SBORNÍK NÁRODNÍHO MUZEA V PRAZE

ACTA MUSEI NATIONALIS PRAGAE

Volumen XXXI B (1975), No. 1—2

REDAKTOR JIŘÍ ČEJKA

JIŘÍ ČIHAŘ

National Museum – Natural History Museum
Department of Zoology

GEOGRAPHICAL AND ECOLOGIC VARIABILITY OF PERCH [PERCA FLUVIATILIS (LINNAEUS)] AND HISTORY OF ITS DISTRIBUTION FROM EURASIA TO NORTH AMERICA

Dedicated to doc. dr. Ota Oliva
on the occasion of his 50th birthday

This work deals with taxonomy and morphology of 560 specimens of fluvial perch (*Perca fluviatilis* L.) from 29 localities throughout the area of distribution of this species from the USA and Canada to Kolyma river in the north-east area of the USSR. It was surveyed that a perch forms numerous local ecologic and geographical forms all over that territory, which correspond with lower taxonomic unities (natio, infraspecies, morpha). Neither sub-species *Perca fluviatilis intermedius* from Kolyma river, described by SVETOVIDOV and DOROFEEVA, nor their hypothesis that the Kolyma perches are an interstage between eurasian and north-american populations and outline direction through which the perch was penetrating from Eurasia to North America in past time, were not confirmed.

The differences between North-american yellow perch and Eurasian perch are relatively small and prove there are two sub-species of the same species and not two independent species.

The contemporary distribution of fluvial perch in Eurasia and North America, relatively small taxonomic differences between *Perca fluviatilis fluviatilis* and *Perca fluviatilis flavescens* or the paleontologic arguments don't support the theory defended now by most of authors, i. e. that Eurasian perch penetrated to North America through north-pacific land bridge (Beringuiade). They rather indicate (as well as in case of some other fresh-water fishes) their distribution occurred from Europe to North America.

The author is presenting a new work-hypothese: perch and some other fresh-water fishes settled in North America from Europe in the time of glacial retreat, probably in last Würm glacial period, i. e. cca thirteen to fifteen thousand years B. P. through the brackish sea water along thawing arctic ice. Migration was probably supported by sea flows of that time and made easy by bigger extent of territories. Distribution of perch throughout different river basins was then made possible by connection of river and lake basins along foot of the receding ice sheet. In the north-east Asia, Kolyma and Anadyr mountains formed natural barrier to continuing distribution of perch to east,

in North America its advancement to west was stopped by crest of Rocky Mountains and Mackenzie mountains. Isolation of populations in individual river system and lakes of both continents occurred later than isolation of North-american yellow perch.

Balkhash species *Perca schrenki* was developing isolatedly since Tertiary in refugium, where glacial periods didn't substantially interfered by their influence.

1. Introduction

All animal and plant species, their today's appearance and contemporary geographical distribution are result of a longtime historical development. During ages it has been permanently developing, improving and adapting to the changing conditions of life. Plants and animals that lived for a long time isolated from other populations, were developing during hundreds of generations under pressure of specific conditions. At first, local ecologic and geographical forms had come into being, later, when such an isolated population separated taxonomically even more from the original species, a new species came into existence. It is closely cognate to the initial species though it differs so much that now it can be safely characterized taxonomically.

We know a lot of examples of an inception of new species and subspecies by a geographical isolation — the most popular and historically the oldest being the well-known insular fauna (fauna of Galapagos, fauna of Madagascar, the remarkable fauna of Australian region and many others) up to the cases of isolation occurring in times relatively recent (from the geological point of view) that are little known now and unsufficiently studied, too.

Fresh-water fish is the animal group, probably the most convenient one for the detailed and thorough studies of development of the animals in past geological epochs. Compared with the other vertebrates, they have many perfections as far as the phylogenetic studies are concerned. One is the fact their existence mostly depends very closely on fresh-water environment, on biotop very strictly marked off. They cannot — as the over-land vertebrates or sea fauna — change their stand as desired, they cannot follow better climatic and food conditions as mammals, birds, reptilians, amphibians or sea fauna.

Another important criterion causing the fresh-water fish is particularly convenient object of phyllogenetic studies is the fact that there are species or groups of species (genus, family) among them with a relatively broad area of distribution. No less important is the fact that we find among fresh-water fishes both groups evolutionarily immensely old, known since the time of the early carbon and groups relatively young, i. e. where we can presume their phyllogenetic development is actually in a full upsurge. Another virtue of fresh-water fishes is also the fact that their classification, development and today's distribution on the Earth is fairly well elaborated.

MYERS, 1938 (cit. DARLINGTON, 1957) divided fresh-water fishes as to their origin and relation to sea water into three basical divisions. The first division is formed by those species of fresh-water fishes which are strictly bound to fresh water and penetrate only rarely to brackish waters, avoiding to enter sea water. Those fishes which live largely in fresh water but suffer no harm in both brackish and sea waters, pertain to the second division. The third division of fishes, so called "peripheal division" (NICHOLS, 1928) concentrates such species of fishes which can live without harm in both fresh water and sea water and often migrate loosely between them.

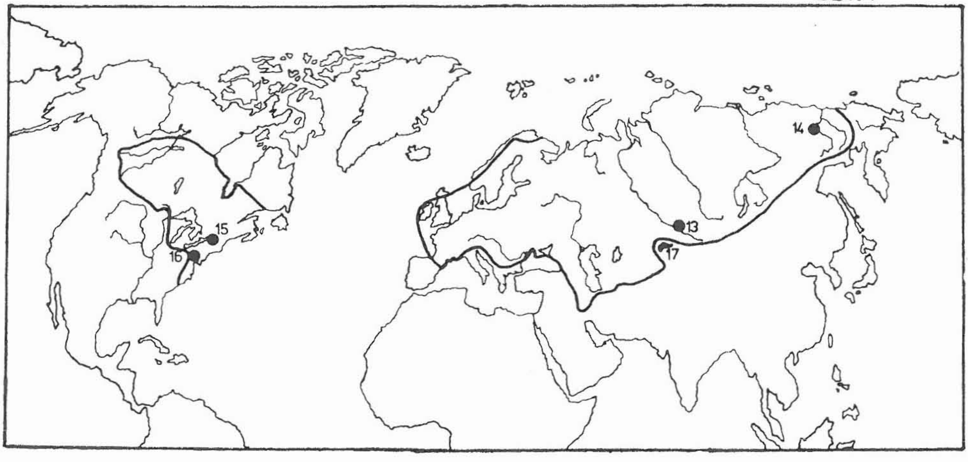
It is evident of what has been told here that the fishes of the first division are the most convenient for phyllogenetic studies, e. x. those fishes which always were and even now are strictly bound on fresh water. The first Meyers division includes Teleosts *(Teleostei)* only, pike, umbra, perch etc. belonging there. Almost seven eights of all fresh-water fishes of the first category belong to order *Ostariophysi (Cypriniformes)* — (of 40 families with more than 5.000 species only 2 families are marine and they include 150 species only).

