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Systematic Position of the Lake Trout, *Salvelinus namaycush*

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IT has been recently proposed (Miller, 1950: 2) that *Cristivomer* again be regarded as a synonym of *Salvelinus*, and hence that the name of this distinctly American lake char[1], more commonly known as the lake trout, should revert to *Salvelinus namaycush* (Walbaum). This name was in use for some time prior to 1878 and was revived five years later (Jordan and Gilbert, 1883: 317). Following the recent proposal, the name *Salvelinus* [= *Cristivomer*] *namaycush* has been used by certain American ichthyologists (Hile, Eschmeyer, and Lunger, 1951: 77; Royce, 1951: 59; Lagler, 1952: 24; Legendre, 1952: 17; and Fry, 1953). The senior author has been collecting morphometric and meristic data on American salmonids (especially on chars) over the past decade and offers some of this material in support of the recent trend. Arguments for the generic recognition of

[1] Although the editors of COPEIA have agreed to follow vernacular names adopted by the American Fisheries Society, one of us (W. M. M.) has prepared a treatise on the use of the word "char" which strongly supports the spelling "charr," preferred by him.

Cristivomer, lately proposed by Stokell (1951: 213–4), are discussed below.

Cristivomer Gill and Jordan, 1878

Cristivomer Gill and Jordan, in Jordan and Brayton (1878: 89). *Nomen nudum.*

Cristivomer Gill and Jordan, in Jordan (1878a: 356, 359). Listed and diagnosed. Two species (*namaycush* and *siscowet*) included; synonymy given; no type designated.

Cristivomer Gill and Jordan, in Jordan (1878b: 430). Additional synonymy.

Cristivomer Gill and Jordan 1878, in Jordan and Gilbert[2] (1883: 317–8). Diagnosed as subgenus of *Salvelinus* with type species (*Salmo namaycush* Walbaum) designated in footnote. *S. namaycush* described, synonymy given, and *siscowet* included as variety. Jordan (1878a) cited as original publication source, with *Cristivomer* credited to Gill and Jordan.

The proposal to synonymize *Cristivomer* with *Salvelinus* has been developing for a long time. Since 1880, ichthyologists who have mentioned this species have frequently expressed some degree of doubt as to its taxonomy. We cannot state the problem any more clearly or concisely than was done thirty-five years ago by William Converse Kendall (1919: 78–80) when he wrote:

> The generic name for the lake trout has undergone several changes since Walbaum in 1794 designated the species as *Salmo namaycush*. After the generic name *Salvelinus* for the char had been generally recognized, the lake trout being regarded as a char, was for some time, by American authorities at least, called *Salvelinus namaycush*.
>
> In 1878 Gill and Jordan bestowed upon it the generic name, *Cristivomer*. The character which distinguished the genus from *Salvelinus* was stated to be a raised crest behind the head of the vomer and free from its shaft, the crest being armed with teeth.
>
> In 1914 C. Tate Regan, of the British Museum, indicated that *Salvelinus fontinalis* possessed a backward extension of the head of the vomer, and in form and dentition was intermediate between a British char and the lake trout. For this reason he considered it advisable to give up the generic name *Cristivomer*. In the same year, in a paper which was in press at the time Regan's conclusion was published, the present writer [Kendall, 1914: 10–11] had stated a like conclusion based, however, on somewhat different characters of the vomers. He had found that some vomers of *Salvelinus stagnalis* from Labrador and *S. aureolus* from Floods Pond, Maine, could not be distinguished from the typical vomer of the lake trout, thus appearing intermediate between *S. fontinalis* and the lake trout. In the addenda to the same publication, however, attention was called to the discrepancy between Regan's and the present writer's observations, and the suggestion offered that neither char possessing lake trout-like vomers was intermediate between the lake trout and the other, but each independently derived from the ancestral form.
>
> Apparently both Regan and the present writer thought they had discovered something new concerning char vomers, but 26 years prior to our publications F. A. Smitt [1886] called attention to a similar situation, citing a specimen from Spitzbergen and one from Greenland which presented vomerine characters similar to *Cristivomer namaycush*. However, Smitt did not recognize even the genus *Salvelinus*. In fact his genus *Salmo* was the same as the subfamily Salmoninae of most recent ichthyologists.
>
> Inasmuch as the *Cristivomer* form of vomer is exceptional rather than the rule in the other chars, they may be regarded as vestigeal [sic]. However, the fact remains that the genera cannot always be distinguished by the character of the vomer.

