# THEORETICAL PAPERS AND REVIEWS

# Homologous Series by Chromosome Number and the Genome Rearrangements in the Phylogeny of Salmonoidei

Yu. P. Zelinsky<sup>1</sup> and A. A. Makhrov<sup>2</sup>

 <sup>1</sup> Department of Zoology, Tolstoy Tula State Pedagogical University, Tula, 300026 Russia
<sup>2</sup> Vavilov Institute of General Genetics, Russian Academy of Sciences, Moscow, 119991 Russia; e-mail: makhrov@vigg.ru Received February 19, 2002

**Abstract**—Published data on chromosome numbers of Salmonoidei are summarized. The existence of homologous variation of chromosome number in different phyletic lines of this suborder is substantiated. It is suggested that the origin of homologous series is related to major genome rearrangements (simultaneous fusion of several chromosomes).

# STRUCTURE AND ORIGIN OF THE GROUP

The reports karyological diversity in animals [1], in particular, in vertebrates [2] including fish [3], are currently available. The ample evidence accumulated in literature provides the possibility to elucidate the regularities of karyotype evolution in individual fish taxa. In this work, we summarized the published data on the karyotypes of the members of the suborder Salmonoidei.

According to the classification [4] that we follow in this work, this suborder includes the families Salmonidae, Coregonidae, and Thymallidae. Salmonoidei are distinguished from other representatives of the order Salmoniformes by a number of traits (see [5] for review). However, the most important specific feature of Salmonoidei is their polyploid origin.

Svardson [6] proposed that the species that are currently included in the order Salmoniformes constitute a polyploid series with the basic chromosome number of 10. He distinguished groups with a diploid chromosome number of 58 to 60 (hexaploids), 80 to 84 (octaploids), and 102 (decaploids). Later, it was revealed that the Atlantic salmon *Salmo salar* and the brown trout *S. trutta*, which are far apart by chromosome number, are similar by DNA content in the cells [7]. The distinction between these species by chromosome number is related to chromosome fusion or partition rather than polyploidy [8].

Shortly afterwards, several authors [9–11] supposed that all species of Salmonidae, Coregonidae, and Thymallidae have a tetraploid origin. This viewpoint was confirmed by further studies. It was revealed that genome duplication had occurred before the separation of three groups; that is, they had a common tetraploid ancestor (see [12] for review). The analysis of karyotypes of related diploid species suggested that the common ancestor of Salmonoidei had 112 chromosomes and 144 to 156 chromosome arms [13].

# KARYOTYPES OF THE EXTANT SALMONOIDEI

To date, karyotypes have been studied in several dozens of Salmonoidei species (Fig. 1). As it is impossible to provide all references to original works within the limits of this review, we used the data from published reviews [3, 13, 16–18, 28–30].

In representatives of the family Thymallidae, karyotypes are closest to the ancestral karyotype. They have about 100 chromosomes and a considerable number of chromosome arms. During the evolution of Salmonidae and Coregonidae, chromosome number significantly decreased by chromosome fusion [14]. Salmonidae and Coregonidae are characterized by karyotypes with a diploid chromosome number near 80 or 60 (Fig. 1). Thus, current data confirm the existence of the groups revealed by Svardson (Fig. 2). In particular, these groups are distinguished in a recent review [17].

The karyotypes with a chromosome number about 80 have independently originated in Coregonidae and Salmonidae. Evidently, these karyotypes have also independently appeared in phyletic lines of taimen (*Hucho*) and other Salmonidae. Both taimen and lenok (*Brachymystax*) species, which are distinguished by a relatively great chromosome number, have a group of four pairs of small metacentric chromosomes, which is absent in other Salmonidae [14].

