ACTA UNIVERSITATIS CAROLINAE — BIOLOGICA 1975—1976: 37—67 1978

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MORPHOLOGICAL VARIATION IN THE GENUS THYMALLUS CUVIER, 1829 AND RECOGNITION OF THE SPECIES AND SUBSPECIES

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Dedicated to the 50th birthday of Assist. Prof. Dr. Ota Oliva CSc.

Received January 10, 1976

Abstract: The study is concerned with a new systematic division of the genus *Thymallus* Cuvier, 1829 into five species - *Thymallus thymallus* from Europe, Siberia, Alaska and Canada, *Thymallus brevirostris* from N-W Mongolia, *Thymallus baicalensis* from the Bajkal lake, *Thymallus grubei* from the Amur river basin and *Thymallus nigrescens* from the Mongolian lake Khövsgöl. *Thymallus thymallus* was subdivided into four subspecies - *Thymallus thymallus thymallus* from Europe, *Thymallus thymallus arcticus* from Siberia, *Thymallus thymallus signifer* from central Alaska and Canada, *Thymallus thymallus mertensi* from the coast of Alaska and the basins of the rivers Anadyr and Kamchatka.

INTRODUCTION

We intended originally to make a comparative study of the morphological characters of grayling populations from two rivers of Mongolia, i. e., the Shishkhid and Kherlen collected during our expedition to this country in 1969 (from June to September). In view of the wealth of data and evaluations of the outer morphology of the individual grayling populations (SVETOVIDOV, 1936; IOGANZEN, 1945; KIRILLOV, 1972; TUGARINA, 1972; OLIVA and NAIKSATAM, 1974) we decided to compare all these data and pay increased attention to the geographical variation of morphological signs in members of the genus *Thymallus* in the area of their distribution in Eurasia including graylings populations from Alaska and Canada (WALTERS, 1955; MCCART and PEPPER, 1971). This provided a sound basis for our discussion on the systematic division of the genus and on the geographical distribution of the individual species and subspecies received in this genus.

MATERIAL AND METHODS

A survey of the materials employed, the number of fishes examined, the approximate geographical localisation, is given in Table 1. The localities have been arranged in the order of their increase

in northern latitude and eastern longitude (calculated by multiplication of the values of both coordinates). The same arrangement has been used in the figures on geographical variation. The method of measuring graylings in our material (rivers Shishkhid and Kherlen) is that used by BERG (1948, p. 170) for salmonids. We measured a total of 36 different morphological characters, but employed 9 signs only in our evaluation of morphological variability, i. e., the number of gill rakers on the first gill arch, the number of lateral line scales, predorsal distance, head length, dorsal and pectoral fins length, length of caudal peduncle and length and width of maxilla. All these signs are considered to be most important in the differentiation of the individual graylings forms (SVETOVIDOV, 1936).

Table 1. *Sources of the data used, and numbers of specimens from the various areas*

Area	No. specimens	Lat.	Long.	Source
Vltava R.	26	49 °N	14 °E	OLIVA and NAIKSATAM (1974)
Danube R.	40	49	16	OLIVA and NAIKSATAM (1974)
Sola R.	—	50	16	SOLEWSKI (1960)
Roumania	60	45	24	VASILIU (1967)
Ural R.	40	53	57	ŠAPOŠNIKOVA (1964)
Mesna R.	100	68	45	SVETOVIDOV (1936)
Khövd R.	5	48	90	SVETOVIDOV (1936)
Khendekt L.	25	50	90	GUNDRISER (1966)
Teleckoe L.	75	51	88	IOGANZEN (1945)
Enisej R.	40	53	90	SVETOVIDOV (1936)
Khövsgöl L.	9	51	100	SVETOVIDOV (1936)
Shishkhid R.	50	52	99	own data
Kherlen R.	15	47	110	own data
Bajkal L.	145	54	107	SVETOVIDOV (1936)
Amur R.	11	54	140	SVETOVIDOV (1936)
Aldan R.	41	65	135	KIRILLOV (1972)
Kamchatka R.	117	56	160	TUGARINA (1972)
Chistoe L.	25	60	150	TUGARINA and DEGTEVA (1971)
Kolyma R.	23	69	155	SVETOVIDOV (1936)
Kolyma R.	100	69	155	KIRILLOV (1972)
Anadyr'R.	105	66	175	SVETOVIDOV (1936)
Anadyr'R.	102	66	175	TUGARINA (1972)

Our statistical evaluation has been based on coefficient CD (MAYR and al., 1953) involving total variability of the signs under consideration and not only their mean values as does coefficient M_{diff} (for more information see in HOLČÍK and SKOŘEPA, 1971) which is frequently used in ichthyology. Populations for which coefficient CD shows value of more than, or equal to 1.3, or higher than or equal to 1 ($CD \geq 1.3$, $CD \geq 1$) in most signs were considered to be sufficiently differentiated. The graphical evaluation of variation in morphological characters has been arranged similarly to that given by HUBBS and HUBBS (1953). In the figures on morphological differentiation the individual morphologically different populations (as regard the character studied) are joined with full lines (line segments) for $CD \geq 1.3$, or interrupted lines for $CD \geq 1$.

RESULTS

Sexual dimorphism and growth variation in morphometric characters

Before setting out our evaluation of morphological variation in the grayling populations under consideration, attention has been given partly to sexual dimorphism

and partly to variation in the relative growth of the measured morphometric characters. Characters, in which differences among the sexes or among differently sized length group of the same population were identical or bigger than differences among the populations compared, were excluded from a further evaluation.

Sexual dimorphism in the genus *Thymallus* has been studied into great detail by SVETOVIDOV (1936) who obtained with the t-test a reliable confirmation of differences in the length of the pelvic fin and the depth of the dorsal and anal fin in *Thymallus articus baicalensis*. The same author found a significant difference in the depth of the dorsal fin in European graylings. OLIVA and NAIKSATAM (1974) studied sexual dimorphism in European graylings and observed additional differenciating features in the sexes, i. e., the preanal, predorsal and preventral distance and P-V distance. However, their table on p. 200 indicates that these characters were not very distinctive. Additional tests disclosed significant differences in the depth of the dorsal fin and the length of the pelvic fin in male and female graylings from the Vltava river. Sexual dimorphism of the same characters has been reported by ZINOVEV (1963) for graylings from the Kama river. Male and female graylings from the rivers Shishkhid and Kherlen differed solely in the depth of their dorsal fin.

Variation in relative growth was investigated in graylings from the Shishkhid river. Morphometric characters measured in different length groups showed

a) a relative decrease in head length, diameter of oculi, length and width of maxilla, mandibule length, preorbital and postorbital distance, pre-preopercular distance, predorsal, preventral and A-C distance, length of both caudal fin lobes.

b) a relative increase in head depth, preanal and postdorsal distance, minimum and maximum body depth, length of dorsal-, anal-, pectoral- and pelvic fin.

Table 2. *Relative growth of selected morphometric characters in Thymallus a. arcticus (mean values)*

Smitt's length	9.9	14.9	21.7	25.7	29.6
As % of Smitt's length					
length of head	21.1	20.1	18.8	18.4	18.5
occipital head depth	15.0	15.3	15.3	15.2	15.5
length of maxilla	6.8	6.1	5.8	5.9	6.1
width of maxilla	2.1	2.0	1.9	1.9	2.0
predorsal distance	35.9	35.2	34.3	34.3	34.3
postdorsal distance	38.5	38.7	39.4	39.8	39.4
maximum body depth	19.1	21.4	22.6	23.8	25.1
length of caudal peduncle	15.5	15.9	15.1	15.2	15.6
A-C distance	9.6	10.0	9.0	9.2	9.2
minimum body depth	6.9	7.3	7.7	8.1	8.4
length of D	19.8	21.8	22.1	22.7	23.5
length of P	16.7	16.7	16.5	16.9	17.4
number of fish	6	6	9	21	8

The remaining characters, i. e. (interorbital width, length of caudal peduncle and P-V distance change either minimally or irregularly during growth. A survey of the variation in relative growth of sings used as a criterium in studies on morphological

Table 3. *Means and standard errors of the means for selected morphological characters of the various populations and subspecies of (a) Thymallus t. thymallus and Thymallus a. arcticus, and (b) of Thymallus a. arcticus, Thymallus a. baicalensis Thymallus a. grubei and Thymallus a. pallasi*

subspecies	Vltava R. *thymallus*	Danube R. *thymallus*	Mesna R *thymallus*	Enisej R. *arcticus*	Shishkhid R. *arcticus*	Teleckoe L. *arcticus*	Kherlen R. *grubei*	Bajkal L. *baicalensis*	Kolyma R. *pallasi*
lateral line scales	85.0±0.72	80.8±0.56	88.2±0.31	85.5±0.56	82.1±0.46	84.5	93.1±0.64	98.9±0.34	91.6±0.36
gill rakers	23.7±1.03	22.1±0.30	24.1±0.15	17.6±0.17	19.1±0.23	17.5	15.1±0.30	19.4±0.11	19.4±0.13
length of head	20.6±0.41	20.8±0.48	18.8±0.06	17.7±0.14	18.8±0.16	21.4±0.23	18.1±0.20	17.2±0.04	17.7±0.06
length of maxilla	5.2±0.18	5.7±0.07	5.3±0.03	5.8±0.08	5.9±0.05	8.0±0.24	6.2±0.10	5.7±0.02	4.8±0.07
width of maxilla	2.4±0.03	2.5±0.04	1.8±0.01	1.7±0.02	1.9±0.02	2.1±0.12	1.7±0.05	1.4±0.01	1.5±0.02
predorsal distance	33.9±0.73	35.1±0.25	32.5±0.09	32.2±0.26	34.3±0.02	35.9±0.27	30.1±0.27	33.5±0.08	28.5±0.13
length of caudal ped.	14.2±0.38	14.0±0.19	16.2±0.07	17.1±0.16	15.1±0.13	16.1±0.21	16.9±0.18	16.7±0.07	16.8±0.20
length of D	22.3±0.48	22.1±0.39	22.2±0.10	23.3±0.29	22.1±0.23	20.5±0.24	23.7±0.41	19.3±0.08	25.2±0.16
length of P	15.3±0.39	16.2±0.19	14.5±0.06	16.4±0.15	16.5±0.10	15.6±0.12	15.0±0.22	15.6±0.07	16.1±0.10

variation of the individual graylings populations is given in Table 2. Fishes of the two first size groups have not been included in the calculation of basic statistical data. This is in accord with ZINOVEV (1963) who concluded on the basis of detailed study on relative growth variation in graylings from the Kama river that the individual proportions changed most up to a body length of 17.5 cm.

The extent of differences in the individual signs among the size groups may be illustrated on the »length of pectoral fin«. The values assessed for this character in the last three size groups were these: 16.5, 16.9; 17.4; respectively. The value of the t-test between the first and last group was 2.9 (CD = 0.66). This evaluation enabled an estimation of differences in the remaining signs of the individual size groups.