In reversing his stand of 1914, Kendall in this paper held that differences in the morphometric proportions and direction of striae of the ethmoid bone justify the reestablishment of the genus *Cristivomer*. He presented proportional measurements from 3 or 4 ethmoids of each of four species of chars but of no other genera of the family.

A major factor in the retention of *Cristivomer* as a full genus has been that no comparative tabular or photographic evidence has been published that would permit one to compare *namaycush* objectively with other species of *Salvelinus*, especially with regard to the vomerine structures. It was the lack of such presentation in the many rehashed descriptions found in the huge general literature on salmonoids, and especially on chars, that inspired Morton to spend much time measuring, counting, and dissecting hundreds of specimens in order to obtain concrete comparative data on the better-known characters, or possibly to uncover some better ones. Results so far have impressed upon him chiefly that he has only scratched the surface of a very time-consuming problem. He has in preparation a revision of *Salvelinus*, and much of the data thus far obtained are utilized in the present account. In the section that follows, the best characters that have been used by others (or discovered in this study) to distinguish the lake trout from other chars are discussed in some detail.

The morphometric and meristic data included herein demonstrate that *S. alpinus* is intermediate between *S. namaycush* and the other American species considered. Such data further indicate that *S. alpinus* is a connecting link

[2] The date of publication of this volume is usually given as 1882, the year printed on the title page. However, as Jordan (1885: 789) pointed out, the volume was issued "about April 1, 1883." We are grateful to Carl L. Hubbs for this reference.

between typical lake-spawning chars, such as *namaycush*, and stream-spawning chars, such as *fontinalis*. Without access to more extensive series of the numerous Asiatic forms of *Salvelinus* (Berg, 1948: 269–95, figs. 156–171a), the comparisons cannot be considered exhaustive. The authors believe, however, that sufficient data are presented below to render a sound decision on the systematic status of the lake trout.

Differential Characters

Vomer.—The nature of the vomerine bone and of its dentition has been utilized as a major character for the generic recognition of *Cristivomer*. The character may be stated thus: vomer with a long, blade-like, raised crest extending backward from the head of the bone and free posteriorly from its shaft, the crest armed with a uniserial row of strong teeth. *Salvelinus* (*sensu stricto*), on the other hand, is generally credited with having the teeth confined to the head of the vomer (see Stokell, 1951: Figs. 2–3).