This work is concerned with a contemporary ecologic and geographical variability of perch, it compares fluvial perch (*Perca fluviatilis* L.) from Eurasia and North America and tries to explain the reasons of its actual remarkable geographical distribution.

The perch, fish of genus *Perca* belongs to fishes plentifully found in a big part of holarctic area. They are living in fresh-waters of the immense area of the northern hemisphere all over Europe (with the exception of southern Mediterranean peninculas — Iberian, Apenines and southern part of Balkan), in rivers and lakes of northern parts of Asia in Arctic Ocean basin and the tributary rivers. They are found in Balkhash and Alakul lakes, too. In the east, the area of their contemporary distribution ends by Kolyma river basin. In eastern parts of North America

Picture No. 1
Map of distribution of *Perca fluviatilis* in holarctic sphere (after BERG 1949 and DARLINGTON 1957). The limits of distribution area are inked in thick line, black ringlets indicate places the investigated material comes from:
13 — Ob river, 14 — Kolyma river, 15 — Canada, 16 — U. S. A., 17 — Balkhash Lake, where endemic species *Perca schrenki* lives.

Obr. 1



the perch is living from Labrador up to Georgia, up to the system of Mississippi river and in the upper part of Mackenzie river system, in Little Slave Lake (according to BERG 1949 and SCOTT and CROSSMAN 1973) (picture No. 1).

In the wide area inhabited by fish of genus Perca, two, resp. three species are known. In Balkhash and Alakul and tributary rivers of these lakes the resident perch *Perca schrenki* formed two ecologic forms, substantially different from the European perch and the North-american yellow perch. According to BERG, 1949, there are these main differences between *P. schrenki* and *P. fluviatilis:*

Table No. 1

	Perca fluviatilis	*Perca schrenki*
The first dorsal fin	higher than the second one	lower than the second one
Number of scales in the lateral line	min. 55	max. 55
Back edge of the first dorsal fin	with black spot	without black spot

The opinion as to the taxonomic classification of perch from eurasian and north-american fresh waters are not yet quite uniform. Some authors consider the Eurasian and North-american yellow perch as two independent species *Perca fluviatilis* L. and *Perca flavescens* Mitchill (MITCHILL 1814, SCOTT and GROSSMAN 1969, STERBA 1959 etc.), others (BERG 1949, SVETOVIDOV and DOROFEEVA 1963, KIRILLOV 1972 etc.) consider North-american yellow perch as the mere sub-species of Eurasian perch *Perca fluviatilis flavescens* Mitchill.

In the immense area of Eurasia and North America, many geographical and ecologic forms of perch were described (EDDY and SURBER 1947, BERG 1949, POKROVSKIJ 1951, NIKOLSKIJ 1956, HUBBS and LAGLER 1958, ABDURACHMANOV 1962, SVETOVIDOV and DOROFEEVA 1963, KIRILOV 1972 etc.); as to BERG 1949 and SVETOVIDOV and DOROFEEVA 1963, the perch from the most eastern parts of the USSR, from Kolyma river basin, is the interstage between perch of the Old and the New World that suggests which way the perch of past time was distributing from his eurasian ancient home eastward to North America.

The aim of this work is primarily an attempt to compare the Eurasian and North-american perch population as far as the taxonomic signs and body proportions are concerned and the solution of the rather unclear question of their taxonomic pertinence. The work also tries to precise the sphere of influence of geographical and ecologic factors on exterier and meristic signs of perch of the wide territory inhabited by this species, to verify data about the fact the perch of Kolyma river is the interstage between Eurasian and North-american yellow perch, eventually an attempt to adumbrate the most probable ways through which the perch in holarctic region was spreading during past time.

I give my thanks to all foreign colleagues — ichthyologues, who sent me the samples of perches from the distant regions, making the solution of the task possible. Thanks to their help a numerous all-world collection of perch, practically from the whole area of their contemporary distribution came into existence in the National Museum of Prague. I give my thanks for granting study materials to prof. A. N. Svetovidov, dr. B. G. Jogansen and prof. F. N. Kirillov (USSR), prof. W. Frost (Great Britain), dr. W. Klausewitz (GFR), dr. A. Grimaldi (Italy), dr. W. Steffens (GDR), + dr. G. Schultz (Austria), dr. E. J. Grossman (Canada), dr. E. A. Lachner (USA), dr. M. Berg (Norway), dr. M. Papadopol (Rumania), dr. M. Olsson (Sweden) and dr. J. Bartel (Poland).

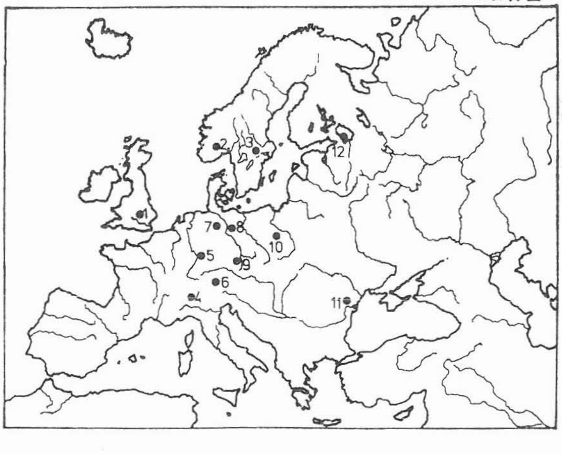
I must also give my best thanks to my colleagues — paleontologues dr. J. Beneš, dr. R. Horný and dr. R. Prokop of the National Museum of Prague and to dr. N. Obrhelová from the Institute of Geology of Academy of Sciences in Prague, whom I consulted all problems connected with history and ways of distribution of perch from Europe to North America with.

2. **Material and methods of work**

My work is based on results gained by studies of 560 perches from the different regions of holarctic area. Localities the respective material comes from are marked by black circlets on pictures No. 1 and 2. Picture No. 1 also demonstrates the area of the distribution of perch in eurasian and north-american waters.

Meristic signs and proportions which I investigated at all fishes can be seen in resumé tables included at the end of this work. I carried out the measurements according to already deep-rooted methods by slide millimeter rule, fishes were weighted on the sensitive mail scales accurate to 1 gram. Works requiring magnification were executed under binocular microscope with interchangeable lens.

Obr. 2



Picture No. 2
European localities the investigation material comes from: 1 — England, 2 — Norway, 3 — Sweden, 4 — Italy, 5 — GFR, 6 — Austria, 7 — GDR, 9 — Czechoslovakia, 10 — Poland, 11 — Rumania, 12 — Ladoga Lake.

Number of fishes of the particular localities, data of collection and names of collectors or donators are included in table No. 2. All fish material, fixed in 70% of alcohol, is deposited in ichthyological depositary of the National Museum of Prague under resp. Nos. 6598—7256.