The characters employed in the study on morphological variability were influenced neither by sexual dimorphism nor relative growth variation to such an extent that it would not permit their use in the present study.

Morphological characters in populations of the European and Siberian grayling

For this purpose, data were obtained on grayling populations from these localities: *Thymallus t. thymallus* from the rivers Vltava, Danube and Mesna; Thymallus a. arcticus from the rivers Enisej, Shishkhid and lake Teleckoe. Average values of the compared characters and their mean errors are shown in Table 3. In total the populations differed 12 times (CD $\geq$ 1.3), i. e., 5times in maxilla width, 3 times in the number of gill rakers, twice in the length of the caudal peduncle and twice in the length of the pectoral fin (Table 5). Graylings from the Danube differed from those from the Enisej in three signs, graylings from the Enisej and Mesna and from the Shishkhid and Mesna in two signs, graylings from the Mesna and Vltava, Mesna and Danube, Enisej and Vltava, Shishkhid and Dabune differed in one sign. No differentiating characters were found between graylings from the Vltava and Danube, and between those from the Enisej and Shishkhid - in both cases the geographical position of each of the two localities was very close. A grayling population from the lake Teleckoe, (situated at roughly 600 km SW of the locality Enisej, for which no statistical values were available in the first two signs - we had data on the centres of intervals only, did not differ from any population of the other localities investigated in the remaining 7 signs. However, the centres of intervals of the two first signs, i. e., the number of gill rakers and lateral line scales, suggested that graylings from the lake Teleckoe might not have differed even in these characters from the remaining populations. The situation was similar in a grayling population from the river Ural for which only mean values and ranges were available: in all instances, these values were very close to those assessed for graylings from the Vltava and Danube. Thus, between graylings from the Ural river and those from the other localities i. e., from the rivers Mesna, Enisej, Shishkhid and the lake Teleckoe, differences may be similar to those occuring between populations from the latter localities and those from the rivers Vltava and Danube. Interesting results might be obtained

from a comparison grayling populations from the localities Shishkhid *(Thymallus a. arcticus)* and lake Bajkal *(Thymallus a. baicalensis)* situated at a distance of 300—400 km from one another. Population from the first locality differed from the earlier mentioned localities four times while graylings from the lake Bajkal differed from the same localities sixteen times!

Morphological characters in various subspecies of the Siberian grayling

The data used in this comparison were obtained from grayling populations of the lake Teleckoe, the rivers Enisej, Shishkhid, Kherlen, Kolyma and from the lake Bajkal. A survey of average values and mean errors of the characters under consideration is given in Table 3. In total, these populations differed 21 times which is almost two times more than differences in the same number of populations of two different species *(Thymallus thymallus* and *Thymallus arcticus)*. Additional differences could be recorded in the number of lateral line scales and gill rakers in graylings from the lake Teleckoe in comparison with populations from the remaining localities. All populations differed 6 times in predorsal distance, 4 times in the number of lateral line scales, 3 times in the length of dorsal fin, twice in head length, and in length and width of the maxilla. This suggest a remarkably higher morphological variability inside the species *Thymallus arcticus* than that observed between different species, i. e., *Thymallus thymallus* and *Thymallus arcticus*. Apart from other factors, this phenomenon might be ascribed to the considerable distance between the compared populations and, hence, to the influence of extremely different climatic conditions. The former group of grayling populations, except for that from the Mesna river were concentrated roughly along the 50th parallel.

Inside the species *Thymallus arcticus* (Table 5), grayling populations from the river Shishkhid differed from those from the Kherlen in three signs; the same applied to populations from the rivers Shishkhid and Kolyma and from the river Kherlen and lake Bajkal; differences in two characters were found between grayling populations from the lake Teleckoe and the river Kherlen, the lake Teleckoe and the river Kolyma, the river Enisej and the lake Bajkal, the Shishkhid and Bajkal, the Kolyma and Bajkal. Differences in one character occured between grayling populations from the lake Teleckoe and the Bajkal, the Kherlen and the Kolyma. No differences were found between grayling populations from the lake Teleckoe and those from the Enisej and Shishkhid, which again are closely adjoining localities. The morphological comparison of characters from graylings of the rivers Shishkhid and Kherlen (Table 4) will be treated more comprehensibly because it will be based on our own count and measurements. Data on values of coefficient CD will be given in instances only, where they either surpass or equal one ($CD \geq 1$). Both populations differed in head depth, predorsal, postdorsal distance, maximum and minimum body depth, length of caudal peduncle, A-C distance, length of pectoral fin, number of lateral line scales, number of scales above lateral line and number of gill rakers,

Table 4. *Morphometric and meristic characters of Thymallus a. arcticus (Shishkhid river) and Thymallus a. grubei (Kherlen river) and the values of CD coefficient (CD>1)*

Systematic character	Shishkhid river M ± m		CD	Kherlen river M ± m	
Smitt's length	25.7	0.91		19.5	0.75
As % of Smitt's length					
length of head	18.5	0.16		18.6	0.20
preorbital distance	4.1	0.05		3.8	0.07
long. diameter of eye	4.8	0.13		4.9	0.10
postorbital distance	9.9	0.06		10.1	0.08
occipital head depth	15.3	0.11	1.53	13.0	0.19
prepreopercular distance	13.6	0.14		14.3	0.13
interorbital width	6.1	0.05		5.5	0.10
length of maxilla	5.9	0.05		6.2	0.11
width of maxilla	1.9	0.02		1.7	0.05
length of lower jaw	9.8	0.09		10.1	0.09
predorsal distance	34.3	0.22	1.85	30.4	0.27
preventral distance	45.3	0.24		44.3	0.18
preanal distance	70.8	0.18		68.9	0.23
postdorsal distance	39.6	0.17	1.26	43.0	0.36
maximum body depth	23.8	0.31	1.67	18.3	0.19
length of caudal peduncle	15.3	0.13	1.08	16.7	0.18
A-C distance	9.1	0.12	1.12	10.9	0.19
Addip-C distance	9.6	0.12		10.0	0.21
minimum body depth	8.1	0.09	2.10	6.3	0.06
P-V distance	28.2	0.15		26.7	0.33
V-A distance	26.8	0.26		25.1	0.30
length of D	22.8	0.23		22.9	0.41
length of A	8.9	0.12		8.9	0.18
length of upper caudal lobe	19.3	0.15		18.2	0.12
length of middle caudal rays	8.5	0.12		6.9	0.23
length of P	16.9	0.10	1.51	14.5	0.22
length of V	16.7	0.16		15.5	0.31
depth of D ♂♂	19.7	0.69		15.6	0.75
depth of A ♀♀	11.7	0.27		9.9	0.30
depth of D ♀♀	15.9	0.35		9.5	0.27
depth of A ♂♂	12.3	0.62		11.7	0.55
nonramified rays in D	7.2	0.14		6.7	0.33
ramified rays in D	14.0	0.11		13.5	0.22
nonramified rays in A	3.8	0.07		3.5	0.13
ramified rays in A	9.0	0.09		8.2	0.10
lateral line scales	82.1	0.46	1.56	93.1	0.63
scales above lateral line	7.3	0.06	1.90	9.0	0.01
scales below lateral line	8.4	0.07		9.4	0.10
gill rakers	19.1	0.23	1.51	15.1	0.30

i. e., in total in 11 characters out of the 35 characters investigated (depth of the dorsal fin was not evaluated).

In view of the variability in the individual characters, different values of coefficient CD might be expected from a comparison of another couple of populations of these subspecies. This can be confirmed on the data given by SVETOVIDOV (1936) for graylings from the river Enisej *(Thymallus arcticus arcticus)* and from the river Amur *(Thymallus arcticus grubei)*. A comparison among these populations and, simultaneously, with our populations of the pertinent subspecies suggested that the diffe-

rentiating characters - depth of head, predorsal distance, maximum and minimum body depth and number of lateral line scales - were common to all possible combinations. In this, these characters may be considered the most important ones for a differentiation between the two populations. In addition, they are well suited for characterizing differences in their proportions. The graylings from river Kherlen *(Thymallus arcticus grubei)* differ from graylings from the river Shishkhid *(Thymallus arcticus arcticus)* in the shape of the maxilla which in *Thymallus a. grubei* is longer and lower (salmonid-shaped mouth). However, variability of these two characters is considerably high and, hence, coefficient CD does not reach the requires limits. Another remarkable feature in graylings from Kherlen is a wide orange-red band (roughly 11 % of length according to SMITT) extending through the middle of the body from the base of the pelvic fin to the base of the dorsal fin. This coloured band was mentioned by DYBOWSKI (1869) for that subspecies and also for the graylings from the lake Bajkal. SVETOVIDOV (1936) recordet it for graylings from the Bajkal *(Thymallus arcticus baicalensis)* and from Amur basin *(Thymallus arcticus grubei)*. It is mentioned by him also from an occasional *Thymallus arcticus arcticus*. It was not observed in our graylings from the river Shishkhid *(Thymallus arcticus arcticus)*.

Of the nine selected key characters, the two populations differed in four, i. e., number of lateral line scales, number of gill rakers, length of the pectoral fin and predorsal distance. The graylings from the river Shishkhid differed from those from the rivers Vltava and Danube in one of these characters only, while graylings from the river Kherlen differed from those from the Vltava and Danube in four and five characters out of the 9 principal signs! The morphological difference in populations of two different subspecies of the Siberian grayling *(Thymallus arcticus arcticus* and *Thymallus arcticus grubei)* showed to be considerably greater than that between the two species *(Thymallus thymallus* and *Thymallus arcticus)*. The external morphology of graylings from the river Shishkhid is very close to that of graylings from Europe; this however, does not apply to graylings from the river Kherlen, (Photos 1a, 1c, 2b).

The problem of separate identity of the species *Thymallus grubei* DYBOWSKI, 1869 or its arrangement to the species *Thymallus arcticus* as the subspecies *grubei* (see the recent revision by SVETOVIDOV, 1936) is still in need of clarification. The results of our studies permitt to suggest that graylings from the Amur basin might be considered to belong to the independent species *Thymallus grubei* DYBOWSKI, 1869.

Morphological characters within the genus Thymallus

The localities covering roughly the total area of distribution of the genus *Thymallus* in Eurasia are listed in Table 5. The selection was restricted by a statistical elaboration of the individual populations under consideration of coefficient CD.

