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Chromosomal Variability, Genome Reorganization in Phylogeny, and the Systematics of *Salmo* and *Parasalmo* Species (Salmonidae)

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Abstract—We analyzed the literature on the number of chromosomes and chromosome arms in the *Salmo* and *Parasalmo* species. Occurrence of large-scale genome reorganizations during the phylogeny of *Salmo salar* and *Parasalmo* species was demonstrated. We also discuss a possible mechanism of these reorganizations. Similar reorganizations could possibly took place during the phylogeny of other genera of the salmonid family, *Salvethymus* and *Parahucho*. This suggests that similar karyotypes of endemic Pacific salmonids genera, *Oncorhynchus, Parasalmo, Parahucho,* and *Salvethymus* may be of independent origin. Thus, similarity of the karyotypes cannot serve as a basis for merging Pacific genera of salmonids, especially for merging *Parasalmo* with *Oncorhynchus*.

INTRODUCTION

During the evolution of many animal species, including fish, polyploidy played a significant role (Ohno, 1970; Kirpichnikov, 1974; and Vasilyev, 1985). In particular, it is known (Svardson, 1945; Ohno, 1970; Allendorf and Thorgaard, 1984) that the salmonid family evolved through polyploidy. During recent years, it was shown that other genome reorganizations can also be very important in evolution (Altukhov, 1989; Stegnii, 1993; and Vorontsov, 1999).

In this study, we tried to substantiate the possibility of significant genome reorganizations during the evolution of the Atlantic salmon, *Salmo salar* L. and Pacific salmons of the genus *Parasalmo* (Salmonidae). This can also help to determine the taxonomic status of the group *Parasalmo*, which is currently debated in the literature.

SYSTEMATIC RELATIONSHIPS OF NOBLE SALMONS

According to immunological, osteological, and karyological traits, as well as DNA characteristics (Dorofeeva, 1967, 1975; Novikov,1973; Mednikov, Akhundov, 1975), noble salmon can be divided into three major groups: (1) brown trout (*Salmo trutta*) and similar endemic species, such as *S. ischchan* (Lake Sevan, Armenia), *S. letnica, S. carpio, S. marmoratus* (Mediterranean basin), and also *S. platycephalus* (Behnke, 1968); (2) the Atlantic salmon (*S. salar*); and (3) Pacific noble salmons. The composition and taxonomic status of this group is intensively discussed in the literature.

Traditionally, Pacific noble salmon are merged into the *Salmo* genus (Tchernavin, 1923, 1937; Berg, 1948; Norden, 1961; Rounsefell, 1962; Behnke, 1968; Savvaitova *et al.*, 1973; Dorofeeva, 1975; and Pavlov, 1989). Vladykov (1963) suggested that they should be separated as a subgenus *Parasalmo*.

During the last decades, it has been shown that *Parasalmo*, more than other salmonid species is similar to Pacific salmon of the genus *Oncorhynchus* with respect to many karyological (Viktorovsky, 1978; Vasilyev, 1985; Viktorovsky *et al.*, 1985; and Dorofeeva, 1989) and osteological traits (Glubokovsky and Glubokovskaya, 1981; Dorofeeva, 1989; Sanford, 1990; Stearley and Smith, 1993; Glubokovsky, 1995). Results of allozyme variation analysis (Yamanaka *et al.*, 1967; Ferguson and Fleming, 1983; Osinov, 1999) and DNA variation analysis (Berg and Ferris, 1984; Phillips *et al.*, 1992; Shedlock *et al.*, 1992; Devlin, 1993; McKay *et al.*, 1996; Murata *et al.*, 1996; Kitano *et al.*, 1997; Phillips and Oakley, 1997; Lee *et al.*, 1988; Mednikov *et al.*, 1999; Oakley and Phillips, 1999) also agree with this pattern.

This allows us to consider *Parasalmo* as a separate genus (Glubokovsky and Glubokovskaya, 1981; Kendall and Behnke, 1984; Vasilyev, 1985; Dorofeeva, 1989; Dorofeeva *et al.*, 1992; Glubokovsky, 1995; Ginatulin and Ginatulina, 1998; Makoedov, 1999; Mednikov *et al.*, 1999; Osinov, 1999; and Dorofeeva, 1999). This view is followed in the last edition of the checklist of Russian fish (*Annotirovannyi...*, 1998).

In 1988, the Names of the Fish Committee of the American Fisheries Society and American Society of Ichthyologists and Herpetologists, included Pacific noble salmon in the genus *Oncorhynchus*. But studies which substantiated this decision appeared only later (Smith and Stearley, 1989; Sanford, 1990; Stearley and Smith, 1993).