Table I

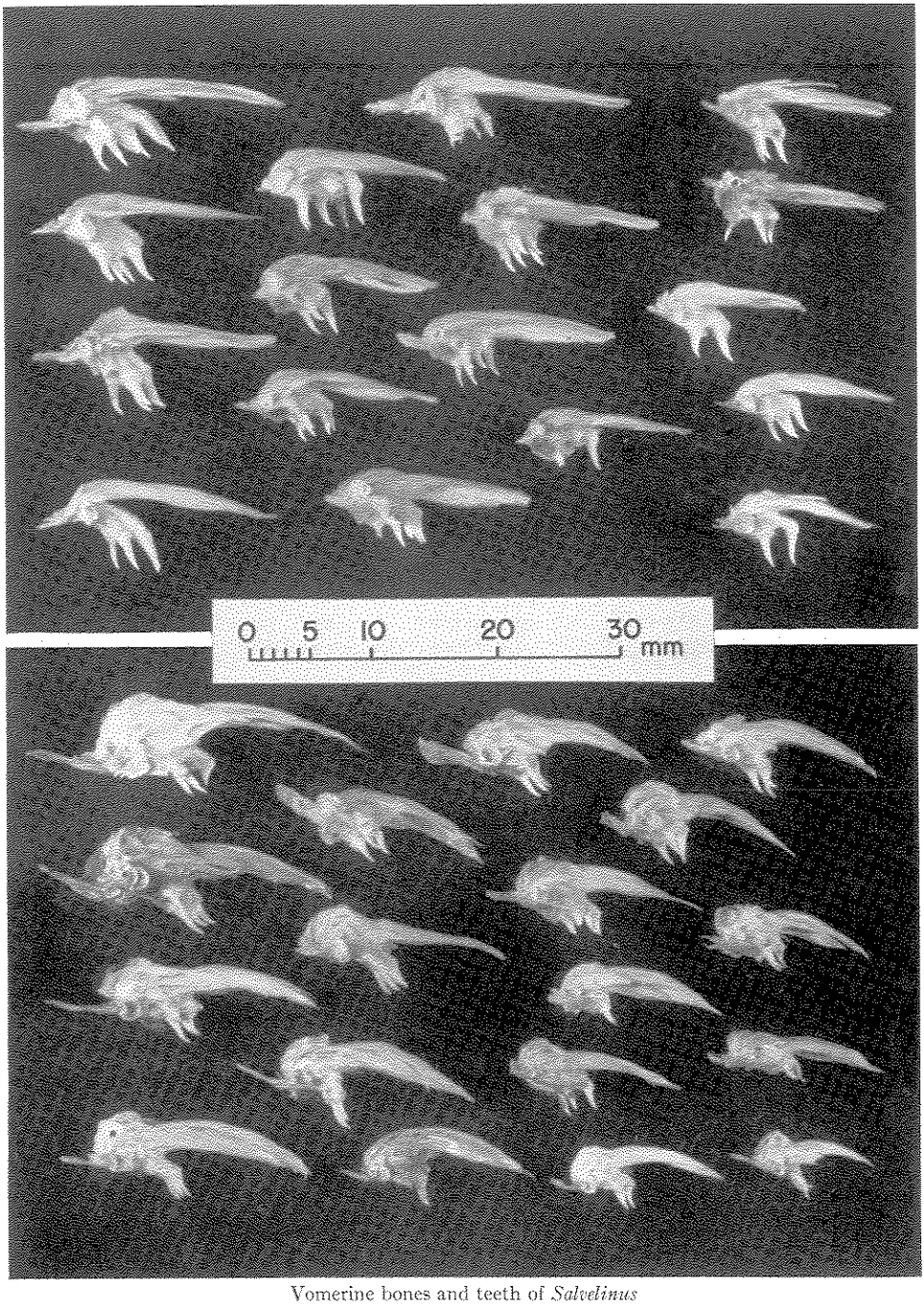
Number of Pyloric Caeca in American Chars (*Salvelinus*)

Number of caeca	Species			
	namaycush	*alpinus*	*fontinalis*	*malma*
16–20	..	..	..	1
21–25	..	..	6	33
26–30	..	1	12	50
31–35	..	5	13	24
36–40	..	11	11	6
41–45	..	12	4	
46–50	..	15	1	
51–55	..	12		
56–60	..	5		
61–65	..	1		
66–70	..			
71–75	..			
76–80	..			
81–85	..			
86–90	..			
91–95	2			
96–100	1			
101–105	2			
106–110	5			
111–115	4			
116–120	7			
121–125	8			
126–130	6			
131–135	3			
136–140	5			
141–145	3			
146–150	4			
151–155	..			
156–160	2			
161–165	1			
166–170	2			
Range.....	95–170	30–64	23–46	20–39
Specimens..	55	62	47	114
Mean.....	126.7	46.0	32.5	27.9

