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A contribution to the systematics of the Chukchi char of the genus Salvelinus

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K sistematike chukotskikh gol'tsov roda Salvelinus

A contribution to the systematics of the Chukchi char of the genus Salvelinus

by

V. V. Barsukov

(Zoological Institute of the Academy of Sciences of the USSR)

In the summer of 1955 we collected char from Lavrentiya 3*
Bay and neighbouring lakes, and also from Lake Estikhet, located beside Provideniya Bay (Chukchi peninsula).

The shallow, small, tundra lakes in the vicinity of Lavrentiya Bay (their length ranges from 100 - 200 m, one - about 1 km) are connected with the sea by way of various channels and the Nunyamka river. Lake Estikhet has a completely different character. Its depth, based on interrogatory data, exceeds 100 m. It is in essence a fiord 11 - 12 km in length and about 2 km in width, cut off from the sea by a low neck of land; the possibility cannot be excluded that in it only

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* The numbers in the right-hand margin indicate the corresponding pages in the original text (Tr.).

the upper layer of the water is fresh. The shores are represented by the steep slopes of hills, devoid of a plant cover; only at the northern and southern (facing the sea) ends of the lake is the shore fairly low and with a partially tundra-type character. There is no connection with the sea.

It is natural that char living in such differing conditions could also be differentiated morphologically. Such differences in the char from Lake Estikhet have already been found. On the basis of one specimen from this lake L. S. Berg (1948a) described the distinct species - Salvelinus andriashevi Berg, which is closely related, in his opinion, to S. leucomaenis. Additional material which has been obtained has permitted a critical evaluation of L. S. Berg's conclusions. In contrast, the char from the lakes in the vicinity of Lavrentiya Bay have not previously been studied by anyone.

We present a comparison of the char from Lavrentiya Bay with the char from the neighbouring lakes and with the char from Lake Estikhet. The length [1] of the sea-run char from Lavrentiya Bay was 28.7 - 48.7 cm, of the lake char from the vicinity of the latter (hereafter, for the sake of brevity, we will call these the Lavrentiyan lake char) - 26.5 - 44.8 cm, and of the Estikhet char - 21.5 - 37.5 cm. 14 specimens from each locality were studied.

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[1] The length of the body is always indicated from the end of the snout to the end of the middle rays of the caudal fin. The char were measured after preservation in alcohol for seven months. During this time the body length of the char from Lavrentiya Bay was shortened, on average, by 3.8%. The shortening of the body proceeds unevenly: the head, for example, is shortened to a lesser degree than the body. All of this, undoubtedly, diminishes the precision of the comparison, though not to the extent as to make this completely impossible.

The mentioned groups of char are well differentiated from one another primarily by the form of the body. In the sea-run char the body is fusiform, though compressed from the sides, while in the lake char the body is teretely-elongate and thick (Figures 1 - 5). The Lavrentiyan lake char are shallow-bodied in comparison with the sea-run char, while the Estikhet char, though not differing from the sea-run char in the greatest depth of the body, are differentiated by an even greater thickness than is the case in the Lavrentiyan lake char[1]. It is true that the form of the body of the char is strongly dependent on their nutritional state (Zabolotskii, 1936; Mikhin, 1955), but in the present case the differences in the body thickness between the mentioned groups of char are apparently not due to differences in their fat content: judging by the X-ray photographs[2], the latter differences are slight. 4

It is possible that the terete character of the lake char may be explained by the smaller range of their movements, by an adaptation to very rapid though short surges. In fact, the body form of the lake char approximates in its terete character the body form of the pike. The dorsal, anal and ventral fins are somewhat displaced backwards (to a somewhat greater degree in the Estikhet char than in the Lavrentiyan lake char). The possibility cannot be excluded that in their

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1 A char obtained from a sea lagoon near the settlement of Sireniki was found to be just as shallow-bodied and elongate as the Lavrentiyan lake char. In the thickness of its body, however, it resembled the sea-run char.

2 On the X-ray photographs of many of the specimens there could be seen the boundary between the fat layer and the muscles, especially on the back in front of the dorsal fin.

way of life the lake char resemble the pike, in connection with which there may be noted in them similar changes in the form of the body and of the fins. The above are only preliminary suppositions; the relationship between the body form of fishes and the character of their locomotion is very complicated and needs to be studied with the help of physicists specializing in the field of the movement of bodies in an aqueous medium.

The head in the lake char is somewhat longer than in the sea-run char, while the length of the upper jaw and the length of the snout in the males of the lake char is somewhat decreased: the sexual dimorphism becomes less markedly expressed.

The positioning of the upper jaw in relation to the eye in individuals of the same size is approximately the same in all three groups. The width of the maxillary bone in relation to its length increases from the sea-run char to the Lavrentiyan lake char and even more to the Estikhet char. In all three groups at a body length of about 28 cm and more, almost simultaneously with the extension of the upper jaw past the posterior margin of the eye, there becomes evident the protuberance on the lower jaw and the depression for this on the upper jaw; this is expressed more markedly in the males than in the females. The upper jaw protrudes slightly over the lower jaw in most of the sea-run and Lavrentiyan lake char and in all of the Estikhet char. Its tapering in side view in this mentioned series in general decreases very slightly; in the Estikhet char this decrease is evident also from the dorsal view: the snout becomes somewhat blunter.

The depth of the notch in the caudal fin varies considerably in all three groups, and on the average it increases slightly, as does the depth of the caudal peduncle in relation to the greatest depth of the body.

The number of rays in the unpaired fins and also the number of supporting elements in these (excluding the elements of the caudal fin) in the cited series in general increases but only very slightly. In the number of vertebrae all three groups are fairly similar, as they are also in the number of gill rakers. However, the number of rays of the branchiostegal membrane decreases somewhat on the average. In the Lavrentiyan lake char the gill rakers are somewhat shorter than in the sea-run char; in the Estikhet char they are of about the same length, though thinner.