Several studies put forward many arguments against such a taxonomic reorganization. In particular, investigations of DNA variation revealed a clear difference between *Parasalmo* and *Oncorhynchus* species (Ginatulina and Ginatulina, 1998; Mednikov *et al.*, 1999). The differences between these genera with respect to osteological (Dorofeeva, 1999) and genetic traits (Osinov, 1999) are comparable to differences between other genera of salmonid fish.

The Pacific salmon are represented by several species: *O. mykiss*, *O. clarki*, *O. gilae*, and *O. chrysogaster*, as well as an array of populations with unclear systematic status (Behnke, 1992). On the basis of osteological data, a fossil fish *Rabdofario lacust* Cope 1870 from the pleistocene and myocene of No America is considered a close relative of the living sp cies *O. mykiss*. In this case, according to the priori rule, the genus name of Pacific salmon should be *Rab ofario* (Stearley and Smith, 1993).

KARYOLOGICAL VARIABILITY OF NOBLE SALMONS

The number of chromosomes in brown trout vari from 76 to 84, and the number of chromosome ar ranges, from 92 to 104 (Table 1). The number of ch mosomes, documented in the work by Ojima *et* (1963) significantly differs from the data obtained other investigators, and therefore is not included in the table. Very similar traits are also characteristic other species, related to trout: 2n = 80–82, NF = 9

Table 1. Karyological variability of the brown trout

Region	2n	NF	Data source
White Sea	80	100	Zelinskii, 1990
Baltic	84	–	Prokof'eva, 1934
Baltic	78	98	Kaidanova, 1975
Sweden	80	96	Svardson, 1945
Sweden	80	100	Nygren *et al.*, 1971
Germany	80	–	Lieder, 1956
Poland	80	100–102	Wornicki *et al.*, 1998
Onezhskoe Lake	80	100	Makhrov *et al.*, 1990
Scotland	80	101, 102	Hartley, Horne, 1984
Spain	79, 80	102	Moran *et al.*, 1989
Spain	80	100–102	Martinez *et al.*, 1991
Spain	80	–	Sanchez *et al.*, 1991
Spain	80	100	Abuin *et al.*, 1996
Italy	80	100	Capanna *et al.*, 1973
Yugoslavia	80	98, 100	Sofradzija, 1982
Yugoslavia	80	100	Al-Sabti, 1985
Greece	80	100	Karakousis *et al.*, 1992
Greece	76	92	Karakousis *et al.*, 1992
Romania	80	104	Raicu, Taisescu, 1977
Black and Caspian seas	80	98	Dorofeeva, 1965
Caucasus	78–84	98–104	Rukhkyan, 1989
Aral Sea Basin	80	98	Mazik and Toktosunov, 1986
North America	80	–	Wright, 1955
North America	80	–	Phillips, Ihssen, 1985
North America	80	–	Phillips, Hartley, 1988
Japan	80	98	Ueda, Ojima, 1984
?	78–80	102	Zenzes, Voiculescu, 1975
?	80	–	Gjedrem *et al.*, 1977
?	80	100	Pendas *et al.*, 1993

100 in *S. ischchan* (Dorofeeva, 1967; Rukhkyan, 1989; Toktosunov and Mazik, 1991), 2n = 80, NF = 96–100 in *S. letnika* (Dimovska, 1959), 2n = 80, NF = 98 in *S. carpio* (Merlo, 1957), 2n = 80, NF = 108 in *S. marmoratus* (Pohar and Al-Sabti, 1978; Al-Sabti, 1985).

The modal number of chromosomes in populations of the Atlantic salmon varies from 54 to 60, and the number of chromosome arms varies from 72 to 74 (Gjedrem *et al.*, 1977; Phillips and Ihssen, 1985; Garcia-Vazquez *et al.*, 1988; Phillips and Hartley, 1988; Moran *et al.*, 1983; Wornicki *et al.*, 1994; Abuin *et al.*, 1996a; Perez *et al.*, 1999; see also references in the reviews by Zelinskii, 1985 and Semenova, 1998).

The number of chromosomes in populations of *Parasalmo mykiss* is 58–65, with the constant number of arms 104 (Aref'ev and Agapov, 1987). The values documented in recent publications (Phillips and Hartley, 1988; Frolov, 1989; Palm and Paaver, 1990; Behnke, 1992; and Veloso *et al.*, 1992) lie within this range. The monograph by Behnke (1992) also includes data on the number of chromosomes and chromosome arms in *P. clarki*: 2n = 64–68, NF = 104, in *P. gilae*: 2n = 56, NF = 106, *P. chrysogaster*: 2n = 60, NF = 104, and in populations of unclear systematic status from Mexico: 2n = 64, NF = 104.

