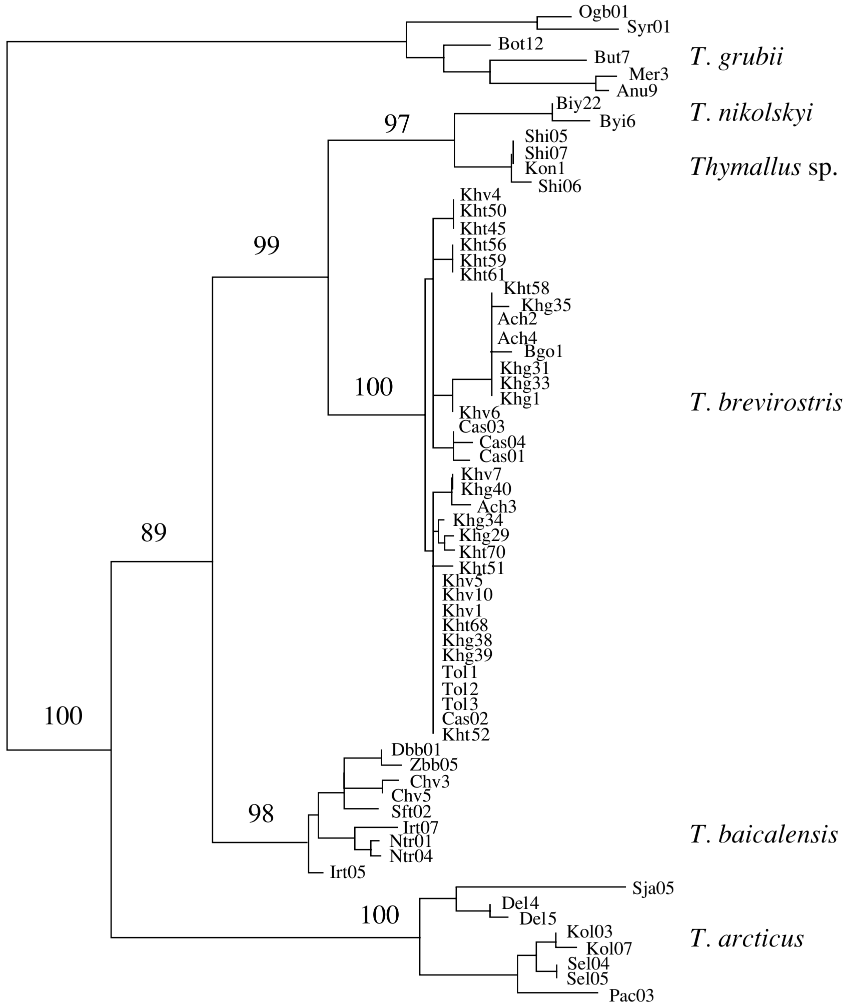

Fig. 6. NJ phylogenetic tree of graylings *Thymallus* depicted on the basis of the distances of Kimura-2 parameter of whole control region of mitochondrial DNA calculated between 65 sequences. The Amur River basin: Ogb, Onon River; Syr, Sypchegurka River (Ingoda River); Mer, Amgun River; Anu, Anyui River. Tatar Strait: Bot, Botchi River; But, Buta River. Upper Ob River basin: Biy, Biya River. Angara–Yenisei basin: Irt, Irkutsk Reservoir; Ntr, Nizhnyaya Tunguska River; Kon, Konui River (Abakan River); Shi, Shishkid Gol River (Darkhat Depression). Central Asian basin: Khv, Ktg, Khovd River (Kht, Lake Khoton Nur; Khg, Lake Khurgan Nur); Tol, Lake Tolbo Nur; Ach, Lake Achit Nur; Bgo, Bokhmoroon Gol River; Cas, Lake Khokh Nur. Basin of Lake Baikal: Dbb, Dagar Gulf; Zbb, Zavorotnaya Gulf; Chv, Lake Khuvsgul; Sft, Terkhin Gol River (upper reaches of the Selenga River). Basin of White Sea: Sja, Syamzhen'ga River. Basin of Laptev Sea: Del, delta of the Lena River. Basin of east Siberian Sea: Kol, Kolyma River; Sel, Indigirka River. Basin of Pacific Ocean: Pac, Burnt River (British Columbia, Canada). Haplotypes of individuals tentatively classified as *T.* cf. *arcticus.*

representatives of genus *Thymallus* was recorded by some characters including *c, f, lmx*, and *lmd.*

The samples of graylings from the basins of the upper reaches of Khovd, Dzabkhan, and upper Ob (Biya) rivers were studied with the method of principal components (PCA). First two principal components accounted by meristic characters for 79.1% of total variance. The loads of characteristic vectors are presented in Table 6. Maximum positive loads on the first principal component gave the rays in dorsal fin (D_1, D_2, and D), and negative the number of pyloric caeca (*pc*); maximum positive load on the second principal component belonged to the number of scales in lateral line (*ll*). It is seen in scatter plot (Fig. 8) that differentiation by meristic characters was absent in west Mongolian graylings, whereas the individuals of the upper Ob grayling from the Biya River diverge with them almost without overlapping.

Cluster analysis of grayling samples from water bodies of Eurasia and North America, representing different taxi of genus *Thymallus*, performed with UPGMA method by the complex of 12 meristic characters (Table 7) also revealed low level of divergence in west Mongolian forms (Fig. 9).

Additional analysis, including the data on Mongolian grayling from Lake Kyndykty-Kol (Gundrizer,

Table 3. Distribution of haplotypes of grayling *Thymallus* from the studied water bodies of Mongolia, forming the branch *T. brevirostris*

Water body	*n*	Haplotypes																	
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
		Khv 4	Kht 50	Kht 56	Kht 58	Khg 35	Khv 6	Khv 7	Khg 34	Khg 29	Kht 51	**Cas 2**	**Cas 3**	**Cas 4**	**Cas 1**	Ach 3	Bgo 1	Kht 70	Ach 2
Khovd River	6	1					1	1				3							
Lake Khoton Nur	10		2	3	1						1	2						1	
Lake Khurgan Nur	9				3	1		1	1	1		2							
Lake Tolbo Nur	3											3							
Lake Khokh Nur	4											1	1	1	1				
Bokhmoroon Gol River	1																1		
Lake Achit Nur	3															1			2
Sum total	36	1	2	3	4	1	1	2	1	1	1	11	1	1	1	1	1	1	2

Note: The names and numbers are presented of haplotypes of individuals, in which these haplotypes were found first. Numbering of haplotypes in the columns (1–18) is arbitrary. Haplotypes given in boldface (Cas1–Cas4) were placed earlier in GenBank with access codes AY168386–AY168389.