The teeth on the basibranchial in all of the char are situated in one row along the margins of the "tongue", though in some of the individuals from all three groups there are also teeth present on the middle of the "tongue". The number of such individuals and the maximal number of such teeth increases from the sea-run char to the Lavrentiyan lake char and even more to the Estikhet char.

The greatest difference is found in the number of the pyloric caeca. In the sea-run char there are 22 - 31 of these, in the Lavrentiyan lake char - 40 - 54, and in the Estikhet char - 30 - 48. This feature is subject to very considerable individual variations. It may be expected that with an increase in the number of observations there will be found transitional values even between the sea-run and the Lavrentiyan lake char which differ so markedly in this feature.

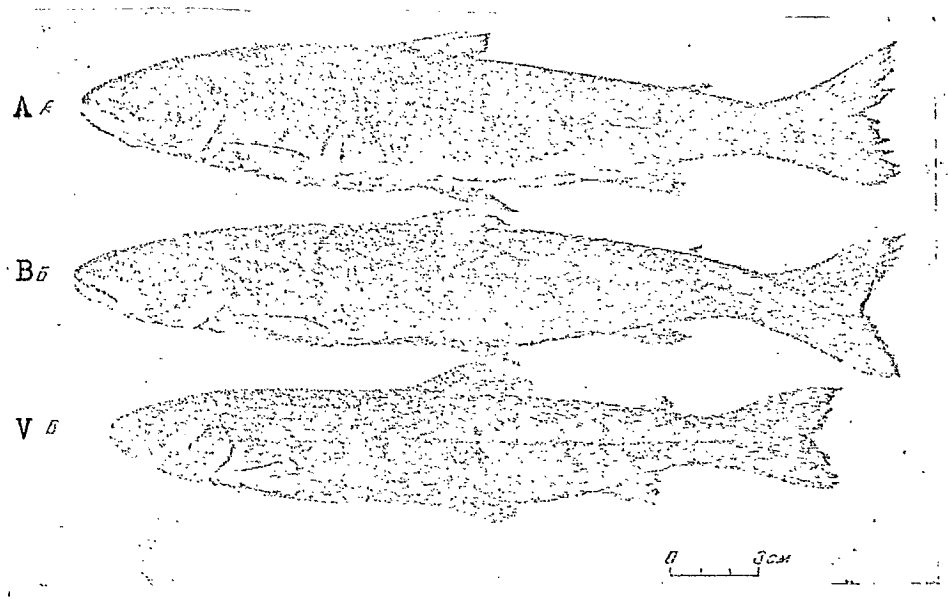

Рис. 1. Гольцы длиной 22—28 см (вид сбоку)

А — проходной голец (самка II стадии, IX 1955 г.); *Б* — озерный лаврентьевский (самец II стадии, 13.IX 1955 г.); *В* — эстихетский (самец IV стадии, 10.VIII 1955 г.)

Figure 1. Char 22 - 28 cm in length (side view)

A - sea-run char (stage II female, September 1955); B - Lavrentiyan lake char (stage II male, 13 September 1955); V - Estikhet char (stage IV male, 10 August 1955).

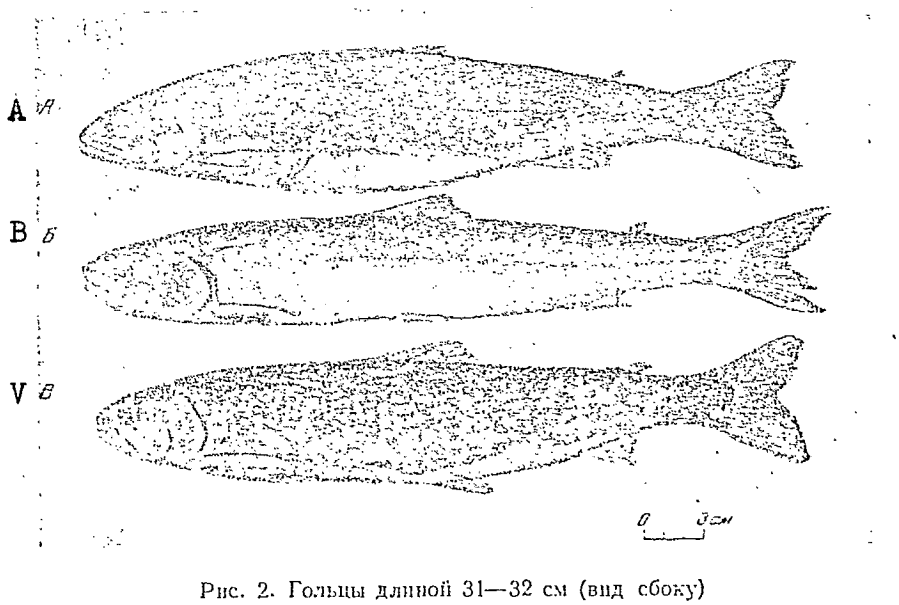

Рис. 2. Гольцы длиной 31—32 см (вид сбоку)

А — проходной голец (самец II стадии, 3.IX 1955 г.); *Б* — озерный лаврентьевский (самка II стадии, 13.IX 1955 г.); *В* — эстихетский (самка IV стадии, 10.VIII 1955 г.)

Figure 2. Char 31 - 32 cm in length (side view)

A - sea-run char (stage II male, 3 September 1955); B - Lavrentiyan lake char (stage II female, 13 September 1955); V - Estikhet char (stage IV female, 10 August 1955).