The forms with the karyotypes including about 60 chromosomes have independently originated in at least six (!) different phyletic lines of Salmonidae and Coregonidae. These are species of the genera *Oncorhynchus* and *Parasalmo*, the Sakhalin taimen *Parahucho perryi*,

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(a)	2n	100	90	80	70	60	5	0	
SAL	MONIDAE	•	Ι	•	Ι	•		NF	Reference
Brachymystax		•	1		1	•			
<i>B. l</i>	enok		* *		I			102-124	[3, 14–16]
Hucho		•	1	•	1	•			
H. I	hucho		I	*.	I			106-114	[3, 17]
<i>H. t</i>	aimen	•	1	****	1	•		112	[13]
Onc	corhynchus	•	I	•	I	•			
0.8	gorbuscha	•		•		•	***	100-104	[3, 13, 17]
0. k	keta	•	I	•	*	•		94–102	[3, 17–19]
0. k	kisutch	•		•		xoxoyoxox		100-112	[3, 13, 17–21]
0. r	nasou	•	I	•	I	* .		100-104	[3, 17, 22]
0. r	1erka	•		•		• **	*	100-104	[3, 17]
0. t	schawytscha	•	I	•	*	•		100-104	[3, 17, 18, 23]
Par	ahucho	•	1	•	1	•			
<b>P</b> . p	perryi	•	I	•	I	*.		100	[3, 17]
Par	asalmo	•		•		•			
<i>P.a</i>	<i>ipache</i>	•	I	•	I	•	*	106	[17]
<i>P. a</i>	, iquabonita	•	1	•	1	****	*	104	[13, 17]
Р. с	hrysogaster	•	I	•	I	*		102-104	[17, 30]
Р. с	larki		1		*	***		104	[13, 30]
P. g	gilae	•	I	•	I	•	*	106	[30]
<i>P</i> . <i>n</i>	nvkiss	•	1	•	1	***		104-108	[17, 19, 24–31]
<i>P</i> . s	p.	•	I	•	I	* .		104	[30]
Sali	no	•	1			•			
S. c.	arpio	•		*	I	•		98	[31]
S. is	schchan	•		***		•		96-100	[31]
S. le	etnika		I	*	I			104	[31]
S. n	narmoratus	•	1	*	1	•		108	[31]
S. se	alar		I	•	I			72–74	[31, 32]
S. ti	rutta	•	1	<del>xxxxy</del> yxx *	1	•		92–104	[31, 33–35]
Salı	mothymus	•	I	•	I	•			
S. 0	btusirostris	•		*.		•		94	[3, 17]
Salv	velinus	•	I	•	I	•			
S. a	lbus	•		<b>,</b> %%%%%		•		98–100	[13, 17, 36]
S. a	lpinus	•	I	* *****	I	•		96–100	[3, 6, 13, 17, 37–39]
S. b	oganidae	•		• ***		•		98	[13]
<i>S. c</i>	onfluentus	•	I	• *	I	•		100	[17]
S. e.	lgyticus	•		• ****		•		98	[13]
S. fa	ontinalis	•	I .	***	I	•		100	[3, 13, 17]
S.k	ronocius	•		<del>३०१०१०१</del>		•		100	[13]
S. le	epechini	•	I	*	I	•		100	[40]
S. le	eucomaenis	•		***		•		100	[3, 13, 17]
S. le	evanidovi	•	I	****	I	•		98	[17]
S. n	nalma	•	:	*** * ***		•		98–100	[3, 17, 36]
S. n	amaycush	•	I	* .	I	•		100	[17]
S. p	luvius	•	:	***		•		100	[17]
S. s	chmidti	•	I	***	I	•		98	[13]
S. ta	aranetzi	•		****		•		98	[13]
<i>S</i> . s	p.	•	1	*.	I	•		98	[17]
Sal	vethymus	•		•		•			
<i>S. s</i>	vetovidovi	•	I	•	I	•	*	98	[13]
L	2 <i>n</i>	100	90	80	70	60	5	0	

**Fig. 1.** Chromosome number (2n) and the number of chromosome arms (NF) in different Salmonoidei species: (a) family Salmonidae; (b) families Coregonidae and Thymallidae.