Table 4. Average values of *p*-distances between haplotypes representing different taxi of grayling *Thymallus*

Taxon	*T. grubii*	*T. nikolskyi*	*T. baicalensis*	*T. arcticus*	*T.* cf. *arcticus*	*T. brevirostris*[1]	*T. brevirostris*[2]	*Thymallus* sp.
T. grubii	–							
T. nikolskyi	0.042	–						
T. baicalensis	0.035	0.020	–					
T. arcticus	0.040	0.037	0.025	–				
T. cf. *arcticus*	0.040	0.016	0.016	0.030	–			
T. brevirostris[1]	0.040	0.015	0.016	0.031	0	–		
T. brevirostris[2]	0.041	0.015	0.016	0.031	0.001	0	–	
Thymallus sp.	0.043	0.007	0.020	0.036	0.014	0.013	0.013	–

Note: *T. grubii*, the upper Amur River, rivers of Tatarskii Strait; *T. nikolskyi*, the upper Ob River; *T. baicalensis*, Baikal and Angara–Yenisei basins; *T arcticus*, delta of the Ob River, rivers Indigirka, Kolyma, Burnt (Canada); *T.* cf. *arcticus*, the upper Khovd River; *T. brevirostris*[1], the Khovd River basin (lakes Khoton Nur, Khurgan Nur, Khokh Nur, Achit Nur, the Bokhmoroon Gol River); *T. brevirostris*[2], the Khovd River basin (Lake Tolbo Nur); *Thymallus* sp., upper reaches of the Yenisei River (the Shishkid Gol River).

1966) by ten meristic characters[13], demonstrated the belonging of fishes from this lake to the samples from water bodies of western Mongolia, which we analyzed. The other species and subspecies of grayling distributed along the branches in various combinations with different levels of divergence.

[13] Dendrogram is not presented.

DISCUSSION

As it was noted above, available literature data about the peculiarities of external structure of Mongolian

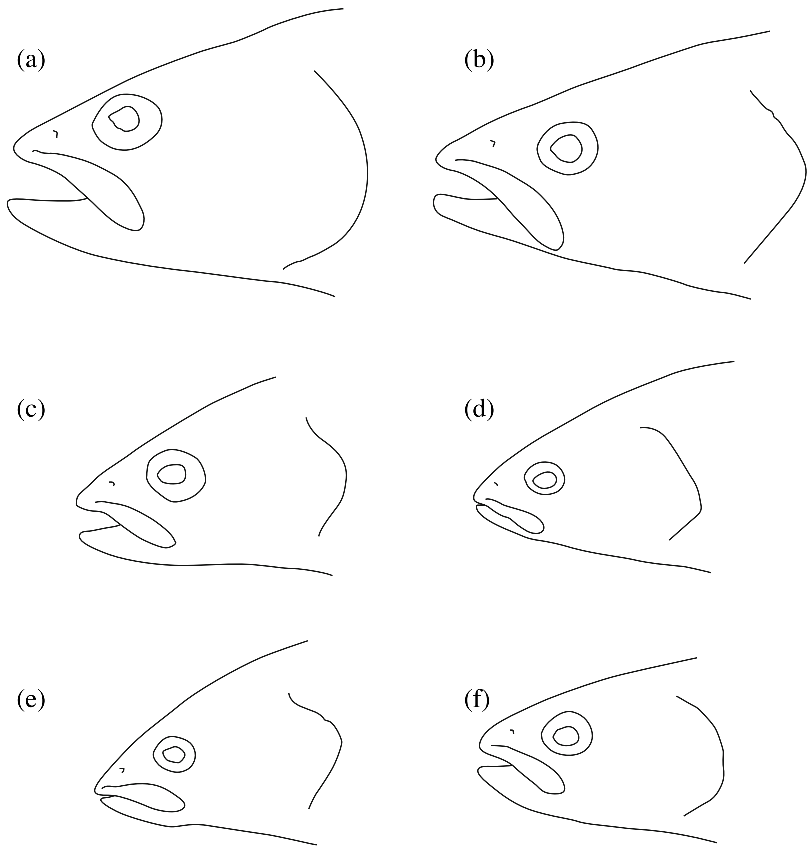

Fig. 7. External outlines of the head of large predatory (a, b) and small benthos-eating (c–f) forms of Mongolian grayling *Thymallus brevirostris* from water bodies of Altai: (a) Lake Khoton Nur; (b) Lake Khurgan Nur; (c) Lake Tolbo Nur; (d) Bogdoin Gol River; (e) Lake Kyndykty-Kol; (f) Lake Khoton Nur.

grayling are contradictory. Disagreement in estimates of taxonomic characters resulted in the fact that researchers classified individuals of this form, not only to different species, but even to different genera. This is true first of all for the sizes of maxilla and mandible, presence of teeth, and some other parameters of the head.

It is the opinion of Gundrizer (1966) that upper jaw in slow-growing individuals of Mongolian grayling from the lakes not reaching eye center, and reaching behind it in fishes inhabiting the river; the latter fishes have more developed teeth. Slightly pointed snout and slightly elongated upper jaw with well-pronounced, though small, teeth are typical for Mongolian grayling from Lake Tolbo Nur and to some extent for individuals from the Bogdoin Gol River (Tugarina and Dashidorzhi, 1972) and Lake Kyndykty-Kol (Gundrizer, 1966). It should be noted that if the fishes with such phenotype could somehow be synonymized with Arctic grayling, it could be done for the predatory form of Mongolian grayling from the upper reaches of the Khovd River and lakes Khoton Nur, Khurgan Nur, and Khokh Nur. The difference between both classified forms is well seen in the length of the jaws and head shape (Baasanzhav et al., 1988). Mongolian grayling from water bodies of western Mongolia resembles by head shape taimen and partly lenok. Analysis of head characters in graylings from the Khovd River basin revealed the populations well distinguished according to these characters as well as populations intermediate by these characters (Table 5). Unlike other taxi of genus *Thymallus*, graylings from the Khovd River basin have teeth, not only on jaws, but also on vomer, and articulation of mandible bone with cranium is behind the vertical of posterior orbit edge.