Graylings from the Bajkal differed in the largest number of cases (26) from the remaining grayling populations; the next in succession were graylings from the river Kherlen (24), from the Danube (21), the Mesna (20), the Anadyr and Kolyma (19)

Table 5. *Coefficients of difference among populations of grayling in number of gill rakers, lateral line scales, predorsal distance, length of head, length of caudal peduncle, length of dorsal and pectoral fins, length and width of maxilla (from left above to right below)*

	Vltava R. 11 + (7) = 18	Danube R. 21 + (5) = 26	Mesna R. 20 + (12) = 32	Khendekt L. 18 + (7) = 25	Teleckoe L. 8 + (7) = 15
Vltava R.	—	0	1	1	0
Danube R.	0.22 0.57 0.22 0.04 0.07 0.04 0.35 0.36 0.40	—	(13)	2	0
Mesna R.	0.07 0.47 0.13 0.73 0.75 0.03 0.30 0.09 2.20	0.59 1.12 1.02 0.59 1.18 0.03 0.96 0.58 1.93	—	3(1)	0(3)
Khendekt L.	0.84 1.70 0.08 0.05 0.93 0.40 0.42 0.75 —	1.30 0.84 0.64 0.09 1.32 0.35 0.18 0.52 —	2.20 2.20 0.56 0.84 0.41 0.62 1.24 1.40 —	—	0
Teleckoe L.	— — 0.33 0.20 0.52 0.40 0.10 0.96 0.27	— — 0.20 0.12 0.69 0.35 0.27 0.93 0.34	— — 0.75 1.10 0.04 0.55 0.68 1.18 0.27	— — 0.75 0.28 0.28 0.05 0.50 0.80 —	—
Enisej R.	0.97 0.06 0.31 0.98 1.00 0.70 0.44 0.44 1.53	1.52 0.54 0.86 0.80 1.40 0.28 0.18 0.10 1.45	2.50 0.32 0.11 0.90 0.55 0.40 1.39 0.71 0.15	0.32 1.22 0.50 1.13 0.10 0.74 0.00 0.43 —	— — 0.93 0.95 0.55 0.72 0.50 0.89 0.28
Shishkhid R.	0.69 0.43 0.08 0.55 0.94 0.34 0.14 0.52 1.44	0.90 0.18 0.28 0.48 1.34 0.39 0.58 0.21 0.36	1.68 0.98 0.84 0.00 0.56 0.04 1.53 0.94 0.52	0.31 1.12 0.37 0.59 0.90 0.45 0.06 0.28 —	— — 0.45 0.83 0.36 0.43 0.51 0.89 0.14
Kherlen R.	1.34 1.24 0.78 0.86 1.03 0.32 0.01 0.75 1.97	2.26 1.98 1.88 0.70 1.50 0.37 0.57 0.58 1.77	3.30 0.84 1.17 0.59 0.51 0.54 0.34 1.41 0.12	1.46 3.20 1.70 1.00 0.00 0.91 0.80 0.14 —	— — 1.69 1.22 0.31 0.82 0.31 1.29 1.00
Bajkal L.	0.66 1.76 0.85 1.32 0.90 0.88 0.11 0.43 3.38	0.85 2.38 0.62 1.02 1.32 0.82 0.29 0.00 2.78	1.67 1.48 0.53 1.88 0.34 1.51 0.78 0.82 1.42	0.46 3.46 0.00 1.60 0.11 0.56 0.55 0.80 —	— — 0.73 1.69 0.23 0.39 0.00 1.00 0.57

Table 5. *Coefficients of difference among populations of grayling in number of gill rakers, lateral line scales, predorsal distance, length of head, length of caudal peduncle, length of dorsal and pectoral fings, length and width of maxilla (from left above to right below)*

	Vltava R. 11 + (7) = 18	Danube R. 21 + (5) = 26	Mesna R. 20 + (12) = 32	Khendekt L. 18 + (7) = 25	Teleckoe L. 8 + (7) = 15
Kolyma R.	0.64 0.87 1.24 1.01 0.91 0.70 0.26 0.26 2.45	0.80 1.18 2.20 0.82 1.30 0.75 0.04 0.82 2.20	1.50 0.49 1.70 0.99 0.38 1.23 0.97 0.56 1.05	0.42 2.20 2.18 1.18 0.06 1.41 0.23 1.30 —	— — 2.00 1.36 0.26 0.80 0.76 1.17 0.55
Anadyr' R.	0.89 1.10 0.69 1.08 0.23 0.79 0.16 0.07 1.40	1.36 0.29 1.54 0.85 0.39 0.83 0.17 0.67 1.34	2.40 1.93 0.92 1.14 0.73 1.22 0.76 0.25 0.25	0.00 0.88 1.32 1.34 0.96 1.54 0.50 1.25 —	— — 1.48 1.48 0.43 1.34 0.09 0.96 0.24

Table 5. *Continue. The first number below each locality are cases when CD ≧ 1.3, the second in parentheses are cases when CD ≧ 1.*

	Enisej R. 8 + (7) = 15	Shishkhid R. 14 + (6) = 20	Kherlen R. 24 + (10) = 34	Bajkal L. 26 + (6) = 32	Kolyma R. 19 + (11) = 30	Anadyr 19 + (11) = 30
Vltava R.	1(1)	1	2(2)	3	1(2)	1(2)
Danube R.	3	1	5	3(1)	3(1)	3
Mesna R.	2	2	2(1)	5	2(2)	2(2)
Khendekt L.	0(2)	0(1)	3(1)	2	4(1)	3(1)
Teleckoe L.	0	0	2(2)	1(1)	2(1)	3
Enisej R.	—	0(1)	0(1)	2	0(1)	0(1)
Shishikhid R.	0.59 0.42 0.74 0.55 1.03 0.35 0.06 0.10 0.46	—	4(1)	2(1)	3(1)	1(1)
Kherlen R.	1.10 0.98 0.76 0.24 0.12 0.11 0.88 0.47 0.02	1.50 1.56 1.85 0.36 1.08 0.46 1.50 0.41 0.57	—	3	1(1)	2(2)
Bajkal L.	0.75 1.41 0.51 0.38 0.22 1.44 0.56 0.14 0.44	0.11 2.35 0.37 0.98 0.90 0.07 0.58 0.28 1.68	2.81 0.85 1.64 0.70 0.13 2.38 0.35 0.77 0.97	—	2(1)	3(2)
Kolyma R.	0.70 0.66 1.20 0.08 0.15 0.54 0.25 0.90 0.55	0.10 1.37 2.17 0.55 0.90 0.93 0.22 1.04 1.29	1.22 0.23 0.64 0.20 0.06 0.42 0.56 1.31 0.79	0.00 0.89 2.13 0.53 0.06 2.22 0.26 1.00 0.14	—	1
Anadyr' R.	0.35 0.90 0.59 0.25 1.14 0.66 0.40 0.78 0.00	0.32 0.61 1.46 0.53 0.10 1.06 0.39 0.90 0.40	1.52 3.20 0.04 0.08 1.12 0.55 0.40 1.22 0.00	0.50 3.50 1.34 1.00 0.95 2.33 1.05 0.85 0.75	0.46 2.18 0.57 0.22 0.60 0.12 0.14 0.25 0.50	—

respectively. Graylings from the Vltava, the lake Teleckoe and the Enisej differed in the least number of cases from the remaining populations, i. e., in 11, 8 and 8 cases respectively. However, in the first case (the Vltava), the standard deviation for the number of lateral line scales and the gill rakers may have been overestimated, while for the second case (lake Teleckoe) measurements only were available. On the average, the individual grayling populations differed from the remaining populations in 15.4 cases.

By introducing the criterium $CD \geq 1$ we might obtain a better arrangement of the individual populations. In that case populations of graylings from the rivers Kherlen, Mesna, lake Bajkal, Anadyr and Kolyma differed from the remaining populations in 34, 32, 32, 30 and 30 instances. All populations concerned inhabit the northern, northeastern or eastern (Kherlen) parts of the area of distribution of the genus *Thymallus* in Euroasia. Populations from the southwestern and south parts (the rivers Vltava and Danube, the lakes Khendekt and Teleckoe, the rivers Enisej and Shishkhid differ in 18, 26, 25, 15, 15 and 20 signs which indicates their lower morphological variability. It is of interest that the employment of Mdiff criteria for the differentiation of the individual populations enables the finding of significant differences in morphological characters in graylings from neighbouring water basin. This may be illustrated on a comparison in *Thymallus brevirostris* from the Dzavkhan basin and in that from lake Khendekt (Khövd basin). Of the 28 different characters we found significant differences in the values of 17 characters (i. e. Mdiff > 3) (TUGARINA and DAŠDORŽ, 1972).

Further information on possible relationships among grayling populations investigated in this study can be obtained from the figures on geographical variability; and on morphological differences.

Number of lateral line scales: (Figs 1, 2) average values increase roughly north- and eastwards. By contrast to this trend higher values in the number of lateral line scales were obtained from graylings of the lake Bajkal and the river Kherlen, lower values in graylings from the river Khövd and the lake Khendekt, and also in grayling populations from the rivers Anadyr and Kamchatka. The sudden decrease in the number of lateral line scales in graylings from Anadyr (80.9; 79.3) and Kamchatka (75.4) is in good agreement with similar low values in this sign in graylings from the coast of Alaska (MCCART and PEPPER, 1971) (Fig. 18). Generally, grayling populations placed earlier in the group with a higher morphological variability, (i. e., from the northern, northeastern and eastern parts of distribution) displayed higher average values in the number of lateral line scales. Thus, graylings from the rivers Mesna, Kherlen, lake Bajkal, rivers Kolyma, Amur, the lower Enisej, the Lena and Kara have 88.2, 93.1, 98.9, 87.6, 93, 98 and 90 lateral line scales respectively, while graylings from the southwestern, and southern parts of their area of distribution are less variable in their morphology and have a lower number of lateral line scales, i. e., graylings from the rivers Vltava, Danube, Sola, from Roumania (VASILIU, 1967), from Scandinavia (SMITT, 1866, 1887) and from the river Ural (ŠAPOŠNIKOVA, 1964)

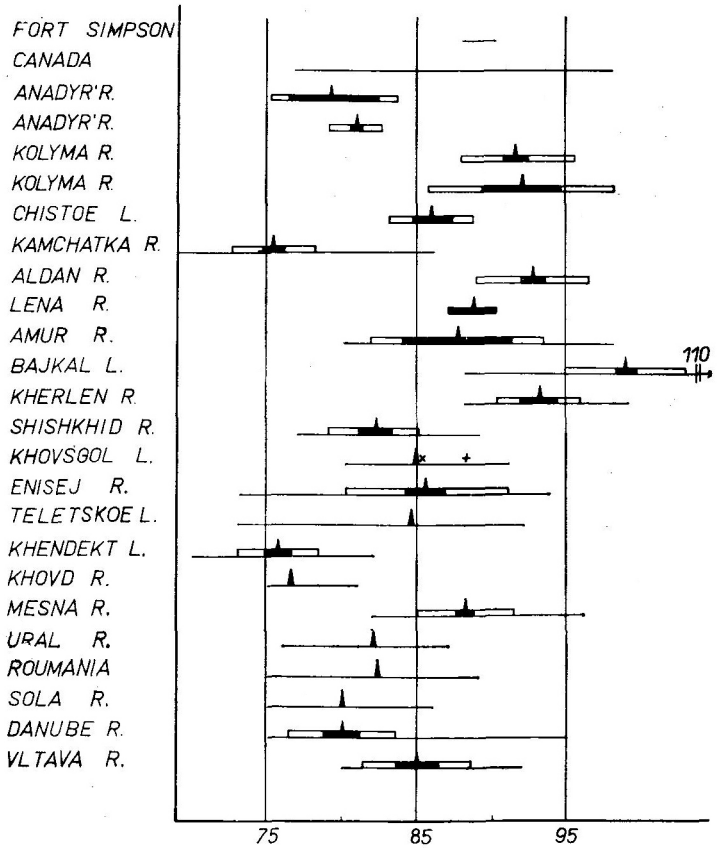

Fig. 1: Geographical variation of scales in lateral line (x-two specimens leg. Dašdorž, + eight specimens leg. Országh)

