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A systematic review of the genus *Salvelinus*

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14.1 Introduction

> *The members of this genus are by far the most active and handsome of the trout, and live in the coldest, cleanest and most secluded waters. No higher praise can be given to a Salmonid than to say, it is a charr.*
> Jordan & Evermann (1896)

> *There is no other group of fishes which offer so many difficulties to the ichthyologist with regard to the distinction of species as well as to certain points in their life history as this genus.*
> Günther (1866)

Although Günther included *Salvelinus* as a subgenus of *Salmo*, the above quotations concisely provide the reasons for devoting a volume of works to this most beautiful and enigmatic group of fish. The delicate beauty of the charrs, their secretory habits, the associated landscape and remoteness of their habitats have given rise to a wealth of folklore and a rich vocabulary of common names. Man's historic interest in charrs is all out of proportion to the number of species, their abundance or commercial significance.

Ichthyologists have devoted considerable study on charrs for two centuries. Today, the taxonomic arrangement of the genus is still plagued by the confusion surrounding the distinction of species, as was mentioned by Günther more than 100 years ago. Despite modern methods and principles available to systematic study such as the biological species concept, phylogenetic systematics, biochemical and cytological systematics and

computer-aided techniques of data analyses (and the contributions in this volume) there will not be general agreement on the number of species recognized in the genus. I must admit that I am not overly confident of my interpretation of the data in relation to the number of species I recognize as valid. In this review I will focus attention on the most confusing areas, contrast opposing points of view, ask the questions in need of answers and try to keep an open mind.

14.2 Distribution of the genus

The genus *Salvelinus* is Holarctic in distribution and includes the most northerly distribution of any fish found in freshwater. In Europe the southen extent of the range includes Great Britain, Ireland, and Alpine lakes of central Europe to northern Italy. Across Siberia in the U.S.S.R., charr, with a few notable exceptions, do not generally occur far (a few hundred km) from the Arctic Ocean. The southernmost extension of the range in the Far East is Honshu Island, Japan. In North America, the original range of *Salvelinus* included Pacific Ocean drainages southward to the Sacramento River system, California, and Atlantic Ocean drainages to northern Georgia. Anadromous stocks of all species except *S. namaycush*, which lack anadromous stocks, are typically more northern in distribution; from northern Norway in Europe to the sea of Japan in the Far East. Anadromous North American stocks extend southward to Oregon in the Pacific Ocean and to Newfoundland in the Atlantic, although semi-migratory, estuarine brook charr, *S. fontinalis*, are common to Massachusetts. Throughout the range of anadromous charr, resident, nonmigratory charr occur, often sympatrically, with anadromous stocks. A major point of taxonomic disagreement on species recognition concerns resident lacustrine charr stocks, often strikingly distinct from sympatric, anadromous charr or two or more reproductively isolated lacustrine stocks living in the same lake. Do they represent distinct species comparable to other animal species, or only slight modifications of a single species which have established reproductive isolation by initiating temporal and/or spatial spawning differences in relatively recent geological times (during the past few thousand years)? Almost all of the taxonomic confusion and disagreement on species determination concerns the *Salvelinus alpinus* "complex", charr commonly known as arctic charr and dolly varden charr – a phylogenetic group I recognize as the subgenus *Salvelinus*.

14.3 General aspects

14.31 *Phylogenetic groups within the genus*

As a starting point for evaluation of species recognition and relationships within the genus, I recognize three, divergent phyletic lines which can be considered as subgenera (Behnke 1972). Two of these lines, represented by the lake charr, *Salvelinus namaycush*, and the eastern brook charr, *S. fontinalis*, are endemic to North America. The lake charr consists of a single species. It is the most morphologically divergent charr and the most highly specialized predator, attaining, by far, the largest size of any *Salvelinus* – to 47 kg (Scott & Crossman 1973). The lake charr can be segregated in the subgenus *Cristivomer*. The eastern brook charr, *S. fontinalis*, is a widely distributed, more generalised species in eastern North America, and generally recognized as a single species with few taxonomic problems. The subgenus *Baione* can be used to emphasize the distinction of *S. fontinalis* from other species in the genus. I also recognize a charr, known only from a single lake, now probably extinct, *Salvelinus agassizi*, as a valid species in the subgenus *Baione* (Behnke 1972).

In my scheme of charr classification, all other charr, with the possible exception of *S. leucomaenis* are considered in the subgenus *Salvelinus* (type of the subgenus, as of the genus, is *S. alpinus*). The "kundsha" charr of the Far East, *S. leucomaenis*, can not be assigned to the other phylogenies with authority. Savvaitova (this volume) believes that the affinities of *S. leucomaenis* lie with the North American charr (subgenera *Cristivomer* and *Baione*). The karyotype of *leucomaenis* given by Viktorovsky (1975) of 2N = 84 − 86 also suggests such affinities. The distinctive spotting on the body of *leucomaenis*, with large, oblong, light lemon-colored spots is most similar to *S. namaycush*. Formerly (Behnke 1972) I included *S. leucomaenis* n the subgenus *Salvelinus* and for the present zork will treat *leucomaenis* in the subgenus *Salvelinus* section while recognizing that the evidence is far from conclusive concerning the true relationships of this species.

The separation of the major phylogenies within the genus, however, has not reached a point where reproductive isolation can be ensured by sterility barriers. That is, all species within the genus can be hybridized producing fertile offspring (see Dangel *et al*. 1973, for list of known hybrid combinations and also references in Marshall 1977).

14.311 *Notes on nomenclature*

There are two aspects to the problem of determining the validity of species of *Salvelinus*. One concerns documenting and interpreting the evidence of phylogenetic divergence (degree of differences between forms) and the other concerns the validity of binomial or trinomial names as governed by the international rules of zoological nomenclature; particularly in regards to the type locality on which the name is based.

The generic name *Salvelinus* to segregate the charrs from other salmonid fishes is based on an old common name for charrs – "salvelin". Nilsson (1832) first proposed *Salvelini* as a group name to separate the charrs within the genus *Salmo*. Richardson (1836) first used *Salvelinus* as a genus although its common acceptance in the literature did not occur until the late nineteenth century and it is still common practice in Scandinavian literature to treat the charrs in the genus *Salmo*.

In my opinion, the generic status of charrs is well substantiated. Among salmonid genera, species of *Salvelinus* are distinct from species of *Salmo* end *Oncorhynchus* by the absence of teeth on the shaft of the vomer and from species of *Hucho* and *Brachymystax* by the presence of only light colored spots on the body (absence of black spots). No doubtful species suggesting intermediacy between *Salvelinus* and other genera is known. Fertile hybrids between *Salvelinus* and other genera never have been reported. Cavender (this volume) reviews the generic diagnosis of *Salvelinus* in detail.

The type species and their type localities of the three subgenera are: *Salvelinus* – *S. alpinus*, Swedish Lappland; *Cristivomer* – *S. namaycush*, Hudson Bay drainage; *Baione* – *S. fontinalis*, Long Island, New York.

Of particular importance regarding decisions on the taxonomy of the *S. alpinus* complex concerns recognition of the dolly varden charr as a full species and use of the specific name *S. malma*. Previously (Behnke 1972), I pointed out that the dolly varden charr in North America deserved full species status but nomenclatorial problems could arise due to the fact that the type locality for the name *malma* is Kamchatka.

In this volume, Morrow's paper on analysis of dolly varden charr, demonstrates the close similarities between the charr of northwestern Alaska [the charr called the western Arctic group of *S. alpinus* by McPhail (1969) and *S. alpinus* by McPhail & Lindsey (1970)] and the most common charr of northeastern Siberia, including Kamchatka. in the major characters used in charr taxonomy – numbers of vertebrae, pyloric caeca and gill rakers. Morrow concludes that these northwestern Alaska charr – a group characterized typically by 21–22 gill rakers, 66–68 vertebrae and 25–30 pyloric caeca extending north of the Alaskan Peninsula to the Mackenzie River – should be classified as *S. malma* and not *S. alpinus*.

Also in this volume, Savvaitova, as she has stated many times in the past, expresses her conviction that *S. malma* is a synonym of *S. alpinus*.

The original separation of a common ancestral charr into northern and southern stocks may have occurred as early as or earlier than the first glacial period of that early pleistocene in the North Pacific Ocean region. It is probable that in interglacial periods, the ancestral southern stock (*malma*) and ancestral northern stock (*alpinus*) came into

contact and introgression occurred, obscuring clear-cut genetic segregation. I attribute the separation of northern and southern groups and North American and Asiatic subdivisions of the southern group of *malma* to subsequent glacial periods.

The key to the validity of the species *S. malma*, concerns the relationships of the common anadromous charr of Kamchatka; a charr characterized by typical mean values of 21–22 gill rakers, 66–68 vertebrae and 25–30 pyloric caeca. Is the Kamchatkan anadromous charr ("*S. malma malma*") more closely related to the southern groups of dolly varden charr in North America and Asia than it is to the charr of northern Sweden, Norway, Karelia and Kola Peninsula (type of *S. alpinus*)? If so, then *malma* is a valid species. If not, much nomenclatorial revision will be called for.

On the basis of our present knowledge, this question can not be given an authoritative answer. In Alaska, both the northern and southern groups of "*malma*" live with *S. alpinus* with reproductive isolation. North of Kamchatka, in the region of the Chukotsk Peninsula, East Siberian Sea, charr occur, which, based on the works of Barsukov (1960) and Savvaitova (1961), can not be clearly assigned to *malma* or *alpinus*. More recent and comprehensive studies, however, demonstrate *S. malma* and *S. alpinus* occur sympatrically with reproductive isolation in waters of the Chukotsk Peninsula and appear to be identical to their counterparts in western Alaska (Chereshnev 1978a, 1978b).

Walbaum's description of "*Salmo malma*" in 1792 was not based on examination of specimens, nor a type specimen nor a specific type locality. There are diverse forms of charr in Kamchatka – anadromous, nonanadromous in rivers and small brooks and lacustrine specialized stocks in lakes in addition to a morphologically and ecologically distinct from known as the "kamen golets" or stone charr. Walbaum's *S. malma*, then, is an abstraction of a composite of forms. No one, to my knowledge, has recognized this nomenclatorial poblem and acted as a "First Reviser" to produce an adequate redescription of *malma* from Kamchatka.

I will, at least in part, assume such a role for this volume by designating the most common form of the anadromous charr of Kamchatka as the imputed type for the name *malma*, based on Walbaum's statment: "Adscendit fluvios Kamschatkae". More restrictive geographical limits can be placed on the type locality by restricting it to those rivers on Kamchatka draining into the Okhotsk Sea, as the name *malma* is derived from the language of the natives living on the Okhotsk Sea Coast (Berg 1948). It is clear that Walbaum's binomial descriptions are not original works (Briggs 1965) but, in the case of the salmonid fishes named from Kamchatka, ultimately were based on the work of George Wilhelm Steller who produced two large volumes of work on Kamchatkan fishes. For a more thorough definition and redescription of *S. malma* of the type locality, a careful examination of Steller's work may provide some valuable clues concerning what particular group of charr from what area comprised his "*malma*".

The many publications of Savvaitova and her coworkers have well documented the taxonomic characters of Kamchatkan charr, including anadromous stocks (see references in this volume and in Marshall 1977). As mentioned previously, the taxonomic characters of anadromous Kamchatkan charr are virtually identical to the anadromous charr of northwest Alaska and I agree with Morrow that they represent a group of common evolutionary heritage which should be classified as a single subspecies. *S. malma malma* is the correct name for this subspecies if the common anadromous charr of Kamchatka is accepted as Walbaum's *S. malma*.

It must be understood that the type localities of original descriptions and redescriptions of the typical charr of these localities, when necessary, are an integral part of any decisions concerning *Salvelinus* taxonomy.

14.312 *Principles and methods of classification*

In the twentieth century the emergence of a synthesis of evolutionary thought developed clearer concepts and goals of taxonomy and a sharper focus on the nature of species. This modern era has often been called the "new systematics" (Huxley 1940, Dobzhansky 1951, Mayr 1963, 1969, Simpson 1961).

Except for a few die-hard numerical taxonomists ("pheneticists"), the goal of modern taxonomy is to achieve a system of classification most accurately reflecting phylogenetic relationships. There is considerable turmoil between the strict phylogenetic taxonomists of the Hennig school and the "traditionalists" on how to achieve such a classification and on the philosophical and scientific bases of classification, as can be observed in the pages of current issues of the journal Systematic Zoology.

Although the current turmoil on methods and principles of systematic zoology has a salubrious effect of stimulating new ideas and has sharpened and expanded the thought content in the systematic literature, I see little immediate impact toward a solution to the systematic problems of *Salvelinus*.

New characters are needed to detect all of the major and minor branching sequences in the phylogeny with a high degree of authority. This is not possible based on our present knowledge. Thus, speaking of plesiomorphic (primitive) and apomorphic (derived) characters and "sister groups" without a well-founded basis for assumptions on a character state would be little more than playing games.

The matter of discovering the characters necessary for a more correct assessment of the evolutionary dichotomies in the *Salvelinus* phylogeny is the concern of taxonomic methods.

Since the time of John Ray and Peter Artedi in the seventeenth and early eighteenth centuries, fishes have been grouped and classified by comparing similarities and differences of morphological and anatomical features. Arguments are often voiced that such ancient methods used to produce a basis of classification should be replaced by information developed from modern techniques allowing examination and comparisons of karyotypes and gene loci. Such arguments are without validity, however, because of the long history of demonstrated efficacy of morphologically based classification. Traditional taxonomy has proven effective because, as we now know, a thorough examination and extraction of information from phenotypic characters is an indirect examination and comparison of the expression of whole genotypes. Undoubtedly, further significant contributions to *Salvelinus* taxonomy will be made by traditional type studies such as Cavender's (1978) work demonstrating the validity of the bull charr, *Salvelinus confluentus*, in western North America. Cavender's painstaking and detailed comparisons of general morphology, osteology, structure of gill rakers, etc., demonstrated a clear-cut divergence of the bull charr from the southern dolly varden – two groups which do not consistently differ in the number of gill rakers, pyloric caeca or vertebrae, the characters most frequently used in charr taxonomy.

In a genus such as *Salvelinus* where parallelism and convergence can limit the amount of information available from morphological comparisons, significant contributions can be expected from the fields of biochemical taxonomy and cytogenetics. To date, however, input from these methods has not provided much insight into determining the validity of species or detecting evolutionary divergences.

Tsuyuki *et al.* (1966) compared muscle myogen from *S. namaycush*, *S. fontinalis*, *S. alpinus* and *S. malma* (specific localities of specimens not given) and found "striking similarities" between them. Zakharova *et al.* (1971) did not detect clear-cut differences from immunological analyses of *Salvelinus* (*alpinus*, *malma*, *leucomaenis* and "stone charr" of Kamchatka). Most distinctions were expressed in *leucomaenis* and in stone charr. They concluded that *malma* is a synonym of *alpinus*. On the other hand, Omelchenko (1975), comparing hemoglobins of Kola Peninsula *S. alpinus* with Kamchatkan *malma*, concluded they are valid species.

The chromosomal comparisons of Kamchatkan charr by Vasilyev (1975) and by Viktorovsky (1975, 1976) do not completely agree in the diploid number of "*malma*" (typical model numbers of 76–84). Vasilyev believed the Kamchatkan "*malma*" is a synonym of *alpinus* whereas Viktorovsky found a pair of submetacentric chromosomes in Kamchatkan *malma*, not found in Kola Peninsula *alpinus* and concluded they are two distinct species. It is likely that true polymorphism occurs in Kamchatkan *malma* karyotypes similar to rainbow trout, *Salmo gairdneri* (Thorgaard 1976), which will make evolutionary interpretation more difficult. What is necessary, in my opinion, before

karyotype studies can yield more definitive interpretive data, are more refined techniques such as chromosomal banding to detect homologies of specific chromosomes and chromosomal sections between karyotypes, allowing a tracing of evolutionary divergences associated with Robertsonian fusion, translocations and inversions so that primitive and advanced traits of the karyotype can be more intelligently discussed.

Nyman's (1972) "new approach" to *Salvelinus* taxonomy compared polymorphism of the esterase enzyme in many Scandinavian charr populations. Esterase is what I consider to be an evolutionary labile character, subjected to rapid change under natural selection, particularly by temperature regimes. That is, it is character subject to convergence similar to gill raker number. Of particular interest to me was Nyman's comparison of sympatric charr stocks from some of the same lakes in Sweden that I had examined morphologically (Behnke 1972). My conclusion based on phenotypic similarities was that the sympatric pairs in each lake are more closely related to each other than to any populations outside of the lakes. Nyman's data on the allelic frequencies producing the different esterase patterns supported my opinion, yet Nyman stated that the sympatric pairs actually represent two ancient species which happen to appear so similar due to "introgression". There is no basis for such a conclusion and it contradicts his own data.