(b)	2n	100	90	80	70	60	5	0	
CORI	EGONIDAE	•	1	•		•		NF	Reference
C all	sonus hula	•		• ******		•		96-97	[6, 13, 17]
C an	aulorum	•	I	****	I	•		98	[13]
$\begin{bmatrix} C & an \\ C & ar \end{bmatrix}$	tedii	•		***		•		94-106	[13] [13]
$C_{au}$	tumnalis	•	1	***	*	•		96-104	[13, 16, 17]
C ch	adary	•		<del>kokolok</del>		•		98-100	[16, 17]
C ch	uneaformis	•	1	*	1	•	***	94	[17]
C ho	vi	•		*		•		94	[17]
$C_{Lay}$	varetus	•		*****	k	•		94–104	[3, 13, 16, 41–48]
C. m	uksun			****		•		100	[13, 17]
C. na	SUS				1	***		92–98	[13, 17]
C. ni	gripinnis			*		•		94	[17]
C. pe	led		1	* ***	k <del>ikiki</del> k			92–96	[13, 16, 17]
C. tu	gun		****					106	[16]
C. rei	ighardi			*	1			100	[17]
C. sa	rdinella			**				96–100	[13, 17]
C. sci	hinzii				*				[3]
C. us	suriensis			***				100	[13, 17]
C. wa	artmanni	•		*		•			[3]
C. zei	nithicus	•	I	*	I	•		94–98	[3, 17]
Prose	opium	•		•					
P. ab	yssicola	•		•	*	•		100	[17]
P. co	ulteri	•		* *		•		100–102	[13, 17]
P. cy	lindraceum	•		• *	I	•		96–100	[13, 17]
P. ge	mmiferum	•		•		* .		100	[17]
P. spi	ilonotus	•	I	• :	*	•		100	[17]
P. wi	lliamsoni	•		• *		•		100	[17]
Steno	odus	•	I	•	I	•			
S. leu	icichthys	•		• **:	*	•		92–108	[13, 16, 17]
			I		I				
THYM	MALLIDAE	•		•		•			
Thym	allus	•	I	•	I	•			
T. are	cticus	******		•		•		146–168	[3, 16, 17]
T. bre	evirostris	***	I	•	I	•		150	[16]
T. gri	ubei	****		•		•		148–150	[16, 17]
T. thy	mallus	** ***	*	•	I	•		150–170	[3, 16, 17, 42, 49]
								ļl	
	2n	100	90	80	70	60	5	0	



the Atlantic salmon, the longfinned char *Salvethymus svetovidovi*, the broad whitefish *Coregonus nasus*, the Bonneville cisco *Prosopium gemmiferum*.

# DIVERSITY OF CHROMOSOME NUMBER AS MANIFESTATION OF THE LAW OF HOMOLOGOUS SERIES

The series of forms of Salmonoidei with a chromosome number close to 80 and 60 can be considered a particular case of homologous series described by Vavilov [50]. As we know, homologous series by chromosome number have not so far been detected. However, similar concepts were used to describe the evolu-

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tion of karyotypes. White [1] justified the principle of homologous change, though he renamed this conception later. Bulatova [51] described "karyological chains that are basically homologous." Bogdanov [52] described the series of homologous variation by specific features of meiosis.

Several authors reported parallelism of chromosomal rearrangements in different taxa of Salmonoidei. The trend toward decreasing chromosome number, which is exhibited in the evolution of Salmonidae and Coregonidae, is related to genome diploidization in these families, which are tetraploid by origin (see [17] for review).



Extending the idea of homologous series to karyological traits seems to be valid. As Mednikov noted, "Homologous series are formed by heritable changes of phenes rather than by genes" [53, p. 29]. Chromosome number can be considered a phene. Homologous series by chromosome number are traced within genera and families but not within individual species. This is caused by the fact of usual occurrence of reproductive isolation between the forms that considerably differ in chromosome number, which "automatically" makes them different species.

## MAJOR KARYOTYPE REARRANGEMENTS IN THE PHYLOGENY OF SALMONOIDEI

In what follows briefly describe possible mechanisms underlying the formation of homologous series by chromosome number in Salmonoidei. We assume that karyotypes of Salmonidae and Coregonidae with a small chromosome number (2n near 80 and 60) have appeared via major genome rearrangements followed by fusion of several chromosomes. The simultaneous fusion of a number of chromosomes was described in rodents (*Ellobius tancrei*) [54]. Major genome rearrangements were detected in many allopolyploids (see [55] for review); therefore, they are possible in Salmonoidei as well. The assumption about major genome rearrangements were made earlier in the studies of allozyme variation [56] and DNA structure [57] in a number of Salmonoidei species.

The karyotypes with 2n near 80 could arise by paired fusion of all acrocentric chromosomes of the karyotype that was close to the primitive karyotype of Thymallidae (2n = 100, NF = 160). All species of

Salmonidae and Coregonidae may have undergone such a rearrangement with the possible exception of the tungen (*Coregonus tugun*) and lenok species, whose distinction from Thymallidae is not very marked.