Table No. 2

No.	Locality	Date of collection	Collector (donator)	No. of fishes
6598—6617	Ob river, Tomsk, USSR	1967	Jogansen	20
6618—6675	Mondsee, Austria	1967	Schultz	35
7122—7144	Mondsee, Austria	1967	Čihař	30
6658—6714	Krapina Lake, Rumania	1968	Papadopol	57
6764—6793	Windermere Lake, Great Britain	1968	Frost	31
6794—6804	Main by Seligenstadt, GFR	1967	Burkhardt	11
6806—6845	Lago Maggiore, Italy	1968	Grimaldi	40
6846—6851	Mälaren, Norway	1967	Vicant	6
6852—6875	Västervik, Sweden	1967	Osters	24
6877—6926	Ladoga, Balansk. guba, USSR	1967	Gavrilova	50
6927—6933	Diametralsperre, GFR	1968	Stein	7
6934—6938	Walchensee, GFR	1906	Wendt	5
6939	Spechbachweiter, GFR	1906	Wendt	1
6959—6967	Diametralsperre, GFR	1968	Stein	9
6968—6969	Seerahn, Mecklenburg, GDR	1969	Horák	2
6970	Schweinergartensee, GDR	1969	Horák	1
6971—7005	Grosser Mügelsee, GDR	1967	Schäfer	35
7006—7027	Lake by Mamaia, Rumania	1970	Provazník	22
7028—7077	Slapy dam, Czechoslovakia	1966	Čihař	50
145—7184	Wzdydze lake, Poland	1970	Bartel	40
7240—7256	Kolyma river, USSR	1971	Kirillov	17
6716—6729	Youth res., Garrett, Canada	1967	Johnson	14
6730—6763	Frontenac, St. Lawrence river Big Bay, Canada	1967	Crossman	34
6940	Miles Creek, Maryland, USA	1949	Van Densen	1
6941—6943	Small Fyke, N. Y., USA	1911	Need	3
6944	Severn river, USA	1949	Sanderson Zimmermann	1
5945	Potomac river, Glymont, USA	1897	Petrel	1
6946—6948	Lake Murray, Chaplin, USA	1954	Derrick	3
6949—6952	Kenora d., Sandy Lake, Canada	1966	Rower	4
6953—6958	Hastings, Ontario, Canada	1966	Rower	6

3. **Geographical and ecologic variability of perch**

We can notice considerable intraspecies variability in the whole immense area the perch is distributed. Probably almost in every bigger lake, two ecologic forms of perch can be found — the first one, subtle, lives in large shoals in bank shallows, in water growth etc. and grows in average more slowly then the other form, pelagic, which doesn't form large shoals. The food of the first form is mostly benthic fauna and zooplancton; the bigger, pelagic form of perch is ravenous and feeds mostly on little fishes (SVETOVIDOV and DOROFEEVA, 1963).

POKROVSKIJ 1951, who had gone into problems of intraspecies variability of fluvial perch in the USSR territory discovered that in individual fluvial systems and geographically isolated posts the perch forms big amount of ecologic varieties, mutually differing by colouring, growth-rate and way of life. Some geographical forms, as for example perch from Zaisan Lake (DIANOV 1955, cit. SVETOVIDOV and DOROFEEVA 1963) were described as independent sub-species, even when it seems that this is probably the question of lower taxons. It can be seen in tables, included at the end of this work, that there are many similar forms existing throughout the area of distribution of fluvial perch. We can cite as a typical example the perch from Mondsee Lake in the Austrian Alps, perch from the lower flow of Danube or from Lago Maggiore, Italy. It would be probably more convenient to formulate the whole question so that the perch creates now numerous local forms all over the area of distribution which are sometimes approximating the geographical forms (subspecies), sometimes the systematical lower categories (natio, infraspecies, morpha). It is probable that where the geographical isolation had occurred earlier in past, perch populations differed from the initial species more than where the geographical isolation happened in times relatively recent.

Perca schrenki of Balkhash and Alakul Lakes certainly isolated as the first one from the original old home. Balkhash Lake is one of the classical refugiums (microclimately protected territory), the ice ages didn't substantially influenced. Therefore, the local typical perch could go developing since the Tertiary, quite isolated from the others.

As far as fluvial perch (*Perca fluviatilis* L.) is concerned, the most striking differences, exceeding considerably in some signs the divergences among subspecies, are between perch of Old and New World; the permanent polemics of ichthyologues on the systematic lay-out of perches of both regions give evidence of it. The differences confirm that in this case the geographical isolation had occured before the isolation of some perch populations of eurasian and north-american continent. It may be supposed that the influence of environment which participated on development of perch of both continents, were not at all substantially different; both the climate and the ecologic factors of regions the perch lives today in Eurasia and North America are in the main very similar. I shall give heed to these problems in the following chapters.

Very interesting facts can be found if we compare meristic signs of individual perch populations according to geographical latitude and

Tab. 3 — Meristic signs of *Perca fluviatilis* from south to north.

Locality	Number of scales			Number of fin rays		
	later. line	trans-versal	prae-dorsal	D1	D2	A
U. S. A.	56,27 52—62	8,07 7—10	15,13 12—17	13,25 XII—XV	I—III, 11—15	II, 7—8
Canada	53,75 50—59	7,08 6—8	17,42 14—21	12,31 XII—XIV	0—III, 12—15	II, 7—9
Rumania	58,41 53—66	8,79 8—11	14,50 12—18	13,50 XII—XIV	0—II, 12—15	II, 7—9
Italy	68,39 62—72	9,57 8—11	15,61 13—19	13,82 XIII—XIV	I—II, 13—16	II, 8—10
Austria	64,67 61—72	9,23 8—11	14,90 11—18	13,82 XIII—XVI	I—II, 13—15	II, 7—9
Czechoslov.	62,60 59—68	10,33 9—12	15,10 13—17	13,90 XIII—XV	I—III, 13—15	II, 8—9
GFR	63,27 55—68	9,91 8—12	14,36 11—18	14,03 XIII—XV	I—II, 12—15	II, 8—9
GDR	61,56 56—67	9,33 8—10	14,87 12—18	14,15 XIII—XV	I—III, 13—15	I—II, 7—10
England	63,70 61—67	9,07 7—10	13,67 11—17	13,80 XII—XV	0—II, 13—15	II, 8—10
Poland	68,23 62—76	9,97 9—11	15,69 13—20	14,00 XIII—XV	I—II, 13—15	II, 6—10
Sweden	60,92 55—66	9,17 8—10	15,83 13—19	14,38 XIII—XV	I—II, 13—15	II, 7—10
Ladoga	64,08 58—70	9,72 8—11	16,04 13—21	14,60 XIII—XV	I—II, 11—15	II, 8—10
Norway	63,00 61—65	10,17 9—12	15,50 14—18	14,17 XIV—XV	I—II, 13—14	II, 8—9
USSR (r. Ob)	71,55 64—78	10,30 9—12	14,30 12—16	14,65 XIII—XVI	I—II, 12—14	II, 7—9
USSR (r. Kolyma)	60,24 57—66	9,59 9—10	15,65 14—18	15,18 XIII—XVII	I—II, 13—15	II, 8—9

longitude (tables No. 3 and 4). Only one taxonomic sign — number of rays in the first dorsal fin — has in average slightly increasing tendency from the south northward and from the west eastward. The other signs coincide all over the area of distribution of Eurasian perch. If we notice some signs of fishes from different localities (tables No. 3 and 4) more at large, we can see that some of the populations differ conspicuously from the other ones. For example the perch of Kolyma river has in average the biggest number of rays in the first dorsal fin, the North-american yellow perch has the least of all (table No. 5). As far as the number of scales in the lateral line is concerned (table No. 6), it is almost