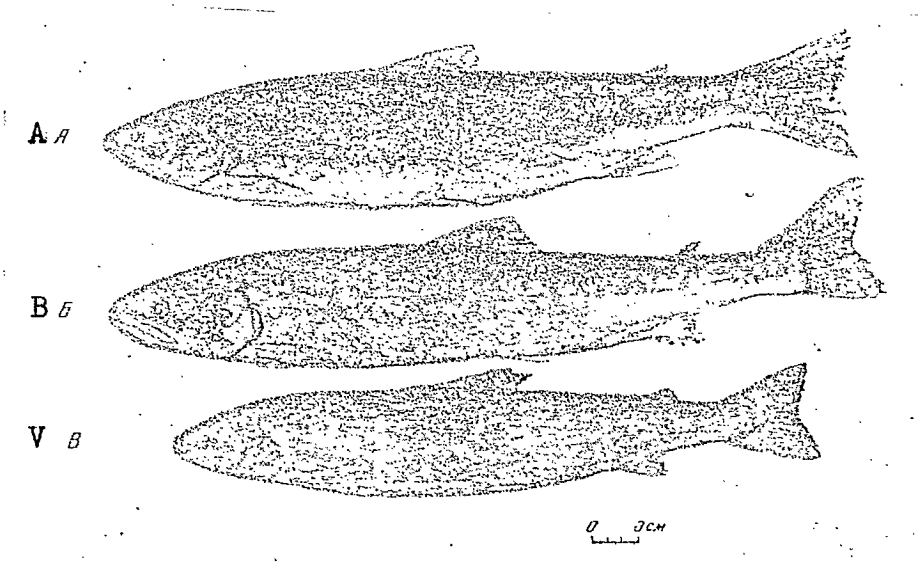

Рис. 3. Гольцы длиной 33—39 см (вид сбоку)

А — проходной голец (самка II стадии, 3.IX 1955 г.); *Б* — озерный лаврентьевский (самец II стадии, 13.IX 1955 г.) *В* — эстихетский (самец IV стадии, 10.VIII 1955 г.)

Figure 3. Char 33 - 39 cm in length (side view)

A - sea-run char (stage II female, 3 September 1955); B - Lavrentiyan lake char (stage II male, 13 September 1955); V - Estikhet char (stage IV male, 10 August 1955).

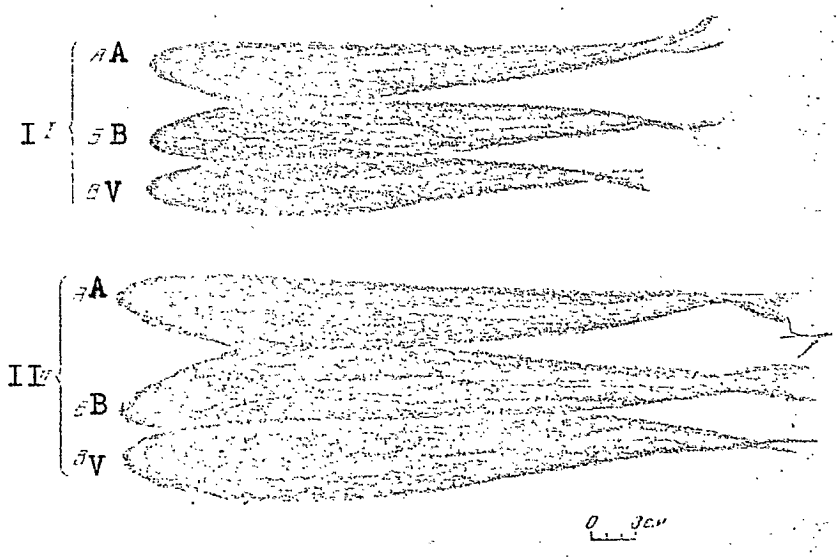

Рис. 4. Гольцы длиной 22—32 см (вид сверху)

I — те же гольцы, что на рис. 1; *II* — те же гольцы, что на рис. 2

Figure 4. Char 22 - 32 cm in length (dorsal view)

I - the same char as in Figure 1; II - the same char as in Figure 2.

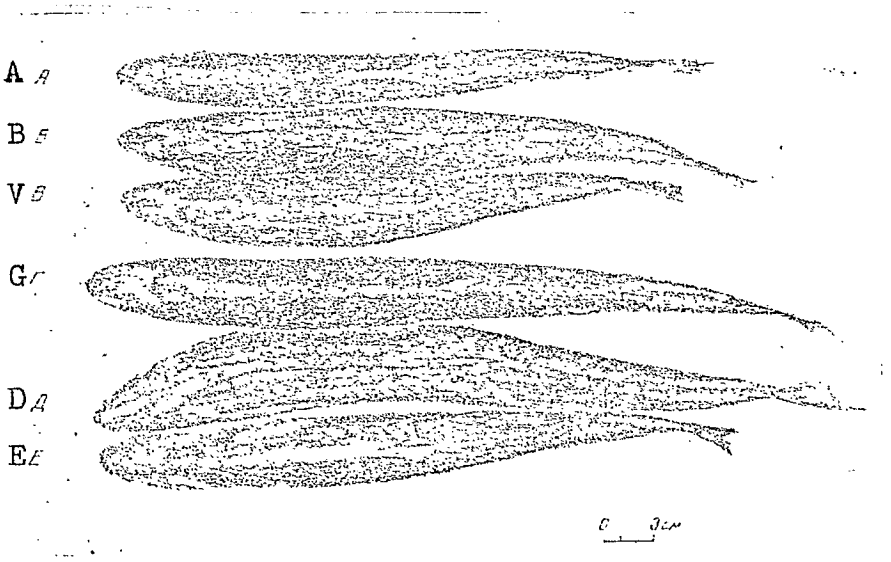

Рис. 5. Гольцы длиной 33—39 см (вид сверху)

А — проходной голец (самец II стадии, 3.IX 1955 г.); *Б* — озерный лаврентьевский (самец II стадии, 13.IX 1955 г.); *В* — эстихетский (самка IV стадии, 10. VIII, 1955 г.); *Г, Д* и *Е* — те же гольцы, что на рис. 3

Figure 5. Char 33 - 39 cm in length (dorsal view)

A - sea-run char (stage II male, 3 September 1955); B - Lavrentiyan lake char (stage II male, 13 September 1955); V - Estikhet char (stage IV female, 10 August 1955); G, D and E - the same char as in Figure 3.