Earlier, we scrutinized the possible mechanisms for the formation of karyotypes with a chromosome number near 60 exemplified by the Atlantic salmon and salmon species belonging to the genus *Parasalmo* [31]. Note that the species with such karyotypes are characterized by a higher chromosomal variability than related species with a chromosome number near 80. Apparently, this is related to the fact that karyotypes with a chromosome number near 60 formed relatively recently and the "balancing" of their chromosome set has not yet been completed.

For example, the embryos of the broad whitefish *C. nasus*, compared to other Coregonidae, are characterized by a very high frequency of such chromosomal aberrations as bridges and by very high mortality [58]. Chromosomal polymorphism is more frequently found in the Atlantic salmon and the rainbow trout *Parasalmo mykiss* than in the brown trout (see [31] for review). The data presented by Mitrofanov [59, pp. 102–103] indicate that the spontaneous chromosomal variation is greater in pink salmon *Oncorhynchus gorbuscha* than in chum salmon *O. keta*.

Homologous series by chromosome number that we detected in the present work indicate that one should be cautious using karyological traits in the taxonomy of Salmonoidei.

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#### REFERENCES

- 1. White, M.J.D., *Animal Cytology and Evolution*, Cambridge: Cambridge Univ., 1973.
- Birshtein, V.Ya., *Tsitogeneticheskie i molekulyarnye* aspekty evolyutsii pozvonochnykh (Cytogenetic and Molecular Aspects of Vertebrate Evolution), Moscow: Nauka, 1987.
- 3. Vasil'ev, V.P., *Evolyutsionnaya kariologiya ryb* (The Evolutionary Karyology of Fishes), Moscow: Nauka, 1985.
- Annotirovannyi katalog kruglorotykh i ryb kontinental'nykh vod Rossii (An Annotated Catalogue of Cyclostomata and Fishes of Russian Continental Waters), Moscow: Nauka, 1998.
- 5. Dorofeeva, E.A., Salmon and Trout of Eurasia: Comparative Morphology, Systematics, and Phylogeny, *Doc-*



toral (Biol.) Dissertation, St. Petersburg: Zoological Institute, RAS, 1999.