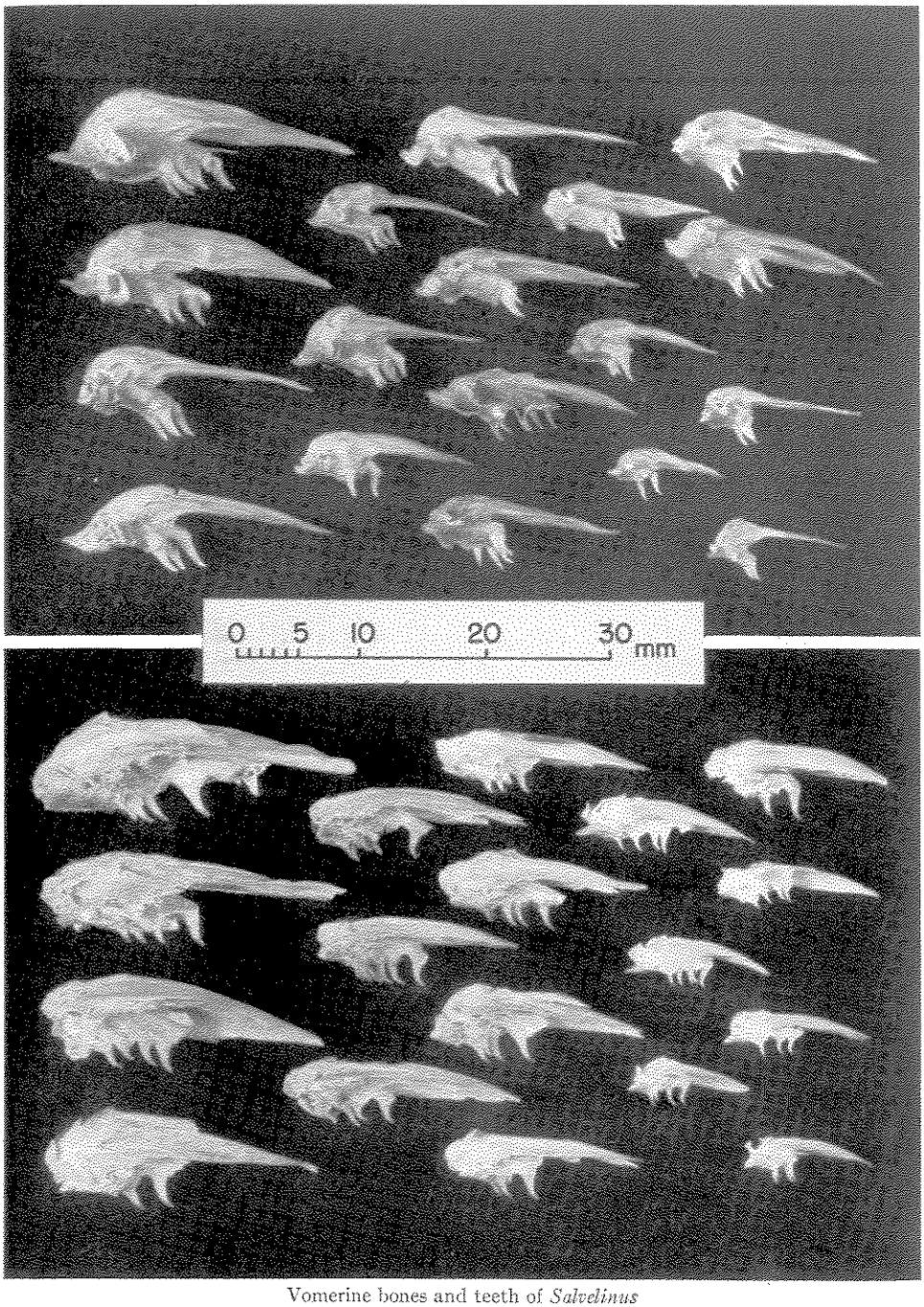
The vomers (Pls. I–II) of *Salvelinus fontinalis* (Mitchill), *S. malma* (Walbaum), *S. alpinus* (Linnaeus) and *S. namaycush* (Walbaum) were collected from various age groups to show the variations that may be encountered. It is noteworthy that the vomers vary considerably in shape, including, in other species, the "crested" form described as typical of *Cristivomer namaycush*. We recognize that the crested vomer tends to be better developed in *S. namaycush* than it is in other species of the genus *Salvelinus*, but the structure varies so much within the several species that its use for specific separation is much restricted (e. g., to distinguish *fontinalis* and *namaycush*).

Pyloric Caeca.—The lake trout may be distinguished from other species of *Salvelinus* by its more numerous pyloric caeca, which number 95–170 in contrast to fewer than 65 in *alpinus*, *fontinalis* and *malma* (Table I). This feature was noted in Goode (1887: 462), who wrote: " 'The lake trout', remarks Bean, '. . . seems to have no parallel in Europe and is well separated from American species by its peculiar vomer and its large number of pyloric caeca (about 150)'." This character is not often mentioned in the literature but we believe it is one of the most diagnostic for *namaycush*, for the lake trout seems to be approached in this character only by *alpinus*.