Tab. 4 — Meristic signs of *Perca fluviatilis* from west to east

Locality	Number of scales			Number of fin rays		
	later. line	trans- versal	prae- dorsal	D1	D2	A
Canada	53,75	7,08	17,42	12,31	0—III, 12—15	II, 7—9
U. S. A.	56,27	8,07	15,13	13,25	I—III, 13—15	II, 7—8
England	63,70	9,07	13,67	13,80	II, 8—10	II, 8—10
Norway	63,00	10,17	15,50	14,17	0—II, 13—15	II, 8—9
Italy	68,39	5,57	15,61	13,82	I—II, 13—16	II, 8—10
GFR	63,27	9,91	14,36	14,03	I—II, 12—15	II, 8—9
GDR	61,65	9,33	14,87	14,15	I—III, 13—15	I—II, 7—10
Austria	64,67	9,23	14,90	13,82	I—II, 13—15	II, 7—9
Czechoslovakia	62,60	10,33	15,10	13,90	I—III, 13—15	II, 8—9
Sweden	60,92	9,17	15,83	14,38	I—II, 13—15	II, 7—10
Poland	68,23	9,97	15,69	14,00	I—II, 13—15	II, 6—10
Rumania	58,41	8,79	14,50	13,50	0—II, 12—15	II, 7—9
Ladoga	64,08	9,72	16,04	14,60	I—II, 11—15	II, 8—10
USSR (r. Ob)	71,55	10,30	14,30	14,65	I—II, 12—14	II, 7—9
USSR (Kolyma)	60,24	9,59	15,65	15,18	I—II, 13—15	II, 8—9

Tab. 5 — Number of rays in the 1st dorsal fin

Locality	Number of spec.	XII	XIII	XIV	XV	VI	VII	Average
Canada	36	17	17	2	—	—	—	12,31
U. S. A.	16	3	8	3	2	—	—	13,25
England	30	1	4	23	1	—	—	13,80
Italy	28	—	5	23	—	—	—	13,82
Norway	6	—	—	5	1	—	—	14,17
GFR	34	—	4	25	5	—	—	14,03
GDR	39	—	2	29	8	—	—	14,15
Austria	39	—	10	27	1	1	—	13,82
Czechoslovakia	30	—	4	25	1	—	—	13,90
Sweden	24	—	1	13	10	—	—	14,38
Poland	30	—	4	22	4	—	—	14,00
Rumania	34	1	15	18	—	—	—	13,40
Ladoga Lake	50	—	1	18	31	—	—	14,60
USSR (r. Ob)	20	—	1	9	6	4	—	14,65
USSR (Kolyma)	17	—	1	4	2	9	1	15,18

Tab. 6 — Number of scales in the lateral line

Locality	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	Average
U. S. A.	—	—	1	2	2	2	1	2	2	—	2	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	56,27
Canada	2	5	6	6	6	1	4	3	1	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	53,75
England	—	—	—	—	—	—	—	—	—	—	—	1	5	8	7	7	1	1	—	—	—	—	—	—	—	—	—	—	—	63,70
Italy	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1	2	2	3	6	1	6	4	2	—	—	—	—	—	—	68,39
Norway	—	—	—	—	—	—	—	—	—	—	—	2	1	—	1	2	—	—	—	—	—	—	—	—	—	—	—	—	—	63,00
GFR	—	—	—	—	—	1	—	—	—	1	2	3	4	10	2	2	6	2	1	—	—	—	—	—	—	—	—	—	—	63,27
GDR	—	—	—	—	—	—	2	—	2	2	7	6	6	5	4	3	1	1	—	—	—	—	—	—	—	—	—	—	—	61,56
Austria	—	—	—	—	—	—	—	—	—	—	—	2	2	3	3	9	1	3	6	1	3	4	1	—	—	—	—	—	—	64,67
Czechoslovak.	—	—	—	—	—	—	—	—	—	1	1	5	8	5	4	4	1	—	1	—	—	—	—	—	—	—	—	—	—	62,60
Sweden	—	—	—	—	—	1	—	—	3	5	3	2	3	2	2	2	1	—	—	—	—	—	—	—	—	—	—	—	—	60,92
Poland	—	—	—	—	—	—	—	—	—	—	—	—	1	—	2	2	4	4	2	4	5	3	2	—	—	—	1	—	—	68,23
Rumania	—	—	—	3	1	—	5	4	4	6	4	2	2	1	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	58,41
Ladoga Lake	—	—	—	—	—	—	—	—	1	3	1	4	4	6	10	5	6	5	3	1	1	—	—	—	—	—	—	—	—	64,08
USSR (r. Ob)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1	—	1	2	1	2	4	4	2	—	1	—	1	71,55
USSR (Kolyma)	—	—	—	—	—	—	—	2	3	3	3	1	1	2	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	60,24

coincident with the majority of Eurasian perch populations; the fishes from Ob river vary conspicuously with the in average highest number of scales in the lateral line (71, 55), perch from the lakes at the lower flow of Danube (in average 58, 41), perch of Sweden and of Kolyma river have the least number of scales. The American yellow perch has in average smaller number of scales in the lateral line as well as less rows of scales above the lateral line than the Eurasian perch (Canada 7,08 in average, USA 8,07, Eurasian fishes 8.79—10,33 in average).

The perch of Canada (17,42) and of Ladoga Lake (16,04) have the biggest number of scales before the insertion of the first dorsal fin (Squammae praedorsales, table No. 7). Fishes of Rumania (13,50) and the English locality Windermere (13,80) have the smallest number of scales before the dorsal fin. In transversal line (table No. 8) perch of Canada and USA, of Eurasian localities than fishes from England have the least number of scales (9,07), perch of Czechoslovakia the biggest one (10,33).

It can be seen in the above mentioned examples that the different values of North-american and Eurasian perch are relatively considerable and must be assigned to the rather long-time geographical isolation, but the differences between the systematic signs of perches of individual Eurasian and North-american localities are substantially smaller. It may suggest that their geographical isolation (if there is any isolation at all) from the coherent area of species' distribution occurred later.