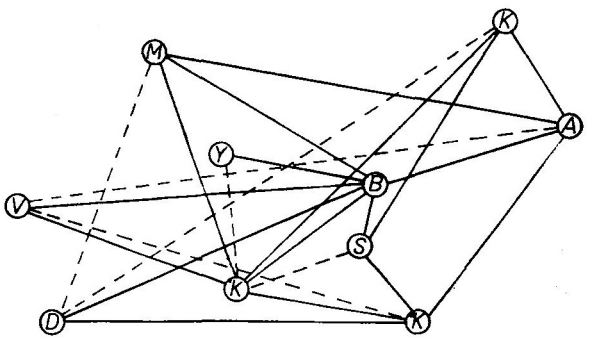

Fig. 2: Morphological differences among localities in scales of lateral line K Kolyma, 'K Khendekt, "K Kherlen, A Anadyr, B Bajkal, S Shishkid, Y Enisej. M Mesna, D Danube, V Vltava, T Teleckoe). Full lines for CD>1.3, interrupted lines for CD>1.

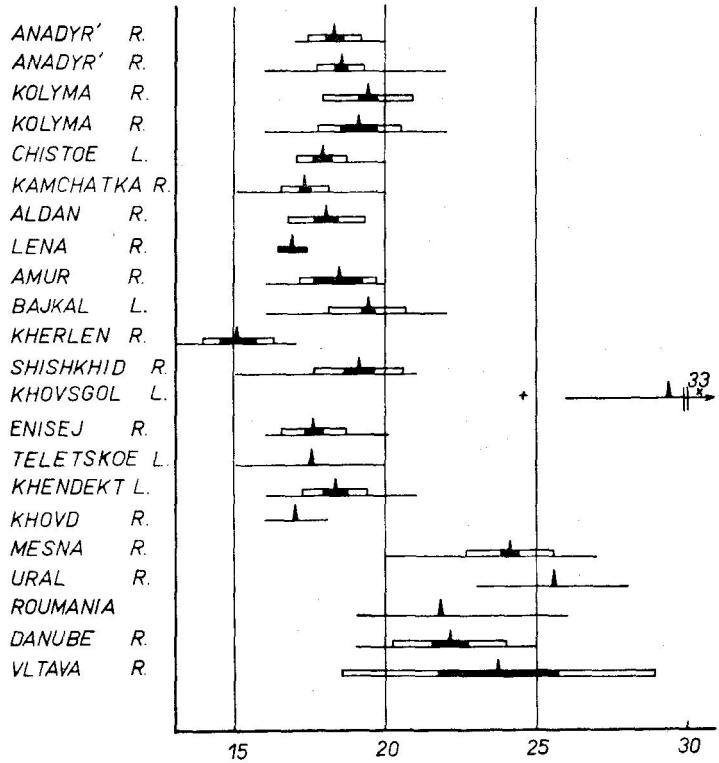

Fig. 3: Geographical variation of gill rakers

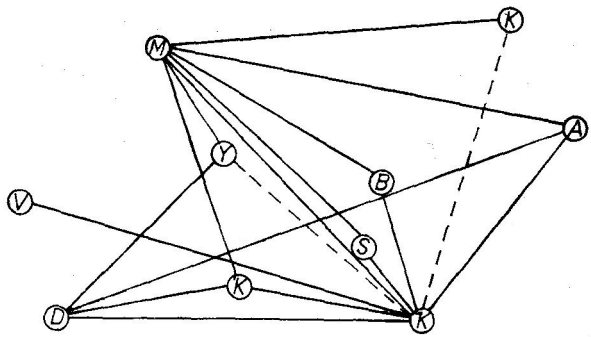

Fig. 4: Morphological differences among localities in number of gill rakers.

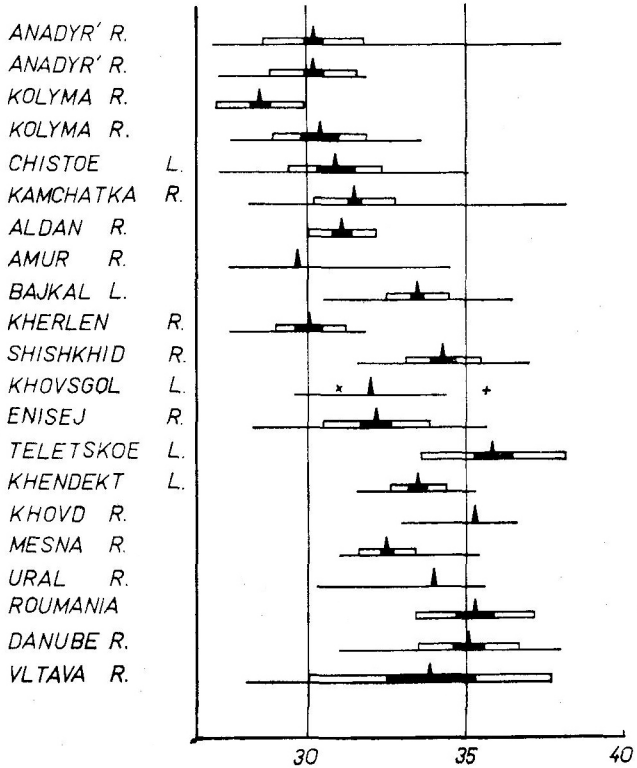

Fig. 5: Geographical variation of predorsal distance

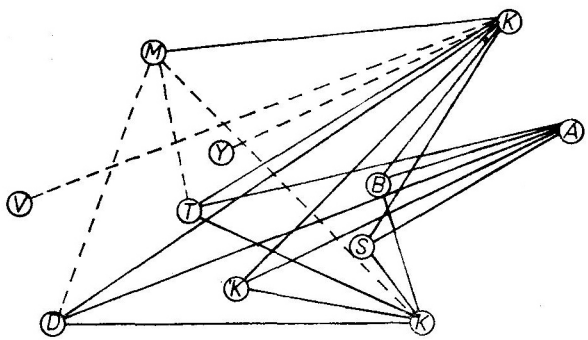

Fig. 6: Morphological differences among localities in predorsal distance

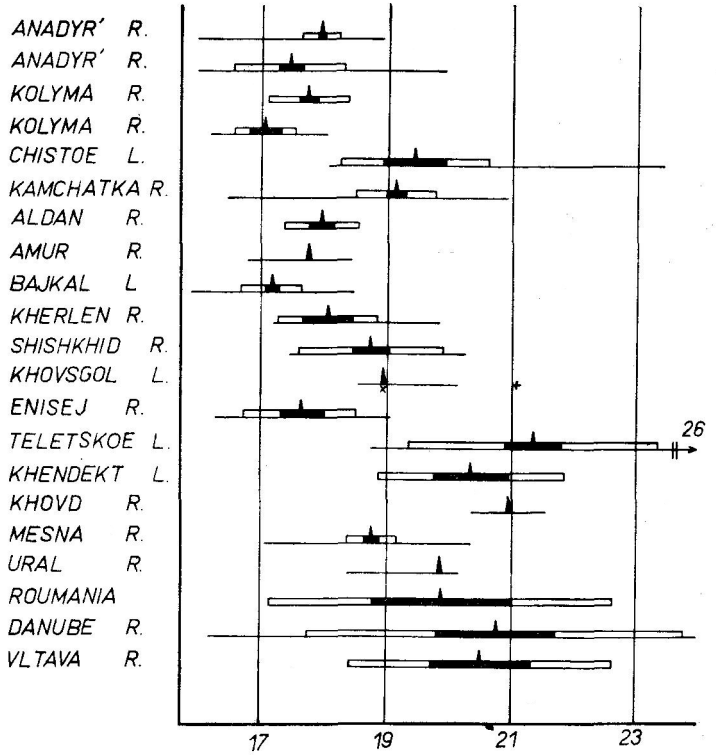

Fig. 7: Geographical variation of head length

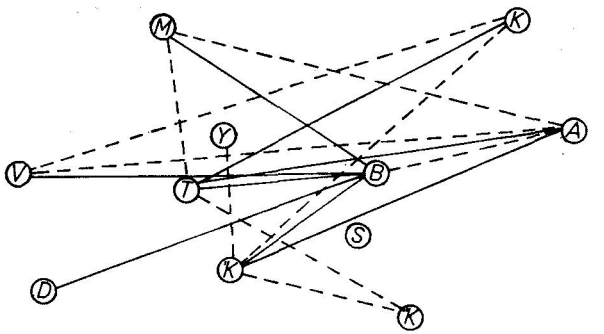

Fig. 8: Morphological differences among localities in head length

have 85, 80.8, 80.4, 82.4, 82.1 and 82.1 lateral line scales respectively. In the Asian part of grayling distribution, in the upper Enisej river, the lake Teleckoe and the river Shishkhid, they have 85.5, 84.5 and 82.1 lateral line scales respectively whereby we do not mention the low number of lateral line scales in *Thymallus brevirostris*. In fig. 2 on morphological differences the most frequent connection established is that of localities with extreme values. It concerns populations from the lake Bajkal and Khendekt, rivers Anadyr and Kherlen, from which extend 7, 7, 5, 5 line segments respectively.

Number of gill rakers in the first gill arch: (Figs 3, 4) according to this character grayling populations can be divided into three groups. Grayling from all European localities with a medium number of gill rakers (20—26); those from the lake Khövsgöl *(Thymallus nigrescens)* with a high number of gill rakers (26—33); all grayling populations from Asia with a low number of gill rakers (14—21). Within the last group, the lowest number of gill rakers was found in graylings from the river Kherlen (15.1). Grayling populations belonging to the species *Thymallus brevirostris* do not differ from other Asian populations in the low number of gill rakers. The graphical illustration of morphological differences emphasizes extreme values in populations from the rivers Mesna and Kherlen (line segments 7 and 9).