The sea-run and the lake char from Lavrentiya Bay are similar in their coloration: their sides are silvery, the back and upper part of the head are greenish (in the sea-run char) or grey with a brown tinge (in the lake char). After fixation there appear on the sides indistinct dark transverse bands, and there become clearly evident the white spots on the back and sides; all of this, in the Lavrentiya Bay forms, is expressed in a somewhat more pronounced fashion in the sea-run char than in the lake char. In the Estikhet lake char, however, the transverse bands are even more pronouncedly expressed; moreover, in many of the individuals the back is covered with discrete dark spots which are larger than the eyes in their

size (in fixed individuals; the coloration of the living individuals was not observed). However, on the basis of the degree of maturity of the gonads, with which changes in coloration of char are closely associated, the Estikhet char are clearly differentiated from the sea-run char and from the lake char from Lavrentiya Bay (see below).

The meristic characteristics and measurements of the studied forms of char are presented in Table 1.

Thus, all three groups of char are well differentiated from one another. If all of the char are mixed together, they may be sorted out anew without error on the basis of the form of the body and the coloration [1]. Nevertheless, there are no adequate grounds for considering these mentioned groups to be distinct species. In almost all of the features they are connected by gradual transitions, and with an increase in the number of observations they may also prove to be connected in the remaining features.

The char from Lake Estikhet were separated out into a distinct species by L. S. Berg (1948a) on the basis of the small number of gill rakers (14) in the specimen, No. 31 107 (Collection of the Zoological Institute of the Academy of Sciences of the USSR), which he studied. However, when this specimen was checked there were found 19 rakers on the right first arch and 21 on the left arch. In general, therefore,

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[1] It is obvious that sea-run char were absent from the studied lakes beside Lavrentiya Bay. They were not found here because of the small number of observations, or because they move into these lakes at a different time, or because they never enter these lakes; this question remains open.

Table 1.

Meristic and plastic features of the studied forms of char

Таблица 1

Счетные и пластические признаки исследованных форм гольцов

	Indices Показатели и признаки and features	A Залив Лаврентия у пос. Пинакуль B проходные гольцы	C озерные гольцы	D Озеро Эстихет, озерные гольцы
	Дата . Date	3—7.IX 1955	13—16.IX 1955	10.VIII 1955
	Глубина, м . Depth, m	0,5—3	1—2	1—2
	Половой состав	10 ♀♀ II	7 ♀♀ III	3 ♀♀ II-III, 5
	Make-up by sex	4 ♂♂ II	7 ♂♂ II	♀♀ IV, 2 ♂♂ II, 4 ♂♂ IV, V, VI
a	Лучей в спинном плавнике	III—IV—11—12 (15,8)	III—IV 11—12 (16,0)	IV—V11—12 (16,3)
b	Лучей в анальном плавнике	III—V 9—11 (14,3)	III—V 9—11 (15,0)	IV—V 10—11(15,3)
c	Лучей в хвостовом плавнике	44—50 (47,0)	44—50 (47,2)	43—52 (48,4)
d	Позвонков	67—69 (67,6)	67—70 (68,9)	67—69 (67,8)
e	Жаберных тычинок	21—25 (23,4)	20—25 (23,1)	19—29 (23,7)
f	Жаберных лучей	10—13 (11,3)	10—13 (11,2)	9—12 (10,6)
g	Зубов на basibranchiale . .	6—11 (8,5)	7—16 (10,3)	7—16 (10,8)
h	Пилорических придатков	22—31 (26,4)	40—54 (46,6)	30—48 (36,6)
i	Длина головы, % длины тела			
	самки ♀♀	17,3—19,5 (18,3)	18,3—22,1 (19,4)	18,1—19,5 (18,9)
	самцы ♂♂	18,7—20,4 (19,7)	19,2—21,2 (20,0)	19,5—22,1 (20,3)
j	Высота головы через затылок	11,0—13,8 (12,2)	11,3—14,7 (12,4)	11,3—13,2 (12,1)
k	Наибольшая высота тела	16,5—19,4 (17,9)	15,2—17,6 (16,5)	16,1—18,7 (17,8)
l	Высота хвостового стебля	6,1—7,1 (6,6)	5,8—6,8 (6,2)	6,5—7,5 (7,0)
m	Толщина головы в области praeoperculum	8,4—9,4 (8,9)	8,4—10,0 (9,2)	9,3—11,0 (9,9)
n	Толщина тела у начала D	8,0—10,4 (9,0)	10,3—11,9 (11,0)	11,3—13,6 (12,5)
o	Антевентральное расстояние	42,5—46,6 (44,2)	43,8—52,6 (48,7)	47,0—50,9 (48,9)
p	Длина верхней челюсти, % длины головы			
	самки ♀♀	44,5—52,0 (46,5)	44,9—48,0 (46,4)	44,1—48,8 (46,5)
	самцы ♂♂	45,4—52,0 (49,2)	44,7—50,9 (47,5)	43,9—54,0 (46,9)
q	Длина рыла			
	самки ♀♀	25,7—31,2 (28,6)	27,0—29,2 (28,3)	27,1—29,7 (28,4)
	самцы ♂♂	28,5—32,1 (30,7)	27,7—30,6 (29,3)	25,9—31,1 (28,4)

A - Lavrentiya Bay near the settlement of Pinakul'
B - sea-run char, C - lake char.
D - Lake Estikhet, lake char.