- Svardson, G., Chromosome Studies on Salmonidae, *Rep. Swed. State Inst. Freshwater Fish. Res. Drottningholm*, 1945, no. 23, pp. 1–151.
- 7. Rees, H., The Question of Polyploidy in the Salmonidae, *Chromosoma*, 1964, vol. 15, no. 3, pp. 275–279.
- Pegington, C.J. and Rees, H., Chromosome Size in Salmon and Trout, *Chromosoma*, 1967, vol. 21, no. 4, pp. 475–477.
- Behnke, R.J., A New Subgenus and Species of Trout, Salmo (Platysalmo) platycephalis, from Southcentral Turkey, with Comments on the Classification of the Subfamily Salmoninae, Mitt. Hamburg. Zool. Mus. Inst., 1968, vol. 66, pp. 1–15.
- Massaro, E.L. and Markert, C.L., Isozyme Patterns of Fishes: Evidence for Multiple Cistrons for Lactate Dehydrogenase Polypeptides, *J. Exp. Zool.*, 1968, vol. 168, no. 2, pp. 223–238.
- Ohno, S., Wolf, U., and Atkin, N.B., Evolution from Fish to Mammals by Gene Duplication, *Hereditas* (Lund, Swed.), 1968, vol. 59, no. 1, pp. 169–187.
- 12. Allendorf, F.W. and Thorgaard, G.H., Tetraploidy and the Evolution of Salmonid Fishes, *Evolutionary Genetics of Fishes*, New York: Plenum, 1984, pp. 1–53.
- 13. Frolov, S.V., *Izmenchivost' i evolyutsiya kariotipov lososevykh ryb* (The Variation and Evolution of Salmonid Karyotypes), Vladivostok: Dal'nauka.
- Viktorovskii, R.M., Makoedov, A.N., and Shevchishin, A.A., The Chromosome Sets of *Brachymystax lenok* and Siberian *Hucho taimen* and Divergence of Salmonid Genera, *Tsitologiya*, 1985, vol. 27, no. 6, pp. 703–709.
- Ginatulina, L.K., Kartavtseva, I.V., Shedko, S.V., and Nemkova, G., Karyological Analysis of Two Forms of Brachymystax lenok (Pall.) from Sympatric and Allopatric Populations of Primorye, Modern Achievements in Population, Evolutionary and Ecological Genetics (MAPEEG-1998): Int. Symp., Vladivostok—Vostok Marine Biological Station (September 3–8, 1998), Vladivostok, 1998, pp. 6–7.
- 16. Makoedov, A.N., Kariologiya, biokhimicheskaya genetika i populyatsionnaya fenetika lososevidnykh ryb Sibiri i Dal'nego Vostoka: sravnitel'nyi aspekt (Karyology, Biochemical Genetics, and Population Phenetics of Salmonids from Siberia and the Russian Far East: A Comparative Aspect), Moscow: Psikhologiya, 1999.
- 17. Phillips, R.B. and Rab, P., Chromosome Evolution in Salmonidae (Pisces): An Update, *Biol. Rev.*, 2001, vol. 76, no. 1, pp. 12–25.
- Gorshkova, G.V., Several Specific Karyotypic Features of Pacific Salmon Species, *Tsitologiya*, 1978, vol. 20, no. 12, pp. 1431–1434.
- Shelenkova, N.Yu., The Structure and Variation of the Karyotype in Kamchatka Blueback Salmon and Several Other Salmon Species, *Abstract of Cand. Sci. (Biol.) Dissertation*, Leningrad: Institute of Cytology, USSR Acad. Sci., 1987.
- Chevassus, B., Guyomard, R., Chourrout, D., and Quillet, E., Production of Viable Hybrids in Salmonids by Triploidization, *Genet. Sel. Evol.*, 1983, vol. 15, no. 4, pp. 469–478.
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- Lozano, R., Ruiz Rejon, C., and Ruiz Rejon, M., An Analysis of Coho Salmon Chromatin by Means of C-Banding, AG- and Fluorochrome Staining, and In Situ Digestion with Restriction Endonucleases, *Heredity*, 1991, vol. 66, part 3, pp. 403–409.
- 22. Frolov, S.V., Chromosomal Nucleolar-Organizing Regions as a Population Marker of Salmon *Oncorhynchus masou* (Brevoort), *Genetika* (Moscow), 1995, vol. 31, no. 6, pp. 833–838.
- 23. Yamazaki, F., Arai, K., and Terao, T., Chromosomes of the Hybrids between Masu Salmon and Chinook Salmon, *Bull. Fac. Fish. Hokkaido Univ.*, 1987, vol. 38, no. 1, pp. 34–37.
- Flajshans, M. and Rab, P., Chromosome Study of Oncorhynchus mykiss Kamloops, Aquaculture, 1990, vol. 89, no. 1, pp. 1–8.
- 25. Klinkhardt, M.B. and Buuk, B., Die Chromosomen der Regenbogenforelle (*Salmo gairdneri*), *Zeitscchrift fur Binnenfischerei*, 1990, vol. 37, no. 7, pp. 226–228.
- Aref'ev, V.A., Mikodina, E.V., and Dushkina, L.A., Steelhead (Rainbow) Trout as a Possible Test Subject of Cytological Monitoring in Aquaculture, *Rybn. Khoz., Ser. Akvakul'tura*, VNIIERZh, 1996, no. 1, pp. 15–35.
- Ostberg, C.O. and Thorgaard, G.H., Geographic Distribution of Chromosome and Microsatellite DNA Polymorphisms in *Oncorhynchus mykiss* Native to Western Washington, *Copeia*, 1999, vol. 99, no. 2, pp. 287–298.
- Colihueque, N., Iturra, P., Estay, F., and Diaz, N.F., Diploid Chromosome Number Variations and Sex Chromosome Polymorphism in Five Cultured Strains of Rainbow Trout (*Oncorhynchus mykiss*), *Aquaculture*, 2001, vol. 198, pp. 63–77.
- Aref'ev, V.A. and Agapov, V.S., Karyotypic Characterization of rainbow trout Cultivated in NEKM, *Geneticheskie issledovaniya morskikh gidrobiontov* (Genetic Studies in Marine Hydrobionts), Moscow: Vses. Inst. Rybovod. Okeanogr., 1987, pp. 182–203.
- 30. Behnke, R.J., *Native Trout of Western North America*, Bethesda, Md.: Am. Fish. Soc., 1992.
- Zelinskii, Yu.P. and Makhrov, A.A., Chromosome Variation, Phylogenetic Genome Rearrangement, and Taxonomic Relationships of *Salmo* and *Parasalmo* Species (Salmonidae), *Vopr. Ikhtiol.*, 2001, vol. 41, no. 2, pp. 1–8.
- Loginova, G.A. and Krasnoperova, S.V., An Experiment on Hybridization of Atlantic Salmon Salmo salar and Pink Salmon Oncorhynchus gorbuscha (A Preliminary Communication), Tr. Polyarn. Nauchno-Issled. Inst. Morsk. Rybn. Khoz. Okeanogr., 1981, no. 45, pp. 112– 120.
- Woznicki, P., Jankun, M., Kucharczyk, D., et al., Cytogenetic Characterization of Sea Trout (Salmo trutta) from Poland, Copeia, 1999, no. 2, pp. 501–505.
- 34. Woznicki, P., Jankun, M., and Luczynski, M., Chromosome Studies in Brown Trout (*Salmo trutta* m. Fario) from Poland: Hypothetical Evolution of the 11th, 12th, and 14th Chromosome Pairs in the *Salmo* Karyotype, *Cytobios*, 1997, vol. 91, pp. 207–214.
- 35. Woznicki, P., Sanchez, L., Martinez, P., *et al.*, A Population Analysis of the Structure and Variability of NOR in *Salmo trutta* by Ag, CMA3 and ISH, *Genetica* (The Hague), 2000, vol. 108, no. 2, pp. 113–118.