Predorsal distance: (Figs 5, 6) average values decreased in all populations in northward and eastward direction regardless of the species or subspecies. The continuity of the genus is reflected in the course of these values. The graphical illustration of morphological variability (fig. 6) elucidates the whole situation in that the largest number of differentiating line segments occured in localities with extreme values (the rivers Kolyma, Anadyr, Kherlen: 8, 5, 5 line segments respectively; (the rivers Danube, Mesna and the lake Teleckoe - 4 line segments each).

Head length: (Figs 7, 8) again this character indicates a decrease in average values north- and eastward except for grayling populations of the species *Thymallus brevirostris* which in view of the general trend in the development of this sign attain higher average value. This also can be seen from the fig. 8 in which the largest number of line segment start off from localities inhabited by *Thymallus brevirostris*, e. g., the lake Khendekt (5). It is of interest that the same number of differentiating line segments starts off from the locality lake Teleckoe; the average value of this character, however, is slightly higher than that recorded for *Thymallus brevirostris* in spite of the fact that this locality is inhabited by the *Thymallus arcticus* (according to IOGANZEN, 1945). The number of differentiating line segments is low for grayling populations from the rivers Vltava and Danube; also in this case this may be ascribed to a large variability in the length of the head of these populations (standard deviation is very high - CD coefficient attain a low value).

Length of dorsal fin: (Figs 9, 10) average values of this character increase in grayling populations from localities situated more to the North or East. The only exception are populations of *Thymallus brevirostris* and *Thymallus arcticus baicalensis* from the lakes Khövd and Bajkal. The largest number of differentiating line segments