Tab. 7 — Number of praedorsal scales

Locality	10	11	12	13	14	15	16	17	18	19	20	21	Aver.
U. S. A.	—	—	2	1	2	4	3	2	—	—	1	—	15,13
Canada	—	—	—	—	1	4	5	9	9	3	4	1	17,42
England	—	3	4	7	6	7	2	1	—	—	—	—	13,67
Italy	—	—	—	2	4	8	6	6	1	1	—	—	15,61
Norway	—	—	—	—	1	3	1	—	1	—	—	—	15,50
GFR	—	1	1	6	9	11	4	—	1	—	—	—	14,36
GDR	1	—	1	5	9	10	7	3	3	-	—	—	14,87
Austria	—	1	3	8	6	3	7	9	2	—	—	—	14,90
Czechoslov.	—	—	—	3	6	10	9	2	-	—	—	—	15,10
Sweden	—	—	—	3	3	4	6	4	3	1	—	—	15,83
Poland	—	—	—	1	3	10	10	2	2	—	1	—	15,69
Rumania	—	—	2	6	11	6	7	1	1	—	—	—	14,50
Ladoga Lake	—	—	—	4	5	11	11	10	6	—	2	1	16,04
USSR (Ob)	—	-	1	4	6	6	3	—	—	—	—	—	14,30
USSR (Kol.)	—	—	—	—	2	7	5	1	2	—	—	—	15,65

Tab. 8 — **Number of scales in the transversal line**

Locality	6	7	8	9	10	11	12	Average
U. S. A.	—	5	5	4	1	—	—	8,07
Canada	2	19	14	—	1	—	—	7,08
England	—	1	5	15	9	—	—	9,07
Italy	—	-	1	11	15	1	1	9,57
Norway	—	-	—	2	2	1	1	10,17
GFR	—	—	2	7	19	4	2	9,91
GDR	—	—	2	22	15	—	—	9,33
Austria	—	—	7	17	14	1	—	9,23
Czechoslovakia	—	—	—	—	20	7	2	10,33
Sweden	—	—	4	12	8	—	—	9,17
Poland	—	—	—	5	21	4	—	9,97
Rumania	—	—	12	18	3	1	—	8,79
Ladoga Lake	—	—	3	23	23	1	—	9,72
USSR (r. Ob)	—	—	—	3	10	5	2	10,30
USSR (r. Kolyma)	—	—	—	8	8	1	—	9,59

We can see similar differences when comparing results of measuring body proportions at perch of individual localities. In the table No. 9 and 10 there are dissimilar values of some localities, perceptibles at the first sight, wrenching very often the average. Perch of Rumania, Alpine lakes of Mondsee and Lago Maggiore, Polish lakes, perch of England, of Ladoga Lake, of Scandinavia, Ob river and Kolyma river basins belong there. Practically almost each of the contemplated localities considerably differ from the others in some habitual signs of perch. The similar differences we can notice at perch of Canada and the USA.

We shall try now to characterize fishes of individual localities of the eurasian and north-american continent more in details (see tables No. 3, 9, 10):

a) **Perches of Rumanian lake at the estuary of Danube** have in average very small number of scales in the lateral line. They are relatively small, with big head (in average 33,2 % of body lentgth). Their dorsal fin is considerably moved backward as well as the ventral fins. Compared with other localities'fish they have the second dorsal fin slightly higher in average. The distance between their eyes is relatively small. There are 5—10 outstanding dark cross stripes on their flanks.

b) **Fishes of Lago Maggiore in Italian Alps** have in average the most scales in their lateral lines (68,39) of the European perches. They have considerably more scales before the base of the first dorsal fin, too. Their head, compared with the body length, is relatively short, their dorsal fins and ventral fins are moved more forward than at the other fishes and the distance between eyes is rather big.

c) **Perches of the Alpine lake of Mondsee in Austria** have relatively big amount of scales in lateral line (61—72), the first ray of the first dorsal fin is very short (73.7 % of the length of the second ray) and many (7—11) outstanding dark stripes on their flanks.

They form a typical low-body form; the height of their body is in average only $^1/_4$ of the body length, while at perch of all other localities it is $^1/_3$. The Mondsee perch has relatively short caudal fin and short ventral fins, its first dorsal fin is relatively low. This fish has its mouth subtler than the perch of other localities, its nasal pores rather distant and considerably big eyes. Its head, compared with other perch, is rather slender. The total habitus of that fish is narrowly connected with the ecologic factors of the Alpine glacial lake and it is probably stabilized to a certain extent thanks to rather long standing geographical isolation of that locality. The Mondsee perch constitutes a stunted form similar to that we know at crucian carp (*Carassius carassius m. humilis* Heckel), even though in that case the reasons are undoubtedly both ecologic (rather poor, cool conditions of life) and geographical (isolation of locality).

The analysis of the digestive tract of some perches of Mondsee confirm that the main food of this fish is the minute planctonic crustaceans, benthic fauna, even insect fallen on the water surface. The fact their food is very minute is also confirmed by the considerable length of their gill rakers (it will be stated later).

d) **Perches of Slapy dam in Central Bohemia** have in average maximum of scales above the lateral line (squammae lineae lateralis) of all the studied fishes (10,33). The ventral fins and caudal fin are relatively long, dorsal and anal fins rather high. The eyes of that perch are rather distant and are situated at the back of head.

e) **Fishes of Diametralsperre and the other localities in the GFR** have in average big number of rays in the first dorsal fin (14,03). They are characterized by a long, broad head and heavy body. Their caudal fin is rather short, the mouth big and the eyes relatively small.

f) **Perches of North-german Grosser Mügelsee (GDR)** are characterized by a considerable number of scales in the lateral line (average 61,56). They have strikingly long base of the first dorsal fin. Their nasal pores are relatively close to each other.

g) **Perches of Polish take Wzdydze** are of low-body form. They have big number of scales in the lateral line (average 68,23). Their body is strikingly slender and on flanks pressed down. Their body at the caudal peduncle is relatively higher than at other localities'perch. The fins are mostly short and lowlying. These fishes have their eyes set very close.

h) **Perches of English lake Windermere** have in average smaller number of scales above the lateral line than the majority of Eurasian fishes (average 9,07) and relatively few praedorsal scales (average 13,67). They have rather small number of rays in the first dorsal fin; therefore they bear resemblance to the North-american yellow perch. Their head is short, high and broad. The dorsal fin is situated more in front than of majority of other localities'perch. The body is considerably pressed down on the flanks.

i) **Fishes of Ladoga Lake** have big number of scales before the insertion of the first dorsal fin. Their anal fin is situated rather in the back. Their body is considerably broad and head rather narrow. The dark cross stripes on their flanks are little perceptible.

j) **Perches of Sweden** have relatively few scales in the lateral and transversal lines. The base of their first dorsal fin is relatively very long. The caudal fin is long too, the second dorsal fin is relatively high. Mouth of Swedish perch is rather big, its body in the caudal part is high. Cross stripes on flanks are little perceptible.

k) **Fishes of Mälaren in Norway** have in average big number of scales above the lateral line (average 10,17) and belong to robust perch group. Their body is high and strong, the second dorsal fin is relatively long--lying but with a very strong base. The mouth is big, nasal pores rather distant, their eyes are small — one set far from the other. Their body is rather high in the caudal fin (the same as perch of Sweden). They have 6—7 little perceptible dark cross stripes on their flanks. Material of these fishes is relatively poor (6 specimens only), it seems that by habit they are similar to Swedish perch.

l) **Perches of Ob river in the USSR** have the biggest number of scales in the lateral line (71,55) and big number of rays in the first dorsal fin (average 14,65). Their dorsal fins are rather high, with short bases. Their eyes are set considerably in front. Head is narrow. Their body is relatively very low-lying in the caudal part.

m) **Perches of Kolyma river** have relatively few scales in the lateral line (average 60,24), considerable number of scales in front of the base of the first dorsal fin and the biggest amount of rays of the first dorsal fin (average 15, 18). They strikingly differ from the North-american yellow perch. Compared with the others, they have very short head, high and strong body, very long caudal fin and high anal fin. Their eyes are small. The body on Kolyma river perch is relatively high in the caudal part.

n) **Perches of the USA,** as well as the Canadian fishes, have contrary to Eurasian perch several different meristic and plastic signs. They differ by bigger number of rays in the first dorsal fin, bigger number of scales in the lateral line and in transversal line, lesser number of scales in front of the base of the 1st dorsal fin. They considerably differ even in some plastic signs; rather small number of fishes of the USA and their small size unfortunately don't permit to compare them with Canadian perch. In spite of it it is noticeable that in North-american territory there is similar interspecies variability among perches of several localities as among Eurasian perches.

o) **Canadian perches** differ substantially from the Eurasian ones. Thanks to numerous materials they can help to comparing Eurasian and North-american yellow perch. I'll deal with this problem in the 4th chapter.