All these make it possible understanding the causes, according which some researchers (Svetovidov, 1936; Berg, 1948; Pivnička and Hensel, 1978; Zinov'ev, 2005) assumed the probability of hybridization between Siberian and Mongolian graylings, and Ioganzen (1945) found common characters in them. It became possible to judge definitely about this on the basis of our results of morphological and molecular genetic analyses.

It is obvious from the results of cluster analysis by the complex of meristic characters (Fig. 9) that discussed forms of west Mongolian graylings compose one branch similar to NJ-tree. However, the taxi, validity of which is beyond question, and the areas of which are well distant, can also differ at very low level as, for

Table 5. Variations of some parameters of the head in graylings *Thymallus* from western Mongolia

Character	*Thymallus brevirostris*							*Thymallus* cf. *arcticus*		
	Lakes Khoton Nur and Khurgan Nur	Lake Tolbo Nur	Lake Khokh Nur	Lake Khoton Nur	Lake Kyndyk-ty-Kol	Bogdoin Gol River	Lake Khar Nur	Lakes Khoton Nur and Khurgan Nur	Lake Khoton Nur	Khovd River
	own data			Baasanzhav et al., 1988	Gundrizer, 1966	Tugarina and Dashidorzhi, 1972	Shatunovskii, 1983	own data	Baasanzhav et al., 1988	
	n = 21	*n* = 3	*n* = 7	*n* = 27	*n* = 25	*n* = 65	*n* = 260	*n* = 29	*n* = 27	*n* = 31
L_{Sm}, mm	468.0 298.0–665.0	280.4 255.0–294.5	359.5 297.0–419.0	342 180–556	294.5 221–338	289.9 205–413	– 304–579	260.7 212.5–365.8	254 174–399	209 147–287
c	22.0 20.6–23.5	20.8 20.1–21.2	22.0 21.3–23.1	22.22 18.2–23.6	20.4 18.8–26.0	– 19.6–23.5	– 20.1–21.2	19.6 18.0–21.2	18.7 17.5–20.5	19.9 18.9–21.7
In % *c*										
ao	33.1 30.0–35.7	31.6 30.8–32.9	31.3 28.6–32.8	26.4 22.1–30.4	20.3 18.7–24.7	–	– 24.8–30.9	29.8 27.0–34.0	24.0 20.8–26.9	24.0 21.0–27.0
lmx	33.4 30.0–37.0	30.7 28.8–31.6	32.7 30.6–36.3	34.6 30.7–37.5	30.3 27.2–33.7	31.5 25.6–36.5	34.2 30.0–38.0	27.6 24.8–30.0	29.0 26.0–32.2	29.0 26.3–31.3
lmd	59.3 51.5–62.9	55.4 53.5–57.0	55.5 53.0–57.3	56.5 50.7–62.7	55.4 51.6–60.4	– 46.6–67.5	56.0 50.0–64.8	52.3 49.1–56.3	53.0 46.8–58.8	50.5 46.3–53.0

Note: Above the line, average value; under the line, the range.

example, the Bureya–upper Ob and Amur–European graylings. One of probable cause of this is observed in fishes from genus *Thymallus* parallelism in variations of their characters (Zinov'ev, 1980). Observed disagreement suggests that diagnostics of above named pairs of taxi cannot be performed by one complex of analyzed characters, and application in taxonomy of this group of morphological criterion without accounting the data of molecular genetics, peculiarities of body color, and the dorsal fin pattern is not always sufficient and efficient.

As it was noted, despite the significant difference by meristic characters, some similarity exists between west Mongolian and the upper Ob graylings in components of the dorsal fin pattern, its form and size, and body color. Genetic and geographical closeness allows assuming their divergence from common ancestor, populating water bodies of Mongolia in Tertiary period. On this basis the revealed differences can be considered as the result of environmental conditions occurred after the breakdown of relationship between Central Asian and the Ob River basins. The same can be said about the grayling from the Shishkid Gol River, which preserved much less common with Mongolian and the upper Ob graylings signs of external structure despite the genetic closeness to these forms. The difference between genetically close, but phenotypically different, forms living at the junction of the areas suggests specific characters of microevolution processes run under conditions of isolation over relatively similar time from the moment of their divergence.

It becomes obvious from the results obtained in the course of our study that none of grayling forms inhabited the Central Asian basin, and the sites of the upper reaches of the Ob and Yenisei rivers cannot be classified with Arctic grayling, the area of which is restricted mostly by the lower reaches of large rivers of Arctic coast from Northern Dvina to Canada, Alaska, and other North American states (Koskinen et al., 2002; Stamford and Taylor, 2004; Froufe et al., 2005; Knizhin et al., 2006c; Weiss et al., 2006, 2007; Knizhin and Weiss, 2007). Hence, water bodies of the Central Asian basin and namely the system of the Khovd River are inhabited only by one species, Mongolian grayling; the upper Ob River, by the upper Ob grayling (*T. nikolskyi*); and the upper reaches of the Yenisei River, by the upper-Yenisei grayling. These forms are characterized in comparison with other known species of genus *Thymallus* by relative genetic closeness, but have at the same time the complex of diagnostic characters confirmed their taxonomic independence.

There several hypotheses about probable ways of evolution of graylings and particularly about the origin of west Mongolian forms. The first hypothesis was suggested by Benke (1965), who conceded the origin of Mongolian grayling (*Phylogephyra*) from small-mouth benthos-eating form (*Thymallus*) as, for example, inconnu (*Stenodus*) from whitefish (*Coregonus*). The

Table 6. Loadings of eigenvectors on the first two principal components for 12 meristic characters of graylings *Thymallus* (vector length equals to square root from own value)

Character	Principal components	
	1	2
ll	0.132	0.976
D_1	0.562	0.010
D_2	0.751	0.282
D	0.799	0.213
P	0.320	0.292
V	0.373	0.087
A_1	0.291	0.234
A_2	0.259	0.108
sb.	0.122	0.090
rb.	–0.422	0.045
vert.	0.383	0.335
pc	–0.965	0.189

second hypothesis [the result of investigations of Tugarina and Dashidorzhi (1972) analyzed morphological features of Mongolian grayling *T. brevirostris* and geological and hydrological histories of the region in Pliocene–Pleistocene time] assumes that this species can be considered a relict of the Tertiary period, i.e. the