a - Rays in dorsal fin
b - Rays in anal fin
c - Rays in caudal fin
d - Vertebrae
e - Gill rakers
f - Branchiostegal rays
g - Teeth on basibranchiale
h - Pyloric caeca
i - Length of head, as % of body length
j - Depth of head through occiput
k - Greatest depth of body
l - Depth of caudal peduncle
m - Thickness of head in region of praeoperculum
n - Thickness of body at the origin of D
o - Anteventral distance
p - Length of upper jaw, as % of length of head
q - Length of snout

Note (to Table 1). In parentheses - arithmetical mean. The anterior ray of the dorsal fin on the X-ray photographs is sometimes visible only as a dot. This occurs especially frequently when there are counted five unbranched rays. At times the last unbranched ray is indistinctly differentiated from the branched rays. The bases of the two last, smallest, branched rays are always set more closely together than are the bases of the other branched rays. These two rays were considered as one, as has been generally accepted (Hubbs and Lagler, 1949; Oliva, 1950, and others). The anterior, and sometimes also the following, pterygiophore of the dorsal fin is shorter than the others, and is more weakly ossified. It is possible that it is composed of two-three pterygiophores that have fused with one another. The anterior pterygiophores, in contrast to the posterior pterygiophores, do not have a supplementary element extending to the neighbouring ray. Such an element always extends towards the posteriormost doubled rays, although the basic element under the latter is generally reduced. In front of the dorsal fin there are 15 - 18 pterygiophores that do not bear rays. The anterior of these are very weakly ossified and are poorly evident. Generally they become clearly evident only beginning with the third spinous process, and very rarely - with the first. All that has been said concerning the rays and pterygiophores of the dorsal fin refers also to the anal fin, although, of course, there are no pterygiophores that do not bear rays in front of the anal fin. A fusion of vertebrae was found only in two of the Estikhet char. In one of these the fifth and sixth vertebrae from the tail (counting the urostyle, as was also done during the counting of the total number of vertebrae) were each composed of two fused vertebrae; in the second specimen the 24th vertebra was composed of seven fused vertebrae. If the fused vertebrae are counted as one, then in the Estikhet char there would be 63 - 69, with an average of 67.2 vertebrae.

as was shown above, the Estikhet char was found to be very similar, with regards to the number of gill rakers, to the sea-run S. malma. An error in the counting of the gill rakers or a slip of the pen[1] induced L. S. Berg to place the Estikhet char in a close relationship with S. leucomaenis. There are no other grounds for making such a close relationship. The coloration of the Estikhet char in no way resembles the coloration of S. leucomaenis. In the latter the sides and back, and sometimes also the upper part of the head, are covered with distinct large light-coloured spots which are larger than the eyes. In the Estikhet char, however, the light-coloured spots on the back and on the sides are smaller than the eyes and are weakly evident.

The juvenile char from Lake Achchen, studied by A. G. Kaganovskii (1955) and described by him as S. taranetzi Kaganowsky, most probably belongs to a landlocked form of char, similar to the Estikhet char, since it very closely resembles the latter, both as to the number of the pyloric caeca (32 - 42) as well as the coloration. In three specimens of S. taranetzi 15.3 - 21.1 cm in length[2], preserved in the collections of the Zoological Institute of the Academy of Sciences of the USSR, the following counts were made from the X-ray photographs: D IV-IV 11 - 11, A III-III 10 - 10, 68 vertebrae. On the basis of the mentioned features, and also on the basis of the number of gill rakers, these specimens in no way differ from

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[1] Possibly, the number 19 was written down by L. S. Berg in such a way that it was read by him as 14.

[2] These lengths are somewhat less than those cited by A. G. Kaganovskii for the reason mentioned at the beginning of this paper.

the other forms of the malma* that I studied. It is true that the body in these specimens was markedly less deep and also thinner than in the adult Estikhet char, the anteventral distance was somewhat smaller, the head slightly longer, the notch in the caudal fin was larger, the length of the upper jaw (42.6 - 45.3% of the length of the head when measured from the end of the snout to the posterior end of the maxillary bone) and the length of the snout (as a % of the length of the head) were smaller. All of these differences, however, may well be a consequence only of aging variability. Thus, the separation of the char from Lake Achchen into a distinct species is premature.

At the present time the systematics of the genus Salvelinus is in such a state that it is fairly difficult to determine the systematic position of the above-mentioned forms of char. In the first place there arises the question of the independence of the species S. malma, to which there belong both the sea-run char from Lavrentiya Bay, as well as, to all appearances, also the lake char from the vicinity of this bay and from Lake Estikhet and Lake Achchen.

An analysis of the literature data, our collections and a survey of the specimens of S. alpinus and S. malma in the collections of the of the Zoological Institute of the Academy of Sciences of the USSR have led us to the following conclusions: 1) there is found a very large intraspecific individual variability, and in some features also an age, sex and seasonal variability, within both species; 2) this variability in both species is so similar that they should not be

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* Translator's note. For the sake of consistency the Russian vernacular name "malma" is retained here, rather than translating this as "Dolly Varden".

considered as distinct species (Table 2). This same opinion was held previously by L. S. Berg (1916) and by other authors (Soldatov, 1932; Pravdin, 1928; Lindberg and Dulkeit, 1929). Later L. S. Berg (1932) began to consider the malma as a distinct species; however, the diagnosis of the species in the 1932 and 1948 editions of this work by L. S. Berg is essentially in no way different from the diagnosis of the subspecies in the 1916 edition.

The question of the independence of the subspecies S. alpinus alpinus and S. alpinus malma requires further elaboration, namely a checking of their distinguishing features on a large number of individuals from different parts of the distribution range of both of the subspecies. Without such a check it is not possible to determine the boundaries of the contiguity of their distribution ranges. Moreover, without such a check it is not possible to make any statement as to whether S. malma is a synonym, subspecies or group of subspecies of S. alpinus. 11

This question is inseparably associated with the elaboration of the systematics of the entire genus as a whole.