We can see there is considerable inter-species variability inside the continuous area of distribution of the *Perca fluviatilis* species as far as meristic signs and plastic signs. Same as BERG 1949, POKROVSKIJ 1951, ABDURACHMANOV 1962, KIRILLOV 1972 and many other authors, the author of this publication is of the opinion the question is mostly non-geographic, ecologic forms, mutually connected by many transient populations. However no difference of all the investigated Eurasian perches is clean-cut enough to entitle to designating independent subspecies. HOLČÍK and SKOŘEPA 1971, concluded the same opinion as to the roach (*Rutilus rutilus* L.) when studying the inter-species variability. According to BERG 1949, they are mostly either infra-species, or ecologic forms (morpha) and in some cases — perch of the Alpine lakes, Ob river, Kolyma river and English lake Windermere — we can consider them as natio; in these cases they are geographically independent population (SUVOROV 1948), isolated for a rather long period.

While studying the inter-species variability of *Perca fluviatilis*, considerable attention was given to number and shape of gill rakers on the first gill arch. Some authors (BERG 1949, POKROVSKIJ 1951 etc.) consider this sign as a criterion for taxonomical studies; they have been particularly studying the relation between the length of gill rakers and gill filaments, varying expressively (as was stated correctly by SVETOVIDOV and DOROFEEVA 1963) according to the length of fish.

The results of this work prove that number of gill rakers of perch is in all localities almost coincident throughout the area of distribution. Smaller differences are probably caused by relatively little number of the investigated material. I chose a sample of 15 fishes only, of the approximately coincident body length and from each locality, to avoid possible differences caused by varying size of compared fishes. It is known (ČIHAŘ, 1958) that the number of gill rakers depends considerably on the length of fish body. Number of gill rakers can be seen in the table No. 11 and table of numerosity No. 12 on page 72 of this work.

Table No. 11 — The average number of gill rakers on the first gill arch

Rumania	Italy	Austria	ČSSR	GFR	GDR	Poland
20,2 (18—23)	23,0 (21—25)	20,9 (17—74)	20,7 (17—25)	21,8 (17—24)	22,6 (20—25)	23,9 (21—29)

England	Ladoga	Sweden	Norway	Ob	Kolyma	USA	Canada
23,2 (22—25)	22,6 (20—24)	23,0 (22—25)	22,5 (21—24)	23,0 (21—26)	20,2 (18—23)	20,3 (19—21)	19,0 (18—21)

Identical with other fishes, the length of gill rakers of perch, too, is connected very closely with the type of food received, with what the fish is mostly fed on. Therefore it is not possible to consider the

Tab. 12 — Number of gill rakers on the first gill arch

Locality	17	18	19	20	21	22	23	24	25	26	27	28	29	Aver.
U. S. A.	—	—	1	4	3	—	—	—	—	—	—	—	—	20,3
Canada	—	4	3	2	1	—	—	—	—	—	—	—	—	19,6
England	—	—	—	—	—	1	7	1	1	—	—	—	—	23,2
Italy	—	—	—	—	1	2	3	2	1	—	—	—	—	23,0
Norway	—	—	—	—	1	2	2	1	—	—	—	—	—	22,5
GFR	1	—	—	1	1	2	4	1	—	—	—	—	—	21,8
GDR	—	—	—	2	1	2	4	3	1	—	—	—	—	22,6
Austria	1	—	—	—	3	4	5	1	—	—	—	—	—	20,9
Czechoslovakia	—	—	—	1	3	7	5	2	2	—	—	—	—	22,4
Sweden	—	—	—	—	—	3	2	1	1	—	—	—	—	23,0
Poland	—	—	—	—	—	1	2	4	1	—	—	—	1	23,9
Rumania	—	—	2	3	3	—	2	—	—	—	—	—	—	20,2
Ladoga Lake	—	—	—	2	—	2	2	4	—	—	—	—	—	22,6
USSR (r. Ob)	—	—	—	—	1	4	1	3	—	1	—	—	—	23,0
USSR (Kolyma)	—	1	3	3	—	2	1	—	—	—	—	—	—	20,2

length of gill rakers as reliable criterion for taxonomic evaluation. We can see in picture No. 3, where the first gill arches of different environment, length and shape of individual gill rakers are schematically demonstrated, how closely the length of gill rakers is connected with food. It is remarkable that long rakers of planctonofagous perch have on surface bigger number of fine protrusions, the whole system being a very effective filtering apparatus, collecting microscopis morsels. As to the length of gill rakers we can divide our perches into 4 main groups, with many continuous transitions existing between:

1st group (very short gill rakers — 1 : 2):* perch of Ladoga Lake, Canada and Sweden;

2nd group (short gill rakers — 1 : 1,5):* perch of the USA, GFR, Kolyma river and Norway;

3rd group (gill rakers medium size — 1 : 1):* perch of Czechoslovakia, GDR, England and Ob river;

4th group (very long gill rakers — 1,5 : 1):* fishes of Poland, Rumania, Italy and Austria.

The analysis of the contents of digestive organs of these fishes confirmed that perch with the longest gill rakers feed mostly on subtle food

---

* Numbers in brackets signify the proportion of gill rakers'length to gill filaments' length.

(zooplancton, little insect larvae etc.), fishes of the 2nd and 3rd groups on coarse morsels (bigger insect larvae, small fishes), perch of the last group almost solely on fishes.

4. **Perch of Eurasia and North America**

Opinions on taxonomy and systematic relations between Eurasian and North-american perch are far from clear. Many authors (MITCHILL 1814, GÜNTHER 1859, STEINDACHNER 1878, DAY 1880, 1884 etc.) concluded, after comparing and evaluating systematic signs of both continents'perch that the differences between them are so conspicuous that they justify the classification of North-american yellow perch as an independent species *Perca flavescens* Mitchill, but JORDAN and GILBERT 1882, raised many objections to those conclusions. Even SMITH 1893, reached a conclusion that both perches are only subspecies of one species, his opinions being later confirmed by BERG 1905, 1949, POKROVSKIJ 1951 and many other authors. The standpoint that the North-american yellow perch is a good species is supported even today by many ichthyologues (SCOTT and GROSSMAN 1969, 1973, STERBA 1959 etc.).