Henricson & Nyman (1976) used more sophisticated techniques of multivariate analysis to study enzyme polymorphism, parasites, food, age and growth of sympatric charr stocks in three lakes in Swedish Lappland. There is no doubt that sympatric and reproductively isolated stocks exist, but their conclusions that three "species" of charr invaded Swedish waters in postglacial times is not very enlightening without a discussion of these three "species", their nomenclature and distribution.

In the future, real biochemical contributions to *Salvelinus* taxonomy will result from more refined techniques and greater expertise examining the products of several gene loci (20–30 or more). I would emphasize, however, that interpretation of these results may be limited by the probable discordance between the evolutionary rates of genes governing intermediate metabolism (those studied from electrophoresis of their products) and the genes determining morphological traits. In many fish groups studied to date, the biochemical data on evolutionary divergence agrees with a taxonomy based on morphology for some (Avise & Smith 1977) but not for others (Turner 1974, Avise *et al*. 1975). That is, protein evolution, as determined from electrophoretic studies, may not have a direct cause and effect relationship with phenotypic divergence and speciation (Bell 1976). The caution that must be exercised for assessing quantitative data of genetic affinities and divergence, often expressed as scores of genetic distance, genetic identity, similarity, etc., as input to taxonomic problems, is apparent from studies demonstrating comparable genetic similarity expressed in gene loci between man and the chimpanzee as is found between subspecies of species in the mouse genus *Mus* and the lizard genss *Anolis* (Avise 1974, King & Wilson 1975) – an enormous amount of genetic information remained untapped by such studies.

A promising technique, theoretically avoiding the above problem, is DNA hybridization, where DNA of a large part of the genotype (redundant DNA) can be compared. The test is based on the assumption that the more similar are the strands of DNA, the more solidly they will join together when combined and the more energy (heat) required to disassociate them. Quantitative data then can be obtained from the temperature necessary to separate DNA strands from any two oganisms (the higher the temperature the closer the genetic relationship).

The DNA hybridization technique has not yet been widely applied in ichthyology (Gharrett *et al*. 1977). My impression is that the technique as presently used is in need of further refinement to obtain useful data below the generic level so that the affinity scores are truly a reflection of actual evolutionary divergence and similarities. In this volume an interesting article is presented on DNA hybridization studies of Eurasian *Salvelinus* (Mednikov *et al*.). The anadromous charr of the Kamchatka River (what could be called "topotype" specimens of the taxon *S. malma*) were compared with charr from 15 other localities. I would generally agree with the distance scores between the anadromous *malma* of the Kamchatka River and *S. leucomaenis* (greatest or most dissimilar) and with

the "stone charr" (called *S. malma kuznetzovi* in the article, but I believe this is an erroneous use of the subspecies name). I do not agree with the DNA hybridization data indicating the extremely close genetic identity of anadromous *malma* to the charr called *S. neiva* (a typical *S. alpinus*) and certainly do not agree to the closest indicated affinities of all tested – anadromous *malma* to Kola Peninsula *S. alpinus* (a charr that is close geographically and morphologically to the type of *S. alpinus*). The problem appears to be that the experimental error in DNA hybridization studies to date is such that the genetic differences accumulated in evolutionary lines separated for less than a few million years can not be accurately assessed. Mednikov & Akhundov (1975) performed DNA hybridization experiments with the anadromous trout of Kamchatka, *Salmo mykiss* (called *S. penshinensis* in their publication), comparing it with non-anadromous Kamchatkan trout, steelhead trout, *Salmo gairdneri*, from Oregon, Atlantic salmon, *S. salar*, brown trout, *S. trutta*, and a domesticated hatchery stock of *S. gairdneri* (called *S. irideus*). The "relationships" of anadromous *S. mykiss* and anadromous *S. gairdneri* were virtually identical, which is in agreement with my opinion that *mykiss* and *gairdneri* are the same species (Behnke 1966). The position of *S. trutta* and *S. salar* appears to be correctly remote from *S. mykiss*, but the DNA values of the hatchery stock of *S. gairdneri*, lies half way between *S. mykiss* and *S. trutta* – not at all in accord with evolutionary reality.

The studies by Mednikov *et al*. (1977) on the whitefish genera *Coregonus* and *Prosopium*, does seem to approximate phylogenetic relationships, particularly in the distance between *Prosopium* and *Coregonus* and the clustering of species associated with the subgenera *Coregonus* and *Leucichthys* in the genus *Coregonus*. In this case the time of separation of the phyletic lines has allowed sufficient divergence to overcome the "noise" of experimental error.

A point I would emphasize is that no matter what technique is used, efficacy depends on the ability to detect unique genetic events occurring in one phyletic line and not its "sister" line since the point of divergence from a common ancestor. Evolutionary divergences occurring in the past 1–2 million years, as is likely to be the case in the *S. alpinus* complex, may not have accumulated sufficient unique events, to yield conclusive results from gene loci data or DNA hybridization. Concerning the time period involved and the manifestation of genetic differences, there seems to be much in common between what may be called subspecies of both *S. alpinus* and *S. malma* and the evolution of the races of man, *Homo sapiens*. The races of man exhibit conspicuous morphological differences; for example, Australian Aborigines can be readily differentiated from Scandinavians simply by visual analysis. However, all races of man are remarkably similar in gene loci (Mitton 1977). Relatively few of the 1 000 000's of gene loci of an individual are amenable to study and the chance of discovering unique genetic events between two diverging evolutionary lines diminishes with decreasing time since various branching points originate in a phylogeny.

In many parts of the world charr assume considerable importance as a commercial or sporting fish. Because of this I would make a plea for research workers to attempt to find broader applicability of the information developed from systematic studies beyond the confines of taxonomy. Basic information on various life history traits, ecology, environmental optima and limitations, food habits, age and growth, interaction with associated fauna and behavioral observations are critical for intelligent management, exploitation, propagation and acclimatization.

Of prime importance for systematists is to make clear to biologists involved in fisheries management that a small genetic difference, not recognized taxonomically, can result in great differences in life history, behavior and ecology between two populations subjected to different evolutionary programming, and these differences are of major importance for fisheries management (Trojnar & Behnke 1974).

Workers familiar with the taxonomic problems of *Salvelinus*, realize the fallacy of the typological approach to charr taxonomy (where every population which looked different was named as a new species). Fisheries management programs may also be hampered by the typological approach to management whereby all members of a given taxon (species or subspecies) are assumed to respond identically to different environmental parameters.

The enormous amount of genetic diversity incorporated into the various evolutionary lineages in *Salvelinus* comprises a great natural resource whose use and development by man remains largely untapped. To illustrate this point, the differential survival found between two local populations of the most stable *Salvelinus* species, the lake charr, *S. namaycush*, can be cited. In New York State lake charr from two sources, Upper Saranac Lake and Seneca Lake, have long been used for propagation and introductions into other lakes. In a study from 1964 and 1968, comparing the survival from introductions of more than 400 000 lake charr in nine lakes, it was found that the survival of lake charr derived from the Saranac Lake strain was 16 fold greater than the Seneca Lake strain (Plosila 1977). I doubt that the genetic basis governing such a survival difference could be detected other than by examining the interaction of the two genotypes in different environments and measuring survival. It should be obvious that all members of the taxon *S. namaycush* do not respond identically to different environments and a typologically based management program utilizing *S. namaycush* is operating at reduced capacity by failing to study, experiment and make use of the genetic resources available within the taxon.

14.4 Taxonomic complexes

14.41 *Subgenus* Salvelinus (*the* Salvelinus alpinus *complex*)

This discussion attempts to evaluate the evidence for recognizing evolutionary lines responsible for the present confused state of species determination in arctic charr and dolly varden charr. The kundsha charr, *S. leucomaenis*, can be omitted from this discussion for even Savvaitova (this volume) agrees with me that there are no doubts for regarding *leucomaenis* as a well defined species and it does not enter into the problem of delineating the two major groups I call arctic charr (*S. alpinus*) and dolly varden charr (*S. malma*), except for the determination of the dubious relationships of the Japanese charr known as *S. pluvius*.

I will also examine the evidence presented by Savvaitova who claims that only one group, *S. alpinus*, is involved and all the variability expressed in various populations in different geographical areas is either a direct result of environmental influences on meristic characters or rapid evolution (a few thousand years at most) under similar environmental stimuli acting on a single ancestral *alpinus* so that what I call *S. malma* is nothing more than a series of *S. alpinus* populations which happen to be very similar to each other because of convergent evolution.

I realize that the characters most frequently used in charr taxonomy, the numbers of gill rakers, vertebrae and pyloric caeca are highly variable and may be subjected to relatively rapid evolutionary change under different selective pressures. Two geographically isolated populations may have similar gill raker numbers because of convergent evolution and not because of derivation from a common ancestor. However, if the numbers of vertebrae and pyloric caeca are also in accordance with gill raker number (for example, agreeing with typical dolly varden or typical arctic charr counts) in the two geographically isolated populations, then the evidence is much more convincing of recent derivation from a common ancester.

In the Far East, the lacustrine charr population in Lake Shikirebetsu, Hokkaido, Japan, described as *Salvelinus miyabei*, has 24–28 (25.7) gill rakers (Maekawa 1977). Typical gill raker number for the "dolly varden" charr of Hokkaido is 20–22 and only about 16–18 for the charr on the main island of Honshu. Previously, I had suggested that "*S. miyabei*", might represent a southern penetration of *S. alpinus* (Behnke 1972). The vertebrae counts given for the Lake Shikirebetsu charr are 59–63 (61), which is typical of "*malma*" of Hokkaido (Maekawa 1977). I have not seen pyloric caeca values given for "*miyabei*", but if they average less than 30 I would agree with Maekawa (1977) that *miyabei* is a lacustrine specialized subspecies of *S. malma*. If pyloric caeca counts average 45 or more, it would be a definite indication that gene flow from *S. alpinus* has influenced

the charr in Lake Shikirebetsu.

Lake Dalneye and Lake Nachikin, in two different drainages of Kamchatka, have similar populations of lacustrine charr (Savvaitova 1976). They are sharply differentiated from the typical "*malma*" of Kamchatka in their higher number of gillrakers (23–29 [24.8 and 26.7]) and pyloric caeca (35–60 [48.0 and 48.8]). These lacustrine populations of Lake Dalneye and Lake Nichikin occur sympatrically with typical Kamchatkan "*malma*". Savvaitova (1976) believes these lacustrine charr are only "ecotypes" that bear close similarities not because of derivation from a similar common ancestor but because of rapid convergent evolution from the typical anadromous charr of Kamchatka. The final chapter is yet to be written on the evolutionary affinities of the lacustrine charr of Kamchatka. Similar populations likely occur in other lakes such as Lake Kronotskoe, where Viktorovsky (1976) claims there are three distinct, sympatric and reproductively isolated stocks of charr. As more detailed evidence is compiled on Kamchatkan lacustrine charr with 25–26 gill rakers and 45–50 pyloric caeca, I believe it will clearly demonstrate a *S. alpinus* influence from the north, either via headwater transfer from the Lena or Indigirka rivers into the Okhot River ("*S. neiva*") and subsequently Kamchatkan connections of the Okhot River via the Paleo Penzhina River (Volobuyev 1976) or, more probably, directly along the seacoast. Chereshnev (1978a, 1978b) found both the typical anadromous form of *maima* typically with 21–23 gill rakers and 20–30 pyloric caeca and an artic charr with numbers of gill rakers, pyloric caeca and vertebrae about identical to the values found in the lacustrine charr stocks of Lake Dalneye and Lake Nichikin, in waters of the Chukotsk Peninsula where "*alpinus*" has both lacustrine and anadromous stocks and is sympatric with "*malma*".

Unfortunately, two papers by Glubokovsky, published in the Soviet journal, Biologiy Morya (1977 no.s 3,4), were not received before my manuscript was completed, and only their abstracts were seen. Glubokosky's 1977 publications concerned the charr of the Kamchatkan River basin with the description of a new species, *Salvelinus albus*. I assume that the new species is based on the lacustrine *alpinus*-like charr of Kamchatka. I eventually foresee that the arctic charr (typically with 24–27 gill rakers, 40–50 pyloric caeca and 65–70 vertebrae) of Kamchatka, western Alaska and the Chukotsk Peninsula will be recognized as a subspecies of *S. alpinus*. The names *S. andriashevi* Berg 1948 and *S. taranetzi* Kaganovsky 1955 are available for this taxon, but would need redescriptions as discussed later.

Savvaitova certainly deserves credit for accomplishing an enormous amount of taxonomic and ecological research on Far Eastern Charr, but she has shackled herself uncompromisingly to the concept of a single polymorphic species giving rise to similar "ecotypes" by convergent evolution ("homologous parallel variation") to explain all apparent divergence in the *Salvelinus alpinus* complex. Her taxonomic conclusions are impaired by continually ignoring all supplementary evidence available from geological and zoogeographical studies necessary to more firmly associate taxonomic characters with the climatic and geological events initiating evolutionary divergence and, in some cases, perhaps subsequent introgression which are responsible for the present diversity we see. For example, the zoogeography, divergence and taxonomic confusion of the whitefishes of the genus *Coregonus*, has much in common with the problems of *Salvelinus*. Undoubtedly, similar climatic and geological events and similar glacial refugia and dispersion routes are involved. Shaposhnikova (1974) presented considerable data on the Siberian "pyzhan" whitefish, *Coregonus lavaretus pidschian* (or *C. pidschian*). This whitefish of the *C. lavaretus* complex has a distribution from Murmansk and the White Sea eastward across Siberia to the Beaufort Sea of North America – a distribution that can be virtually superimposed on the major part of the range of the *S. alpinus complex*. Of particular significance for correlating isolation and divergence in glacial refugia, dispersal routes and area of introgression between incipient divergent groups of both whitefish and charr is the occurrence of a highly distinctive group of whitefish (*Coregonus baunti*) with about 30–36 gill rakers in headwater lakes of the Lena River basin. Some of these same lakes also contain *Salvelinus alpinus erythrinus* (Savvaitova 1977), representing a disjunct and relict distribution of *S. alpinus*.

Also noteworthy is the occurrence of three distinct and sympatric stocks of the "pyzhan" whitefish in Lake Taimyr on the Taimyr Peninsula which also has divergent, sympatric charr stocks.

Ustyugov (1976) discussed the origin of two groups of Siberian cisco, *Coregonus sardinella*, in the Yenisei River basin in relation to past climatic, geologic and hydrologic factors as a probable cause of the observed divergence. Ancestral *Salvelinus* were also exposed to these same factors.

Soviet ichthyology has a rich heritage of zoogeographical literature to provide insight and understanding to problems of fish distribution and speciation, particularly exemplified in the works of L. S. Berg and G. U. Lindberg. A more thorough understanding of the information available in the Russian literature would, I believe, cause Savvaitova to reject her statement made in this volume that all of the diversity in the *S. alpinus* complex is attributable to events of the past 10 000 years — that is, no isolation and divergence before that time has played a role in producing the present diversity.

Two distinct populations of kokanee salmon, *Onchorhynchus nerka*, differing by more than 10 gill rakers (32.7 vs. 43.0) occur in Lake Kronotshoe, Kamchatka. This lake has been isolated from invasion from the sea for 10 000–15 000 years (Kurenkov 1977). To me, this indicates that more than one wave of salmonid fishes invaded Kamchatka to produce the present diversity and that similar factors are responsible for the diversity found both in the salmon and the charr of Lake Kronotskoe.

Biochemical taxonomic methods may prove useful to trace dispersion routes of different evolutionary lines of charr as was the case in the study of lake whitefish in North America by Franzin & Clayton (1977).

I am in agreement with Savvaitova that sympatric occurrence with reproductive isolation is not sufficient evidence by itself for species recognition. Innate reproductive homing behavior in salmonid fishes can maintain reproductive isolation between two or more stocks with little genetic divergence (Behnke 1972). Reproductive isolation associated with major morphological differences such as found in charr stocks of Karluk and Fraser Lake, Alaska and in Lake Dalneye and Lake Nachikin, Kamchatka, does strongly indicate to me that the two distinct, sympatric stocks represent separate invasions by two ancestral species rather than independent divergence within each lake from a single ancestor ("convergent" sympatric speciation).

14.411 *Divergence within the* S. alpinus *complex*

It was mentioned previously that there are two aspects regarding problems of *Salvelinus* taxonomy. One concerns the documentation, comparison and ranking of diversity, attempting to correctly associate it with phylogenetic divergence and the other aspect is the names applied to the imputed divergence.