Basibranchial Teeth.—Jordan (1878a: 356) indicated that "a band of stout recurved teeth on the hyoid bone" is one of the stated characteristics of the genus *Cristivomer*. The teeth on the basibranchial bones (usually incorrectly called hyoid teeth) are numerous and multiserial in the lake trout and generally weaker and usually uniserial or biserial in the other species of *Salvelinus*. Partly on the basis of the nature of the basibranchial teeth, Regan (1914: 405) proposed to distinguish three groups of *Salvelinus*: the *alpinus* group, with uniserial dentition; the *fontinalis* group,



Vomerine bones and teeth of *Salvelinus*
Above: S. fontinalis from Kearneyville, West Virginia; January 15, 1942.
Below: S. malma from Karluk Lake, Alaska; summer, 1941.



Vomerine bones and teeth of *Salvelinus*

Above: S. alpinus from Karluk Lake, Alaska; summer, 1941.
Below: S. namaycush, juveniles, from Lake Michigan; 1942, 1946, and 1952.

without basibranchial teeth; and the *namaycush* group, with these teeth in a long patch.

Recently Stokell (1951: 213) has written that "The second character by which Regan [1914] proposed to separate his groups, namely, the hyoidal dentition, also fails in respect of *Salvelinus fontinalis*. It has been shown elsewhere (Stokell, 1940) that this species may or may not have teeth on the hyoid, and that when present these teeth are variable in number and degree of development. It is therefore impossible to separate *fontinalis* from other chars of the genus *Salvelinus*, and the proposed intermediate group must be abandoned. *Cristivomer*, however, has a multiserial arrangement of the hyoidal teeth and differs in this feature from all species of *Salvelinus* recorded." It was unfortunate that Stokell had not had the opportunity to examine specimens of *S. alpinus*. Our observations of the basibranchial teeth of chars, although not as extensive as desired, have shown that those of *alpinus* are intermediate between those of *malma* and of *namaycush*, and that the basibranchial teeth of *malma* bridge the gap between those of *fontinalis* and of *alpinus*. In more than a dozen American specimens of each of four species of *Salvelinus* examined by us independently, *namaycush* was invariably found to possess a multiserial arrangement of strong basibranchial teeth; *alpinus* had fewer rows of weaker teeth but definitely in two or more rows; in four of twenty specimens of *malma*, no basibranchial teeth could be found and in the remainder there were 1 to 14 usually rather weak teeth in a median or uniserial arrangement; and basibranchial teeth were lacking in all but two of forty-one specimens of *fontinalis*, each of which had a single tooth at the base of the second gill arch (Stokell, 1940, found as many as 1 to 7 teeth in this species). Similar variation in these teeth occurs in species of the genus *Salmo*.

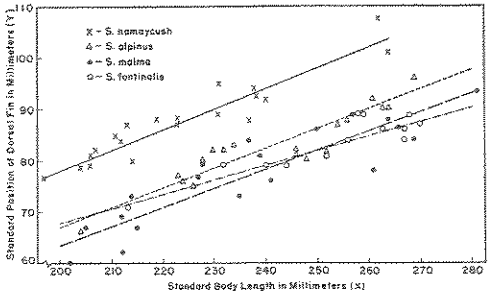


Fig. 1. The relationship between position of the dorsal fin and standard body length in four species of *Salvelinus*.

The regression formulae are as follows: $y = -0.3 + .394x$ (*namaycush*); $y = -9.2 + .381x$ (*alpinus*); $y = -9.1 + .365x$ (*malma*); and $y = 11.1 + .284x$ (*fontinalis*).

Dorsal Fin Position and Forking of Caudal Fin.—From several morphometric characters that specifically characterize *Salvelinus namaycush*, we have selected the position of the dorsal fin and the forking of the caudal fin as the most diagnostic and as perhaps the most practical and available characters to supplement the very distinctive color pattern for quick diagnosis in the field or laboratory. For convenience of tabulation, data from similar size groups were selected for plotting these characters (Figs. 1 and 2). The standard body length is the projected lineal

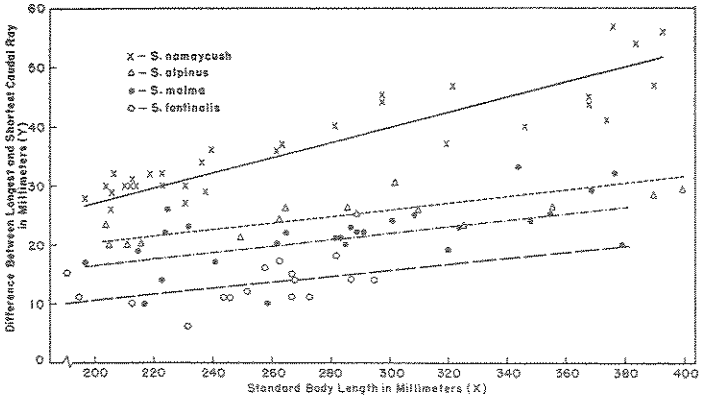


Fig. 2. The relationship between forking of the caudal fin and standard body length in four species of *Salvelinus*.