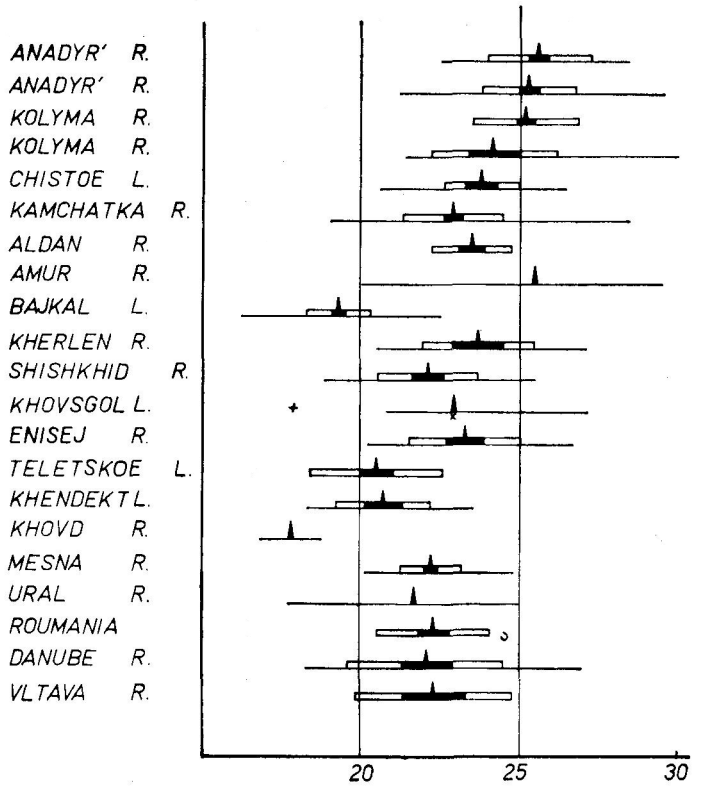

Fig. 9: Geographical variation of lentgh of dorsal fin

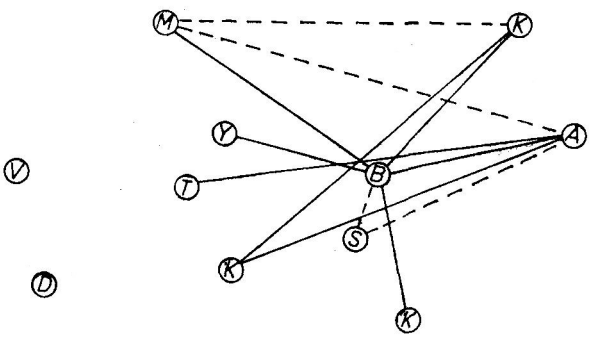

Fig. 10: Morphological differences among localities in length of D

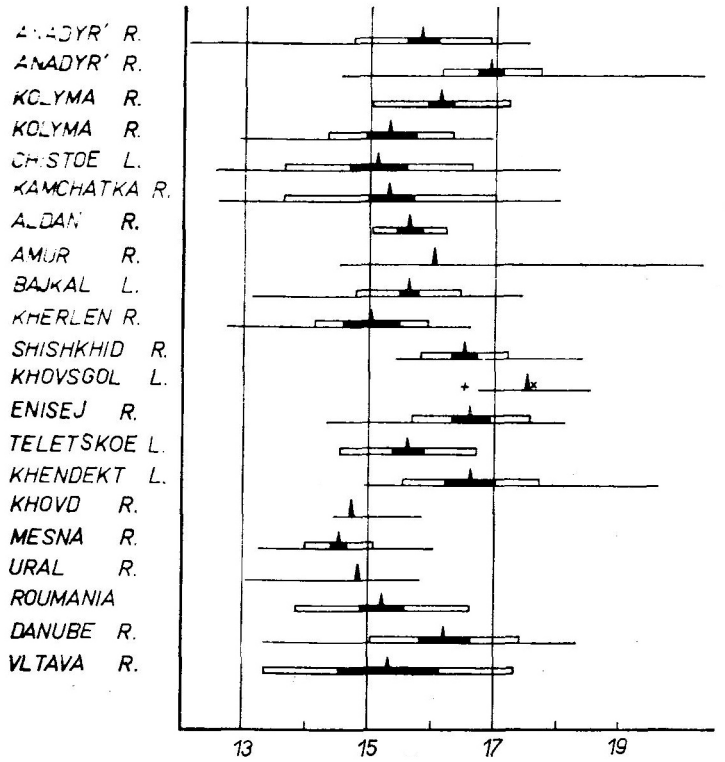

Fig. 11: Geographical variation of length of pectoral fin

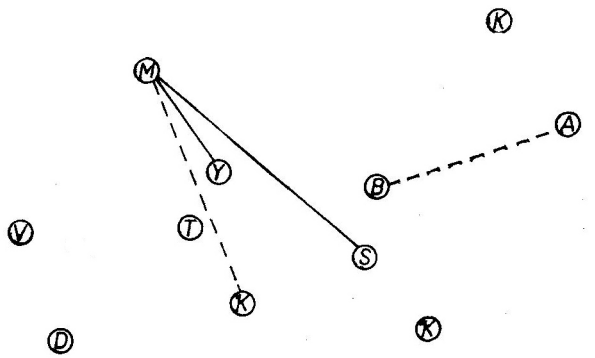

Fig. 12: Morphological differences among localities in length of P

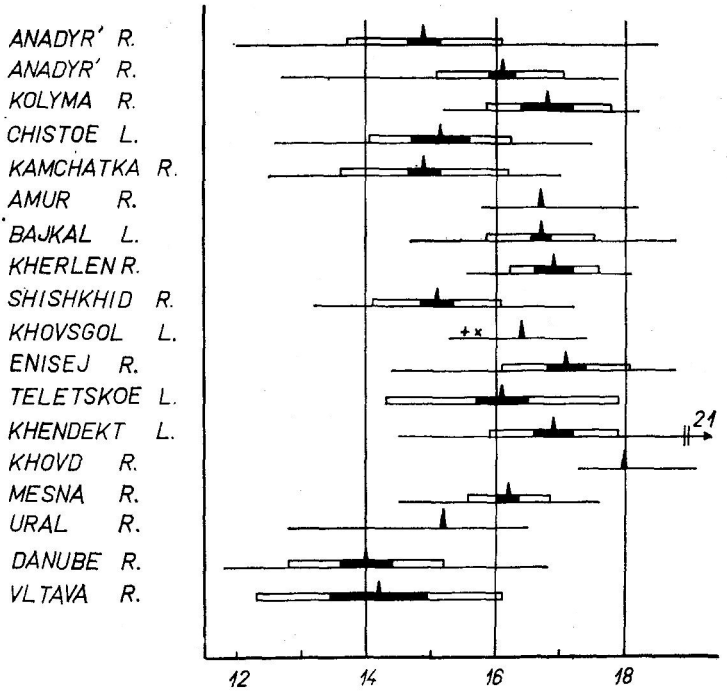

Fig. 13: Geographical variation of length of caudal peduncle

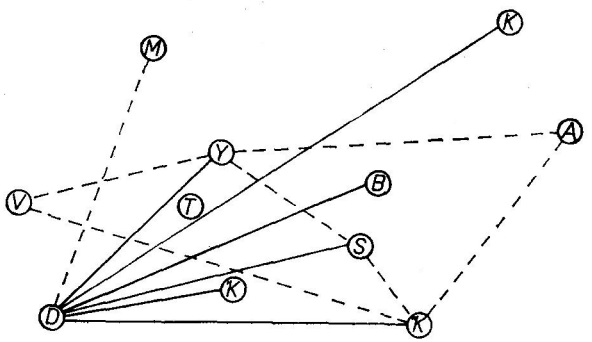

Fig. 14: Morphological differences among localities in length of caudal peduncle

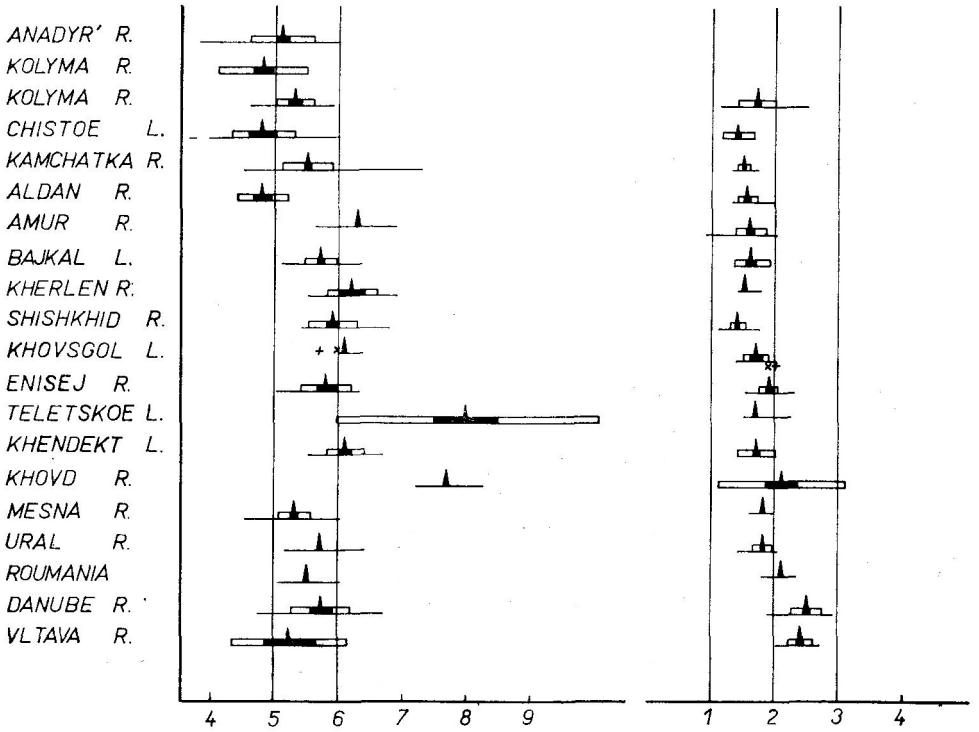

Fig. 15: Geographical variation of length and width of maxilla

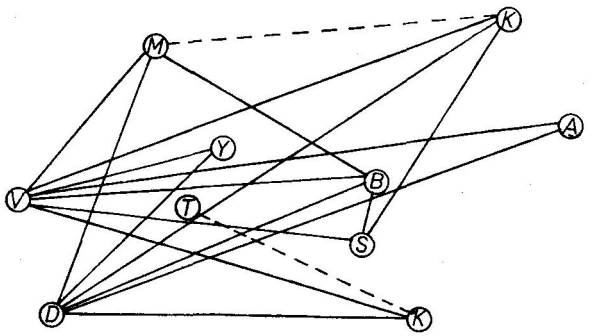

Fig. 16: Morphological differences among localities in width of maxilla

and thus the more extreme values are attained by graylings from the Bajkal (6 line segments) and from the river Anadyr (5 line segments), etc.

Length of pectoral fin: (Figs 11, 12) the geographical variability of this sign is similar to that of the foregoing character. An exception from the general trend are graylings from the lake Khövsgöl *(Thymallus nigrescens)*. The lowest values have been recorded for graylings from the river Mesna and, hence, this locality sends off the largest number of differentiating line segments (3).

Length of caudal peduncle: (Figs 13, 14) except for graylings from the rivers Vltava and Danube for which average values are low, those of all other populations are roughly equal as regards this character (16—17 % of length according to Smitt) with an occasional exception. A clear picture of the situation is given in the graphical illustration of morphological differences seven differentiating line segments for graylings from the Danube (it may be similar in graylings from the Vltava river if it were not influenced by the high variability).

Maxilla width: (Figs 15, 16) a decrease in average values in northern and eastern direction is indicated for all populations. Maximum values reached by populations from the rivers Vltava and Danube, minimum values from the river Kolyma (see graphical illustration of morphological differences).

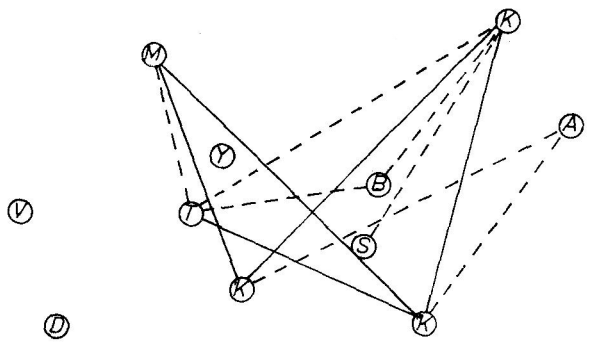

Fig. 17: Morphological differences among localities in length of maxilla

Maxilla length: (Figs 15, 17) average values form an arch with maximum values at its peak for localities with Thymallus brevirostris, followed by populations from the rivers Kherlen, Amur etc. For populations in Europe and the Far East, values of maxilla length were almost equal.

From the results presented it is evident there are two large groups of populations linked with one another by a complete series of morphological signs independent on the systematic position. Group 1 comprises populations inhabiting the northern and northeastern areas of distribution of the genus. Typical for this group are a large morphological variability in the individual populations, a high number of lateral line scales (roughly 90) and a low number of gill rakers (14—21) common to all

populations. An exception are graylings from the river Anadyr, and from the river Kamchatka in which the number of lateral line scales is low (80.9 or 79.3 and 75.4 respectively). Another exception are graylings from the river Mesna with a higher number of gill rakers (24.1); this feature forms the link with the second group, while in the number of lateral line scales, the length of caudal peduncle and the length of head it belong to Group 1.

Group 2 includes populations inhabiting the southwestern and souththern area of distribution of the genus. Typical of this group are: a low geographical variability as pointed out earlier by OLIVA and NAIKSATAM (1974) for European populations, a low number of lateral line scales (85 at the maximum) and a medium number of gill rakers (20—26) (European populations). Within this group *Thymallus nigrescens* from the lake Khövsgöl differs in the higher number of gill rakers (26—33), *Thymallus brevirostris* in the longer head and maxilla and in the smaller number of gill rakers. The small number of lateral line scales is common to the whole group.

The morphological unity and relationships among the individual populations are demonstrated by several characters responsible for an uninterrupted transition from one group to another. The characters involved are mainly predorsal distance, maxilla width and length of pectoral fin (except from *Thymallus nigrescens)*.

DISCUSSION

The boundaries dividing the individual continents are frequently considered to be analogous to the boundaries dividing the areas of distribution of individual systematic units. According to DARWIN (1860) large distances between the areas of distribution of two doubtful forms are often responsible for the fact that these forms are identified as independent species. The genus *Thymallus* is an excellent example of such a division. European populations have been listed to the species *Thymallus thymallus,* those from beyond the Ural separating Europa from Asia to the species *Thymallus arcticus* with the subspecies *arcticus, pallasi, grubei* and *baicalensis.* In addition two more independent species, i. e., *Thymallus brevirostris* from NW Mongolia, and *Thymallus nigrescens* from the lake Khövsgöl have been described from the Asian continent. Originally, *Thymallus signifer* (RICHARDSON, 1836) was described from Alaska and Canada, at present, however, it is listed generally to the species *Thymallus arcticus* (see in SCOTT and CROSSMAN, 1973). Two more species, i. e., *Thymallus montanus* and *Thymallus tricolor* have been described from the American continent.

Frequently the correct taxonomic position can be determined only on the basis of detailed studies on populations throughout their area of distribution. On the other hand, one should not overlook that the more knowledge is available of the geographical variability of a species, the more difficult it is to assess the boundary of the possible subspecies (MAYR, 1965). HUBBS and MILLER, (1965) added that the

speciefic or subspecific level of such populations can be determined only if based on an experimental analysis of sexual isolation.

Under consideration of the earlier suggested differentiating criteria, our opinion on the individual species or subspecies of the genus *Thymallus* is this:

Thymallus thymallus, Thymallus arcticus

According to PROBATOV (1936) contact between the two species is established in the river Kara (N-Ural) with *Thymallus thymallus* as the dominant species (97 % of the catches). BORISOV (1932, cit. SVETOVIDOV, 1936) recorded the incidence of *Thymallus arcticus* in the Pechora river. The morphological differentiation of the two species is most difficult since all differentiation signs are considerably variable and overlap each other. This has been confirmed by SVEDOVIDOV (1936) who eventually differentiated the species on the basis of the general habitat (p. 219). Should there be two independent species with a common incidence in the Kara river, and apparently also in the Pechora river, then Thymallus arcticus would have to be present in other rivers of the N.- and NW-parts of the European USSR.

Grayling populations of *Thymallus thymallus* from the Mesna river were similar to the remaining Thymallus thymallus populations in several characters such as the number of gill rakers. In the other characters (the number of lateral line scales, the length of caudal peduncle), they were similar to populations of *Thymallus arcticus*. The latter two characters are dependent to a certain degree on the more northern location of the river Mesna. The more southernly situated populations of *Thymallus arcticus* have a smaller number of lateral line scales and a shorter caudal peduncle similar to those characters in *Thymallus thymallus*.

LINDBERG (1972, pp. 228—283) demonstrated that after the catastrophes of the glacial period and transgressions of the oceans, rivers in the North, West and East of Europe were repopulated by fish populations from the Danube river, the only locality with remnants of Neogene species. The same author (p. 288) inferred that the Siberian grayling was of European origin, i. e., from the ancestral stock of the Danube. This suggests (see earlier in the text) that

1) populations of the European and Siberian grayling are, at present, differentiated to such a degree, that a »recent« return of the Siberian grayling to Europe did not lead to the crossbreading of the two species

2) there is a continuous transition from one population to another (from Europe to Siberia), we should remember that the morphological differentiation between the European and Siberian grayling is extremely difficult; if they have reached a stage of just originating species then they cannot exist together and if they do exist, they have to crossbreed. This may lead to a considerable morphological variability of the individual specimens which may impede differentiation. We are in favour of the second alternative.

Concerning the species *Thymallus arcticus*, we observed a considerable morphologi-

cal variability in the individual populations. A feature common to them was the high number of lateral line scales, with the exception of populations from the southern border of the area of distribution of this species (Upper Enisej, Shishkhid) in which the number of lateral line scales was low and which displayed generally a less morphological variability.

There is a smooth transition between the subspecies *Thymallus a. arcticus* and *Thymallus a. pallasi*. Remarcable differences were observed in populations from the Amur basin reffered to as *Thymallus arcticus grubei* DYBOWSKI, 1869. These differed from the remaining populations (Table 5) most frequently (34 times) in 9 characters thus forming a continuation of the north- and north eastern group of populations, but from the subspecies *Thymallus arcticus pallasi* dispersed more to the north, they differed in the length of maxilla, small number of gill rakers (Figs 3, 4). It should be remembered that by contrast to northern Europe and partly also to Asia, the Amur river basin had not been affected by an iceberg which means that grayling populations of this river basin are of original ancestral stock similar to grayling populations from northwestern Mongolia listed to the independent species *Thymallus brevirostris*, populations from the lake Khövsgöl again listed to the independent species *Thymallus nigrescens* and population from the Bajkal *(Thymallus arcticus baicalensis)*. It should be logical to arrange all these borderline groups of populations to independent species, i. e., *Thymallus grubei* DYBOWSKI, 1869; *Thymallus brevirostris* KESSLER, 1879; *Thymallus nigrescens* DOROGOSTAJSKIJ, 1923 and *Thymallus baicalensis* DYBOWSKI, 1874.

The closeness between European and Siberian grayling populations suggests that after the withdrawal of the iceberg grayling migrated from Europe (the Danube river) to the northeast similar to the migration of grayling populations from the North-American refuges to the »West«. It could not be brought the light at which site the two (East and West) groups met, whether their genetical differentiation was sufficient to make impossible crossbreeding or whether they formed transitional populations. WALTERS (1955) considered *Thymallus signifer* to be conspecific with *Thymallus arcticus* but failed to support his suggestion with detailed characteristics.