The data on the chromosome variability of noble salmon are presented in Table 2. Chromosomal mosaicity is characteristic of brown trout, rainbow trout, and Atlantic salmon. In addition, intra- and inter-population chromosomal polymorphism was documented in all three species, although it is less characteristic of the brown trout (by Hartley and Horne, 1984). This points to intense evolution of the karyotypes in both the Atlantic salmon and the rainbow trout.

Following the genome doubling, which brought about the appearance of salmonid fishes, their evolution was characterized by a reduction of the number of chromosomes. Therefore, the most advanced species are characterized by a lower number of chromosomes (Kirpichnikov, 1974; Viktorovsky, 1978; Allendorf and Thorgaard, 1984; Vasilyev, 1985; Viktorovsky *et al.*, 1985; and Hartley, 1987). The karyotypes of the brown trout and related endemic species are the most primitive. Let us consider mechanisms that could bring about a reduction in the chromosome number during the phylogeny of the Atlantic salmon and Pacific noble salmons.

GENOME REORGANIZATION IN THE ATLANTIC SALMON EVOLUTION

The difference in the number of chromosomes between the brown trout and the Atlantic salmon is associated with chromosome reorganizations rather than loss or addition of separate chromosomes (Rees, 1964; Pegington and Rees, 1967). Differential staining revealed that certain chromosomes of the Atlantic salmon evolved by means of the lumping of two chromosomes, similar to chromosomes of modern brown trout (Amaro *et al.*, 1996).

Table 2. Karyological Variability of noble salmons

Group	2n	NF
Brown trout and related endemic species	76–84	92–104
Atlantic salmon	54–60	72–74
Pacific noble salmons	56–68	104–106

Because the Atlantic salmon differs from the brown trout not only by a lower number of chromosomes but also by the number of chromosome arms, it seems obvious that the phylogeny of this species was characterized by tandem chromosome fusion. In this way, the telomere of one chromosome connected with the telomere or centromere of another chromosome, thereby forming acrocentric (one-armed) chromosomes. The possibility of such a process is confirmed by observations of chromosomal associations during the mitosis (Zelinskii, 1985), as well as by the possibility of spontaneous tandem fusion of chromosomes in the cell culture of the Atlantic salmon (Sanches *et al.*, 1993).

Characteristics of the distribution of heterochromatin regions in chromosomes of the Atlantic salmon and brown trout are in agreement with the tandem chromosome fusion hypothesis (Hartley and Horne, 1984; Phillips and Hartley, 1988). Both species have heterochromatin in the centromere region. In the Atlantic salmon, heterochromatin was also found on the 3–4 telomeres and in the 10–13 regions, localized on the arms of large acrocentric chromosomes. Most probably, these heterochromatin regions are associated with former centromeres. DNA sequences, characteristic of telomeres, have also been found on the arms of some long chromosomes in the Atlantic salmon (Abuin *et al.*, 1996b). However, this observation has not been confirmed by further work (Perez *et al.*, 1999).

As no intermediate forms between the Atlantic salmon and the brown trout have ever been found, it is reasonable to suppose that these tandem chromosome fusions occurred simultaneously, during a large-scale genome reorganization. For example, one-time merging of chromosomes has been documented in a rodent: *Ellobius tancrei* (Vorontsov, 1999).

It has been supposed (Zelinskii, 1985) that tandem fusion of all chromosomes took place in the gamete of a trout-like ancestor of the Atlantic salmon. In this way, genome with n = 20 and NF = 25 was formed from the haploid number of chromosomes, similar to the brown trout modal number (n = 40, NF = 50). Lumping of such a gamete with an unchanged gamete resulted in the creation of a zygote with 2n = 60 and NF = 75. This karyotype is close to the karyotype of the modern Atlantic salmon.

The fish created in this way could reproduce by means of nonmeiotic gynogenesis. An important fact supporting this hypothesis is that gynogenesis is possible in females of the hybrid between the Atlantic salmon and the brown trout (Johnson and Wright, 1986; Galbreath *et al.*, 1997). Small chromosomal reorganizations could occur in the gynogenetic fish during several years, which would make the karyotype more stable. Later, this form could return to sexual reproduction. A similar transition is thought to have occurred in polyploid species (Vasilyev, 1985).

It seems less possible that genome reorganization could occur only in one zygote of a troutlike ancestor of the Atlantic salmon. In this case, different-sex individuals of the Atlantic salmon could evolve after the gametes of this individual merged with normal gametes.

Most probably, trivalents formed first in the meiosis of the Atlantic salmon; i.e., it was a multiple heterozygote with respect to Robertsonian translocations. As a result of a continuous drift, alternative genotypes, represented by merged and split chromosomes, become common in the gene pool of the Atlantic salmon, so that bivalents currently predominate in the meiosis of this species (Zelinskii, 1985). However, the process of the genome "homozygotization" is currently not finished, and chromosomal polymorphism is very characteristic of this fish species.