Most of the following discussion on divergence is based on the most frequently used characters in taxonomic publications on *Salvelinus*, the numbers of gill rakers, pyloric caeca and vertebrae. The degree of difference in these characters between various groups of the *alpinus* complex is not directly correlated with actual genetic divergence in all cases. As mentioned, two phyletic lines, the bull charr and the southern dolly varden charr in North America have reached full species status without consistently differing in the number of gill rakers, caeca or vertebrae. There are, however, consistent differences in these characters in charr of different geographical areas which can be assumed to be representative of the evolutionary lines giving rise to these charr. Low numbers of pyloric caeca (<30) are "*malma*-like", high numbers (>40) "*alpinus*-like". High gill raker numbers (>25) are *alpinus*-like and low numbers (<20) are "*malma*-like". Consistent agreement of high or low values are associated with particular geographic regions. They do not occur randomly and sporadically throughout the range of the complex. Vertebrae numbers are not so consistently associated with *alpinus* or *malma* except that the lowest numbers (<62) are always found in the southern dolly varden, particularly in the charr native to Honshu Island, Japan (*S. pluvius* or *S. malma pluvius*) where mean values below 60 are frequently encountered. The highest vertebrae numbers are found in some arctic *S.*

alpinus (67–69), but Kamchatkan charr (type locality of *S. malma*) and northern dolly varden of Alaska typically have 66–68 vertebrae.

Extremes in the values of these characters can be evaluated with the assumption that the extreme groups are the groups which have been least effected from introgression and may represent the most divergent lines resulting from the earliest isolation and speciation. The zoogeographical evidence agrees with this assumption.

If the charr with the highest number of gill rakers is taken as the "extreme *alpinus*", these charr typically with 26–32 (means of about 27–30 or more) exemplify this trait. Charr with such gill raker numbers are found in the Alpine lakes of Europe, the Transbiacal region and the Taimyr Peninsula of Siberia, in lakes of the Okhot River basin draining into the Okhotsk Sea, and in North America, eastward from the Mackenzie River to Hudson Bay, but they also occur in headwater lakes draining into the Arctic Ocean west of the Mackenzie River. The Alpine lake charr are strictly lacustrine, the Taimyr Peninsula and North America charr are both lacustrine and anadromous. The highest gill raker counts are found in disjunct relict populations far from the sea and evidently represent dispersion of this group (called the "high Arctic" group in Savvaitova's chapter 5) during a period when suitable environmental conditions existed for *Salvelinus* in Siberian rivers far from the present sea coast, perhaps during a time of postglacial marine transgression. These relict interior populations consist of the charr named *S. alpinus erythrinus* from Lake Frohlika with 27–31 (29.2) gill rakers (Savvaitova *et al*. 1977). This same charr also inhabits several lakes in the Vitim River drainage of the Lena River basin. Figure 2 of Savvaitova's chapter (this volume) illustrates a mean value of approximately 36 gill rakers for an unidentified charr population. Savvaitova has informed me that this charr occurs in Lake Lepindo of the Lena basin in the Transbaical region. As mentioned in a previous paper (Behnke 1972) I counted 31, 32, 32 gill rakers in three specimens of charr from Lake Darpir in the headwaters of the Kolyma River basin. Shaposhnikova (1971) presented some additional data on the charr of Lake Darpir. Savvaitova & Smolyanov (1967) counted 30 and 31 gill rakers in two large specimens of charr from Lake Khantaiskoye in the interior region of the Yenisei River basin. Volobuyev (1976) counted 27–34 (30.3) gill rakers in the charr of Lake Ueginskoye of the Okhot River basin. Volobuyev (1977) obtained slightly higher counts in charr from Korral Lake of the same basin where two forms of charr are found, a short-lived dwarf form and a normal form. The dwarf form averaged 31.2 and the normal averaged 31.1 gill rakers.

This lacustrine charr, named *S. neiva* by Taranets (1933) occurs in several lakes of the Okhot River system (draining to Okhotsk Sea). The lacustrine charr of the Okhot River basin seems very close to the charr of Lake Darpir in the headwaters of the Kolyma. The headwaters of the two drainages are very close and several elements of the fish fauna of the Okhot River were derived from past connections to the Kolyma and possibly the Indigirka (Volobuyev 1976). Such headwater transfer of an ancestral charr with about 30 gill rakers — a "pre-adapted" lacustrine form — is a more logical explanation to explain the widespread occurrence of "*S. neiva*" in several lakes than to invoke the theory of separate invasion of each lake by the typical *S. malma* of the Okhotsk Sea, which, by a "series of parallel homologous variations" (convergent evolution) independently produces identical populations. As I have formerly discussed (Behnke 1972), the Taimyr Peninsula is an area of zoogeographical interest with Baikal elements in its fauna. The Taimyr Peninsula was largely submerged by the last marine transgression and I would agree with Savvaitova that the few thousand years the lakes have been available on the Taimyr Peninsula is insufficient time for the charrs to speciate to the degree they have with several examples of distinct, sympatric lacustrine stocks and lacustrine and anadromous stocks. I see no obstacle to the assumption that the present Taimyr charr were already divergent in their high gill raker number during the marine transgression and invaded the Taimyr lakes from interior refugia after the sea receded. The zoogeographical evidence, particularly the existence of *S. alpinus erythrinus* in interior lakes supports such a theory. Savvaitova *et al*. (1977) placed the origin and distribution of *S. alpinus erythrinus* in the upper pliocene — beginning of pleistocene, or well over 1 000 000 years ago. Such timing is in

contradiction to Savvaitova's statement in this volume that all of the *S. alpinus* complex diversity can be explained by events during the past 10 000 years. There is an enormous gap between 1 000 000 years and 10 000 years. What occurred during this time? It seems highly improbable to me that one branch of the *alpinus* complex, *S. a. erythrinus*, has persisted essentially undifferentiated for over 1 000 000 years, during which time all other lines in the complex disappeared only to suddenly reappear 10 000 years ago and then differentiate with an "explosive" rate of evolutionary change. It is more reasonable to assume that during the last million years, the *alpinus* complex was fractioned, diverged and introgressed several times to produce the present geographic variability.

The Taimyr charr appears very similar to the North American charr with about 25–31 gill rakers found from the Mackenzie River to Hudson Bay and this similarity, in my opinion, is due to common ancestry and not convergent evolution. If this is true then this charr once had a continuous distribution which was interrupted by the last glacial epoch or by events since then resulting in its replacement in intervening areas by *S. malma*, other divergent groups of *S. alpinus* and/or introgressed *malma-alpinus*.

The charr of the Alpine lakes of Europe probably represent an earlier separation from this common ancestral *alpinus* stock with high numbers of gill rakers. The presence of a highly differentiated charr in the Bodensee, the "Tiefseesaibling", which I recognize as a full species, *S. profundus* (Behnke 1972), attests to the antiquity of *Salvelinus* associated with the Alpine lakes of Europe. It is premature to assign subspecific designations to the *S. alpinus* with the highest gill raker counts on any real basis of genetic relationships. When this task is faced in the future, however, the following options are available: an all inclusive subspecies to cover all *Salvelinus* with the highest number of gill rakers (Alpine Lakes, Taimyr Peninsula, interior Siberian lakes and North America) would be *S. alpinus salvelinus*. Linnaeus used the binomials "*Salmo salvelinus*" "*Salmo umbla*" and "*Salmo salmarinus*" for Alpine lake charr. By precedence, *Salvelinus alpinus salvelinus* for the charr of the Alpine lakes has been the most commonly used subspecific designation.

If *S. alpinus salvelinus* is restricted to Alpine lake charr of Europe, the oldest available name to apply to the other groups with high gill raker numbers is *S. alpinus erythrinus* from "*Salmo erythrinus*" of Georgi's description of the Lake Frohlika charr in 1775. The present use of this subspecies could be expanded to include the Taimyr Peninsula charr and the North American charr. Several more recent names have been given to charr from the Taimyr area (Behnke 1972).

If a subspecific designation is restricted to the North American group with high numbers of gill rakers, a decision on the correct name may be a problem. The oldest potential names are "*Salmo stagnalis*" and "*Salmo rivalis*" proposed by Fabricius for Greenland charr in 1780. After the last glaciation, Greenland was exposed to invasion by two groups of charr from the sea. The charr with numerous gill rakers would be expected to disperse along the west coast of Greenland from Baffin Bay and Davis Strait. The east coast may have received charr from a group characteristic of Scandinavia, Great Britain and Iceland with about 21–28 gill rakers (*S. alpinus alpinus* in a broad sense) and introgression may have occurred between these groups in southern Greenland. A redescription of "*S. stagnalis*" should be made. I examined six specimens of charr from Greenland at the British Museum. One specimen (1955.9.14.1) from Strindborg, Norofjord, N.E. Greenland has 25 medium-long gill rakers. Five specimens (1957.9.20.1–40) from Britannia Lake, N.E. Greenland, have 26–28 (27) long, fine gill rakers.

The above mentioned groups of charr can be considered the "extreme" form of *S. alpinus*. Before considering the less extreme groups of *S. alpinus* and attempting to find a demarcation point between *alpinus* and *malma* I will examine the other extreme in the complex – the southern dolly varden of North America and the charr of Japan in the Far East, with gill rakers typically of 16–18 and with clear-cut differences in numbers of vertebrae and pyloric caeca from *S. alpinus*. These charr are the most visible results of an early separation of the *S. alpinus* complex.

SHORT PAGE

14.412 *Extremes in "malmoid" characters*

The extreme in morphological divergence in charr associated with Pacific Ocean drainages is found in the southern part of the range consisting of two major groups – the southern dolly varden charr, including both Asia and North America and the "bull" charr, *Salvelinus confluentus*, in North America. Perhaps these two major groups are sister groups of the first dichotomy from the earliest isolation of part of the *S. alpinus* complex south of the Bering Strait. The geographical demarcation of the southern dolly varden in Asia includes the area south of the Amur River mouth (southern Okhotsk Sea), Sakhalin, Hokkaido, Honshu and the Asiatic mainland draining into the Sea of Japan. In North America, the southern dolly varden ranges in Pacific Ocean drainages from California to the Alaskan Peninsula and westward across the Aleutian Islands. North of this area, the "northern" dolly varden is found: northern Okhotsk Sea, Kamchatka, northward around Chukotsk Peninsula to the Arctic Ocean (probably about to Kolyma River) and in North America, north of the Alaska Peninsula to the Mackenzie River. The southern and northern dolly varden differ mainly in the number of gill rakers and vertebrae (mean values typically 16–21 and 59–64 in southern and 21–23 and 66–68 in northern). The southern dolly varden can be provisionally separated into three groups. In respect to vertebrae and gill raker numbers, the North American group is relatively uniform with no obvious clines or geographically unique subgroups. Vertebrae counts are higher in the North American group with typically mean values of 62–64. The gill raker counts are consistently low, typically averaging 17–18. In the Far East, a group characterized by the lowest vertebrae counts of about 58–59 and low gill raker numbers (16–18) is associated with Honshu Island, Japan (southernmost distribution of the genus) and with the Kuril Islands (Savvaitova & Movchan 1973). There is also a trend for lower pyloric caecal numbers (20–25 vs. 25–30) to be associated with the lowest values of vertebrae and gill rakers. On Sakhalin and Hokkaido, populations exhibit higher numbers of vertebrae and gill rakers (61–63 and 19–22) which is likely attributed to past introgression with the northern form. Viktorovsky (1976) reported karyotype differences between southern *malma* and northern *malma* in the Far East. The southern *malma*, listed as *S. malma curilus* and *S. malma krascheninnikovi* by Viktorovsky were found to have a diploid number of 84–86 whereas the Kamchatkan *S. malma malma* were reported to have 76–80 chromosomes. Vasilyev (1974) found 80–82 chromosomes in Kamchatkan *malma*.

In regards to the evolutionary reality of the groups discussed and for consideration of the validity of the name *malma* and various other names, it is important to know what the situation is in those areas where the southern dolly varden has been exposed to contact with the northern dolly varden and with arctic charr. Have they hybridized to produce a broad or narrow clinal zone of intergradation? Have they maintained reproductive isolation in sympatry?

14.413 *Areas of contact in North America*

In North America the distribution of the northern dolly varden meets the southern dolly varden on the Alaskan Peninsula where the Aleutian range separates the two forms. Southern dolly varden occur in south slope drainages and the northern form in north slope drainages. One or the other form of dolly varden exist sympatrically with arctic charr in several lakes in this region. It should be mentioned here that two groups of *S. alpinus* are also found in Alaska. In the Alaska Peninsula area of group typically with mean values of 23–25 gill rakers and 45–50 caeca (52.5 in Aleknagik Lake) is found in lakes on both sides of the Alaskan Peninsula. This is the group called the Bristol Bay-Gulf of Alaska *S. alpinus* by McPhail (1961). Also McPhail's eastern Arctic group of *alpinus* with about 25–30 gill rakers is found in headwater lakes in drainages tributary to the Beaufort Sea west of the Mackenzie River (McCart & Craig 1971, Behnke 1972). The southern dolly varden is known to occur with the Gulf of Alaska-Bristol Bay group of *S. alpinus* in Fraser Lake and Karluk Lake on Kodiak Island and in a lake on one of the

Shumagin Islands south of the Alaska Peninsula (McPhail 1961, Morrow, this volume). Northern *malma* occurs with this same group of *S. alpinus* in Brooks Lake, Aleknagik Lake and in a lake on the Seward Peninsula (McPhail 1961). I will again make clear that I am considering McPhail's northern *malma* and his western Arctic-Bering Sea *alpinus* to be one and the same group which I call the northern dolly varden or northern *S. malma*.

In the northern part of its range (Beaufort Sea drainages), the northern dolly varden comes in contact with the eastern Arctic *alpinus*. The northern dolly varden is typically anadromous here and the eastern Arctic *alpinus* is a resident lacustrine fish. The northern dolly varden also exists as resident stream stocks, typically isolated in small spring-fed streams inland to the Brooks Range in both coastal and Yukon River tributaries (McCart & Craig 1973, Morrow 1973, McCart & Bain 1974). Morrow's "new species", *Salvelinus anaktuvukensis* (Morrow 1973), represents northern dolly varden populations isolated in small stream habitat in the Brooks Range.

No documented example is known of sympatric occurrence of northern and southern *malma*. Morrow (this volume) found populations of northern and southern *S. malma* and *S. alpinus* (Bristol Bay-Gulf Alaska group) in the Yukon River basin but all are allopatric. McPhail (1961) presented data on the *S. alpinus* in Aleknagik Lake and on the northern dolly varden in a stream tributary to the lake (Hansen Creek). Thirty specimens of dolly varden from Hansen Creek had 19–24 (21.9) gill rakers, 66–70 (67.6) vertebrae and 21–30 (26.7) pyloric caeca. Morrow (this volume) lists a gill raker count of 17–19 (18.6) for five specimens from Aleknagik Lake. No vertebrae counts are given for these specimens and a larger sample from this Aleknagik Lake population would be necessary to confirm the occurrence of the southern form of *S. malma* with the northern form and with an *S. alpinus* population in the Aleknagik watershed. Previously (Behnke 1972) I mentioned the occurrence of a *malma* with 65–69 (66.9) vertebrae and 20–24 (21) gill rakers in Willow Creek, a tributary of the Susitna River, south of the Alaska Range, near Anchorage, Alaska, which is within the distributional range of the southern *malma*. Morrow (this volume) points out that headwater stream transfers have allowed fish to pass from coastal drainages into the Yukon and from the Yukon to the Susitna. The significant point here is that the northern form has penetrated into the range of the southern form and has maintained its integrity and was not "absorbed" into the southern form by hybridization. The taxonomic status of *Salvelinus* in the whole Susitna drainage is not known in relation to the distribution and possible sympatric occurrence of the two forms of dolly varden. The charr from most of the vast network of Alaskan waters are essentially unstudied. Undoubtedly, many more examples will be found of sympatric occurrence between *malma* and *alpinus* and probably between the two forms of *malma*.

The significant conclusion that can be drawn from the Alaskan charr data of McPhail (1961) and Morrow (this volume) is that there are two distinct forms of *S. malma* and two less distinct forms of *S. alpinus* occurring in Alaska and no population yet examined, appears to be the result of hybridization between any of the four groups. The southern *malma* is distinct from the northern *malma* in its lower numbers of vertebrae and gill rakers (63–64 and 16–18 vs. 66–68 and 20–23). Both groups of *malma* consistently differ from any *alpinus* population in pyloric caecae number (25–30 vs. 40–50) and the two groups of *alpinus* differ in gill raker number (23–25 vs. 25–30). The evidence clearly indicates an earlier separation resulting in *S. malma* and *S. alpinus* (early pleistocene or before) and a later segregation in both *malma* and *alpinus* which gave rise to the two groups in each species present today in Alaska. The map of McPhail & Lindsey (1970, Fig. 2) showing maximal extent of the last glaciation and glacial refugia, along with discussions of isolation and postglacial dispersal of several arctic fishes, provide a logical explanation of the origin of the two forms of *malma* and the two forms of *alpinus*.