BERG 1949, proves besides it — basing on comparing of gill rakers and gill filaments'length — that perch of the most distant north-east Siberia is a certain transient form between Eurasian perch and the North-american yellow perch. We already mentioned what an unreliable taxonomic sign this criterion is. Berg's opinion was later confirmed by POKROVSKIJ 1951, who defined also a volume of inter-species variability of perch in the USSR territory with more precision, using large material and studying considerable amount of signs.

Relation between the length of gill rakers and gill filaments is a rather variable sign, but the next one, studied by BOULENGER 1895, later by POKROVSKIJ 1951, SVETOVIDOV and DOROFEEVA 1963, is relatively constant. It is a relation between the length of the first ray of the first dorsal fin and the length of the second ray, resp. between the length of the first ray of the first dorsal fin and the length of the first ray of the anal fin.

I have studied this sign of all Eurasian and American perch localities and I cannot agree with the opinions of the mentioned authors, same as KIRILLOV 1972; when studying perch of Kolyma, he reached such a variability of this sign that he couldn't confirm opinions neither of POKROVSKIJ nor of SVETOVIDOV and DOROFEEVA, that the Kolyma river perch is, thanks to this sign, existing between Eurasian and North-american perch, forming a transitient form between them.

Consequent to the table No. 13 on the page 74 of this work, the first ray of the first dorsal fin of Kolyma river perch is in average slightly shorter but not so expressively as it was found by the mentioned authors on relatively scanty material. Further of their affirmations that from West to the East the length of the first ray D1 goes down, must be taken with certain reserve (table No. 13). Almost same values were found for example at perch of Kolyma river, Rumania and Austrian lake Mondsee, of England and Ob river; the fishes of Poland, England, Northgerman

Tab. 13 — Length of the 1st ray of D1

Locality	Length of the 1st ray D1 to:		Body length mm	Number of specimens
	2nd ray of D1	longest ray A		
U. S. A.	59,2 (50—65)	59,8 (40— 83)	63—145	9
Canada	61,6 (46—83)	72,0 (45— 97)	151—213	58
England	76,3 (66—86)	104,8 (93—119)	146—207	31
Italy	81,1 (58—92)	112,6 (86—128)	117—208	40
Norway	78,8 (70—89)	123,0 (88—142)	207—254	6
GFR	81,4 (74—84)	117,2 (104—136)	149—258	22
GDR	80,2 (68—89)	124,3 (100—167)	123—195	38
Austria	73,7 (59—82)	83,8 (59—100)	92—113	65
Czechoslovakia	81,0 (73—90)	120,7 (100—161)	128—161	50
Sweden	82,3 (64—93)	115,6 (106—129)	160—250	24
Poland	75,3 (57—83)	104,6 (63—125)	100—153	40
Rumania	76,0 (69—85)	92,4 (79—104)	108—143	79
Ladoga Lake	85,7 (75—93)	110,5 (102—120)	168—233	50
USSR (r. Ob)	80,5 (75—87)	104,4 (81—182)	109—171	20
USSR (Kolyma)	72,1 (60—85)	82,8 (64—111)	232—257	17
SVETOVIDOV and DOROFEEVA, 1963:				
European part of USSR	70,0—93,9	86,9—133,3	60—270	30
river Jenisej	63,4—92,2	74,6—148,6	84—114	6
river Lena	55,2—90,0	56,1—124,1	46—243	10
river Kolyma	36,9—80,4	33,0—121,5	43—249	15
Perca flavescens	34,8—65,7	36,3— 81,2	48—239	16
POKROVSKIJ, 1951 (cit. SVETOVIDOV and DOROFEEVA 1963):				
river Kolyma	72,0—84,0	73,5—96,1	—	6
Perca flavescens	52,0—69,0	50,0—83,2	—	4

Grösser Mügelsee, of Norway, Sweden and Italy had in average the longest first ray D1. It is evident that BERG, POKROVSKIJ, SVETOVIDOV and DOROFEEVA considerably over estimated the importance of that sign when comparing the Eurasian and North-american perch.

SVETOVIDOV and DOROFEEVA describe Kolyma river perch as an additional independent subspecies *Perca fluviatilis intermedius* SVETOVI-

DOV and DOROFEEVA 1963; they base on comparing the length of the first ray of the first dorsal fin, on comparing craniologic and some paleontologic discoveries of Krcak peninsula to the east of Kolyma river, where the remnants of *Perca fluviatilis* were found in Quarter stratum by LEBEDEV 1960.

Both authors recapitulated all their existing knowledge on taxonomy of *Perca fluviatilis fluviatilis* and *Perca fluviatilis flavescens* and defined some signs both these subspecies differ from each other and from newly described subspecies *Perca fluviatilis intermedius,* too. Their conclusions are shown in table No. 14:

Table No. 14

Sign investigated	*P. fluviatilis fluviatilis*	*P. fluviatilis intermedius*	*P. fluviatilis flavescens*
number of scales in the lateral line	57—77	56—62	54—62
frontal edge D1 in relation to P	before P	before or above P	before or above P
crest occipitale	high	high	low
cranium	broad	broad	narower
distance between eyes in % of head length	21,4—26,1	20,6—29,0	17,9—24,6
length of the 1st ray D1 to the 2nd ray D1	55—94 %	37—74 %	35—69 %
number of rays in D1	XIII—XVIII	XII—XVI	XIII—XV
number of rays in A	II/7(8—9)10	II 7—9	II 7—8
number of vertebras	(39, 40) 41—42 (43—44)	39—41	40—41

If we compile the values, gained by studies of big amount of perches and presented in this publication into a similar table and supply them with additional facts and other authors'data, the situation looks different (table No. 13, 15).

Hence it follows that all the studied signs of Kolyma and other Eurasian perches cover over so much that a description of Kolyma perch as an independent subspecies is nor really well-fonded. Even in this case, equally to perch of some other localities, the question is more a mere local form than a subspecies.

As far as Eurasian and North-american yellow perch is concerned, even now differences are so much outstanding (minor number of scales in the lateral line, position of a dorsal fin, in average shorter first ray of the first dorsal fin, lower height of the caudal peduncle than of Eurasian perch etc., see table No. 3, 9, 10, 13, 15), that it is possible fully confirm the authorisation of an independent North-american subspecies *Perca fluviatilis flavescens* Mitchill, obviously not as an independent species. Differences between *Perca fluviatilis fluviatilis* and *Perca fluviatilis flavescens* are well visible even in number of rays of the first

Table No. 15

Investigated sign	*P. fluviatilis fluviatilis*	*P. fluviatilis of Kolyma r.*	*P. fluviatilis flavescens*
No. of scales of the lateral line	(53)55—76(78)	57—66	50—62
frontal edge D1 in relation to P	before, above	before, above	before, above
distance between eyes in % of head length	21—33 %	26—29 %	21—27 %
length of the 1st ray D1 to the 2nd ray D1	57—93 %	60—85 %	46—83 %
no. of rays in D1	XII—XVI	XIII—XVII	XII—XV
no. of rays in D2	I—III, 12—16	I—II, 13—15	I—III, 12—15
no. of rays in A	I—II, 7—8	II, 8—9	II, 7—8
no. of scales before D1	11—21	14—18	12—21
no. of scales in transversal line	7—12	9—11	6—10
praedorsal dist.	33—38	30—34	28—35
length of the caudal peduncle	18—27	19—23	16—26

dorsal fin (table No. 11), in number of scales of lateral line, in transversal line and praedorsal scales, too (see table No. 6, 7, 8).