Investigators who have been involved with the char of the Alps, Scandinavia and also of Lake Ladoga and Lake Onega (Fries et al., 1895; Buresch, 1925; Andersson, 1942, and others) have noted the very strong variability of the coloration and form of the body in S. alpinus[1], in particular they

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[1] Large variation on the coloration and form of the body is also found in S. fontinalis. It is known that S. fontinalis reared in a deep still pond has a short deep body; in a shallow rapid stream - a long thin body; on a dark silty bottom in a shaded place - dark, deep tones of coloration; on a light-coloured bottom, covered with gravel - light-coloured, delicate tones (Livingstone-Stone, cited by Day, 1887).

Table 2.

A comparison of the characteristics of the char Salvelinus alpinus and S. malma.

Characteristic	S. alpinus	S. malma
Upper jaw	1. In juveniles and poorly grown forms it does not extend past the posterior margin of the eye, in old individuals it extends past this.	1. The same, although it generally extends somewhat further past the posterior margin of the eye.
	2. Wider in the lake forms than in the sea-run forms.	2. The same, although on average it is only slightly narrower in the sea-run forms.
	3. In the adults on the upper jaw there is a protuberance which fits into a depression on the lower jaw; during the spawning period this protrusion in the males is reinforced by a fatty outgrowth (in the sea-run forms).	3. The same, although the outgrowth in the males of the sea-run forms is possibly developed somewhat more strongly.
Coloration	1. In the sea the back and the upper part of the head are bluish or greenish, the sides and venter are silvery, on the back and sides there are weakly evident light-coloured spots, which are larger below the lateral line than above the latter.	1. The same, although the spots on the back are apparently somewhat more numerous.
	2. In lakes in the coloration of the back and the upper part of the head there predominate brown or grey tones of varying intensity, often spreading also onto the sides; venter sometimes goldenish.	2. The same.

Table 2 (continued)

Characteristic	S. alpinus	S. malma
	3. During spawning the light-coloured spots on the sides, and also the venter, the pectoral, pelvic and anal fins acquire a red or orange colour, which is often more intensive in the males than in the females; the anterior margins of the fins remain light-coloured. The vividness of the spawning coloration and the duration of its retention vary considerably.	3. The same.
	4. Juveniles and poorly-grown forms bear 13 - 15 dark transverse bands on their sides; the back is sometimes covered with large dark spots.	4. The same.
Number of vertebrae	58 - 65	59 - 70
Number of rays in dorsal fin	III-IV 8-12	III-V 9-12
Number of rays in anal fin	III-V 7-10	III-V 7-11
Number of rays in pectoral fin	I 11-14(15)	I 11-14
Number of rays in pelvic fin	I(II) 7-8(9)	I 7-8(9)

Table 2 (concluded)

Characteristic	S. alpinus	S. malma
Number of transverse rows of scales	190 - 280	232 - 270
Number of gill rakers	16 - 32, on average 23 - 29	16 - 33, on average 23 - 29
Number of branchiostegal rays	(9)10 - 12(13)(14)	(9)10 - 12(13)
Pyloric caeca	28 - 62	22 - 54
Maximal length, cm	88	74
Diameter of eggs, mm	4.0 - 5.5	3.7 - 5.5

N o t e . In composing this table we made use of our own observations and studies by other authors (Krasheninnikov, 1786; Pallas, 1811; Kessler, 1864; Varpakhovskii, 1899; Shmidt, 1904; Berg, 1909, 1909a, 1948, 1949; Isachenko, 1912; Soldatov, 1923; Pravdin, 1928; Lindberg and Dulkeit, 1929; Lindberg and Taranets, 1929; Probatov, 1934; Esipov, 1935; Tarants, 1933, 1936; Rudakova, 1941; Mukhomediarov, 1942; Heckel and Kner, 1858; Seeley, 1886; Day, 1887; Fatio, 1890; Fries, Exström and Sundevall, 1895; Jordan and Evermann, 1896; Bade, 1901; Evermann and Goldsborough, 1907; Vogt and Hofer, 1909; Dahl, 1929; Buresch, 1925; Steinmann, 1936; Andersson, 1942; Oliva, 1951; Needham and Vaughan, 1952; Sprules, 1952; Grainger, 1953; Walters, 1953, 1953a). In S. malma the eggs were measured after fixation in alcohol.

noted that the body form ranged from flattened, as in the herring, to cylindrical, as in the eel. Naturally, variation is also found in the form and comparative dimensions of different parts of the body: the snout, jaws, eyes, opercula fins etc. (Day, 1887, and others). Variant forms, differing with respect to the form of the body and the coloration, are found both in different lakes as well as within one and the same lake. Commencing from the end of the 19th century, all of these variant forms have been included, on adequate grounds, in one and the same species, S. alpinus, which also includes the sea-run form, although previously they were described under various species names: Salmo salvelinus L., S. umbla L., S. alpinus L., S. salmarinus L., S. rutilus Nilsson, S. carbo- 12
narius Strönn, S. schrankii Fitzinger, S. monostrictus Heckel et Kner, S. distichus Heckel, S. ventricosus Nilsson, S. salvelino-stagnalis Smitt, S. lepechini Gmelin, S. autumnalis Pallas etc. To this same species Salvelinus alpinus belong the sea-run and lake char of Iceland, which were previously referred (in part) to Salmo nivalis Günther (Seeley, 1886; Oliva, 1951); the char of Spitzbergen, previously S. stagnalis (Fabr.); the sea-run char of the whole of the Arctic coast of Eurasia and North America; and the char from Lake Baikal, previously S. erythrinus Georgi (Berg, 1948). It is true that according to L. S. Berg (1948) the European lake char, with the exception of those from the lakes of Swedish Lapland, represent the distinct species Salvelinus lepechini, which is differentiated from the sea-run S. alpinus. Commencing in 1932 L. S. Berg recognized the independence of the species S.