The evidence from the above discussion favors the recognition of separate species for the arctic charr and the dolly varden charr. If the names I have used – *S. malma* and *S. alpinus* – for the Alaskan charr are actually the correct names depends on the relationships of the northern dolly varden to the charr of Kamchatka (type locality of *malma*) and of the arctic charr of Alaska (both groups) to the charr named "*Salmo alpinus*" by Linnaeus in 1758 from "Swedish Lappland".

The northern dolly varden of North America is virtually identical to the anadromous charr of Kamchatka in numbers of vertebrae, gill rakers and pyloric caeca. This close relationship is supported on zoogeographical grounds by comparing the postglacial dispersal and present distribution of anadromous Pacific salmon of the genus *Oncorhynchus*. The chum salmon, *O. keta*, and the pink salmon, *O. gorbuscha*, have a distribution almost identical to the charr I recognize as *S. malma* (all forms); from Japan to the Lena River in Asia and from the Sacramento River to the Mackenzie River and North America.

14.414 *Areas of contact in Asia*

An obvious area where contact between the northern and southern groups of *S. malma* occurred is the Aleutian Islands, a long string of islands extending in an arc across the north Pacific from the Alaskan Peninsula about two-thirds the distance to Kamchatka. The eastern Aleutian Islands, nearest the Alaska Peninsula apparently have the southern dolly varden (Morrow, this volume, Cavender 1978). The western Aleutian Islands may have a charr representing introgression between the northern and southern *malma* characterized by 19–20 gill rakers and 64–65 vertebrae (Morrow, this volume and personal data). The Commander Islands off the east coast of Kamchatka apparently has a charr more further introgressed by the northern form. Savvaitova & Maksimov (1975) published data on the charr of Bering Island of the Commander group. The gill raker number, 20–24 (21.8) is similar to Kamchatkan anadromous charr, but the vertebrae counts of 63–68 (64.5) are intermediate.

When two closely related groups such as the northern and southern dolly varden come into contact without sterility barriers to prevent hybridization, the choice of sympatric occurrence with reproductive isolation or hybridization is decided by the environment. If niche diversity is sufficient to favor the maintenance of two ecologically discrete stocks then natural selection will act to enforce reproductive isolation by negative selection against hybrids. The small watersheds on the Aleutian Islands probably are not sufficiently large and diverse to allow sympatric occurrence of both the northern and southern dolly varden – but Aleutian charr have been only superficially examined to date.

As mentioned, the "southern dolly varden" of the Far East consists of two main groups based on number of vertebrae and gill rakers. The most divergent form with 16–18 gill rakers and typically 58–59 vertebrae is associated with Honshu Island, Japan, and the Kuril Islands (Oshima 1961, Savvaitova & Movchan 1973, Maekawa 1977). Savvaitova (this volume) mentions a "continuous clinal variability of characters" in the Far Eastern charr. There is no published evidence to support her view. Savvaitova's own data demonstrate a sharp break between the charr of Kamchatka and the Kuril Islands immediately to the south, in 6–8 vertebrae and 2–5 gill rakers without any clinal transition between them.

The other southern group of *malma* in the Far East is associated with Sakhalin and Hokkaido and the Asiatic mainland south of the Amur River. The higher number of vertebrae (61–63) and gill rakers (20–22) is likely associated with introgression from the northern form. Further studies may demonstrate a rather broad introgression between the two southern forms. Maekawa's (1977) data shows two stocks of anadromous *malma* from the west coast of Hokkaido with mean values of vertebrae of 60 or less. There is no known example of the southern form(s) of *malma* occurring with *S. alpinus* in Asia. As previously discussed, the "*miyabe*" charr of Lake Shikirebetsu, Hokkaido, has a mean number of gill rakers of 25.7, typical of *alpinus* and occurs sympatrically in the lake with a typical anadromous *malma*, but its vertebrae number is similar to Hokkaido *malma*. The question concerning the true relationships of the Lake Shikirebetsu charr remains open. Is it a highly specialized lacustrine form derived from the same ancestor of the Hokkaido *S. malma* or has it at least been influenced from introgression from *S. alpinus* during a period of former contact?

In Kamchatka and the northern part of the Okhotsk Sea (north from Amur River) the northern (type) form of *S. malma* is found. This charr typified by 66–68 vertebrae, 20–23

gill rakers and 20–30 pyloric caeca, extends northward around the Chukotsk Peninsula to the East Siberian Sea. The problem regarding the validity of *S. malma* concerns the charr of this area from Kamchatka to the Lena River where *S. alpinus* and *S. malma* would be expected to come into contact.

Barsukov (1960) studied Chukotsk charr and from the variability found in the charr of Lake Estikhet, near Providence Bay in southern Chukotsk and charr from a lake and in the sea at Lavrent (Lawrence) Bay in eastern Chukotsk, he concluded there were no consistent differences between *S. alpinus* and *S. malma* and *malma* should be considered a synonym of *S. alpinus*. Since then, Savvaitova and most Soviet authors have followed Barsukov and treated *malma* as a synonym of *S. alpinus*. The three samples of Chukotsk charr examined by Barsukov do not differ much in number of gill rakers or vertebrae (mean values of 23.1–23.7 and 67.6–68.9 respectively) but the average pyloric caecal number is 26.4 (typical *malma*) for the Lavrent anadromous charr, 46.6 (typical *alpinus*) for the charr from a lake near Lavrent Bay and 36.6 (intermediate) for the Estikhet charr. However, I recently received two reprints from I. A. Chereshnev of his latest publications on Chukotsk charr (Chereshnev 1978a, 1978b) and detailed personal communication. Chereshnev examined a series of specimens from Lake Estikhet and found 22–28 (25.0) gill rakers and 33–51 (42.0) pyloric caeca. He also found a similar charr (typically 24–27 gill rakers and 35–50 pyloric caeca) in rivers of the Peninsula where it is sympatric with typical northern *malma* characterized by 21–23 gill rakers and 20–23 pyloric caeca. The spotting and coloration of the dolly varden and arctic charr of the Chukotsk Peninsula are quite distinct. Chereshnev (1978a) found no overlap in the numbers of spots below the lateral line between 157 anadromous dolly varden and 130 anadromous arctic charr. He also noted that the arctic charr spawns in lakes and the dolly varden in streams. The shape of the gill rakers is consistently different: short, blunt, and curved in dolly varden, but long and attenuated in arctic charr.

Kaganovsky (1955) described a new species for the anadromous charr he found in Lake Achchen, near Providence Bay. The diagnosis of *Salvelinus* "*tarenetzi*" of L. Achchen included 23–25 gill rakers and 32–42 pyloric caeca. Chereshnev (1978a) verified that both anadromous dolly varden and anadromous arctic charr are sympatric in Lake Achchen where each is recognized by the common names, "kimkhyn" for the dolly varden and "lyginnen" for the arctic charr. Chereshnev examined 25 specimens of the artic charr from Lake Achchen and found 24–28 gill rakers and 34–47 pyloric caeca. In 1964, I examined the three specimens (types?) of "*S. taranetzi*" of Lake Achchen in the collection of the Zoological Institute of the Soviet Academy of Sciences, Leningrad (32104), and counted 24, 26 and 28 gill rakers. The rakers are very long and fine, typical of *S. alpinus*. Also at the Zoological Institute of the Soviet Academy of Sciences in Leningrad, I examined 14 specimens of *Salvelinus* from Lake Estikhet (35493 and 35492a) which were discussed by Barsukov (1960). My gill raker count varied slightly from Barsukov's (22–29 [24.0] vs. 19–29 [23.7]). I would point out that I count every gill raker including all rudimentary rakers which are often not counted by Soviet ichthyologists. If rudimentary gill rakers are not counted, differences in total number will be found between young and adults of the same population because the rudimentary rakers in small fish (ca. 75 mm–150 mm) typically develop as the fish grows.

One specimen among the collection from Lake Estikhet is highly distinctive from the other 13 specimens. This specimen of 299 mm standard length, is of a darker, almost purple color, the maxillary is narrower, the teeth on the head of the vomer are well separated from the palatine teeth (essentially continuous in the other 13 specimens), the head is relatively longer with a more acute snout and the scalation is much finer (more numerous scales). I counted 47 scales above the lateral line in the specimen (vs. 37–41) in the other 13 charr from L. Estikhet and 30 scales from the origin of the adipose fin to the lateral line (vs. 21–27). Scale counts on *Salvelinus* are notoriously difficult to make with accuracy and scale counts made by two workers on the same sample of specimens will not likely agree, but counts made by the same person, if in error, should be consistent in this error and thus comparable.

It is possible that this "aberrant" specimen in the Lake Estikhet collection was inadvertently mixed from another collection during previous examinations. If not, there is little doubt in my mind that two distinct and reproductively isolated stocks exist in Lake Estikhet. They may not differ in most meristic characters (the "aberrant" specimen has 24 gill rakers), but my evaluation suggests considerable genetic differentiation is represented between this one specimen and the other 13 specimens in the collection from Lake Estikhet.

Certainly the last glacial period particularly the existence of the Bering Land Bridge with its terrestrial connection between the Chukotsk Peninsula of Asia and the Seward Peninsula of Alaska would suggest similar pairs of *alpinus* and *malma* should be found in some lakes of the Chukotsk Peninsula and some lakes of western Alaska. This, indeed, now appears to be true. The anadromous dolly varden seems to be essentially identical from Kamchatka, the Okhotsk Sea, throughout the Chukotsk Peninsula, and from the Alaskan Peninsula to the Mackenzie River. An arctic charr, typically characterized by 24–27 gill rakers, 35–50 or more pyloric caeca and 65–70 vertebrae, has essentially the same distribution. This form of arctic charr occurs as lacustrine stocks in Kamchatka and Alaska and as both lacustrine and anadromous stocks in waters of the Chukotsk Peninsula.

The genetic affinities between the arctic charr associated with the Bering Sea and Chukotsk Sea drainages and the charr of the type locality of *S. alpinus* (northern Scandinavia) must be more authoritatively determined before a correct classification can be made.

Savvaitova (this volume) believes that the Bering Land Bridge separated "alpinoid" charr from "malmoid" charr, but this belief contradicts her statements to the effect that all diversity in the *S. alpinus* complex occurred in the last 10 000 years. The origin of the Bering Land Bridge is much older and it was already submerged more than 11 000 years ago (Walters 1955).

Savvaitova (1961) presented data from three populations of the East Siberian Sea drainages, west of the Chukotsk Peninsula and east of the Kolyma River. The charr from a lake on Aion Island averaged 22.5 gill rakers, 66.7 vertebrae and 41.5 pyloric caeca. From a lake near the sea in the Chaunsk region these values were 23.4, 69.2 and 37.0. An anadromous stock in the Chaunsk region has 23.5, 68.3 and 33.6. These data indicate that in the area of Chukotsk to the Kolyma River, charr are not readily assigned to *malma* or *alpinus* on the basis of numbers of gill rakers and pyloric caeca, however, I will reserve my opinion on the charr of the Chaunsk region until they are more thoroughly studied. Chereshnev wrote to me that he plans to initiate such studies this year and also plans to include a study on the taxonomy of the charr of the Anadyr River basin, south of the Chukotsk Peninsula.

A geographical demarcation limiting the westward extent of *S. malma* distribution west of the Chukotsk area can not be made on the present data (that is, the boundary, west of which only *S. alpinus* occurs). I know of no taxonomic data on charr from the Kolyma River drainage except for the three specimens with 31–32 gill rakers representing a relict population of *S. alpinus* from Lake Darpir in the headwaters of the drainage. The anadromous and resident charr of the lower Kolyma are expected to be similar to the charr of the lower Indigirka River and lower Lena River drainages which can be considered as *S. alpinus* on the basis of a trend for consistently higher gill raker numbers (23–25) and more numerous pyloric caeca, typically 40 or more. The great variability of charr populations in lakes of the Lena delta region has been cited by Savvaitova (1976) as an example of rapid evolution by *S. alpinus* because these thermokarst lakes are of recent origin. It seems more likely to me that post-glacial mixing of divergent groups produced highly heterozygous stocks so that no two lakes were settled by an identical ancestor.

Thus, *S. malma* is represented by two well-defined groups in North America with examples of both groups occurring sympatrically with *S. alpinus*. In Asia, from the Chukotsk Peninsula southward, an analogous pattern of diversity occurs except that the southern dolly varden of Asia is differentiated from the southern dolly varden of North America and some introgression between the northern and southern forms may have occurred in Asia resulting in some intermediacy in the charrs of Hokkaido and Sakhalin.

14.415 *Groups of arctic charr,* S. alpinus

The charr from the area of the Indigirka River drainage (western section of East Siberian Sea) to the Lena River drainage (eastern Laptev Sea) are assigned to *S. alpinus* on the basis of typical values of 23–25 gill rakers and 40 or more pyloric caeca. I would call attention to a charr found in Lake Ozhogino in the Indigirka River basin, in which Shaposhnikova (1971, Fig. 1) illustrates a highly distinctive vomer with massive teeth. A charr population highly differentiated from other populations within a particular geographic group of *Salvelinus*, suggests a relict of a distinct evolutionary divergence which has been replaced in surrounding waters within the region. If this is the case, then the question becomes: do other populations of this same evolutionary line persist in any other regions of the Holarctic?

West of the Lena River, the Taimyr Peninsula region is an area of great significance for *Salvelinus* taxonomy. The charr stocks, both anadromous and lacustrine, are characterized by high gill raker numbers (24–32) and some unusual charr evidently specialized for deep-water lacustrine life occur sympatrically with "normal" charr.

Previously (Behnke 1972) I discussed the Taimyr charrs and stated that the lacustrine, deep-water charr of Lake Taimyr, could be recognized as a species, *Salvelinus taimyricus*, on the basis of imputed genetic differentiation interpreted from its distinctive morphology and its sympatric occurrence with the typical large (to 14 kg) charr. The geological and climatic history of the Taimyr region with interior pluvial lakes for refugia during the marine transgression period, interconnections with contiguous drainage basins, Baikal elements in the present fauna, and the great diversity of whitefishes (*Coregonus*), provide many clues to explain the origin of the present charr diversity. Concerning *S. taimyricus*, I (Behnke 1972) wrote: "Because of the relatively brief existence of the present lake Taimyr and the marked differentiation of this charr, it is doubtful that this strictly lacustrine form had an autochthonous origin in Lake Taimyr in the past few thousand years. It would not be surprising if future investigations find this same charr in the Norilsk lakes of the Pyasina River basin." Thus, the recent publication by Savvaitova *et al*. (1977) on the deepwater charr of Lake Kapchuk (one of the Norilsk lakes) where the deepwater charr is sympatric with a "normal" charr, was read with great interest. Another deepwater charr, sympatric with "normal" charr was described from Lake Bolshoye Shchuchye, tributary to the Ob River (Amstislavsky 1976). If the deep-water charr of the Norilsk lakes and Lake Bolshoye Shchuchye share a monophyletic origin with *S. taimyricus*, then *taimyricus* should be recognized as a valid species. The high gill raker number ranging from 24–33 is characteristic of *Salvelinus* distributed from the Khatanga to the Yenisei river drainages. Both anadromous and "typical" lacustrine charr of this area are characterized by a long maximum life span (aged to 26 years), highly predacious feeding habits and a large maximum size (to 15 kg). These life history characteristics are similar to the eastern arctic charr of North America (also with similar gill raker numbers) and further indicate a common origin and relatively recent separation of the Taimyr *Salvelinus* and the eastern North American arctic charr.

Charr with about 25–30 gill rakers extend westward to the mouth of the Ob River. Rudakova (1941) found 24–31 (28–29) gill rakers in charr from two lakes, a river and in the sea of Gydansk Bay, between the mouth of the Yenisei and the mouth of the Ob. In the western Kara Sea-Nova Zemlya area a transition toward lower (23–26) gill rakers occurs. Data are sparse on large samples from specific localities but it appears that the charr associated with the Barent Sea is similar to the western Kara Sea, with, perhaps, slightly fewer gill rakers (21–25) (Kolyushev 1971, Berg 1948, and personal data). In this area, however, there occurs stocks with decidedly lower gill raker counts (18–21). Berg (1948) mentioned that six specimens from the Zhemchuzhnaya River, tributary to Chosna Bay of Kanin Peninsula (Barent Sea) have 18–21 gill rakers. At the Zoological Museum, University of Moscow, I examined two charr collected from the Bugrentse River on the Kanin Peninsula (P-3951) with 18 and 19 gill rakers. These charr with 18–21 gill rakers associated with the Kanin Peninsula area are probably relicts of a group which became largely introgressed by the charr with more numerous gill rakers of the Taimyr

region when the two groups came into contact.

I will mention one other highly significant charr specimen in the Moscow collection (P-5412) which is labeled from the Irtish River, a tributary of the Ob River, about 1 000 km from the sea. This specimen has 21 gill rakers.