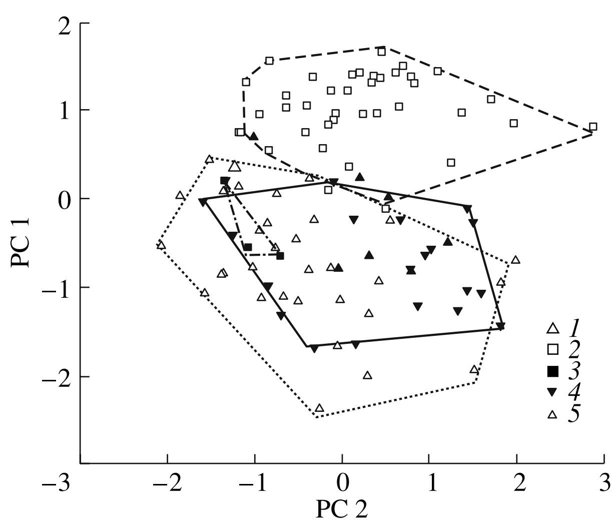

Fig. 8. Scatter plot of individuals from the studied samples of graylings *Thymallus* of Altai water bodies in the space of first two principal components (PC) by 12 meristic characters: *1*, *T. brevirostris* (Lake Khokh Nur, Dzabkhan River basin); *2*, *T. nikolskyi* (Biya River, basin of the upper Ob River); *3*, *T. brevirostris* (Lake Tolbo Nur); *4*, *T. brevirostris* (upper Khovd River, Lakes Khoton Nur and Khurgan Nur); *5*, Arctic grayling *T.* cf. *arcticus* (upper Khovd River, lakes Khoton Nur and Khurgan Nur).

Table 7. Estimates of meristic characters in representatives of genus *Thymallus* from water bodies of Eurasia and North America

Character	*T. brevirostris* $n = 7$	*T. thymallus* $n = 64$	*T. tugarinae* $n = 76$	*T. grubii grubii* $n = 106$	*T. grubii flavomaculatus* $n = 48$	*T. burejensis* $n = 5$	*T. arcticus* $n = 30$	*T. arcticus** $n = 27$	*T. nikolskyi* $n = 39$	*T. baicalensis* $n = 50$	*T. a. nigrescens* $n = 35$
ll	80.7 / 77–84	86.3 / 80–94	82.6 / 75–91	90.6 / 82–102	90.5 / 82–101	83.6 / 80–91	93.3 / 87–110	91.81 / 87–99	81.3 / 76–91	99.5 / 88–110	94.2 / 87–100
D_1	7.4 / 7–8	7.7 / 7–9	9.6 / 8–12	8.2 / 7–11	10.4 / 9–15	9.8 / 9–10	10.2 / 9–12	11.7 / 10–13	8.0 / 6–10	7.8 / 7–10	7.9 / 7–9
D_2	12.1 / 12–13	14.4 / 12–16	15.2 / 13–17	12.6 / 10–16	13.3 / 10–15	14.6 / 14–15	14.0 / 12–16	10.9 / 10–13	15.3 / 14–18	12.5 / 11–15	11.3 / 10–13
D	19.5 / 19–20	22.1 / 20–24	24.9 / 23–26	20.8 / 19–23	23.7 / 21–25	24.4 / 23–25	24.1 / 22–26	22.6 / 21–24	23.3 / 21–25	20.4 / 19–22	19.3 / 18–22
P	14.1 / 14–15	14.2 / 12–16	14.1 / 12–16	14.0 / 12–16	14.4 / 13–16	14.8 / 14–16	14.6 / 13–16	14.9 / 13–16	15.1 / 14–17	14.7 / 13–16	14.5 / 13–16
V	10.0 / –	9.0 / 8–10	10.0 / 9–11	9.1 / 8–10	9.3 / 8–11	9.8 / 9–10	9.3 / 9–10	9.3 / 8–11	9.9 / 9–11	9.8 / 9–11	9.5 / 9–11
A_1	4.3 / 4–5	4.1 / 3–5	4.2 / 4–5	4.1 / 3–5	4.4 / 4–6	4.4 / 4–5	4.0 / 3–5	5.3 / 4–7	4.2 / 4–5	4.5 / 4–5	4.7 / 4–6
A_2	8.0 / 7–9	9.8 / 9–11	9.1 / 8–10	9.0 / 7–11	9.3 / 8–10	9.8 / 9–11	9.4 / 8–10	9.8 / 7–12	9.4 / 8–10	8.9 / 8–11	8.9 / 8–11
sb.	18.6 / 18–19	23.9 / 21–28	18.1 / 16–22	17.8 / 15–21	18.3 / 16–22	20.0 / 19–21	18.7 / 16–21	17.8 / 15–20	19.4 / 17–21	20.7 / 17–23	25.9 / 21–30
rb.	10.1 / 10–11	9.5 / 8–11	9.8 / 8–11	9.8 / 8–12	9.5 / 9–11	9 / –	9.1 / 8–10	8.4 / 7–9	9.3 / 9–10	9.3 / 8–10	9.3 / 8–10
vert.	56.4 / 56–57	52.3 / 51–55	52.5 / 49–55	55.3 / 53–57	55.0 / 53–57	53.2 / 53–54	53.0 / 51–55	57.2 / 56–59	52.6 / 51–55	55.9 / 52–59	55.2 / 54–57
pc	25.6 / 20–29	20.0 / 15–32	14.8 / 11–20	15.1 / 10–22	17.3 / 14–24	18.0 / 15–21	19.9 / 14–29	19.4 / 15–26	20.4 / 17–27	15.8 / 10–21	23.6 / 16–29

Note: *T. brevirostris*, Lake Khokh Nur (basin of the Dzabkhan River); *T. thymallus*, Obr, Gurk, and Socha rivers (basins of Black and Adriatic seas); *T. tugarinae*, Anyui (basin of the lower Amur River) and Khunmakta (northwestern Sakhalin) rivers; *T. g. grubii*, Ingoda and Onon rivers (basin of the upper Amur River); *T. g. flavomaculatus*, Anyui, Merek (basin of the lower Amur River), Buta, and Botchi (Tatar Strait) rivers; *T. burejensis*, the Levaya Bureya River; *T. arcticus**, the Indigirka (East. Siberian Sea basin), the Big Hole River (the Missouri River basin); *T. nikolskyi*, Biya and Bashkaus rivers (basin of the upper Ob River); *T. baicalensis*[14]

[14] Species status of Baikal grayling is discussed in the works by Knizhin and Weiss (2007) and Weiss et al. (2007).], Lake Baikal; *T. a. nigrescens*, Lake Khuvsgul (Mongolia).