lepechini; however, subsequent authors (Steinmann, 1936; Andersson, 1942, and others) quite rightly do not agree with this. According to L. S. Berg, S. lepechini is differentiated from S. alpinus var. salvelinus (Berg, 1916) by the convex forehead and the tapered lower jaw. However, a forehead that is just as convex and a lower jaw that is just as tapered may be encountered also in the sea-run char (in particular, from Lavrentiya Bay). Thus, in Europe initially there were described many species of char, but during the course of the process of the study of these they were fused into one species, which includes within it also the Spitzbergen and the Baikal char.

Nevertheless, as late as 1911 Regan (1909, 1911) considered that the lakes of Great Britain and Ireland were inhabited by many species of char. These species were described on the basis of differences which were, in essence, of the same order as of the European char, without due consideration to age and other variability, sometimes from very scanty material. To this group belong: Salvelinus killinensis (Günther), S. struanensis (Gibson-Maitland), S. willoughbii (Günther), S. perisii (Günther), S. gracillimus Regan, S. inframundus Regan, S. maxillaris Regan, S. mallochii Regan and S. lonsdalii Regan from lakes in Great Britain; S. colii (Günther), S. grayi (Günther), S. trevelyani Regan, S. fimbriatus Regan, S. scharfii Regan and S. obtusus Regan from lakes in Ireland. While describing a multitude of new species of char, Regan also retained Günther's species, in spite of the fact that long before Regan there already began to be expressed

doubts concerning the reality of these species (Kessler, 1864) and later all of these species, as well as S. struanensis (Gibson-Maitland), were united, with full justification, into one species in common with the European species (Day, 1887). Subsequently Huxley (1944), referring to Regan (1926) himself, combined with the European species all of the other species described by Regan, though he left these with the rank of subspecies.

A similar process of amalgamation of previously described species of char has also started in North America.

In North America the following species have been described: S. nitidus (Richardson), S. alipes (Richardson), S. oquassa Girard, S. aureolus Bean, S. parkei (Suckley), S. alpinus (Linné), S. malma (Walbaum), S. fontinalis (Mitchill) and S. namaycush (Walbaum). S. nitidus is generally not mentioned by contemporary authors. S. alipes was reduced to synonymy with S. alpinus by L. S. Berg (1948). Jordan and Evermann (1896) questioned whether S. oquassa was a distinct species or whether this was rather only a subspecies of S. alpinus. S. parkey (Suckley) was initially recognized by Jordan and Evermann as a species, but later Jordan and Gilbert (1899) recognized this only as a subspecies of S. malma and, finally, L. S. Berg (1948) definitively reduced S. parkey to synonymy with S. malma. As was shown above, S. malma and S. alpinus represent one and the same species. Morton and Miller (1954) are apparently also prepared to cast doubt on the validity of S. aureolus as a species. The differences between all of these species (excepting S. fontinalis and S. namaycush), judging by

their descriptions (Richardson, 1836; Bean, 1887, and others), 13
have the same character as those between the European forms of S. alpinus.

Similar differences served as the basis for the description of numerous species of char from the lakes of Siberia and the Far East, among which there was not to be found even one species in common with the char of Europe and North America. Without taking into consideration the sea-run S. alpinus and S. malma, there have been described: S. drjagini Logaschev (lakes in the basins of the Yenisey and Pyasina rivers), S. taimyricus Michin (Lake Taimyr), S. boganidae Berg (Lake Boganidskoe in the basin of the Khatanga river), S. tolmachoffi Berg (lake Esei in the basin of the same river), S. jacuticus Borisov (lake in the delta of the Lena river), S. czerskii Drjagin (lakes in the basins of the Indigirka and Chukoch'ye rivers), S. neiva Taranetz (mountain lakes in the basin of the Okhota river), S. andriashevi Berg (Lake Estikhet) and S. taranetzi Kaganovsky (Lake Achchen, Chukotka). This list could be extended by separating out into a distinct species, on the same grounds, the char from the lakes in the vicinity of Lavrentiya Bay. However, as is quite obvious, a separating-out of a new species may have a reliable basis only in the case when, in a large number of individuals in different parts of the distribution range and during different periods, there is found a complex of morphological characteristics, without transitions, which differentiate these individuals from individuals of other species of the same age and sex, and, moreover, the differences should be irreversible. There are no such data, with

small exceptions, for any one of the described species of char, which makes it very difficult to identify the latter.

How real are the specific characteristics that have been established without due consideration to the different kinds of intraspecific variability is clearly illustrated by the following example (in addition to those presented above). In Lake Taimyr there live two forms of lake char (which is in no way a rarity also for European lakes): a rapidly-growing and a poorly-growing form. V. S. Mikhin (1955) described the latter as a new species, S. taimyricus, while he referred the former to S. drjagini. Conversely, A. V. Podlesnyi and A. A. Lobovikova (1951) assigned the poorly-growing form to S. drjagini, while for the rapidly-growing form they appropriated the specific name S. taimyricus. The above mentioned authors had proceeded along the same path as has Günther, Regan and L. S. Berg, along the path which was well characterized by Regan himself (1926, p. 75): "Once you begin giving specific names to lacustrine forms of char you never know where to stop".