- Frolov, S.V., Karyotypic Difference between Northern Dolly Varden *Salvelinus malma malma* and White Char *Salvelinus albus* from the Basin of the Kamchatka River, *Genetika* (Moscow), 2001, vol. 37, no. 3, pp. 350–357.
- Giedrem, T., Eggum, A., and Refstie, T., Chromosomes of Some Salmonids and Salmonid Hybrids, *Aquaculture*, 1997, vol. 11, no. 4, pp. 335–348.
- Alekseev, S.S., Pichugin, M.Yu., and Krysanov, Yu.E., Studies of Trans-Baikalian Char Salvelinus alpinus (Salmonidae) Introduced in the Red Book of the Russian Federation: Sympatric Form of the Bol'shoi Namarkit Lake (Morphology, Ecology, Karyology), Vopr. Ikhtiol., 1997, vol. 37, no. 5, pp. 588–602.
- Frolov, S.V. and Frolova, V.N., The Karyotype of Chukotka Char of the Estikhed Lake (Eastern Chukotka), *Genetika* (Moscow), 2001, vol. 37, no. 2, pp. 243–247.
- Zelinskii, Yu.P., Polina, A.V., and Medvedeva, I.M., The Karyotype and Adaptation of Freshwater Lake Char of the Genus *Salvelinus* (Salmoniformes, Salmonidae) from the Ladozhskoe Lake, *Zool. Zh.*, 1983, vol. 62, no. 5, pp. 732–736.
- 41. Bargetzi, J.-P., Application de methodes d'analyse biochimique à un probléme taxonomique: Les Coregones du lac de Neuchatel, *Schweiz. Z. Hydrologie*, 1960, vol. 22, no. 2, pp. 641–758.
- 42. Ohno, S., The Enormous Diversity in Genome Sizes of Fish as a Reflection of Nature's Extensive Experiments with Gene Duplication, *Trans. Am. Fish. Soc.*, 1970, vol. 99, no. 1, pp. 120–130.
- 43. Ershov, P.N., The Chromosome Set of Migratory Whitefish of the Varzuga River, Problemy izucheniya, ratsional'nogo ispol'zovaniya i okhrany prirodnykh resursov Belogo morya: Tezizy dokladov IV regional'noi konferentsii (Problems of Studies, Rational Use, and Preservation of Natural Resources of the White Sea: Proc. IV Regional Conf.), Arkhangel'sk, 1990, pp. 153– 154.
- 44. Jankun, M., Rab, P., Vuorinen, J., and Luczynski, M., Chromosomal Polymorphism in *Coregonus lavaretus* Populations from Two Locations in Finland and Poland, *Arch. Hydrobiol.*, 1995, vol. 46, pp. 1–11.
- 45. Jankun, M. and Rab, P., Multiple Polymorphism of Chromosome 1 in the Karyotype of Whitefish, *Coregonus lavaretus* (Salmonidae) from Lake System Saimaa, Finland, *Caryologia*, 1997, vol. 30, no. 2, pp. 185–195.
- Jankun, M., Boron, A., Kirtiklis, L., *et al.*, Cytogenetic and Biochemical Studies of European Whitefish (*Coregonus lavaretus* L.) from Switzerland, *Arch. Hydrobiol.*, 1998, vol. 50, pp. 363–369.