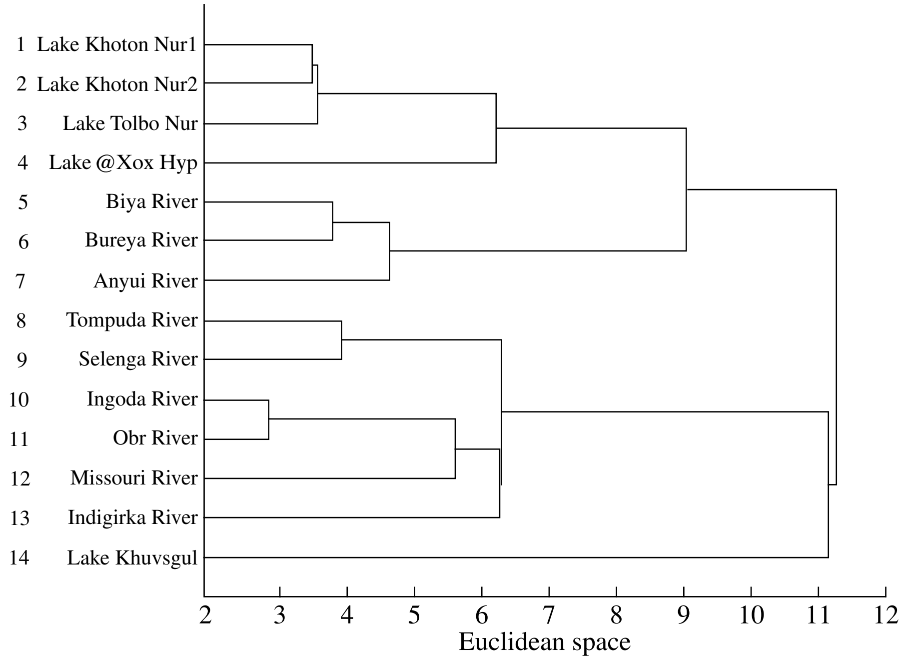

Fig. 9. UPGM dendrogram reflected the level of differences between graylings of western Mongolia and other taxi of genus *Thymallus* by the complex of 12 meristic characters: *1, 3, 4*, *T. brevirostris*; *2*, *T.* cf. *arcticus*; *5*, *T. nikolskyi*; *6, T. burejensis*; *7*, *T. tugarinae*; *8, 9, T. baicalensis; 10*, *T. grubii*; *11*, *T. thymallus*; *12, 13*, *T. arcticus; 14*, *T. a. nigrescens.*

time, when the territory of central and western Mongolia represented a huge freshwater water body. The third hypothesis, the author of which is Makoedov (1999), suggests considering slightly expressed dorsal fin pattern as ancestral character in Mongolian grayling additionally to the presence of developed teeth. This pattern became gradually brightly and more complex in the course of evolution and distribution of derivative forms of graylings continentwide.

We consider that there are no any evidences allowed considering the presence of developed teeth in Mongolian grayling to be the character remained from an ancestor (Svetovidov, 1936; Tugarina and Dashidorzhi, 1972; Makoedov, 1999). According to Mayr (1971: p. 244), “the character could be considered *ancestral,* if it did not change significantly in comparison with homologous character in ancestor”. Recent paleontological data, analysis of which was presented in the works by Sychevskaya (1983), Chereshnev (1996), and Makoedov (1999), do not allow even hypothetical judging about possible evolution predecessor of currently existed graylings, and what the ancestral state of particular character is. In this relation, we should touch the note of Benke (1965) about significant development of teeth in *P. altaica* in comparison with other representatives of genus *Thymallus.* The teeth of the specimen from British Museum, which he, as well as Boulenger (1898), analyzed, were uncovered to the base because of drying of soft tissues. It is that phenomenon that makes it more “toothy” in comparison with representatives of other taxi of genus *Thymallus.* The effect caused by partial destruction of tissues on the jaws in the result of long preservation of fishes in fixative (alcohol, formaldehyde) allows saying about the “toothy” shape of even the Baikal grayling *T. baicalensis*, the specimen of which is long stored in Museum für Naturkunde, Humboldt University, Berlin (no. 7929).

Mongolian grayling cannot be considered the species most close to ancestral form on the basis of results of molecular genetic study (Koskinen et al., 2002; Froufe et al., 2005). Its position on phylogenetic tree as well as that of graylings from the upper reaches of the Ob and Yenisei rivers allows considering that they all are evolutionary young forms in comparison with Amur taxi and Siberian and European graylings. So, it is not likely to consider any known species as a form close to ancestral one.

The hypothesis by Makoedov (1999) about evolutionary transformations of the dorsal fin pattern and the possibility of its using for determination the phylogenetic relationships of graylings also has no proper factual confirmation. Particularly, this author made the conclusion that the pattern of dorsal fin in evolutionary young taxi [east Siberian, Kamchatka, and Alaskan graylings[15] and is characterized by complex configuration, whereas ancestral form has pale fin almost without spots. It is this “type” of pattern he reported for Mon-

[15]It is our opinion that isolation of these subspecies in Arctic grayling is not valid (Knizhin et al., 2006c; Knizhin and Weiss, 2007; Weiss et al., 2007).

golian grayling. However, our investigations demonstrated that the pattern of dorsal fin in populations of this species is no less complex than on other known taxi, and variation presented by Makoedov (1999) is only one of possible variations.[16] If we agree with Makoedov, white Baikal grayling, in which dorsal fin is characterized by pale pattern most of the year, can also be considered as the form close to ancestral form (Knizhin et al., 2006b).