14.416 *Diagnosis of* S. alpinus alpinus

Before the polytypic species, *S. alpinus*, can be authoritatively arranged into subspecific groups, the characteristics of the charr of the type locality ("Swedish Lappland") must be known to define the limits of *S. alpinus alpinus*.

Although the geographical boundaries of "Swedish Lappland" are ill defined, I would include those charr from northern Sweden, northern Norway, the Kola Peninsula and northern Karelia of the U.S.S.R. in both the drainages to the Gulf of Bothnia (Baltic Sea) and the drainages to the Barent Sea. I lack taxonomic data on anadromous charr of the Barent Sea in this region, but will provisionally assume their characteristics are similar to lacustrine populations. Formerly (Behnke 1972) I discussed charr specimens I examined from four lakes in northern Sweden in the Gulf of Bothnia drainage. A total of 48 specimens from eight stocks representing sympatric pairs from each of the four lakes were examined. The variability encompassed in these Swedish charr can provide a relative confident diagnosis of *S. alpinus alpinus* of the "type locality" because their range of variability essentially encompasses the taxonomic data I have on lacustrine charr stocks of the Kola Peninsula, Karelia and Norway. Vertebrae numbers are 61–66, mostly 63–64; gill rakers 21–28, mostly 23–26; pyloric caeca 29–57, with mean values from 39–50; scale counts in lateral series (counted two rows above the lateral line) 176–223, with mean values of 185–213; scale counts above lateral line 34–42 with mean values of 37–40; branchiostegal rays 9–12, typically 10–11; basibranchial teeth present in all specimens ranging from 3–33 with mean values of 6–19.

As discussed in my 1972 publication, the charr of this region (Scandinavia, Kola, Karelia) are noted for numerous examples of sympatric and reproductively isolated stocks occurring in many lakes. Because the taxonomic characters are so similar between sympatric pairs (often more similar between sympatric pairs than to any population outside of the lake), I find no evidence that the sympatric stocks of this region represent two or more species of ancient origin such as *S. alpinus* and *S. malma* or even of diverse *alpinus* groups such as the charr of the Kanin Peninsula with 18–21 gill rakers and the Taimyr charr with 26–32.

My assumption that the charr of "Swedish Lappland" can be considered one highly variable group on the basis of their characters simplifies the delineation of *S. alpinus alpinus*, but also raises the dilemma of having two or more stocks of the same subspecies living sympatrically with reproductive isolation.

Sympatric charr stocks with slight morphological differentiation are typically associated with recently glaciated areas where opportunities existed for numerous stocks of a common ancestor to become isolated for perhaps a few thousand years, sufficient to initiate slight temporal or spatial differences in spawning and slight ecological differences so that when the isolated stocks came into contact where niche diversity favored the maintenance of two or more discrete populations, reproductive isolation was maintained and reinforced.

The Gulf of Bothnia-Baltic Sea region is such an area. Also transfer of fishes (undoubtedly including ancestral *Salvelinus*) occurred between the White Sea and Baltic Sea.

The northern Scandinavian charr (type of *S. alpinus*) is associated with recently glaciated areas. A basic question is: what is the origin of these charr and does this same group (of common ancestry dispersing in postglacial times or persisting as relicts in a glacial refuge area) occur in other regions?

It would appear logical on the basis of taxonomic characters that *S. alpinus alpinus* had its origin from a past hybridization between the charr with the highest number of gill rakers (26–32) now found in the Taimyr Peninsula region and the Alpine lakes of Europe

and the *S. alpinus* group with the lowest number of gill rakers (18–21) now associated with the Kanin Peninsula of the Barent Sea. Such mixing may have occurred in the Baltic Sea basin.

The southernmost population of *Salvelinus* in Sweden occurs in Lake Vättern. On the basis of examination of a single specimen of L. Vättern charr at the British Museum (62, 8–14, 1), it is evident to me that the earliest movement of *Salvelinus* into the first inhabitable waters of Sweden upon glacial retreat, was not from the group of *Salvelinus* now inhabiting the Gulf of Bothnia drainages of northern Sweden (*S. alpinus alpinus*), but from the *Salvelinus* group occurring in the Alpine lakes of Europe with 26–32 gill rakers (*S. alpinus salvelinus*). The Lake Vättern charr specimen has 29 gill rakers. None of the 48 charr specimens I examined from northern Swedish lakes have such a high count.

A few years ago, Dr. Gunner Naevdal of the Institute of Marine Research, Bergen, Norway, sent me 14 charr specimens from three lakes in southern Norway, near Bergen (North Atlantic drainages). Dr. Naevdal pointed out that the lacustrine charr of Norway (North Atlantic drainages) undoubtedly came from anadromous ancestors in relatively recent times. Whitefish of the genus *Coregonus* are not native to these lakes and the charr lakes in southern Norway are at low elevation, near maximum postglacial marine transgression. These Norwegian charr specimens have 22–27 gill rakers, with modes of 24–25 – evidently derived from the same ancestral group as the Gulf of Bothnia *Salvelinus*. This same group with 21–28 gill rakers (*S. alpinus alpinus* in a broad sense) also invaded Great Britain and Ireland from the sea where they now exist only as strictly lacustrine populations.

The charr of Lake Coomarsaharn, Ireland, is evidence that an ancestral group of *Salvelinus* with high numbers of gill rakers also once had access to the British Isles, but have persisted in only one lake, and disappeared from between intervening areas between Lake Coomarsaharn, Ireland, and the European mainland. I have estimated the gill rakers number of Coomarsaharn to be about 28–32 whereas other charr of Great Britain and Ireland have about 21–26 gill rakers (Behnke 1972). The presence of populations of a cisco type of whitefish, typical of the arctic cisco, *Coregonus autumnalis*, in some Irish lakes along with the charr of Lake Coomarsaharn is evidence of a westward movement of salmonid fishes from the Arctic Ocean to the British Isles via the sea in postglacial times. Perhaps the lakes were already inhabited by earlier invaders of *Salvelinus* and *Coregonus* from Scandinavia and only in a few lakes in Ireland were these elements of Arctic salmonid fauna able to persist.

The charr of Iceland most likely are derived from the charr of Scandinavia-Great Britain, which I will consider here as an inclusive group, *S. alpinus alpinus*. Icelandic charr may also have been influenced by invasion from the Greenland area by a charr probably representing the eastern Arctic North American group of *S. alpinus* with about 25–30 gill rakers. Although land bridge connections once occurred from northern Europe to Iceland, the absence of *Coregonus* in Iceland indicates *Salvelinus* invaded from the sea. Comprehensive studies of Icelandic charr have never been attempted.

Fridriksson (1939) published on the charr of Lake Thingvalla (Thingvallavatn), Iceland. Fridriksson believed four sympatric stocks of *Salvelinus* occur in L. Thingvalla which he called "murta", "bleikja", "svart murta" and "urridi". Slight, but significant differences in vertebrae numbers were found (62.27 for "svart murta", 62.75 for "bleikja" and 63.09 for the "murita" – only a few specimens of "urridi" were studied but they had only 60–61). Differences were found in the age and growth of the "bleikja" and "murta". The "bleikja" has more rapid growth, and a longer maximum life span.

Curious to learn more about the charr of L. Thingvalla, I once arranged for Dr. James Adams (presently fisheries biologist, Pacific Gas and Electric Co.) to send me 52 specimens from this lake during a visit to Iceland. I noted six specimens differed from the rest by a more blunt head with a shorter, broader maxillary (evidently "murta"). The 6 specimens have 23–26 (24.7) gill rakers and the other 46 specimens have 23–28 (26.7) gill rakers. Vertebrae counts on all specimens ranged from 58–63 (61.8) which is the lowest I know of in *S. alpinus*.

I have data on two British Museum charr specimens from Lake Myvatn, Iceland. These specimens have 25 and 28 gill rakers. Lake Myvatn is also reported to have sympatric stocks (Lamby 1941).

The systematic status of the *Salvelinus* of Iceland is open to question. Iceland certainly is a significant area deserving intensive study for a better understanding of *Salvelinus* systematics in general and the origin of sympatric stocks in particular.

In northeastern North America, *S. alpinus* has been largely replaced in the southern part of its range by *S. fontinalis*. South of the Gulf of St. Lawrence, *S. alpinus* occurs relatively rarely as relict lacustrine populations. In southern Quebec, north of the Gulf of St. Lawrence, Newfoundland and the southern Labrador, *S. fontinalis* is also dominant and *S. alpinus* occurs sporadically.

These southernmost populations of *S. alpinus* in eastern North America, however, are not relicts of the Arctic Ocean *S. alpinus* (eastern Arctic *alpinus*), but, I believe, represent an *S. alpinus* dispersal from northern Europe via the Atlantic Ocean (probably with the Atlantic salmon, *Salmo salar* and the smelt, *Osmerus eperlanus*).

Three species were described for the eastern North American charr: *Salvelinus oquassa*, the blueback charr of Maine; *S. aureolus*, the golden charr of Sunapee Lake, New Hampshire, and *S. marstoni*, the red charr of Quebec. All of these charrs are essentially similar in their taxonomic characters and can be considered in the same subspecies (*S. a. oquassa*). The slight difference between populations and what would be expected from isolation of several populations of a common ancestor during the last 5 000–8 000 years. These charrs are characterized by 18–24 gill rakers, typically 20–21; 62–66 vertebrae, typically 63–65; and 30–50 pyloric caeca, typically 38–42 (Kendall 1914, Qadri 1974, Vladykov 1954, and personal data).

Thus, it seems highly probable that the two forms of *S. alpinus* in eastern North America represent dispersals in opposite directions with the eastern Arctic form moving from Asia, eastward across the Arctic Ocean to North America where it is now largely restricted east of the Mackenzie River, and the eastern North America form dispersing across the North Atlantic from northern Europe. The two forms have come in contact in postglacial times in the region of Labrador. Backus (1957) presented some limited data on Labrador charr. Gill raker numbers on samples from four populations in northern Labrador are 22–27 (typically 24–25) which is what would be expected from past hybridization between an ancestor with 20–21 gill rakers and one with mean values of about 27–28. Andrews & Lear (1956) also indicate an intermediate number of vertebrae in northern Labrador charr (means of 65.4 to 66.3 in five samples) which would also be expected if an ancestor averaging about 67 vertebrae (east Arctic *alpinus*) was introgressed by a form averaging about 64 (*S. a. oquassa*).

Sympatric occurrence between the two forms of *alpinus* in eastern North America has not been reported, but based on what has occurred in other regions of the Holarctic, it might be expected that sympatric stocks will be found in Labrador differing in vertebrae and gill raker numbers and representing a population of east Arctic derivation and a population of North Atlantic derivation (*oquassa*). One factor which may act against sympatric occurrence of *S. alpinus* in Labrador is the presence and usual dominance of the brook charr, *S. fontinalis*. This is, niche diversity would have to accommodate three *Salvelinus* populations – one *S. fontinalis* and two of *S. alpinus*.

14.417 *Recognition of taxa in the* S. alpinus *complex*

The discussion on divergence in the *alpinus* complex leads to the other aspect of taxonomic problems – that of correct nomenclature. It is premature to discuss recognition of species and subspecies with any authority, but this section is designed to serve as an outline to focus attention on certain groups of potential significance when future studies are carried out to better evaluate the actual relationships within the complex and construct a phylogeny delineating the more ancient and more recent branching points.

I have evaluated the data (admittedly, very inadequate in many cases) in an evolutionary framework to discuss "groups" assumed to be of common origin (mono-

phyletic) characterized by a uniformity of characters and distribution, differing from other such "groups" by consistent differences in characters and distribution patterns. Thus, some of the "groups" I discuss as subspecies may encompass a large geographic area and include a high degree of genetic variability often with sympatric stocks of the same subspecies. I have no objection to anyone recognizing 15 different subspecies for the charr of Great Britain – that would be a matter of individual preference. Such "splitting" may have a practical purpose to help protect or enhance the survival of some populations by designating them as unique taxa and calling attention to them. I would only point out that from my interpretation, all the charr of Great Britain have been derived from a group of charr I recognize as *S. a. alpinus* during the last 10 000 years.

Within a reference frame of geological time, I will assume that what I recognize as subspecies are groups whose origin, in most instances, is no later than the last glacial period (isolated and diverging in a glacial refugium) and what are recognized as species are of much earlier origin, perhaps associated with the first or second period of pleistocene glaciation. These assumptions are highly tentative and provisional. It is well known that rates of morphological divergence often have litte direct relationship to the geological time scale. It is important, however, when techniques are tested, such as "protein clocks", to better quantify genetic relationships and estimated timing of phylogenetic branching sequences, that investigators have some guidelines on what groups potentially have the greatest information to be extracted to answer specific questions. For this reason I am providing an outline of taxa I provisionally recognize to give future investigators an opportunity to "falisfy" my proposed phylogeny.

The arctic charr, *Salvelinus alpinus* – When a species is subdivided into subspecies, the nominate subspecies must be the form of the type locality. Thus, a charr characterized by about 21–27 gill rakers, in northern Sweden is *S. alpinus alpinus*. Charr representing this same group also occur in waters of the Kola Peninsula, Karelia and Norway and gave rise to all of the charr of Great Britain and Ireland, except for the charr of Lake Coomarsaharn, Ireland. The *Salvelinus* east of the Taimyr region from the Lena River to the Indigirka River and probably the Kolyma River have approximately similar values of gill rakers, pyloric caeca and vertebrae as *S. alpinus alpinus*, but this may not be due to common ancestry but rather from introgression. The two hypotheses on the origin and relationships of these charr should be tested when refined techniques associated with a high degree of expertise and an understanding of *Salvelinus* systematics will allow such testing. If separate subspecific recognition is used for this group of charr from the area of the Lena River to the Kolyma River, two names, both given in 1932 must be considered. *Salvelinus czerskii* described by Dryagin in Berg's 1932 edition of the freshwater fishes of the U.S.S.R. for a charr from Lake Agarpypa in the Indigirka basin, and *S. jacuticus* named by Borisov in 1932 in Izdanie Akademii Nauk, for a charr from Lake Aranastakh in the Lena River delta, probably represent the same group. I examined the type specimens of both taxa and observed no differences to indicate origins from different ancestral groups. If this group of charrs is recognized as a subspecies, the validity of *czerskii* vs. *jacuticus* depends on which publication appeared first in 1932. I would reserve judgement on the subspecific status of the charr of Iceland because of the opportunity for invasion by two groups of *S. alpinus* and the occurrence of divergent, sympatric stocks in Lake Thingvalla. Iceland should be considered a high priority area for future studies.

The lacustrine charr of the Alpine lakes of Europe with 26–32 gill rakers are recognized as *S. alpinus salvelinus*. As with *S. alpinus alpinus* in Sweden, many Alpine lakes have two sympatric stocks, a normal or predatory form ("Normalsaibling" or "Wildfangsaibling") and a dwarf form ("Schwartzreiter"). As previously mentioned, I believe the charr native to Lake Vättern, southern Sweden, is *S. alpinus salvelinus* and not *S. alpinus alpinus*.

The "Tiefssesaibling" of the Bodensee and perhaps other alpine lakes is a highly divergent charr which I recognize as *S. profundus*. *S. profundus* will be discussed in more detail later.

The charr of the Taimyr area and interior Siberian lakes with 26–32 or more gill rakers may be of common ancestry with the Alpine charr, but until more data on genetic affinities are available, a separate subspecies should be recognized for this group. *S. alpinus erythrinus* is the oldest available name for this group if the charr with disjunct distribution in interior lakes are of the same common ancestry with the Taimyr charr. On zoogeographical grounds and similarity of characters I see no reason to doubt such close affinities. The charr in lakes of the Okhot River basin, *S. alpinus neiva*, are part of this group. The "*neiva*" charr appears to be very similar to the charr in Lake Darpir, in the headwaters of the Kolyma River and probably had its origin from a headwater transfer from the Kolyma basin into the Okhot basin.

This same pattern of disjunct distribution of this group of charr (*S. a. erythrinus*) occurs in both Asia and North America, indicating a former continuous distribution. This charr was replaced by a different group of *alpinus* in the area of the Lena River to the Kolyma, occurring as relict lacustrine populations in headwaters of the Lena and Kolyma, and was replaced by *S. malma* in Alaska eastward to the Mackenzie River, but again occurring in headwater lakes in the Beaufort Sea drainages west of the Mackenzie River.

If the charr with the numerous gill rakers in North America (eastern Arctic *S. alpinus*) is designated with its own subspecific name, this name probably would be *S. alpinus stagnalis*, but the use of *stagnalis* should be reserved until the Greenland *Salvelinus* are better defined.

Besides the common charr of the Taimyr region, which can be provisionally included as *S. a. erythrinus*, a charr with a unique morphology occurs in Lake Taimyr. If this charr represents an ancient evolutionary line long separated from other Taimyr charr, then it should be recognized as *S. taimyricus*. *S. taimyricus* is discussed later.