The regression formulae are as follows: $y = 1.7 + .127x$ (*namaycush*); $y = 10.1 + .053x$ (*alpinus*); $y = 4.5 + .060x$ (*malma*); and $y = 1.2 + .048x$ (*fontinalis*).

distance from the occiput to the posterior end of the caudal peduncle (DeLacy and Morton, 1943: 85). The standard fin position is the projected lineal distance from the occiput to the origin of the dorsal fin. No overlap is indicated between *namaycush* and any of the three other definitely valid species of American chars. In these characters also *alpinus* is intermediate between *namaycush* on the one hand and *malma* and *fontinalis* on the other.

SCALE COUNTS AND STRUCTURE.—Stokell's observations (1951: 214) of limited material led him to conclude that "All chars of the genera *Salvelinus* and *Cristivomer* that have come under the writer's observation have considerably more cross-rows of scales on the body than scales in the lateral line. The lateral line scales are not composed of hard, transparent material as are those on other parts of the body, but are almost cutaneous in character. They carry no circuli and are flexibly connected. The arrangement differs greatly from that in *Salmo* and *Oncorhynchus*, in which the lateral line scales number approximately the same as the cross-rows and are similar to those on the remainder of the body except that each carries a mucus tube."

Our independent comparative studies of the scales of *Salvelinus* and *Salmo* fail to confirm any fundamental difference in either scale structure or counts. Scales studied were removed from the anterior portion of the lateral line, below the origin of the dorsal fin. The species studied included *Salvelinus alpinus*, *S. aureolus*[3], *S. fontinalis*, *S. malma*, and *S. namaycush*; *Salmo clarki*, *S. gairdneri*, *S. rooseveltl*, *S. salar*, and *S. trutta*; and some of the American Pacific salmons of the genus *Oncorhynchus*.

The differences obtained by counting the scales in the lateral line and those above or below it have long been appreciated. This is why lateral-line scales have been seldom used to distinguish salmonids. Neave (1943) compared the methods and illustrated the differences between scale counts made on the lateral line and those along the oblique rows above the lateral line in three species of *Salmo*. Foerster and Pritchard (1935: 87–90) demonstrated the same thing for the five American species of *Oncorhynchus*. Our counts of *Salvelinus* and of specimens of *Salmo* not studied by Neave are summarized and combined with those of the above authors (Table II). Although very small scales have long been recognized as one of the general characteristics of the genus *Salvelinus*, a perusal of these tables demonstrates that similarly high counts occur in fine-scaled forms of *Salmo clarki* and in *Oncorhynchus gorbuscha*.

In scale structure, the American species of *Salvelinus* and *Salmo* form a rather evenly-graded series from the cutaneous, flexibly connected lateral-line scales of *Salvelinus namaycush* to the almost unmodified scales of *Salmo salar*. In contradistinction to Stokell's observations that the lateral-line scales of *Salvelinus* and *Cristivomer* lack circuli, we find weak to conspicuous circuli in the few specimens of the five species of *Salvelinus* studied by us (see also Cooper, 1951: Pls. I–II). The gradation in scale structure from a coarse-scaled type of *Salmo* into the fine-scaled forms of *Salvelinus* is indicated by the following approximate sequence, arranged from the least modified to the most specialized condition:

Salmo salar.
S. gairdneri kamloops, *S. g. whitehousei*.
S. clarki pleuriticus, *S. c. alpestris*, and *S. roosevelti*.
Salvelinus fontinalis.
S. alpinus, *S. aureolus*, and *S. malma*.
S. namaycush.

Those species listed together appear to be most nearly alike in details of squamation, with no broad gaps between the six groups. The scales of *Salvelinus fontinalis* bear similarities to both the extreme forms of *Salmo* and to the moderately specialized types of *Salvelinus*, thus bridging the gap between trouts and chars.