- Jankun, M., Ocalewicz, K., and Woznicki, P., Replication, C- and Fluorescent Chromosome Banding Patterns in European Whitefish, *Coregonus lavaretus* L., *Hereditas* (Lund, Swed.), 1998, vol. 128, no. 3, pp. 195–199.
- 48. Yakhnenko, V.M. and Mamontov, A.M., Chromosome Polymorphism in Two Subspecies of Lake Baikal Whitefish, *Coregonus lavaretus, VII Int. Symp. on Biology and Management of Coregonid Fishes*, Ann Arbor, Michigan, 1999, p. 110.
- 49. Al-Sabti, K., Using the In Vitro Colchicine Treatment for the Chromosome Studies of the Rainbow Trout (*Salmo gairdneri*) and the Grayling (*Thymallus thymallus*), *Ichthyologia*, 1984, vol. 16, nos. 1–2, pp. 17–22.
- 50. Vavilov, N.I., Zakon gomologicheskikh ryadov v nasledstvennoi izmenchivosti: Linneevskii vid kak sistema (The Law of Homologous Series in Hereditary Variation: Linnaean Species as a System), Leningrad: Nauka, 1967.
- 51. Bulatova, N.Sh., The Evolutionary Branch of Modern Cytogenetics, *Genetika* (Moscow), 1994, vol. 30, suppl., pp. 19–20.
- Bogdanov, Yu.F., Homologous Series in the Variation of Meiotic Traits: Evolution and Conservation, Evolyutsiya, ekologiya, bioraznoobrazie: Materealy konferentsii pamyati Nikolaya Nikolaevicha Vorontsova (1934– 2000) (Evolution, Ecology, Biodiversity: Proc. Conf. in Memory of N.N. Vorontsov (1934–2000)), Moscow: UNTs DO, 2001, pp. 60–75.
- Mednikov, B.M., On the Law of Homologous Series in Hereditary Variation Again, *Priroda*, 1989, no. 7, pp. 27– 35.
- Vorontsov, N.N., *Razvitie evolyutsionnykh idei v biologii* (Development of Evolutionary Ideas in Biology), Moscow: Mosk. Gos. Univ., 1999.
- 55. Soltis, D.E. and Soltis, P.S., Polyploidy: Recurrent Formation and Genome Evolution, *Trends. Ecol. Evol.*, 1999, vol. 14, no. 9, pp. 348–352.
- 56. Altukhov, Yu.P., *Populyatsionnaya genetika ryb* (Population Genetics of Fish), Moscow: Pishchevaya Promyshlennost'.
- 57. Mednikov, B.M., Shubina, E.A., Mel'nikova, M.N., and Savvaitova, K.A., The Problem of the Generic Status of Pacific Salmon and Trout (Genetic Taxonomic Analysis), *Vopr. Ikhtiol.*, 1999, vol. 39, no. 1, pp. 14–21.
- Tsoi, R.M., Sergienko, L.L., and Pak, I.V., Chromosome Mutability in Whitefish Species from River and Lake Ecosystems of the Ob'–Irtysh Basin, *Genetika* (Moscow), 1996, vol. 32, no. 1, pp. 137–139.
- 59. Mitrofanov, Yu.A., *Indutsirovannaya izmenchivost' khromosom eukariot* (Induced Chromosome Variation in Eukaryotes), Moscow: Nauka, 1994.