Besides the eastern *S. alpinus* which I believe is closely related to *S. a. erythrinus*, two other groups of *S. alpinus* express divergence in characters associated with different glacial refugia and dispersion patterns and could be recognized as subspecies. I recognize the eastern North American *alpinus*, occurring mainly as disjunct relicts in the southern extreme of the range as *S. alpinus oquassa*. This group of charr is probably introgressed with the eastern Arctic *S. alpinus* in an area of contact in Labrador. Backus (1957) considered the *S. alpinus* of Labrador to be *S. a. oquassa*. The gill raker counts from Labrador samples given by Backus (22–27) are intermediate between *oquassa* (18–24) and the eastern North American arctic charr (25–32), but the pyloric caecal counts of these three Labrador samples (27–44) is lower than either of the suspected ancestral groups which could have given rise to the Labrador *alpinus*. Dr. James Morrow has provided me with some of his personal data on a sample of 17 specimens of charr from a lake near Nain, Labrador, in the collection of the U.S. National Museum (177650). These charr have 23–26 (24.5) gill rakers and 30–37 (33) pyloric caeca, according to Morrow's counts.

It is premature to speculate on the significance of the low number of pyloric caeca in Labrador charr.

A group of *S.alpinus* characterized by about 23–25 gill rakers and 45–50 pyloric caeca has been called the "Bristol Bay-Gulf of Alaska" *S. alpinus*. This charr also occurs in lakes in the Yukon River basin and, as far as known, has a strictly lacustrine life history. It occurs sympatrically with both the southern and northern subspecies of *S. malma* and is not known to intergrade with the eastern Arctic *alpinus*. No name has ever been proposed specifically for the Bristol Bay-Gulf of Alaska *alpinus*. The closest relationships appear to be with the lacustrine charr of Kamchatka in Lake Dalneye, Lake Nachikin and the lacustrine and anadromous arctic charr of the Chukotsk Peninsula (Chereshnev 1978a).

The last group of *S. alpinus* which could be given subspecific recognition to emphasize the major evolutionary divergences in *S. alpinus* is the charr associated with the Kanin Peninsula of the Barent Sea with 18–21 gill rakers. No name has ever been proposed for this charr. It is a group deserving much more attention in the future.

Tiefseesaibling *Salvelinus profundus* – When I first examined specimens of the "Tiefseesaibling" of the Bodensee, the observable degree of differentiation is such that I could not believe that the Tiefseesaibling is of the same evolutionary group as the other charr of the Alpine lakes of Europe, the "Normalsaibling", "Wildfangsaibling", etc. (*S. alpinus salvelinus*). The Tiefseesaibling occurs with the Normalsaibling in the Bodensee

and differs from the Normalsaibling in the number (20–25 vs. 27–31) and structure of the gill rakers. The most obvious difference, however, is in the general morphology and coloration. A blunt snout, subterminal jaws, large eyes and uniform dull coloration without spots or markings makes the Tiefseesaibling unique among *Salvelinus*.

I have only seen specimens from the Bodensee, but it is reported to occur in other lakes (Berg 1932, Neresheimer 1937, Brenner, this volume). Doerfel (1974) presented further data on the Tiefseesaibling, also based on specimens from the Bodensee.

I would hesitate to speculate on the origins and affinities of the Tiefseesaibling. Is it the last living representative of an ancient phylogeny in the genus? Undoubtedly, most of the uniqueness of the Tiefseesaibling is associated with selection for deep-water life; thus, the Tiefseesaibling may be quite dissimilar in appearance to its progenitor and to its closest living relative, whatever that may be.

A logical place to look for charr with the most recent common ancestry to the Tiefseesaibling would be the Taimyr region and the deepwater charr which occur in some Taimyr lakes.

The Tiefseesaibling was named "*Salmo salvelinus* var *profundus*" by Schillinger (1901). Berg (1932) recognized the species *Salvelinus profundus* (Schillinger). I also recognize the Tiefseesaibling as a valid species.

Because of eutrophication and changing fish faunas in European Alpine lakes, the Tiefseesaibling may be rapidly declining towards extinction. Historical catch data on *Salvelinus* in the Bodensee (Nümann 1972) and in Lac Leman (Laurent 1972), indicates charr occur at only a small fraction of their former abundance. It would be tragic if such a unique and interesting charr became extinct before we have an opportunity to learn more about it, particularly in relation to what secrets it holds for a better understanding of *Salvelinus* phylogeny.

Salvelinus taimyricus of Lake Taimyr – As was previously discussed, a charr with a unique morphology occurs in Lake Taimyr on the Taimyr Peninsula sympatrically with the typical large predatory charr common to the region. The degree of observable morphological differentiation between "*taimyricus*" and the "normal" charr (here grouped with *S. alpinus erythrinus*) is not as great as between the Tiefseesaibling and Normalsaibling, but nevertheless is sufficient to lead me to believe that the sympatric charr of Lake Taimyr did not diverge from a common ancestor within the past few thousand years. The main difference between "*taimyricus*" and the "normal" charr of Lake Taimyr is the distinctive deep-body, slab-sided, almost percoid morphology in *taimyricus*. The head of *taimyricus* is broad with a wide, blunt snout. The fins are greatly enlarged, relative to body size in *taimyricus* specimens compared with other Taimyr charr. *Salvelinus taimyricus* (as best as I can trace its taxonomic history) was named by Mikhin in Berg (1948, addenda to volume 1). A complete description and illustration of *taimyricus* was published by Mikhin (1955).

From my point of view, the validity of *taimyricus* as a full species depends on its degree of genetic relatedness to the common charr of the Taimyr region. Does its morphological uniqueness accurately reflect its genetic divergence? If so, *taimyricus* represents a phylogeny long separated from the phylogeny giving rise to the common charr of the Taimyr region and I would expect other populations of this phylogeny to occur in large, deep lakes as specialized deepwater forms. As mentioned, the deepwater charr, sympatric with normal charr in Lake Kapchuk and in Lake Bolshoye Shchuchye are of particular interest in this regard.

Possible sympatry between North American *S. alpinus* – In contrast to Europe and Asia, there are no well documented cases of sympatric occurrence of two or more stocks I consider as *S. alpinus* in North America, but such examples almost certainly will be found when North American *Salvelinus* are better studied. An area where the two groups of *S. alpinus* in Alaska come together (eastern Arctic group and Bering Sea-Gulf of Alaska group) is in the region of the Kuparuk River and Sagavanirktok River drainages, tributary to the Beaufort Sea. McCart & Craig (1971) reported 24–33 gill rakers (eastern Arctic group) in lacustrine charr from headwater lakes of the Sagavanirktok drainage. Morrow (this volume) presents data on a few charr specimens with 23–26 gill rakers

(Bering Sea, Gulf of Alaska group) in Campsite Lake and an unnamed lake in this same general area. Dr. Morrow kindly supplied further information on these sites. The headwaters of the Sagavanirktok River and the headwaters of the Kuparuk River are very close together and Dr. Morrow is not certain of the drainage relationships of Campsite Lake and the unnamed lake, but believes they are in the Kuparuk Basin.

I would suspect that large lakes with niche diversity in this general region will have both the eastern arctic charr representative and the Bering Sea-Gulf of Alaska *S. alpinus* representative sympatrically, with perhaps *S. malma malma* occurring as a third anadromous population.

The great variability in spotting and coloration mentioned by Backus (1957) for Labrador *S. alpinus* suggests sympatric and reproductively isolated stocks of *S. alpinus* may occur there. Introgression between ancestral groups may have already influenced the *S. alpinus* of Labrador before reproductive isolation, if present, was established. In such a situation, tracing ancestry of sympatric stocks to either the eastern Arctic North American charr or to *S. a. oquassa* may be difficult.

14.418 *Dolly varden charr,* S. malma

As has been discussed above, the dolly varden charr is represented by a few, relatively well-defined groups. As with *S. alpinus* groups, nomenclature to designate particular groups of *malma* (including the name *malma* itself) is highly provisional. Based on the characters and geographical distribution of *S. malma*, discussed in the foregoing sections, the following names are indicated for subspecies recognition of particular evolutionary groups.

Salvelinus malma malma – The common charr of Kamchatka, both anadromous and most of the nonanadromous charr, are typified by modal and mean values of 21–23 gill rakers, 66–68 vertebrae and about 25–30 pyloric caeca. At present, this is the best diagnosis for *S. malma malma*. This same group, the northern dolly varden. *S. malma malma*, occurs in the Okhotsk Sea basin to the Amur River and northward from Kamchatka to the Chukotsk Peninsula in both the Bering Sea and Chukotsk Sea drainages. *S. malma malma* occurs in Alaska, north from the Alaskan Peninsula to the Mackenzie River.

S. malma malma is sympatric with charr I recognize as *S. alpinus* in lakes of Kamchatka and Alaska and in both lakes and rivers of the Chukotsk Peninsula. In the Far East, south of Kamchatka and south of the mouth of the Amur River, two additional groups of *S. malma* are apparent. The extreme form of Honshu Island, Japan and the Kuril Islands. I recognize as *S. malma curilus* and the other form, somewhat intermediate between *S. m. malma* and *S. m. curilus* is commonly recognized as *S. m. krascheninnikovi*.

Salvelinus malma curilus – Based on data cited in earlier sections, the charr living on the Kuril Islands (at least southern Kurils) and in waters of Honshu Island. Japan, is the only charr in the *S. alpinus* complex, typically with fewer than 60 vertebrae (58–59). The gill raker numbers are low (16–18) as are pyloric caecal counts (20–30). I assume that the Kuril Islands charr and the Honshu charr are of recent common origin and for classification purposes represent a single group. The oldest name for this group is "*Salmo curilus*" given by Pallas in 1814 for Kuril charr. Hilgendorf (1876) named the Honshu charr "*Salmo pluvius*" based on specimens from near Nikko. Cavender (this volume) disagrees with such a classification and considers *pluvius* to represent a valid species with closest relationships to *S. leucomaenis*.

Berg (1948) following Taranets (1933) used the designation, *Salvelinus malma krascheninnikovi* morpha *curilus*, for nonanadromous dolly varden in the southern parts of its range in the Far East.

Salvelinus malma krascheninnikovi – On Hokkaido and Sakhalin islands and the Asiatic coast, south of the Amur River to the Yalu River, a form of dolly varden occurs with numbers of gill rakers (20–22) and vertebrae (61–63), somewhat intermediate between *S. malma malma* and *S. malma curilus*. For this group of charr, Taranets (1933)

described *S. malma krascheninnikovi*, based on populations in the southern Okhotsk Sea-Sea of Japan region.

As has been discussed, the lacustrine charr of Lake Shikirebetsu, Hokkaido, with 24–28 gill rakers, described as *Salvelinus miyabei*, is of uncertain relationships. Lacustrine charr populations with similar numbers of gill rakers in Kamchatka, I consider as derivations of *S. alpinus*, but the Lake Shikirebetsu charr has vertebrae counts (61–62) similar to southern *malma* (vs. 66–67 in Kamchatkan "*alpinus*"). The origin and affinities of *S. miyabei* are questions in need of a more critical evaluation. For the present, I would tentatively agree with Maekawa (1977) to consider *miyabei* as a subspecies of *S. malma*, but point out that Yoshiyasu (1973) found differences between the hemoglobins of *miyabei* and *S. malma* of Hokkaido.

The dolly varden in North America – The arrangement of *S. malma* in North America into northern and southern forms by McPhail (1961) must be modified. As has been discussed, McPhail's northern *malma* and western Arctic *alpinus* are the same group which, I believe, is of recent common ancestry with the common charr of Kamchatka, *S. malma malma*. *S. malma malma* in North America occurs from the northern drainages of the Alaskan Peninsula northward to the Mackenzie River. In this range it occurs sympatrically with two groups of *S. alpinus* (typically characterized by 23–25 gill rakers and 25–30 or more gill rakers), with the northern dolly varden being anadromous or a resident stream fish (sometimes lake-river) and *alpinus* as strictly lacustrine populations. In North America, the northern dolly varden is consistently differentiated from the southern dolly varden in numbers of vertebrae (typically 66–68 vs. 62–64) and gill rakers (21–23 vs. 16–18).

Southern dolly varden in North America – The major modification of McPhail's (1961) group of southern dolly varden, is the separation of the bull charr, *Salvelinus confluentus*, from *S. malma*. Although several species were described for western North American *Salvelinus*, the clear-cut distinctions between *malma* and *confluentus* were not known before the work of Cavender (1978). The southern dolly varden occurs from Oregon to the Alaska Peninsula and in the Aleutian Islands. It may have occurred sympatrically with *S. confluentus* in the McCloud River, tributary to the Sacramento River, California, according to Cavender's interpretation of museum specimens. The southern dolly varden of north America is similar to *S. malma curilus* in number of gill rakers (16–18) and pyloric caeca (20–30) but differ significantly in number of vertebrae (typically 62–64 vs. 58–59). The southern dolly varden of North America apparently represents a group long isolated from its nearest relatives of Asia and deserves subspecific recognition. Because of the presence of two species, *S. malma* and *S. confluentus*, in western North America, it is often difficult to associate many of the early names proposed to one species or the other. It is likely that all *Salvelinus* species named from the Columbia River basin represent *S. confluentus*. The earliest name I know of applicable to the southern dolly varden of North America, is "*Salmo lordii*", described by Günther (1866) for a specimen from the Skagit River of Washington and British Columbia. Before the name *S. malma lordi* is used with authority to designate the southern dolly varden of North America, it would have to be clearly demonstrated that Günther's type specimen of *lordi* is indeed *S. malma* and not *S. confluentus*. The Skagit River is tributary to Puget Sound and Cavender found museum specimens of both *malma* and *confluentus* from the Puget Sound area. Seven specimens examined by Cavender from the Skagit River, however, are *S. malma*.

As has been mentioned, there is no documented example of sympatric occurrence of the northern and southern subspecies of *S. malma* in North America and the number of vertebrae and gill rakers reported in charr of the western Aleutian Islands suggests that the two subspecies came into contact and hybridized in this region.

Morton (1970) argued against the use of subspecific recognition for North America *malma*, but he was familiar only with the southern subspecies and did not consider the group I recognize as *S. malma malma* in North America.

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14.419 *The bull char,* S. confluentus

Dr. Cavender kindly sent me a pre-publication copy of his manuscript entitled, "Taxonomy and distribution of the bull trout, *Salvelinus confluentus* (Suckley), from the American Northwest." The following discussion on *S. confluentus* is based on this manuscript (Cavender 1978).

Cavender presented detailed data on 120 specimens of *S. confluentus* from 9 localities and 88 specimens of *S. malma* (southern dolly varden) from 7 localities in western North America. He found a consistent difference between the species in general morphology. In relation to the southern *S. malma*, *S. confluentus* is characterized by a relatively longer, broader and more flattened head; a well developed fleshy knob at the symphysis of the mandibles associated with a notch formed by the premaxillaries; a relatively longer, more massive and curved maxillary; more robust and heavily denticulated gill rakers, especially in relation to the position of the denticles; eyes positioned more dorsally and a more rounded (vs. compressed) body. *S. confluentus* has a large number of branchiostegal rays: 12–15 (13.5) on the right side and 12–16 (13.9) on the left side in the 120 specimens. Cavender found 9–12 (11) and 10–13 (11.6) right and left branchiostegal rays in the 88 specimens of southern *S. malma*. *S. confluentus* was found to typically possess more mandibula pores (12–19 [15.6] for both sides vs. 10–14 [12.1]). The number of vertebrae, pyloric caeca and gill rakers exhibit broad overlap. *S. confluentus* specimens examined by Cavender have 62–67 (64.8) vertebrae vs. 60–66 (62.9) in southern *S. malma*. The tendency for slightly more vertebrae is associated with a relative increase in the number of precaudal vertebrae in *S. confluentus*, evidently an adaptation for enlarging the body cavity for predatory feeding and expansion of the stomach. Gill raker counts are 14–20 (16.6) for *confluentus* and 14–23 (18.1) for southern *malma*. Pyloric caecal counts range from 21–37 (27.8) for *confluentus* and 19–34 (26) for southern *malma*.

S. confluentus probably had its center of origin in the Columbia River basin. From there it dispersed via inland connections to headwater drainages of the Yukon and Mackenzie basins, the North and South Saskatchewan rivers (Hudson Bay drainage), and to the upper Klamath and Sacramento (McCloud River) drainages. A marine dispersal route is hypothesized to extend the known distribution of *confluentus* to the Puget Sound drainages (where it is, or once was, anadromous) and to the Fraser, Skeena and Taku rivers of British Columbia. Based on museum material, Cavender concluded that *confluentus* and *S. malma* were sympatric in the McCloud River, Puget Sound, Skeena River and Taku River. Two specimens from the Skeena River drainage are judged to represent *confluentus* × *malma* hybrids. I have collected hybrids between native *S. confluentus* and introduced *S. fontinalis* in Long Creek of the upper Klamath watershed.