Specific characters of Mongolian grayling such as big head and long jaws with developed teeth can appear during its existence in relatively isolated from other lakes and rivers of internal drainage of the Central Asian basin just after the disappearance of the large freshwater water body existed in the territory of Mongolia. Severe arid conditions resulted in pure food base became probably the cause of appearance of some new adaptations in Mongolian grayling, for example, to vary in wide range the strategy of foraging in ontogenesis: from benthos eating to predation. In the Khovd River basin, extreme forms of nutritional adaptation are known only in graylings inhabiting lakes Khoton Nur and Khurgan Nur. Lakes Tolbo Nur and Kyndykty-Kol and the Bogdoin Gol River are inhabited by populations, the range of food organisms of which is relatively wide and includes zoobenthos, terrestrial insects, and sometimes fishes (Tugarina and Dashidorzhi, 1972; Gundrizer and Popkov, 1984). Water bodies of the Central Asian basin are characterized by different degree of isolation, and food supply of fish in them can also differ significantly (Shatunovskii, 1983). This is seen well from the growth parameters of graylings from different water bodies of western Mongolia (see Table 1). Because of this diverse relatively localized forms of graylings, keen to use optimally food resources and to reproduce, can appear depending on environmental conditions under the influence of natural selection and in the result of adaptive radiation.

Existing of sympatric forms were recorded in some fish species (Svetovidov, 1931; Tugarina, 1981; Savvaitova, 1983; Douglas et al., 1999; Alekseev et al., 2000, 2007; Savvaitova et al., 2000; Østbye et al., 2005; Duguid et al., 2006; Knizhin et al., 2006b; Mina, 2007; etc.). The scenario of their appearance in central Mongolia was described for dwarf Altai osman *Oreoleuciscus humilis* Warpachowski in the Valley of Lakes (Dgebuadze, 2001). This species is presented by sympatric forms: dwarf and large (lake). They differ in growth rate, time of maturing, and nutritional adaptation. Dwarf form of osman can turn into large form depending on the changes of environmental conditions. We cannot consider that similar intraspecies transformations occur in Mongolian grayling because of the absence of good cause for this. However, some analogy is observed. Similar to osman, Mongolian grayling from the upper reaches of the Khovd River is presented by large (predatory) and small (benthos-eating) forms. There is no evidence that the large form appears from the small one. Such process is apparently probable, but it has no mass character. It should be noted that juveniles as well as individuals of older age classes of the same size representing both forms are found in Lakes Khoton Nur and Khurgan Nur. The same situation with existence of two sympatric forms of Mongolian grayling is apparently the case in Lake Chulug-Kol (Tuva). Considered water bodies of the Central Asian basin (Lake Tolbo Nur, Lake Kyndykty-Kol, and the Bogdoin Gol River) are inhabited by populations, which are not differentiated to large and small forms, but have intermediate characters of both forms to different extent. Hence, they represent the links demonstrated the continuous series of variations of external morphological characters and nutritional adaptation of species populations.

Sympatric divergence is usually observed in different fish species in lake systems. The fact that such phenomenon was not earlier described for representatives of genus *Thymallus* can be explained by their greater addiction to the river mode of life, and smaller, to the lake mode of life. Graylings inhabit both rivers and lakes in water bodies of western Mongolia, but total area of river systems in this region is significantly smaller than the area of lake systems. Hence, adaptation of graylings in water bodies of the Central Asian basin would be connected mostly with their ability to adapt to lake existence.

Minimal level of divergence by haplotypes (mostly one or two replacements of bases) in discussed west Mongolian forms of graylings suggests their relatively lower and monophyletic origin. Morphological divergence observed in these forms is the result of significant phenotypic plasticity or habitat differentiation occurred in initial form during relatively short evolutionary time. It is early to judge the degree of reproductive isolation of classified forms of Mongolian grayling prior to performing the analysis of nuclear DNA. It is most likely that exchange of genetic information was not stopped, because sites of reproduction and time of spawning can coincide.

CONCLUSIONS

Summarizing all of the above said, we can conclude that water bodies of western Mongolia are inhabited by Mongolian grayling *T. brevirostris* presented by predatory and benthos-eating forms and by groups with mixed feeding. High level of intraspecies polymorphism and mosaic distribution of its ecological forms in water bodies of the Central Asian basin explain the causes of existed mess in their taxonomic identification. Taking into consideration obtained data, we should expand taxonomic diagnosis of Mongolian

[16] Makoedov (1999) studied individuals of Mongolian grayling from the collection of the Zoological Institute, Russian Academy of Sciences (nos. 11747, 9666, 20812, and 21681) stored in the museum for a long time

grayling at the expense of increase of the ranges of variations in the length of its snout and upper jaw and to add the information about the features of scale cover color and the dorsal fin pattern. The presence of teeth on jaws and vomer and articulation of mandible bone behind the vertical of posterior orbit edge are the stable diagnostic characters of the species.

Genetic identity of forms of Mongolian grayling, their heterogeneity by meristic characters, similarity in the character of variation of body color and the dorsal fin pattern with simultaneous divergence by the length of jaws, development of teeth, head form, and some biological parameters attest to the epigenetic nature of appearance of revealed differences and actively running microevolution process.

Genetic closeness of graylings from the Khovd, upper Ob (Biya River), and upper Yenisei (Shishkid Gol River) rivers and their significant divergence from the other known taxi suggest their common origin from the form populated water bodies of central Mongolia and Altai in Tertiary period.