Grayling populations from the rivers Anadyr and Kamchatka have been listed to the subspecies *Thymallus a. grubei* as natio *mertensi* (SVETOVIDOV, 1936). They are characterised by a remarcably low number of lateral line scales in an area in which all othes populations have on the contrary a large number of scales. In the low number of lateral scales they resemble graylings from the coast of Alaska (Fig. 18) which survive the glacial period in the refuges of the Mississippi (MCCART and PEPPER, 1971) by contrast to graylings from Central Alaska and Canada which survive this period in the Bering refuge. In the latter populations the number of lateral line scales is high (89 in the mean) they have been arranged to the »subspecies *Thymallus arcticus signifer* and are connected with the subspecies *Thymallus arcticus pallasi* from eastern Siberia. Apparently, the graylings from the Anadyr and Kamchatka penetrated Asia from Alaska by way of the Paleoyukon arriving there from the Mississippi

refuge. Similarly LINDBERG (1972, p. 453) mentioned a double invasion of fishes from American continent to Asia. All this might fully justify a re-arrangement of natio mertensi by creating the independent subspecies *Thymallus arcticus mertensi* VALENCIENNES, 1848 (see in TUGARINA, 1972).

Thymallus brevirostris KESSLER, 1879

On the basis of literary data available, i. e., data on populations from the river Khövd and the lake Khendekt (Table 5) it might be concluded that populations of this species differ from all other Asian populations in the longer head (in this character, they are close to graylings from Europe), in the low number of lateral line scales (similar to graylings from the river Kamchatka) and in the long maxilla (this character shows considerable variability). Of interest are graylings from the lake Teleckoe which are similar to *Thymallus brevirostris* in a number of characters (maxilla length, dorsal fin length, head length); in other characters (number of lateral line scales, length of caudal peduncle) they are similar to *Thymallus arcticus* to which they have been assigned by IOGANZEN (1945). They might be also hybrid population as suggested by IOGANZEN (1. c.) and SVETOVIDOV (1936). In view of the fact that according to SVETOVIDOV (1. c.) *Thymallus arcticus* is distributed even in northwestern Mongolia together with *Thymallus brevirostris,* it should be of interest to assess how frequently hybrid populations occur in this area and to investigate the possibility of the existence of transitory forms between the two species, and, in this case naturally without the presence of the independent species *Thymallus brevirostris*. We should keep in mind that the latter species was rearranged by BOULENGER, 1898 (see in SVETOVIDOV, 1936) to the independent genus *Phylogephyra* on the basis of data obtained from individuals from the southern slopes of the Mongolian Altai range and that these may, in fact, have been members of a different species and genus. No further material of graylings is available from this area. The probability of the existence of hybrid populations is supported by a marked morphological variability among the populations of *Thymallus brevirostris* as pointed out earlier in the text.

Thymallus nigrescens DOROGOSTAJSKIJ, 1923

This species was originaly described by DOROGOSTAJSKIJ as *Thymallus arcticus nigrescens*; later, it was given the statute of an independent species by SVETOVIDOV (1936). Two of our specimens obtained by courtesy of Professor A. Dašdorž (place of origin lake Khövsgöl, Fl 23.5 and 20 cm) had 30 and 31 gill rakers, and 83 and 87 lateral line scales respectively, clearly dentate maxillae and mandibles and a marked upper position of the mouth. They resembled closely in the remarkably dark coloration, and long pectoral fins (Fig. 11). However, in other two graylings from the lake Khövsgöl obtained by courtesy of Dr. R. Ergens, the numbers of gill

rakers was similar to that in *Thymallus arcticus* (18.5), the number of lateral line scales (91 or 99) higher, the pectoral fin shorter than those in *Thymallus nigrescens*; also the coloration was lighter. For these reasons, they have been listed to the subspecies *Thymallus arcticus baicalensis* (HOLČÍK and PIVNIČKA, 1969). Finally, the 8 graylings from a tributary of the river Khankha flowing into the lake Khövsgöl (leg. Országh, phot. 1b average length 24.6 cm, average number of gill rakers 24.6, average number of lateral line scales 88.2), were similar to the *Thymallus arcticus* in length of pectoral fin, dorsal fin (the average value of this character was almost the same as in graylings from the lake Bajkal), head length (Fig. 7, 9, 11) and the terminal position of the mouth. However, in the considerably large number of gill rakers which had not been observed in any other population in this area except for *Thymallus nigrescens*, these are again closely related to the latter species; with certain doubts, they might be arranged to it. It is of interest that the two graylings obtained from Professor Dašdorž which unanimously had been assigned to the species *Thymallus nigrescens* differed in the upper position of their mouth at first sight from the specimen referred to as *Thymallus nigrescens* (SVETOVIDOV, 1936 fig. 3). A greater similarity to this figure was observed in the 8 graylings received from Dr. Országh. It appears that these eight graylings together with the one figured by Svetovidov are hybrids of *Thymallus arcticus* and *Thymallus nigrescens* and that the only true *Thymallus nigrescens* specimens are with a mouth in upper position (phot. 2a), and with a large number of gill rakers (30 and more)

If we considered

i) all morphological and geographically-historical differences assessed among grayling populations available for examination

ii) that information on the degree of genetical differentiation of the individual populations and, hence, their crossbreeding in nature along the possible geographical boundaries of the individual forms is still obscure

iii) that apart form the number of gill rakers (this is a very unsettled character with a wide range of variation) no other characters are available to differentiate the individual populations of European and Siberian graylings in spite of the fact that they have been arranged to two different species and can, at present, be differentiated only morphologicaly; other characters are of the clinal type and are unsuitable for the differentiation of the two species

iv) that borderline populations in the southern area of distribution of the genus (NW-Mongolia, the lake Khövsgöl, Bajkal, the basin of the Amur river) have not been affected by the presentace of an iceberg and are inhabited by populations of the original ancestral stock,

we may conclude that at present the genus *Thymallus* received five species.

The polytypical species *Thymallus thymallus* can be separated into these subspecies: *Thymallus thymallus thymallus* (LINNAEUS, 1758), *Thymallus thymallus arcticus* (PALLAS, 1776); *Thymallus thymallus mertensi* VALENCIENNES, 1848; and *Thymallus thymallus signifer* (RICHARDSON, 1836). Grayling populations from NV-Mongolia

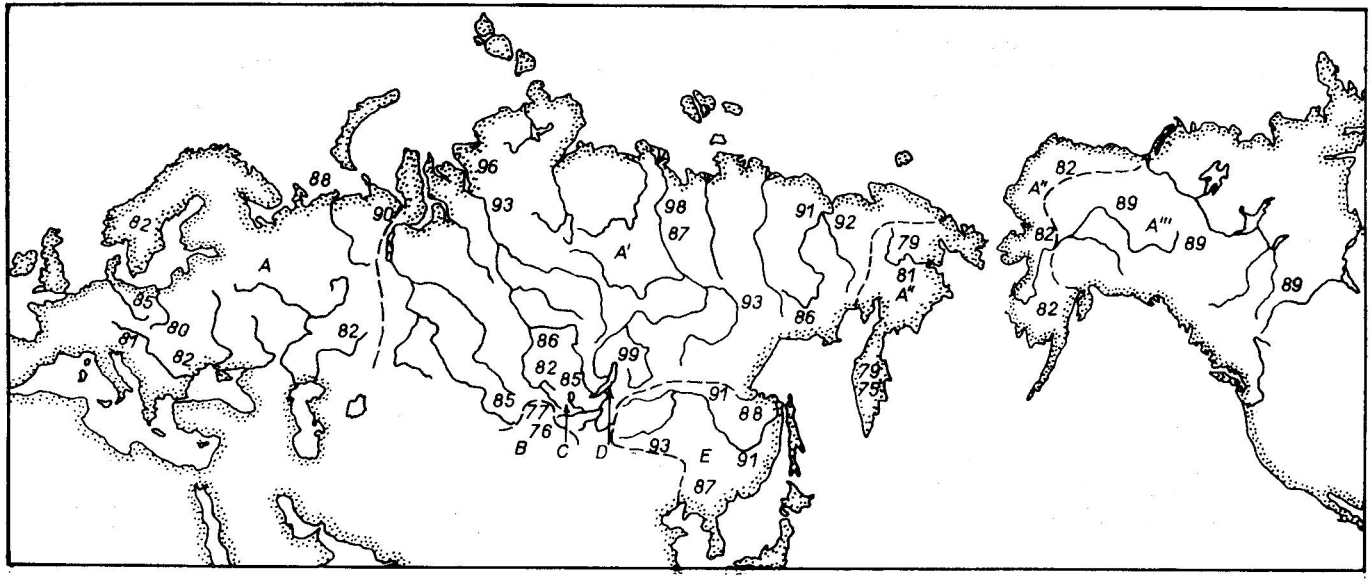

Fig. 18: Map showing probable distribution of *Thymallus thymallus thymallus* (A), *Thymallus thymallus arcticus* (A'), *Thymallus thymallus mertensi* (A''), *Thymallus thymallus signifer* (A'''), *Thymallus brevirostris* (B), *Thymallus nigrescens* (C), *Thymallus baicalensis* (D) and *Thymallus grubei* (E). Individual numbers indicate scales in lateral line from various sources (see in Table 1, BERG, 1948) and MCCART and PEPPER, 1971.

and the lake Khövsgöl had been separated earlier into two independent species, *Thymallus brevirostris* and *Thymallus nigrescens*. In our opinion, grayling populations from the lake Bajkal and the basin of the river Amur also belong to two independent species, *Thymallus baicalensis* and *Thymallus grubei*, although the situation in the Bajkal lake is complicated by the presence of two forms of grayling (SVETOVIDOV, 1936). The geographical distribution of the individual subspecies of *Thymallus thymallus* might be this: *Thymallus t. thymallus* - from Europe up to the Ural; *Thymallus t. arcticus* - throughout Siberia; *Thymallus t. signifer* - Central Alaska and Canada; *Thymallus t. mertensi* - coast of Alaska, basins of the rivers Anadyr and Kamchatka (the whole peninsula). The distribution of the remaining species has been given earlier in the text.