Speciation and zoogeography of other salmonid fishes of western North America suggest similarities to southern *S. malma* and *S. confluentus*, particularly the divergence and dispersal of the cutthroad trout, *Salmo clarki*, represented by a coastal subspecies and several interior subspecies, and the rainbow trout, *Salmo gairdneri*, which includes a coastal group (*S. gairdneri* in a strict sense) and an interior group I have called the redband trout (Behnke 1972), which is also distributed in the Columbia River basin and in the upper Klamath and upper Sacramento drainages.

The reputation of the dolly varden charr as a rapacious predator is largely based on the bull charr *confluentus* – a case of mistaken identity. The greatest size attributed to dolly varden, 18.3 kg for Kootenay Lake, British Columbia (Hart 1973), is also based on *S. confluentus* and not *S. malma*. Much of the life history and ecological data in the North American literature attributed to *S. malma*, will have to be sorted out in view of the fact that many of the authors were working with *S. confluentus* and not *S. malma*.

A logical question concerns the relationships of *S. confluentus*. Is it most closely related to the southern form of *S. malma* or do representatives of the *confluentus* phylogeny live in Asia? Of particular significance in this regard is the "kamen golets" or stone charr of Kamchatka.

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14.420 *The stone charr of Kamchatka*

How much is yet to be learned about the systematics of *Salvelinus* in the Far East is demonstrated by the apparent widespread occurrence of a distinctive but taxonomically unrecognized group of charr commonly referred to as "stone charr". Berg (1948) cites references to stone charr from the earliest literature on Kamchatkan fishes. Citing other authors, Berg mentions reports of stone charr in the Anadyr River, north of Kamchatka and just south of the Chukotsk Peninsula, the Bystraya River of Kamchatka and repeats the observations of Pravdin that two forms of dolly varden inhabit the rivers of western Kamchatka – a short-headed, "typical" form with a shorter, pointed snout and feeble development of the premaxillary notch, and a long-headed form with a longer snout and a well developed premaxillary notch.

The most complete diagnosis of stone charr (from the Kamchatka River) is by Savvaitova & Maksimov (1970). Savvaitova (1970) described the stone charr as a solitary predator with a fusiform body characterized by a sharp rise, or "humping" behind the occiput, and an elongated, very broad, slightly flattened head, The body is black or dark gray with numerous irregularly shaped orange spots on the sides and bright spots on the dorsal fin. A "hook and notch" are very strongly developed on the jaws. Meristic values of the stone charr of the Kamchatkan River are: gill rakers 21–26 (23.2), pyloric caeca 22–35 (29.3), and vertebrae 63–67 (65.6). Savvaitova (1970) concluded that the stone charr is "strongly distinguished" from other *Salvelinus* and ecologically is more similar to the genus *Hucho*, but she considered the stone charr only as an intraspecific form of *S. alpinus*.

The description of the Kamchatkan stone charr, particularly the characteristics of the head and development of the mandibula knob and premaxillary notch is similar to Cavender's (1978) description of *S. confluentus*. The most obvious difference between the stone charr and *S. confluentus* is in gill raker (21–26 vs. 14–20). Such a difference would not be unexpected if the stone charr of Asia and bull charr of North America separated from a common ancestor during or prior to the last glacial epoch. The relationships of the stone charr to *S. confluentus* should certainly be examined using every possible method to evaluate affinities.

A paper in this volume on the genetic divergence of Eurasian charr by Mednikov *et al.* found the stone charr to be the most distinct form, after *S. leucomaenis*, in comparison to the anadromous charr of Kamchatka in DNA hybridization experiments. Table 1 of the article by Mednikov *et al.* lists the stone charr as the "melanistic freshwater form" of the Kamchatka River, "*S. malma kuznetzovi*".

The name *kuznetzovi* was proposed by Taranets (1933) for *Salvelinus* specimens from Lake Ushki (or Ushkovskoye) in the Kamchatka River basin, which Taranets described as *Salvelinus malma* infraspecies *kuznetzovi*. The problem is that Taranets' specimens of "*kuznetzovi*", represent both stone charr and the typical *S. malma* inhabiting the lake. As pointed out, by Savvaitova & Maksimov (1970), two of Taranets' specimens from Lake Ushki are in the collection of the Zoological Institute of the Academy of Sciences, Leningrad (26888). One specimen is a stone charr and one is *S. malma*. The photograph used by Taranets (1933) to illustrate "infraspecies *kuznetzovi*" represents the stone charr. Thus, the description of *kuznetzovi* is based on a composite of both stone charr and *S. malma*. The stone charr is very rare in Lake Ushki according to Savvaitova & Maksimov (1970), occurring only as random strays from the Kamchatka River. Taranets was familiar with stone charr, and if he intended to specifically designate the stone charr as "infraspecies *kuznetzovi*", he would have so stated.

The name *kuznetzovi* can be considered invalid on the basis that it was proposed for a category (infraspecies) not recognized by the international rules of zoological nomenclature. If someone was dedicated to pay homage to Taranets by validating the name *kuznetzovi*, a redescription of Taranets' specimens would be necessary, eliminating the *S. malma* specimens from consideration and designating the stone charr specimen in collection 26888 as the type specimen of *kuznetzovi*.

Much is yet to be learned about the stone charr of Asia – its distribution, geographic variability, and evidence of hybridization. Is it strictly freshwater or do anadromous stocks occur?

Although it is premature to discuss the taxonomic status of the stone charr, I believe it does represent an evolutionary line, sufficiently distinct from *S. malma* and *S. alpinus* to be given specific recognition. If my suggested affinities of the stone charr to *S. confluentus* is supported by future work, the stone charr could be recognized as a subspecies of *S. confluentus*.

14.42 *Salvelinus leucomaenis*

The "kundsha" charr, *S. leucomaenis*, is provisionally included in the subgenus *Salvelinus*, but the probability that its genetic relationships are with the subgenus *Cristivomer* must be seriously considered. As far as known, *S. leucomaenis* is a species strictly of Far East distribution: throughout the Okhotsk Sea drainages of the Asiatic mainland and west coast of Kamchatka, the Bering Sea drainages of the east coast of Kamchatka and the Commander Islands (not known from the Anadyr River, north of Kamchatka); from the southern part of the Okhotsk Sea and to the south. The distribution of *S. leucomaenis* is virtually identical to the southern groups of *S. malma* – Asiatic mainland to Vladyvostok, Sakhalin, Hokkaido, Kuril Islands, and Honshu. Except for the Honshu populations, *S. leucomaenis* is mainly anadromous and may attain a relatively large size (to 6 kg or more). Taxonomic data is sparse on *S. leucomaenis*. The little data available (Berg 1948, Savvaitova 1964, Andreyev & Dulepov 1971) indicates a species relatively stable (compared to other *Salvelinus*) in the range of variability expressed. Pyloric caeca number are low 16–23 (20) for Kamchatka, 11–23 (16.4) for Sakhalin (Savvaitova 1964) and 17 for a specimen from southern Honshu named *Salvelinus imbrius* by Jordan & McGregor (in Jordan & Hubbs 1925). A vertebrae number of 59 is given by Jordan & McGregor for the Honshu specimen and 62–64 (62.6) for 13 specimens examined by Savvaitova from Kamchatka. Gill raker counts of 15–20 (18.5) for Kamchatkan specimens; 12–20 (17.2) for Sakhalin specimens (Savvaitova 1964). Andreyev & Dulepov (1971) gave mean values of 16.8 and 17.9 gill rakers for two Kuril Islands samples. Jordan & McGregor counted 14 gill rakers in the type of "*S. imbrius*".

The most obvious distinction separating *S. leucomaenis* from all members of the *S. alpinus* complex is spotting pattern. *S. leucomaenis* typically has the largest spots of any *Salvelinus*. Large, irregularly shaped, more or less oblong spots of white or light lemon color cover the body and there is a complete absence of small red or orange spots. Color plates of *S. leucomaenis* were published by Oshima (1961) and Yoshiyasu (1969).

There is considerable confusion regarding nomenclature of Japanese *Salvelinus* of Honshu and Hokkaido. The literature ranges from extreme splitting to extreme lumping – grouping all Japanese charr in *S. malma*, with perhaps *leucomaenis* recognized as a subspecies of *malma*. A recent trend (Yoshiyasu 1969, 1973) is to restrict *S. malma* to Hokkaido and revise the species formerly recognized from Honshu (*S. pluvius* and *S. imbrius*) as *S. leucomaenis*. Although the charr names *S. pluvius* from Honshu (which I consider in the *S. malma curilus* group) is evidently quite similar to *S. leucomaenis* of Honshu in the numbers of gill rakers, pyloric caeca and vertebrae, they can be distinguished by the presence of red spots, more pronounced parr marks and smaller light colored spots in "*pluvius*" when compared with *S. leucomaenis*. There is little doubt in my mind that both *S. malma* and *S. leucomaenis* exist as two "good" species on Honshu Island.

It is likely that when adequate taxonomic data on *S. leucomaenis* from throughout its range is available, the Honshu populations will exhibit lower meristic values than Kamchatkan populations. If there is a gradual transition in character values, subspecific recognition would not be warranted. If subspecific recognition is given to the *S. leucomaenis* of Honshu, the validity of "*S. imbrius*", Jordan & McGregor 1925, depends on whether or not the charr named *Salvelinus latus* from Nigata Prefecturate by Ota

(1918) is *S. leucomaenis* or *S. malma*. Oshima (1961) considered *S. latus* as a synonym of *S. pluvius*.

Takeda (1975) and Yoshiyasu & Humoto (1972) published color photographs of color abberations which appear in Honshu charr from two streams. These charr completely lack spots on the body. The "nagare" charr of the Sutani River has a mottled appearance and the 'muhan" charr of the Kanzaki River has a silvery sheen. They occur with normally spotted charr and are similar to the normal charr in other characters. This phenomenon is probably due to color polymorphism exhibited in the two populations. The authors considered the "nagare" charr and the "muhan" charr to be *S. leucomaenis*, but from the distribution (east coast drainages of Honshu) and description of the "normal" charr, I suspect these populations are *S. malma*. Based on meristic characters, however, it would be difficult to assign Honshu charr without spots to either *S. leucomaenis* or *S. malma*.

My personal data on *S. leucomaenis* is based on examination of specimens in the Zoological Museum of the University of Moscow. Two samples collected in 1951 from the Amur River estuary region are labeled *S. leucomaenis*. Collection P-8969 is typical *S. leucomaenis* with very large spots (spots of 6 mm on specimens of 140–150 mm). In 6 specimens I counted 15–19 (16.5) gill rakers. There are about 38–50 scales above the lateral line and 23–28 from the origin of the adipose fin to the lateral line. Collection P-8362, although labeled *S. leucomaenis*, evidently is not this species. I counted 21–24 (22.3) gill rakers in 7 specimens examined and the above mentioned scale counts are 48–62 (54) and 32–38 (34). The spots are smaller, relative to body size, than in specimens of *S. leucomaenis* of collection of P-8969. I would have assumed that the specimens in collection P-8362 are *S. malma*, except for the fact that another collection from the same area, also make in 1951 (P-8049) is labeled *S. malma*, and these specimens have very small spots. The spots on the specimens in collection P-8362 are intermediate between the tiny spots of *S. malma* (P-8049) and the large spots of *S. leucomaenis* (P-8969). The gill raker counts on P-8049 ("*malma*") specimens are 19–23 (21.3), and the scale counts 47–54 (50) and 28–33 (30). The question is: what kind of charr is represented in collection P-8362? I doubt that it is *S. leucomaenis* as labeled. Could it (or P-8049) actually represent a stone charr?

14.43 *Subgenus* Cristivomer

In contrast to the subgenus *Salvelinus*, there is little to discuss in regards to the systematics of the single species, *Salvelinus* (*Cristivomer*) *namaycush*, which I have designated with subgeneric status to emphasize the many distinctions in morphology and ecology associated with this particular phylogeny.

The lake charr is endemic to North America and its distribution is associated with deep, cold lakes, almost entirely within the boundaries of the maximum extent of the last glaciation. The zoogeography of *S. namaycush* was considered in detail by Lindsey (1964). Its dispersion pattern is that of a primary freshwater fish species. Marine waters were not utilized and the apparent absence of interconnecting lakes on the Bering Land Bridge prevented *namaycush* from penetration into Asia.

I have speculated (Behnke 1972) that the origins of *S. namaycush* and *S. fontinalis* in North America resulted from a *Salvelinus* ancestral stock in North America diverging in late pliocene-early pleistocene to fill two salmonid niches – a large, lacustrine predator (*namaycush*) and a smaller, generalized species (*fontinalis*) which is ecologically more similar to *Salmo trutta* and *Salmo gairdneri* than it is to other *Salvelinus*.

The morphological stability exhibited by *S. namaycush* is in sharp contrast to the *S. alpinus* complex and is likely due to the highly specialized ecology of *namaycush*, which limits its expansion into diverse niches, particularly in the presence of other fishes. The lack of geographically differentiated races of *namaycush* suggests that the species has remained essentially unchanged since prior to the last glacial epoch.

The original range of the lake charr includes most of the mainland of northern North America with the southern limits closely associated with the extent of maximum glaciation of the last glacial period. Scott & Crossman (1973) published a distribution may for *S. namaycush* and summarized taxonomic and life history information. *S. namaycush* has been widely introduced outside its original range in the United States and is a popular sport fish. A few introductions have been made into Europe, South America and New Zealand.

The lake charr is a highly specialized predator and its growth potential is well expressed only in lakes where adequate forage occurs in waters of low temperatures (<15°C). Ideal conditions for growth are associated with the abundance of large crustacea such as *Mysis* providing forage for the first few years of life until a size of 400–450 mm is attained, setting the stage for a transformation to a piscivorous diet. Deepwater sculpins (Cottidae) can be an important link between invertebrate prey and larger fishes. In the native range of the lake charr, whitefishes (*Coregonus*), typically are the most important food, but a wide variety of prey may enter the diet.

The lake charr is the largest of all *Salvelinus*. Scott & Crossman (1973) give a maximum size of 46.3 kg for a specimen from Lake Athabasca, Canada. It is also the longest lived charr, commonly reaching 20–25 years or more. *S. namaycush* has been captured at a depth of 467 m in Great Slave Lake (McPhail & Lindsey 1970) and at about the same depth in Lake Tahoe (McAfee 1966).

The high number of pyloric caeca in *S. namaycush* has probably evolved in association with its highly predaceous feeding habits. Scott & Crossman (1973) give a range of 93–208 pyloric caeca but Patterson (1968) found only 81–139 caeca in the lake charr of Swan Lake, Alberta, Canada. Although there is a general trend in salmonid fishes for higher numbers of pyloric caeca to be correlated with more predaceous species such as the lake charr and species of the genera *Oncorhynchus* and *Hucho*, this evolutionary trend must be interpreted with caution. Another predatory charr, the bull charr, *S. confluentus*, typically has fewer than 30 caeca. The highest number of pyloric caeca of all salmonid fishes (200–300) are found in nonpredatory species of whitefish (*Coregonus*).

The number of gill rakers ranges from 16 to 26, typically 20–22 and the number of vertebrae from 61 to 68, typically 64–65.

There are two examples of distinctive sympatric stocks of lake charr. The siscowet of Lake Superior occurs in deeper water and has a higher fat content than the other stocks of *namaycush* in the lake. The siscowet is sometimes recognized as a subspecies, *S. namaycush siscowet*. Hubbs (1929) named a deep-water stock in Rush Lake, Michigan, as *S. namaycush huronicus*. Although the siscowet is ecologically quite distinct from other lake charr, it does not differ in taxonomic characters (Qadri 1967, Khan & Qadri 1970). The point to be stressed here is that within a taxonomically stable species (exhibiting little variability throughout its range), genetic differentiation has occurred in various populations, and this genetic based ecological, physiological and life history variability can be manifested in very different growth and survival rates when exposed to different environments. The publication by Plosila (1977) was cited earlier documenting a 16 fold difference in survival between the offspring of two geographically close populations of *namaycush* when introduced into different environments. The original lake charr of the Great Lakes was not a homogeneous population, but rather several discrete stocks occurred in each lake, differing in spawning areas and life history characteristics; a situation that would be favored by natural selection to maximize effective utilization of a lake charr "niche" in such large environments. The elimination of some of the native Great Lakes stocks by the sea lamprey (probably all native lake charr were eliminated from Lake Michigan, created management problems when reintroduction of *namaycush* into the Great Lakes began. The highly adapted genotypes making up the original genetic diversity of Great Lakes *namaycush* can not be recreated in a relatively brief period of time.