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REFERENCES

1. S. S. Alekseev, M. Yu. Pichugin, and V. P. Samusenok, "Diversity of Arctic Charrs from Transbaikalia in Meristic Characters, Their Position in the Complex of *Salvelinus alpinus*, and the Origin of Sympatric Forms," Vopr. Ikhtiol. **40** (3), 293–311 (2000) [J. Ichthyol. **40** (4), 279–297 (2000)].
2. S. S. Alekseev, R. Baino, N. G. Gordeeva, et al., "Species Formation in Arctic Charrs *Salvelinus alpinus* Complex (Salmoniformes, Salmonidae) from Transbaikalia," in *Proceedings of the Conference on Modern Problems of Biological Evolution, 2007* (GDM, Moscow, 2007), pp. 76–77.
3. A. L. Antonov, "A New Species of Grayling *Thymallus burejensis* sp. nova (Thymallidae) from the Amur Basin," Vopr. Ikhtiol. **44** (4), 441–451 (2004) [J. Ichthyol. **44** (6), 401–411 (2004)].
4. G. Baasanzhav and Ya. Tsend-Ayush, *Mongol orny zagas* (Ulaanbaatar: Ulanbaatar Khot, Ulanbaatar, 2001).
5. G. Baasanzhav, Yu. Yu. Dgebuadze, and V. I. Lapin, "On the Systematics and Distribution of Graylings in Mongolia," in *Proceedings of Coordination Conference on Morphology, Structure of Populations, and the Problem of Rational Use of Salmoniformes* (Leningrad, 1983), pp. 10–11.
6. G. Baasanzhav, Yu. Yu. Dgebuadze, and V. I. Lapin, "On the Study of Graylings from Water Bodies of the Khovd River," in *Natural Conditions, Vegetative Cover, and Fauna of Mongolia* (NTsBI AN RAN, Pushchino, 1988), pp. 319–330.
7. R. J. Benke, "A Systematic Study of the Family Salmonidae with Special Reference to the Genus *Salmo*," in *Subfamily Thymallinae* (Univ. Calif. (Ph. D. Zool, Berkeley, 1965), pp. 233–236.
8. L. S. Berg, "Preliminary Remarks on Euroasian *Salmoninen*, Mainly in the Genus *Thymallus*," Ezhegod. Zool. Muz. Imper. Akad. Nauk **12**, 500–514 (1907).
9. L. S. Berg, *Fishes of Fresh Waters of the USSR and Adjacent Countries*, 4th ed. (Akad. Nauk SSSR, Moscow, 1948), Part 1 [in Russian].
10. V. P. Borovikov and I. P. Borovikov, *Statistica—Statistical Analysis and Data Processing in the Windows Environment* (Filin'', Moscow, 1998) [in Russian].
11. G. A. Boulenger, "On a New Genus of Salmonoid Fishes from the Altai Mountains," Ann. Mag. Nat. Hist. Ser. **I** (4), 329–331 (1898).
12. I. A. Chereshnev, *Biological Diversity of Freshwater Ichthyofauna of the Northeast of Russia* (Dal'nauka, Vladivostok, 1996) [in Russian].
13. N. I. Chugunova, *Guide for Study of Fish Age and Growth* (Sov. Nauka, Moscow, 1959) [in Russian].
14. A. Dashdorzh, A. Dulmaa, and Ya. Tsend-Ayush, "A New Form of Grayling *Thymallus brevirostris kozovi* subsp. n. from the Khovd River Basin," Vestn. Akad. Nauk Mongol. Narodn. Rep., No. 4, 38–45 (1968) [in Mongolian]..
15. Yu. Yu. Dgebuadze, *Ecological Regularities in Fish Growth Variation* (Nauka, Moscow, 2001) [in Russian].
16. E. A. Dorofeeva, *Genus Thymallus*, in *Atlas of Freshwater Fish of Russia,* Ed. by Yu.S. Reshetnikov (Nauka, Moscow, 2002), Vol. 1.
17. M. R. Douglas, P. C. Brunner, and L. Bernatchez, "Do Assemblages of *Coregonus* (Teleostei: Salmoniformes) in the Central Alpine Region of Europe Represent Species Flocks?," Mol. Ecol. **8** ((4)), 589–603 (1999).
18. R. A. Duguid, A. Ferguson, and P. Prodohl, "Reproductive Isolation and Genetic Differentiation of Ferox Trout from Sympatric Brown Trout in Loch Awe and Loch Laggan, Scotland," J. Fish. Biol. A. **69**, 89–114 (2006).

19. A. Dulma, "Zur Fishfauna der Mongolei," Mitt. Zool. Mus. (Berlin) **49**, 49–67 (1973).

20. *Ecology and Commercial Importance of Fish of the Mongolian People's Republic*, Ed. by M. I. Shatunovskii (Nauka, Moscow, 1985).

21. *Fishes of the Mongolian People's Republic*, Ed. by M. I. Shatunovskii (Nauka, Moscow, 1983) [in Russian].

22. 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).

23. 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).

24. A. N. Gundrizer, "On Finding Mongolian Grayling *Thymallus brevirostris* Kessler in Water Bodies of the USSR," Vopr. Ikhtiol. **6** (4), 638–647 (1966).

25. A. N. Gundrizer and V. K. Popkov, "Specific Features of Ecology of Mongolian Grayling *Thymallus brevirostris* Kessler (Thymallidae) in Lakes of Tuvinskaya ASSR," Vopr. Ikhtiol. **24** (1), 69–76 (1984).

26. B. G. Ioganzen, "New Fish Forms from Western Siberia," in *Notes on Fauna and Flora of Siberia* (Tomsk Gos. Univ., Tomsk, 1945), Issue 6, pp. 1–16.

27. D. Jordan, "A Classification of Fishes Including Families and Genera as Far as Known," Biol. Sci. Publ. Univ., Ser. Stanford Univ. **3** ((2)), 77–243 (1923).

28. N. Kashchenko, "Pisces," in *Results of Altai Zoological Expedition of 1898*, Izv. Imper.Tomsk. Univ., **16**, 131–141 (1898).

29. K. Kessler, "Beitr!age zur Ichthologie von Central-Asien," Bull. Acad. Imp. Sci. St.-Petersbourg **25** (3), 282–310 (1879).

30. I. B. Knizhin and S. J. Weiss, "Modern Concepts of the Diversity and Taxonomic Status of Graylings (Thymallidae) from Eurasia," in *Proceedings of the International Scientific and Practical Conference on Protection and Scientific Studies at Specially Protected Territories of Far East and Siberia Dedicated to the 20th Anniversary of Organization of Bureinskii State Nature Reserve, 2007, settlement of Chegdomyn* (Priamursk. Gegraf. O-vo, Khabarovsk, 2007), pp. 103–112.

31. 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)].

32. I. B. Knizhin, S. J. Weiss, B. E. Bogdanov, et al., "Finding a New Form of the Grayling *Thymallus arcticus* (Thymallidae) in the Basin of Lake Baikal," Vopr. Ikhtiol. **46** (1), 38–47 (2006) [J. Ichthyol. **46** (1), 34–43 (2006a)].

33. I. B. Knizhin, S. J. Weiss, and S. Sušnik, "Graylings of Lake Baikal Basin *(Thymallus*, Thymallidae): Diversity of Forms and Their Taxonomic Status," Vopr. Ikhtiol. **46** (4), 442–459 (2006) [J. Ichthyol. **46** (6), 418–436 (2006b)].