Recently, evidence of a large reorganization of the genome during the phylogeny of the Atlantic salmon was obtained at the molecular level. Higher speed of mitochondrial DNA evolution was observed in the Atlantic salmon lineage (Shed'ko, 1991). Significant differences in the repeatable sequences of nuclear DNA between the brown trout and the Atlantic salmon were revealed using the taxonprint method (Mednikov *et al.*, 1999).

It is possible to suggest that the genome reorganization during the phylogeny of the Atlantic salmon was caused by so called "transpositional burst," i.e., a massive one-time transition of mobile genetic elements. Such burst can occur within a single embryonal cell and sometimes cause chromosomal reorganizations, including translocations (Gerasimova, 1990).

REORGANIZATIONS OF *PARASALMO* KARYOTYPES AND THEIR TAXONOMIC POSITION

The karyotypes of *Parasalmo* species are close to those of brown trout but have a smaller number of chromosomes. In the karyotype evolution of *Parasalmo*, therefore, centric chromosome fusions should predominate. Using differential staining method, it has been shown that separate chromosomes of the rainbow trout could evolve by means of centric fusion of chromosomes, similar to chromosomes of the brown trout (Amaro *et al.*, 1996).

In spite of large number of studied populations, there exists no one form with a number of chromosomes intermediate between the brown trout and *Parasalmo* species. This indicates that the evolution of karyological characteristics of *Parasalmo* took place as a result of a single genome reorganization. A possible mechanism could be as follows.

As a result of a centric fusion of acrocentric chromosomes from the haploid set within the gamete, similar to that described in the brown trout ($n = 40$, $NF = 52$), a genome with $n = 26$ and $NF = 52$ has evolved. Merging of such gamete with a normal unchanged gamete creates a zygote with $2n = 66$ and $NF = 104$. This karyotype is in fact characteristic of certain populations of the cutthroat trout (*S. clarki*).

Molecular genetic data also support the hypothesis of a large-scale reorganization of the genome during the *Parasalmo* phylogeny. It was found that differences in DNA between *Salmo* and *Parasalmo* could be associated with a rapid genome reorganizations (Mednikov *et al.*, 1999). It is possible that various DNA sequences were differently affected by this reorganization, and this could explain the differences in the species similarity indices between *Parasalmo* and *Oncorhynchus*, obtained on the basis of various genetic markers (Tsuyuki and Roberts, 1966; Omelchenko *et al.*, 1971; Utter *et al.*, 1973; Chernov and Vorkhsenius, 1987; Thomas and Beckenbach, 1989; McVeigh and Davidson, 1991; Utter and Allendorf, 1994; Shed'ko *et al.*, 1996; Oleinik, 1997; Domanico *et al.*, 1997; Oohara *et al.*, 1997, see also the references above).

Several investigators noted similarities between the karyotypes of *Parasalmo* and *Oncorhynchus* (Chernenko, 1969; Viktorovsky, 1978; Gorshkova, 1978; Gorshkov and Gorshkova, 1981; Anbinder *et al.*, 1982; Vasilyev, 1985; Viktorovsky *et al.*, 1985; and Hartley, 1987), and this is considered as an argument for merging these genera. However, one of the species of the genus *Oncorhynchus*, the chum salmon (*O. keta*), has 74 chromosomes, i.e., much more than the *Parasalmo* species. Because no significant increase in the chromosome number was noted in the evolution of salmonids, the karyotype of the chum salmon could not evolve from a karyotype similar to the *Parasalmo* karyotype. Therefore, *Oncorhynchus* and *Parasalmo* karyotype could only independently evolve from a karyotype similar to that of the trout. Thus, these two groups represent two distinct phylogenic lineages.

Most probably, the genome reorganizations similar to those in *Parasalmo* are not unique in the salmonid fish evolution. For example, a much smaller number of chromosomes is characteristic of the Sakhalin taimen. Thus, it may be considered a closer relative of Pacific salmon (Anbinder *et al.*, 1982; Vasilyev, 1985). An endemic from of arctic chars form Lake Elgygytgyn in Chukot Peninsula (*Salvethymus svetovidovi*) differs from *Salvelinus* species in a small number of chromosomes ($2n = 56$, $NF = 98$, see Frolov, 1993).

All this suggests that very similar karyotypes of endemic Pacific salmonid fish, *Parasalmo*, *Parahucho*, and *Salvethymus*, *Oncorhynchus* evolved independently. This conclusion agrees with the well-substantiated view of parallel karyological evolution of various taxa of this fish family (Frolov, 1997; Makoedov, 1999). The similarity of karyotype cannot be a base for merging the Pacific genera of salmonid fish, in particular, merging *Parasalmo* and *Oncorhynchus*.

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