S. namaycush could become an important species for introduction into other regions of the Holarctic outside of North America, particularly in lakes with an abundance of underutilized *Coregonus*. The approach discussed by Grimas *et al.* (1972) should be followed, whereby several genetically distinct stocks of *S. namaycush* were introduced

into Swedish lakes to utilize *Coregonus* and to compare the response of different genotypes to different environments.

S. namaycush has been long hybridized with *S. fontinalis* to produce a hybrid popularly known as "splake". The splake is a popular sport fish in some areas, having a rapid growth and attaining a maximum size of about 7–8 kg (Berst *et al.*, this volume).

No natural hybrids of *S. namaycush* with any species has ever been reported.

14.44 *Subgenus* Baione

Most commonly, only a single species, *S. fontinalis*, is recognized as the sole representative taxon for this evolutionary line of charrs. I have previously (Behnke 1972) presented the evidence on the validity of *S. agassizi* in the subgenus *Baione*, although *S. agassizi* is presumed extinct.

Salvelinus fontinalis is endemic to north-eastern North America; the northern extent of its range includes Labrador to Nain and tributaries to Ungava Bay, the Hudson Bay drainages south from the Povungnituk River on the east side and south from the Seal River on the west side of Hudson Bay. The distribution extends around the Great Lakes, a small part of the upper Mississippi drainage and southward through the Appalachian Mountains to northern Georgia. MacCrimmon & Campbell (1969) discussed the native and introduced distribution of *S. fontinalis* in detail.

S. fontinalis, and to a lesser extent, *S. namaycush*, are the only species of *Salvelinus* widely established beyond their original range. Although the brook charr is sensitive to slight environmental change and has drastically declined in its native waters affected by man's impact, it has become the most common species in small mountain streams of the western United States, to the detriment of the native cutthroat trout, *Salmo clarki*, which *fontinalis* has largely replaced in such habitat.

The adaptability and success of *S. fontinalis* is populating and establishing dominance in the small streams of the Rocky Mountain region where they now threaten the existence of several rare forms of indigenous *Salmo* has made the nineteenth century prediction of the Rev. Myron W. Reed (who is described by Jordan & Evermann [1902] as a "noble man and an excellent angler") seem ironic as well as quaint. Rev. Reed prophesied an unhappy fate for the brook charr when he wrote:

> This is the last generation of trout-fishers. The children will not be able to find any. Already there are well-trodden paths by every stream in Maine, New York and Michigan. I know of but one river in North America by the side of which you will find no paper collar or other evidence of civilization. It is the Nameless River. Not that trout will cease to be. They will be hatched by machinery and raised in ponds, and fattened on chopped liver, and grow flabby and lose their spots. The trout of the restaurants will not cease to be; but he is no more like the trout of the wild river than the fat and songless reed-bird is like a bobolink. Gross feeding and easy pond life enervate and deprave him. The trout that the children will know only by legend is the gold-sprinkled living arrow of the white water; able to zig-zag up the cataract; able to loiter in the rapids; whose dainty meat is the glancing butterfly.

After the last glaciation, *S. fontinalis* advanced northward and virtually replaced *S. alpinus* throughout northern New England, Nova Scotia, Quebec, Newfoundland and southern Labrador. In this area, *S. alpinus* has persisted mainly as relict lacustrine populations, restricted to deepwater, benthic existence with *S. fontinalis* dominating the littoral areas of the lakes where sympatry occurs. As discussed above, I consider these relict *alpinus* populations as *S. alpinus oquassa*.

In an area from Hamilton's Inlet to Nain, Labrador, *S. fontinalis* is sympatric with resident and anadromous *S. alpinus*. There is little information on this form of *S. alpinus* of northern Labrador, but as mentioned above, it likely represents introgression between the eastern Arctic *S. alpinus* with numerous gill rakers and *S. alpinus oquassa* with fewer gill rakers.

In the Hudson Bay drainages, the range of *fontinalis* overlaps the range of the eastern Arctic group of *S. alpinus* in a few rivers on both the east and west sides of Hudson Bay.

Although *S. fontinalis* is a most highly regarded species and it has generated tremendous amounts of literature (Power, this volume), there is little taxonomic data available, particularly from populations in the southern parts of the range. This lack of taxonomic attention is due to the relative stability of the species. That is, great variability in different populations and the widespread occurrence of sympatric stocks, as is so common in the *S. alpinus* complex, is not known for *S. fontinalis*.

From the literature and personal data, *S. fontinalis* can be characterized by the following values: vertebrae 57–62 (typically 59–60); gill rakers 13–22 (17–19) and pyloric caeca 25–50 (30–40). The most diagnostic characters separating *S. fontinalis* from other *Salvelinus* species is its coloration and markings. Mottled, vermiculated markings occur on the dorsal part of the body and on the dorsal and caudal fins; the lower fins are edged with a black and white border and the small red spots on the body are outlined by a light blue halo (the "halo effect" is sometimes observed in freshwater *malma* to a lesser extent). These traits distinguish *S. fontinalis* from all other charrs. Typically, *S. fontinalis* lacks basibranchial teeth, but I have observed these teeth in Canadian specimens and the occasional presence of these teeth was mentioned by Qadri (1968).

S. fontinalis is the most generalized and adaptable of all charr species. Populations are found in the smallest headwater streams, in ponds and large lakes and in coastal rivers where it may be semianadromous in the northern parts of its range. Typically, the brook charr feeds on invertebrates, but larger individuals may become mainly piscivorous if adequate forage is available. Within a species of such wide distribution, represented by populations living in such diverse environments and exhibiting different life histories, a great amount of intraspecific genetic diversity must exist which is not apparent from morphological comparisons.

Ecologically, *S. fontinalis* can be considered as two major life history types. Typically in the northern parts of its range, the species is characterized by a longer life span, larger size (4–6 kg) and association with environments of greater magnitude – large lakes, rivers and the sea. South of the Great Lakes region and south of northern New England, *S. fontinalis* is typically an inhabitant of small brooks where it has a short life span (3–4 years) and small size (typically 200–250 mm). It is not known if this apparent ecological differentiation is due to a separation of the species into a northern and southern group during past glacial periods, or if, essentially, a homogeneous stock was established in its present range after the last glacial retreat with local differentiation occurring during the past few thousand years. Lennon (1967) mentioned that *S. fontinalis* native to the southernmost part of their range in the southern Appalachian Mountains, have smaller and more numerous red spots than do *fontinalis* from more northern parts of the range.

Dwight Webster and William Flick of Cornell University have studied the fisheries values of several genetically distinct stocks of *S. fontinalis* (Behnke 1972). They have found a greater maximum age and greater potential size to be inherent factors in offspring of parents from large lakes of the Hudson Bay watershed when compared with races of New York State *fontinalis*. Hybridization of Canadian lacustrine stocks with domesticated hatchery stocks of *S. fontinalis* has a great potential in fisheries management. The hybrids retain the greater longevity, growth and survival after stocking, similar to the wild parents, but are relatively simple to rear under hatchery conditions, similar to the domestic parents.

There are two known examples where *S. fontinalis* has occurred sympatrically with other stocks of its evolutionary lineage (subgenus *Baione*). A distinctive charr, lacking the pronounced vermiculations of *fontinalis* was found with typical *fontinalis* in three headwater lakes tributary to the Montreal River, Ontario (St. Lawrence drainage). This charr was described as *Salvelinus timagamiensis* by Henn & Rinkenbach (1925) and is popularly known as the "aurora" charr. Sale (1967) and Qadri (1968) made taxonomic studies on the aurora charr, comparing it to *fontinalis*. Both Sale and Qadri concluded that the aurora charr should be recognized as a subspecies, *S. fontinalis timagamiensis*.

I have examined specimens of the aurora charr and I agree with Sale and Qadri that the genetic differentiation between *timagmiensis* and other *S. fontinalis* is slight, but it was

sufficient to maintain reproductive isolation in sympatry, under original conditions. Hybridization was probably stimulated after "non-native" fontinalis of hatchery origin were stocked into the lakes with aurora charr. Scott & Crossman (1973) doubted that any pure aurora charr are left in the lakes where they were originally found. New populations had been presumed extinct and to represent no more than a "color variant" of *S. fontinalis* this beautiful and rare charr.

The other example of sympatry concerns the brook charr and "silver" charr of Dublin Pond, New Hampshire. The silver charr, I believe, represents a much greater genetic divergence from *fontinalis* than does the aurora charr.

The silver charr, *Salvelinus agassizi* – Little in the way of new information is available to add to my previous discussion on the silver charr of Dublin Pond, New Hampshire (Behnke 1972). The silver charr attracted considerable attention among both ichthyologists and laymen during the nineteenth and early twentieth century but in later years it has been presumed extinct and to represent no more than a "color variant" of *S. fontinalis* (Vladykov 1954). A detailed history of the silver charr and a color plate of this fish is found in Kendall's (1914) publication on New England *Salvelinus*.

No one, however, had discussed the taxonomic position of the silver charr based on a detailed examination of specimens and a critical evaluation of characters until I examined 13 specimens in the collections of the U.S. National Museum (34710, 35355, 39327). The most striking feature I found in specimens of the silver charr is the structure of the gill rakers. The gill rakers are few in number (14–17) and consist, in part, of rudimentary knobs which are strongly denticulated – typical of highly predaceous species such as pikes (*Esox*) and huchen (*Hucho*). The number of pyloric caeca (43–58) is higher than in *S. fontinalis* and also suggests selection for a specialized predator species. My interpretation is that the silver charr did not originate autochthonously in the past few thousand years in Dublin Pond, but represents a divergence from an ancestral *fontinalis* line to fill the specialized predatory charr niche south of the distribution of *S. namaycush*.

The rapid disappearance of the silver charr from Dublin Pond, similar to the disappearance of the aurora charr and the blueback charr (*S. alpinus oquassa*) from their native lakes, illustrates how vulnerable relict charr populations are to extinction from any man-induced environmental perturbations. It is likely that introductions of non-native fishes, particularly the introduction of "non-native" *fontinalis* of hatchery origin, obscured the delicate niche separation and spawning segregation between the native *S. fontinalis* and the silver charr in Dublin Pond.

It is generally believed that the last specimen of silver charr was captured by Kendall in 1912 (Kendall 1914), but Mr. K. E. Hartel of the Museum of Comparative Zoology, Harvard University, notified me that the Museum has 6 specimens (40875) identified as *S. agassizi*, collected from their spawning grounds in Dublin Pond, October 24, 1930. Deepwater charr are notoriously difficult to collect, unless special efforts are made. It is possible that a small population has persisted undetected in Dublin Pond or in other lakes. If my assumption is correct that *S. agassizi* represents an ancient evolutionary line from the phylogeny leading to *S. fontinalis*, then it must have had a much broader distribution. Kendall (1914) believed a charr similar to *S. agassizi* inhabited Christine Lake, New Hampshire (both Cristine Lake and Dublin Pond are in the Connecticut River basin). After the introduction of non-native trouts into Christine Lake, the peculiar native charr disappeared (Behnke 1972) before more could be learned about it.

I still have hopes that in some deep lake of northern New England or southeastern Canada the silver charr persists, waiting to be rediscovered. Sanders & Power (1969) discussed the charr found in Matamek Lake, Quebec. They found *S. fontinalis*, a "red charr", which I assume to be *S. alpinus oquassa*, and a "silver charr". What is the "silver charr" of Matamek Lake?

14.5 Summary and discussion

Our knowledge of the systematics of the genus *Salvelinus* and the recognition of taxa in relation to actual degrees of relationships and branching points of the phylogeny is still in a most rudimentary stage. This volume is the first attempt to assemble an international compendium of current knowledge on the systematics and ecology of the genus and will serve as a foundation for future work.

I have attempted to delinate the evolutionary lines and discuss the recognition of taxa often with little substantiating evidence. My interpretation of the evolutionary divergences and recognition of species and subspecies is highly provisional but can serve as a hypothesis for future workers to falsify and revise.

The earliest divergences in the genus, as interpreted from living species, has produced the three most distinctive evolutionary lines which I recognize as subgenera – *Salvelinus*, *Cristivomer* and *Baione*. At this level, the major unknown concerns the correct assignment of *Salvelinus leucomaenis* – is it more closely related to the *S. alpinus* complex of the subgenus *Salvelinus*, or to the lake charr of the subgenus *Cristivomer*? A recent paper by Viktorovsky & Glubokovsky (1977) presented a phenogram of similarity between 30 populations of *Salvelinus* based on 60 characters derived from examination of skulls using numerical taxonomic methods for analysis of data.

The phenogram neatly segregates *S. malma* from *S. alpinus*, but if a phylogenetic interpretation were to be made based on the first divergence point in the phenogram, two subgenera of *Salvelinus* would be recognized – one for *S. alpinus*, *S. fontinalis* and *S. namaycush* and one for *S. malma* and *S. leucomaenis*, but with the "longheaded" charr of Lake Kronotskoye as the most divergent population of the *malma-leucomaenis* cluster. According to the authors, this separation into Arctic and Atlantic Ocean *S. alpinus*, *S. fontinalis* and *S. namaycush* on one hand, and Pacific Ocean *S. malma* and *S. leucomaenis* on the other, is also supported by the presence of a pair of submetacentric chromosomes in the karyotypes of all forms of *malma* and *leucomaenis*, but not in *alpinus*, *fontinalis* or *namaycush*. Until much more extensive karyotype studies are made, I will reserve judgement on the efficacy of the presence or absence of submetacentric chromosomes as valid indicators of ancient dichotomies in the *Salvelinus* phylogeny and continue to treat *S. malma* as a species in the *S. alpinus* complex.

Virtually all of the problems regarding determination of relationships and recognition of taxa concerns the *Salvelinus alpinus* complex, which includes all of the subgenus *Salvelinus* except for *S. leucomaenis*. In the *S. alpinus* complex I have recognized two major species, *S. alpinus* and *S. malma*, in addition to a species of broad distribution in western North America, *S. confluentus*, and *S. profundus*, a species restricted to one or a few lakes in Europe; and discussed other "tentative" species such as the deepwater charr of Taimyr, *S. taimyricus*, and the stone charr of Kamchatka.

It is obvious that new data will be necessary before the evolutionary relationships within the genus are sufficiently known to allow for more authoritative recognition of species and subspecies. Most of this new data will probably come from studies of karyotypes and gene loci. The most productive studies will combine the expertise of genetic research with expertise on the systematics of the genus so that the most suitable populations are selected for comparisons. That is, an experienced systematist would construct a hypothetical phylogeny based on all available data, and representatives from various major and minor branching points of the phylogeny would be selected for the research. Useful characters to interpret phylogeny and relationships are those that can be associated with a particular branching point in the phylogeny and are found in every member derived from that particular branching point. That is, to detect unique events that have occurred in one evolutionary line but not the other after the original divergence from a common ancestor. Adequate study of all the "groups" I have discussed in this paper, will require international cooperation between research teams.

As a starting point, gene loci data from many loci should be documented between members of the major groups I have assigned to subgeneric status to get an indication of heterozygosity and the number of unique alleles which can be detected between members of the assumed most divergent groups. Within the *S. alpinus* complex, comparisons should first be made between the "extremes" – the *S. alpinus* of the Taimyr region and relict interior populations, the charr of the Alpine lakes of Europe (including *S.*

profundus) and the eastern Arctic North American *S. alpinus*, on one hand to represent the extreme *alpinus* types, and the southern populations of dolly varden in Honshu Island, Japan, and western North America to represent the extreme *malma* types. If consistency and agreement can be found in gene loci and/or karyotype data to clearly detect unique events that have occurred during the phylogenies leading to one extreme or the other, then other groups such as the Kamchatkan *S. malma malma* and "type locality" specimens of *S. alpinus* can be examined in regards to phylogenetic affinities and the validity of the name *malma*.

If such work should prove successful in better delineating *Salvelinus* phylogeny and relationships, I will not be shocked (but perhaps mildly surprised) to find that much of the taxonomic arrangement of the genus proposed in this paper does not bear a close semblance to evolutionary reality.

Besides developing information for taxonomic revisions, systematists can provide useful data on ecology, life history and other aspects of the manifestation of genetic diversity, useful for managing charr populations for sport or commerce. A basic fact of zoogeography is that within a genus or a polytypic species diversity is not equally expressed throughout the distribution of the group, so that some geographical regions may have suitable environments but no native charr highly specialized to most efficiently occupy the various niches such as predator, pelagic plankton feeder, benthic feeder, etc. Carefully evaluated introductions of stocks with evolutionary programming to fill specific niches and establish sympatric and reproductively isolated stocks could be made in an attempt to emulate natural situations in areas where genetic diversity is lacking.

In high Arctic lakes where primary production rates are extremely low, charrs effectively accumulate and convert the energy in the ecosystem into high value protein (Hunter 1970, Skreslet 1973). It could be added that this protein is packaged in an exquisitely beautiful body.

Acknowledgements

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