Key to the indentification of Euro-Asiatic species and subspecies of the genus *Thymallus*

1(2) Mouth in upper position (phot. 2a), gill rakers more than 26 - lake Khövsgöl .... *Thymallus nigrescens*

2(1) Mouth in terminal position (phots 1a, 1c and 2b), gill rakers less than 26

3(6) Scales in lateral line less than 80 (82)

4(5) Head, maxilla and caudal peduncle long (19—24 %, 6—9 % and 17—19 % of Smitt's length respectively - northwest Mongolia .... *Thymallus brevirostris*

5(4) Head, maxilla and caudal peduncle short (16—20 %, 4—6 % and 13—17 % of Smitt's length respectively - Anadyr basin, rivers of the Kamchatka peninsula, coast of Alaska .... *Thymallus thymallus mertensi*

6(3) Scales in lateral line more than 80(82)

7(12) Dorsal fin long (20—28 % of Smitt's length), scales in lateral line between 80(82)—95

8(11) Gill rakers 17—26

9(10) Caudal peduncle long (14—18 % of Smitt's length), gill rakers 17—21 eastward from the Ural Range, exclusively Anadyr and Amur basins and rivers of the Kamchatka peninsula .... *Thymallus thymallus arcticus*

10(9) Caudal peduncle short (12—16 % of Smitt's length), gill rakers 20—26, central, and northern Europe to the Ural Range .... *Thymallus thymallus thymallus*

11(8) Gill rakers 14—17, maxilla long and low (6—7 % and 1.5—2 % of Smitt's length respectively), salmonid shaped mouth (phot. 2b) Amur basin .... *Thymallus grubei*

12(7) Dorsal fin short 17—21 % of the Smitt's length, scales in lateral line more than 95, Bajkal lake .... *Thymallus baicalensis*

CONCLUSIONS

Our conclusions are based on a comparison of 9 selected morphological characters of grayling populations throughout the area of distribution of the genus in Eurasia in addition to graylings from North America with regards to the number of lateral line scales.

1. The selected characters (number of lateral line scales, number of gill rakers, predorsal distance, length of head, length of caudal peduncle, length of dorsal and

pectoral fin, length and width of maxilla) have not been influenced to any extent by either sexual dimorphism or variation in relative growth and have, therefore, been found suitable as a criterium for our comparative, biometric studies.

2. The northern, northeastern and eastern parts of the area of distribution of the genus are inhabited by populations displaying a considerable morphological variability; typical of these populations are a large number of lateral line scales (roughly 90) and a lower number of gill rakers (14—21). An exception are graylings from the rivers Anadyr and Kamchatka, in which the number of lateral line scales are lower. In this they form a link with graylings from the coast of Alaska.

3. By contrast, the southwestern and southern parts of the area in which is the genus distributed, are inhabited by populations with a less distinct morphological differentiation. In these the number of lateral line scales is lower (maximum 85), the number of gill rakers of European populations is of medium size (20—26), of the Asian populations is lower (14—21). A morphological differentiation in populations of both groups could be observed rather in South-North than West-East direction.

4. The values of majority of characters examined formed an uninterrupted line from one population to another and demonstrated thus the morphological unity of the genus (this applies mainly to the species *Thymallus thymallus* and *Thymallus arcticus*).

5. In our opinion, five grayling species may be differentiated in Eurasia and adjoining parts of North. America. These are *Thymallus thymallus* with the subspecies *Thymallus t. thymallus* (from Europe to the Ural), *Thymallus t. arcticus* (troughout Siberia), *Thymallus t. signifer* (Central Alaska and Canada), *Thymallus t. mertensi* (basin of the rivers Anadyr, Kamchatka, coast of Alaska), *Thymallus brevirostris* (NW Mongolia), *Thymallus nigrescens* (lake Khövsgöl), *Thymallus grubei* (basin of the Amur river), *Thymallus baicalensis* (lake Bajkal).

Acknowledgements

We are indebted to our Ministry of Education for financing our expedition to Mongolian People Republic, and to our Ministry of Foreign Affairs for helping in the organisation of the expedition. Our special thanks are due to the Czechoslovak Ambassador in the Mongolian People's Republic, Dr. E. Pátek, and to the First Secretary Mr. F. Budil. We wish to express our thanks to A. Dulmaa CSc., Zoological Institute, Mongolian Academy of Sciences. Professor A. Dašdorž CSc. and to Mr. P. Khorloo from the Mongolian State University for their kind assistance in the collection of our material. We are grateful to Assistant Professor Dr. O. Oliva CSc., Dr. V. Ložek D. Sc. and Dr. S. Frank CSc. for their counsel and stimulating discussions.

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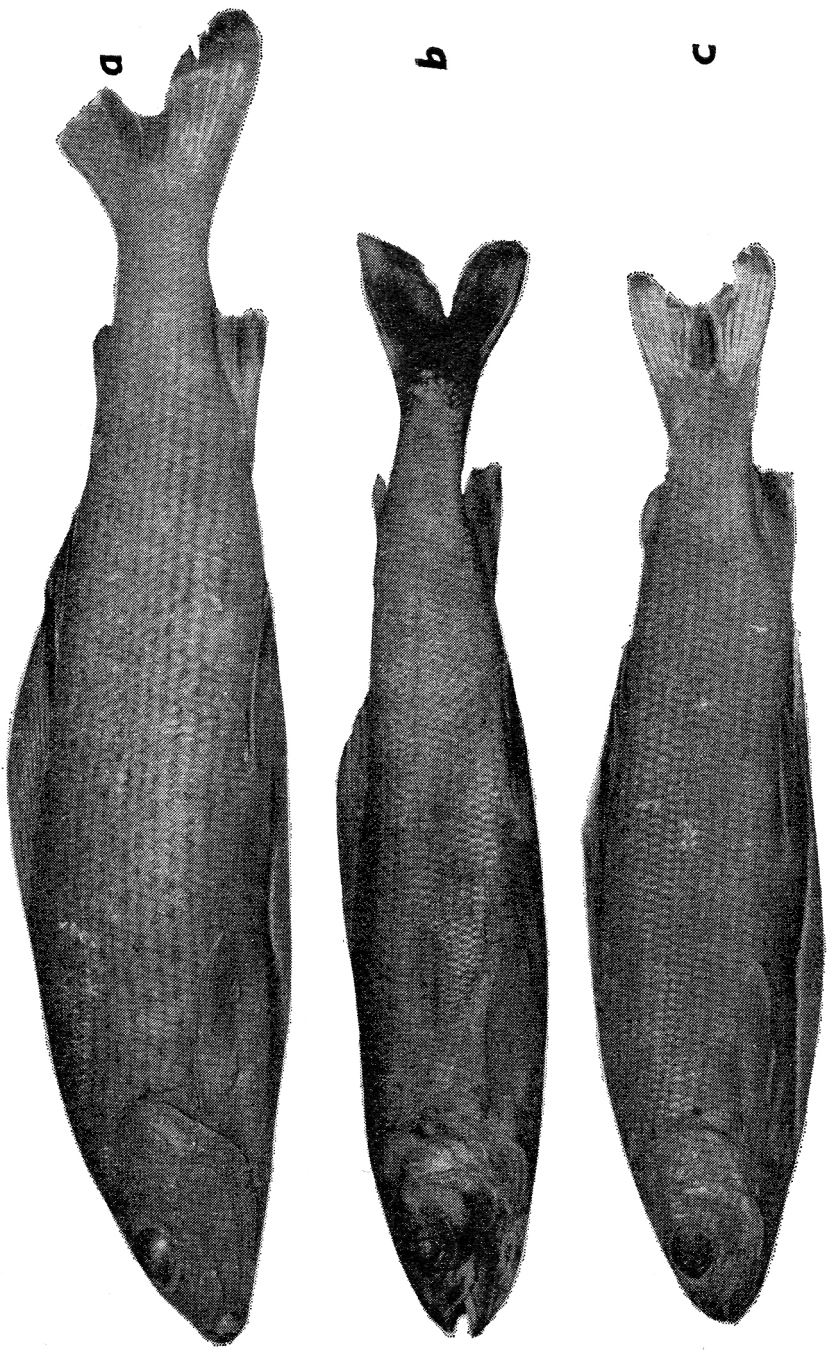
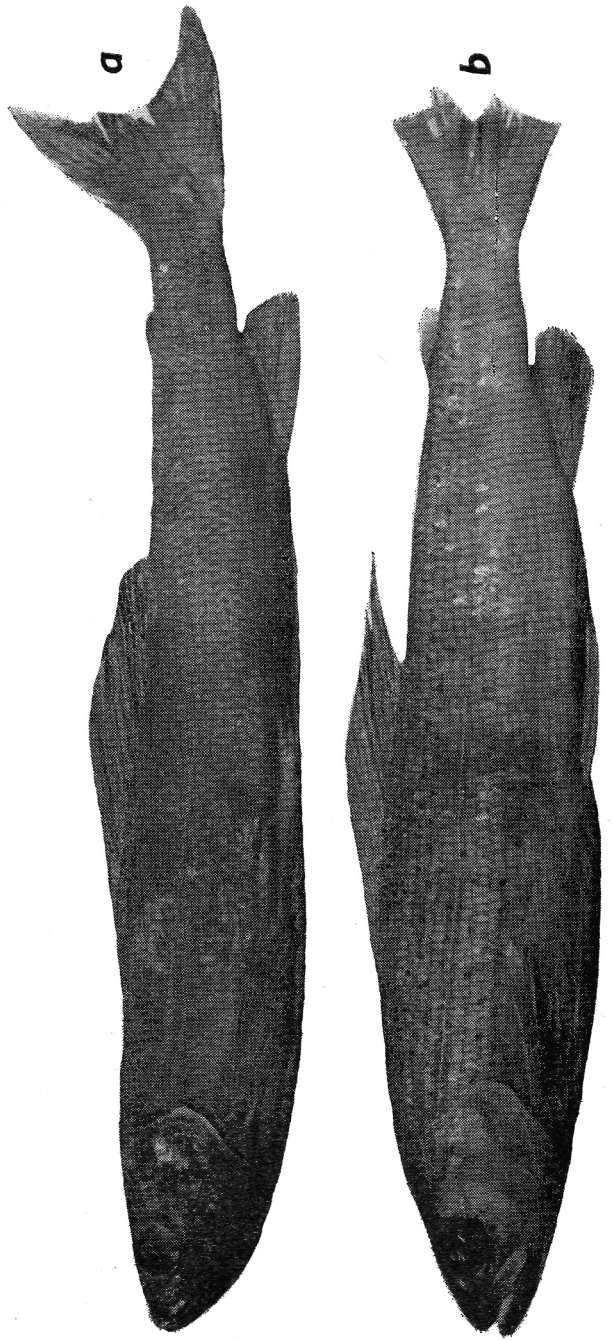


Phot. 1.: a *Thymallus thymallus thymallus* from the Vltava river near Volary (17.—18. 9. 1955, Smitt's length 240 mm)
b *Thymallus nigrescens* from the mouth of the Khankha river flowing into the Khövsgöl lake (13. 7. 1974, Smitt's length 225 mm)
c *Thymallus thymallus arcticus* from the lake Dood about 40 km from the locality Shishkhid (10. 7. 1969, Smitt's length 214 mm)



Phot. 2.: a *Thymallus nigrescens* from the lake Khövsgöl (July 1971, Smitt's length 235 mm)
b *Thymallus grubei* from the river Kherlen (August 1969, Smitt's length 248 mm). All Graylings are in the depot of the Department of the Systematic Zoology, Charles University, Prague