MANDIBULAR PORES.—The presence of well developed pores on the mandible in the lake trout and other chars was mentioned by Stokell (1951: 214, as mucus pits), who thought this feature was almost exclusive to *Salvelinus* and *Cristivomer*. Our observations indicate that these pores are probably most conspicuous and numerous in *S. namaycush* (8 to 11, usually 9 or 10) and less obvious in other chars (4 to 10, usually 7 or 8 in *fontinalis* and *malma*), but that they are developed also in *Salmo clarki* and *S. gairdneri* and in at least *Oncorhynchus nerka*. Thus the number and arrangement of the pores,

[3] We follow current nomenclature. The status of this form is to be treated elsewhere.

TABLE II

A COMPARISON OF CERTAIN SCALE COUNTS IN AMERICAN SALMONIDS

For each taxa is given the range, followed by the number of specimens in parentheses, and, below, the average value of the character

Salvelinus	Number of scales (original data)	
	In lateral line*	In oblique rows
namaycush	121–130 (19) 125	175–228 (30) 196
alpinus	111–130 (12) 122	154–236 (28) 195
fontinalis	109–127 (28) 115	197–236 (25) 218
malma	120–131 (18) 126	186–254 (31) 231

Oncorhynchus	Foerster & Pritchard (1935)		Present study	
	Lateral line	Oblique rows	Lateral line*	Oblique rows
gorbuscha	148–198 (254) 172	169–231 (195) 199	147–180 (3) 166	194–226 (8) 213
keta	124–153 (155) 136	130–153 (135) 139	129–139 (6) 133	137–145 (5) 141
tshawytscha	130–153 (133) 140	133–153 (110) 143	130–138 (9) 134	138–158 (47) 149
kisutch	121–138 (127) 129	118–147 (124) 131	123–132 (10) 128	133–145 (9) 138
nerka	124–138 (145) 131	124–144 (173) 133	122–135 (10) 129	130–146 (16) 138

Salmo	Neave (1943)		Present study	
	Lateral line	Oblique rows	Lateral line	Oblique rows
salar	....	....	106–113 (11) 111	111–118 (11) 115
trutta	105–116 (25) 112	116–136 (25) 125	107–117 (11) 112	120–131 (11) 125
gairdneri†	119–131 (122) 124	123–143 (122) 132	....	125–149 (8) 137
gairdneri‡	114–124 (61) 120	115–130 (61) 122	119–125 (11) 122	146–164 (11) 154
kamloops	121–130 (25) 126	130–155 (25) 143	128	148 ....
clarki§	116–133 (50) 123	146–177 (50) 160	120–129 (6) 122	157–170 (6) 165
clarki¶	116–126 (30) 120	122–154 (30) 137	116–126 (13) 119	180–208 (13) 191

* Sensory pores; approximately the same as the number of scales.
† Anadromous. Our specimens are from Clackamas River, Oregon.
‡ Non-anadromous. Our specimens (UMMZ 130642) are from Rush Creek, Modoc Co., California.
§ The cutthroat trout in the present study are from coastal streams of Oregon and Washington.
¶ Specimens used in our study are *S. c. pleuriticus*, from the Colorado River Basin.

like that of the scales, forms a graded series between chars and trouts.

HYBRIDIZATION.—Although natural hybrids between the lake trout and other chars seem not to have been reported, it has long been known that *S. namaycush* can be crossed with *S. fontinalis* (Bean, 1889: 16–7). Recent studies by Stenton (1950, 1952), have shown that the

fertility of the parents and the development of the hybrids vary with the sex of the parents. When the milt of *fontinalis* was used to fertilize the eggs of *namaycush*, results appeared to be those normal to a natural species; in the reciprocal cross, however, high mortality and many deformed hybrids resulted. The F_1 hybrids seem to be fertile and the sex ratio to be approximately normal, but many F_2 hybrids were abnormal. There is no evidence at this time (October, 1953) that the hybrid will maintain itself under natural conditions. It is clear that there is only a partial genetic barrier to crossing between these species and that this barrier alone would presumably not be sufficient to prevent the normal development of many hybrids, at least to the F_2 generation. Differences in spawning-site requirements and in habits are probably largely responsible for the failure of lake trout and brook trout to hybridize in nature.