34. I. B. Knizhin, A. F. Kirillov, and S. J. Weiss, "On the Diversity and Taxonomic Status of Graylings (*Thymallus*, Thymallidae) from the Lena River," Vopr. Ikhtiol. **46** (2), 182–194 (2006) [J. Ichthyol. **46** (3), 234–246 (2006b)].

35. 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).

36. M. Kottelat, *Fishes of Mongolia. A Check-List of the Fishes Known To Occur in Mongolia with Comments on Systematics and Nomenclature. World Bank Report (NEMO)* (Washington, DC, 2006).

37. S. Kumar, K. Tamura, I. B. Jakobsen, and M. Nei, "MEGA2: Molecular Evolutionary Genetics Analysis Software. Arizona St. Univ. Tempe. Arizona. USA," Bioinformatics **17**, 1244–1245 (2001).

38. E. Mayr, E. Linsley, and R. Usinger, *Methods and Principles of Systematic Zoology* (McGraw Hill, New York, 1953).

39. E. Mayr, *Principles of Systemic Zoology* (McGraw-Hill, New York, 1971).

40. A. N. Makoedov, *Close Relationships of Graylings of Siberia and Far East* (UMK Psikhologiya, Moscow, 1999) [in Russian].

41. M. V. Mina, "Morphological Diversification and Species Formation in African Barbels of the *Barbus intermedius* Complex," in *Proceedings of the Conference on Modern Problems of Biological Evolution, 2007* (GDM, Moscow, 2007), pp. 23–24.

42. K. Østbye, L. Bernatchez, T. F. Naesje, et al., "Evolutionary History of the European Whitefish *Coregonus lavaretus* (L.) Species Complex as Inferred from mtDNA Phylogeography and Gill-Raker Numbers," Mol. Ecol, **14**, 4371–4387 (2005).

43. K. Pivnička and K. Hensel, "Morphological Variation in the Genus *Thymallus* Cuvier, 1829 and Recognition of the Species and Subspecies," Acta Univ. Carolinae-Biologica 1975–1976 **4**, 37–67 (1978).

44. I. F. Pravdin, *Guide on Fish Study* (Pishch. Prom-st', Moscow, 1966) [in Russian].

45. V. I. Romanov, Doctoral Dissertation in Biology (Tomsk. Gos. Univ., Tomsk, 2005).

46. K. A. Savvaitova, "Changes in the Concept of the Biological Species to the Assessment of the Systematic Position of Chars of the Genus *Salvelinus* (Salmonidae)," Vopr. Ikhtiol. **23** (6), 883–893 (1983).

47. K. A. Savvaitova, O. F. Gritsenko, M. A. Gruzdeva, and K. V. Kuzishchin, "Life Strategy and Phenetic Diversity of the Chars of the Genus *Salvelinus* from Lake Chernoe (Onekotan Island, the Kuril Islands)," Vopr. Ikhtiol. **40** (6), 743–763 (2000) [J. Ichthyol. **40** (9), 704–723 (2000)].

48. S. O. Severin and E. A. Zinov'ev, "Kariotypes of Isolated Populations of *Thymallus arcticus* (Pallas) from the Ob River Basin," Vopr. Ikhtiol. **22** (1), 27–35 (1982).

49. M. D. Stamford and E. B. Taylor, "Phylogeographical Lineages of Arctic Grayling (*Thymallus arcticus*) in North America: Divergence, Origins and Affinities with Eurasian *Thymallus*," Mol. Ecol. **13**, 1533–1549 (2004).

50. A. N. Svetovidov, "Materials on Systematics and Biology of Graylings from Lake Baikal," in *Proceedings of*

Baikal Limnological Station (Akad. Nauk SSSR, Moscow, 1931), Vol. 1, pp. 19–199.

51. A. N. Svetovidov, "Euroasian Graylings (Genus *Thymallus* Cuvier), Tr. Zool. Inst. Akad. Nauk SSSR **3**, 183–301 (1936)
52. D. L. Swofford, PAUP* ver. 4.0.b10. Phylogenetic Analysis Using Parsimony and Other Methods. Sinauer Associates, Sunderland, MA, http:paup.csit.fsu.edu/order.html (2002).
53. E. K. Sychevskaya, *History of Formation of Ichthyofauna of Mongolia and the Problem of Faunistic Complexes*, in *Fishes of Mongolian People's Republic: Habitation Conditions, Systematics, Morphology, and Zoogeography*, Ed. by M.I. Shatunovskii (Nauka, Moscow, 1983).
54. R. A. Travers, "Systematic Account of a Collection of Fishes from the Mongolia People's Republic: with a Review of the Hydrobiology of the Major Mongolian Drainage Basins," Bull. Brit. Mus. Nat. Hist. (Zool.) **55** (2), 173–207 (1989).
55. P. Ya. Tugarina, *Graylings of Baikal* (Nauka, Novosibirsk, 1981) [in Russian].
56. P. Ya. Tugarina and A. Dashidorzhi, "Mongolian Grayling *Thymallus brevirostris* Kessler from the Dzabkhan River Basin," Vopr. Ikhtiol. **12** (5), 843–856 (1972).
57. S. Weiss, H. Persat, R. Eppe, et al., "Complex Patterns of Colonization and Refugia Revealed for European Grayling *Thymallus thymallus*, Based on Complete Sequencing of the Mitochondrial DNA Control Region," Mol. Ecol. **11**, 1393–1407 (2002).
58. S. Weiss, I. Knizhin, A. Kirillov, and E. Froufe, "Phenotypic and Genetic Differentiation of Two Major Phylogeographic Lineages of Arctic Grayling *Thymallus arcticus* in the Lena River, and Surrounding Arctic Drainages," Biol. J. Linn. Soc. **88**, 511–525 (2006).
59. S. Weiss, I. Knizhin, V. Romanov, and T. Kopun, "Secondary Contact Between Two Divergent Lineages of Grayling *Thymallus* in the Lower Enisey Basin and Its Taxonomic Implications," J. Fish. Biol. **71** (Suppl. C), 371–386 (2007).
60. E. A. Zinov'ev, "Variation Parallelism in European and Arctic graylings," in *Salmoniformes* (Nauka, Leningrad, 1980), pp. 69–80.
61. E. A. Zinov'ev, Doctoral Dissertation in Biology (Permsk. Gos. Un-t, Perm, 2005).

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