The confused systematics of this genus has naturally given rise to some doubt: is not the genus Salvelinus represented by only a very few, though plastic species? Dymond and Vladykov (1934), Walters (1955) and some other authors have apparently correctly amalgamated many species and subspecies of char into the S. alpinus group, distinguishing only S. fontinalis and S. namaycush. Here also one may add S. leucomaenis. Only for these species is it possible to gain a firm grasp of characteristics, without transitions, which differentiate one species from another. Individuals of all four species are

are encountered in the sea, in rivers and in lakes, but of these S. alpinus is the most eurybiontic. S. leucomaenis is predominantly a sea-run form, S. fontinalis is predominantly a river form, while S. namaycush is predominantly a lake form.

However, S. leucomaenis and S. fontinalis are differentiated without transitions from S. alpinus only by certain features of the coloration, in so far as may be judged by the studies on char that were utilized by me. These features in S. leucomaenis are the large, densely situated, white spots on the back and sides, while in S. fontinalis they are the distinct dark spots on the dorsal and caudal fins. Nevertheless, in the coloration of S. fontinalis, especially of the spawning form, and also during the sojourn of this species in the sea (Bigelow and Schroeder, 1953) there are very many features in common with S. alpinus. How closely related these species are 14
is evident also from the fact that fertile progeny are obtained when they are crossed. In the first generation the hybrids have mixed characteristics, in the second generation there occurs the usual segregation of these characteristics (Vogt and Hofer, 1909; Buresch, 1925), so that there is no need to invoke matrocliny here. It remains only to demonstrate that S. fontinalis is only a race of S. alpinus. The similarity between them is manifested also in the behaviour: the methods of burying the spawned eggs by the females of S. fontinalis and of the sea-run S. alpinus malma are the same (Needham and Vaughan, 1952). The possibility cannot be excluded that S. leucomaenis is also only a peculiar race of S. alpinus malma (Jordan and Hubbs, 1925).

As to S. namaycush, this species is differentiated, without transitional forms, from the others not only by the coloration but also by the number of pyloric caeca (95 - 170, averaging 126.7), and also, apparently, by other characteristics. It is significant that the crossing of this species with S. fontinalis is difficult to achieve: only the first generation of the hybrids are fertile (and even as to this there is some question) and only when the eggs of S. namaycush are fertilized by the sperm of S. fontinalis but not with the reciprocal crossing. Besides the large number of pyloric caeca, S. namaycush is also differentiated by its backwardly displaced dorsal fin (obviously, the pelvic and anal fins are also displaced), by the greater depth of the notch in the caudal fin and by the larger number of teeth, particularly on the basibranchiale (Morton and Miller, 1954), i.e. by those same features which differentiate the lacustrine forms of S. alpinus from the sea-run forms, although these features are more clearly expressed. Further study will probably considerably increase the list of these features; however, the basic task should be the elucidation of their adaptive significance and of the essential nature of the threshold which determines the isolation of the species.

The great diversity of forms of char makes the genus Salvelinus a very interesting subject for profound and protracted study. Let us start with the fact that the freshwater forms of char live in bodies of water that are scattered throughout almost the whole of the Holarctic and which are located both within and outside of the distribution range of the sea-run forms. Moreover, some of these bodies of water, that are

inhabited by the char, have retained their connection with the sea, others have lost this connection recently, while a third group lost this connection a long time ago. There is no doubt that the origins of the freshwater forms of char are very diverse from the temporal aspect, from those that were formed only very recently[1] to those that were isolated over the course of a period which may be measured on the geological scale. A comparison of these forms is particularly interesting. A. N. Probatov (1946), who attempted such a comparison, completely neglected the considerable subjectivity in the application of the systematic categories. It was shown above that the lacustrine forms of the Alpine char, that were separated a long time ago from the sea-run form, are nevertheless united within a single species together with the latter, while the char from the lakes of Siberia and the Far East, which live alongside and sometimes even together with the sea-run char, are divided up into many species, although they are scarcely more differentiated from one another than are the Alpine char, judging by the literature (Lepekhin, 1780; Berg, 1926, 1948; Petrov, 1926; Suvorov, 1927; Borisov, 1932; Smirnov, 1933; Zabolotskii, 1936; Krokhin, 1936; Ostroumov, 1937; Pallon, 1929; Belykh, 1940; Logashev, 1940; Kirillov, 1955, and previously cited authors). At the present time we do not yet have sufficient material, at least on the char of Siberia and the Far East, for a proper comparison of all of these forms.

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[1] Sea-run char easily become transformed into the landlocked form, evidently because of the fact that in the sea they maintain themselves in areas that have a fairly considerable inflow of freshwater (Pirozhnikov, 1949).

Thus, the attempt to determine the systematic position of the char from Lavrentiya Bay and from Lake Estikhet leads us to the following conclusions:

1. The char from Lake Estikhet do not represent the distinct species Salvelinus andriashevi Berg, with a close relationship to S. leucomaenis, as was considered previously. All of the char that were studied by us, sea-run and lake forms, belong to one and the same species, S. malma (Walbaum). To this same species, judging from all appearances, also belong the char from Lake Achchen, which were described as S. taranetzi Kaganowsky. In turn, the species S. malma is no more than a subspecies (group of subspecies, synonym?) of S. alpinus. 15

2. The very large intraspecific variability of char initially led to the description of very many species of char. Later, when this variability began to be taken into consideration, there began the process of of the amalgamation of the mentioned species, which process has evidently not yet been completed up to the present time (with the exception of Europe). At the present time one may speak with confidence only of the reality of the species S. alpinus and S. namaycush, with some doubt - of the reality of S. leucomaensis and S. fontinalis, and with considerable doubt - of the reality of all of the other species of char.

3. The data on char that are available at the present time are all the more inadequate for reaching any reliable judgement as to the reality of systematic units of an intraspecific order. The meagre coverage of studies of the individual, age, sex and seasonal variability of each of the forms

considered separately prevents one from distinguishing the subspecific, racial and suchlike variability. It is therefore better at the present time to refrain from separating out the above-described Chukchi char into particular systematic categories.

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