Discussion

Although *S. namaycush* is distinctly different in several ways from other species of the genus *Salvelinus*, it shares the two prime characters that separate the chars from other salmonid genera, especially *Salmo*. These are: (1) the presence of light spots against a darker background, rather than dark spots against a lighter background (as in *Salmo* and *Oncorhynchus*); and (2) the boat-shaped vomer, with teeth on the head only or on a crest that is extended posteriorly but which is always free from the shaft or connected with it only by a thin septum. In *Salmo* and *Oncorhynchus*, the vomer is long and relatively flat, with the teeth attached all along the shaft. (This difference was well illustrated by Hubbs and Lagler, 1952: 35.)

We agree with Kendall (1919) that "the lake trout represents a line of development distinct from the other chars." Three characters of *Salvelinus namaycush* that are not known to overlap with those of other species of *Salvelinus* are the coloration, the position of the dorsal fin, and the number of pyloric caeca. However, in most characters the Arctic char, *Salvelinus alpinus*, forms a connecting link between *S. namaycush* and the Pacific American and Eastern American brook species, *S. malma* and *S. fontinalis*. Although no overlap is indicated (Fig. 2) in forking of the caudal fin at the larger sizes between *namaycush* and the other three American species of *Salvelinus*, the drawings (Berg, *loc. cit.*) of some of the chars inhabiting eastern Asia show stages somewhat intermediate between the condition in *fontinalis* and *namaycush*. We are convinced that none of the characters of *S. namaycush*, either alone or in combination, is of sufficient importance or consistency to warrant generic separation of this species from the other chars.

As readily noted in the accompanying photographs (Pls. I–II), the major feature that has been used to distinguish *Cristivomer* generically from *Salvelinus*—vomer with an elevated, elongate crest armed with teeth—is not peculiar to *S. namaycush*, and hence this structure cannot be used for recognizing *Cristivomer* at the generic level.

The difference in number of pyloric caeca we regard to be of specific significance only. In many genera of fishes, the development of these structures differs markedly in different species as, for example, the variation from 45 to 195 caeca in *Oncorhynchus* (Clemens, 1935: K105).

In the six forms of *Salvelinus* studied, the basibranchial teeth grade from almost complete absence in *fontinalis* to the strong multiserial teeth of *namaycush*, with no marked break in the character that could be used to justify taxonomic isolation of the lake trout. As in *Salmo*, these teeth seem to be useful for specific rather than generic separation.

We do not attach significance at the generic level to the consistent difference in position of the dorsal fin of the lake trout, and we fail to find fundamental differences in scale structure or number that could be considered of generic importance.

The ability to hybridize with species of *Salvelinus* does not prove that the lake trout should be placed in the same genus, for many widely recognized genera of freshwater fishes are known to hybridize, at least occasionally (e.g., brown trout and brook trout). However, the degree of crossability and the fertility of the hybrids, considered along with the fundamental points of resemblance already discussed, lend support to the view that the relationships of the lake trout are more clearly expressed by classifying this species in the genus *Salvelinus*.

Unlike species, genera are not objective entities. Thus generic concepts vary greatly among systematists and reflect, in the main, the personal judgment of the investigator. A primary function of classification is to reveal natural affinities. We have independently concluded that the relationships of the lake trout are more clearly indicated by referring this species to *Salvelinus* than by isolating it as a monotypic genus. Those who wish to reflect the distinctive characters of the lake trout in its scientific name can readily do so by recourse to the subgenus, *Salvelinus* (*Cristivomer*) *namaycush*.

Summary

In conclusion we have indicated that: (1) A number of characters readily distinguish *S. namaycush* from all other members of the genus. The best of these, we believe, are color pattern, dorsal-fin position, the deeply forked caudal fin, and the large number of pyloric caeca. (2) The supposedly key generic character, a crested vomer, is found in other species of the genus *Salvelinus* and is not developed consistently in the lake trout. None of the other distinguishing characters of this species is regarded by us to be of generic value. (3) The species *namaycush* manifests very clearly all of the essential characters of *Salvelinus*, which we believe to be a recognizable genus. (4) Therefore we support the recent trend among American ichthyologists to suppress the genus *Cristivomer* as a synonym of *Salvelinus*.

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