Several signs, as for example number of rays in the first dorsal fin, are in inconsistence with conclusion of SVETOVIDOV and DOROFEEVA 1963. In the direction from west to the east there is an average increase of rays in the first dorsal fin; the biggest differences are particularly at Kolyma river perch, i. e. from the most eastern area of distribution, and from the North-american yellow perch. The least difference we can see when comparing this sign of West European perch and North-american yellow perch (table No. 16):

Table No. 16 — Average number of rays in D1

Canada	USA	England	Italy	Norway	GFR	GDR
12,3	13,2	13,9	13,8	14,2	14,0	14,2

Austria	ČSSR	Sweden	Poland	Rumania	Ladoga	Ob	Kolyma
13,8	13,9	14,4	14,0	13,5	14,6	14,7	15,2

These facts oppose the conclusion of BERG, POKROVSKIJ, SVETOVIDOV and DOROFEEVA; some facts indicate more that Eurasian perch was not expanding to the American territory across East Asia and Bering bridge, but they can also support completely different theory the last two chapters of this work are dealing with.

5. On history of distribution of fluvial perch from Eurasia to North America

The contemporary habitation of perch in fresh-waters of Eurasia and North America is really remarkable. Area of distribution of *Perca fluviatilis fluviatilis* in Eurasia extends on East up to the basin of Kolyma river only; it seems (as to LEBEDEV 1959) that in ancient times it used to be found more in the east, in Quarter strata of Krcak peninsula in Tchaun bay, but it probably never penetrated to the extreme east of North Asia. Today, it doesn't live as autochton fish nor in the North-siberian neither North-american rivers, disemboguing to Bering sea and Pacific Ocean.

In North-american continent, perch is found as an initial fish in eastern parts only, from Labrador up to Georgia. Its western border is Mississippi river basin and Little Slave Lake in Mackenzie river system. In the last century it was introduced by a man to some waters in Pacific Ocean basin so that its contemporaneous habitation in North America is far from the original distribution of this species on the North-american continent (SCOTT and CROSSMAN, 1973).

According to Mc PHAIL and LINDSEY 1970, the perch was probably distributed continously across North America some time prior to Wisconsin glatiation. They suppose, that this fish survived south to glaciation in the upper Mississippi refuge, in the postglacial age it distributed through the system of glacial lakes in the north and north-western direction. In the same refugium survived after Mc PHAIL and LINDSEY the fishes of genus *Stizostedion* and *Esox,* too. But the paleontological discoveries confirming their oppinion are absent in the perch. SCOTT and CROSSMAN 1973 give the evidence of the percid family in North America from eocene, but the oldest discovery of *Perca fluviatilis* come from late Pleistocene (SMITH 1954). The Eocene founds belong to the fossil genus *Mioplosus.*

Now it is necessary to remark that the similarity and close affinity of ancient and contemporaneous ichthyofauna of Europe and North America doesn't include fish of genus *Perca* only but other genus and families of fishes, too, e. g. *Cyprinidae, Cyprinodontidae,* in the past *Amiidae* and *Lepisosteidae* etc. Some of them will be object of studies in another work that will be published later. Fishes of *Stizostedion* and *Umbra* genus have almost concurrent area of distribution as perch, i. e. they are not found in eastern parts of Asia and in the west of North America (SCOTT and CROSSMAN, 1973).

The initial distribution of perch over the holarctic region indicate that the distribution of this species to North America was being done from Europe (see picture No. 1). However it remains unexplained how and when the perch infiltrated from Europe to North America. Several theories deal with those problems, not only as far as perch is concerned but in regard of affinity and similarity of North-american and European fauna and flora in general (summarized in the publication Löwe and Löwe, 1963). One of them, the well-known Wegener theory or theory of drifts is based on a conspicuous coincidence of meritic lines of Europe and Africa on one side, South and North America on the other side; it presumes that primarily there was one continent (Pangea) only; that primeval land disintegrated sometime in Mesozoic or earlier and during ages the continents separated. This theory cannot be applied to explain the distribution of perch of Europe to North America, because relatively small taxonomic differences between Eurasian and North-american yellow perch indicate that their geographic isolation happened in time substantially succeeding, during the Quarter.

The 2nd theory which presumes the distribution of perch and other fishes from Europe to North America was done through Atlantic connection at the end of Miocene and beginning of Pliocene (LINDBERG 1961, 1962), resp. owing to pristine connection of European and North-american fluvial systems (Paleorhein and Paleohudson) was later dissaproved by the author himself and many other experts.

So, in spite of the fact many cogent arguments confirm that perch and many other fishes penetrated to North America from Europe, most of newer theories have been presuming (BERG 1949, POKROVSKIJ 1951, SVETOVIDOV and DOROFEEVA 1963 etc.) that fluvial perch penetrated in past from Eurasia to North America through today's Bering isthmus, resp. across the land bridge called Beringuiada that had been created in Tertiary and early Quarter and where the migration of Eurasian elements of mammals'species to American continent took place (SIMPSON 1947).

Conclusions, postulated by paleontolog JAKOVLEV 1961, and ichthyologues SVETOVIDOV and DOROFEEVA 1963, are particularly interesting for us. JAKOVLEV, emanating of analysis of paleontologic discoveries, demonstrates that neogenous ichthyofauna of Palearctus and Nonarctus differed mutually much more than recent ichthyofauna and their formation was passing independently. Distribution of most of families, living today in both regions, was in Neogene far from their contemporary distribution.

According to JAKOVLEV 1961, the exchange of ichthyofauna of Eurasia and North America occurred twice in ancient times — once in Paleogene, thanks to direct continual connexion, for the second time in Pleistocene, across the Beringuiada. And according to JAKOVLEV precisely during pleistocenous north-pacific land connexion the perch penetrated from East Asia to North America.

SVETOVIDOV and DOROFEEVA 1963, who are defenders of theory of Eurasian perch penetration to the North-american continent through Beringuiada, are supporting — in case of pike-perch distribution *(Stizostedion)* to North America — quite the reverse opinion. They blame BANARESCU 1960, for considering the distribution from Eurasia across the Bering land bridge in this case and as a main reason against his opinion they quote the contemporaneous distribution of genus *Stizostedion* in Europe (today limited to Europe only). Their arguments are based on ascertainments that any paleontologic discoveries of this genus in more eastern regions of Asia are missing; most eastward the remnants of genus *Stizostedion* were found up to the present time in Pliocene of river Irtysh basin (LEBEDEV 1959) and in Miocene and Pliocene of Altay (SYČEVSKAJA and DEVJATKIN 1962).

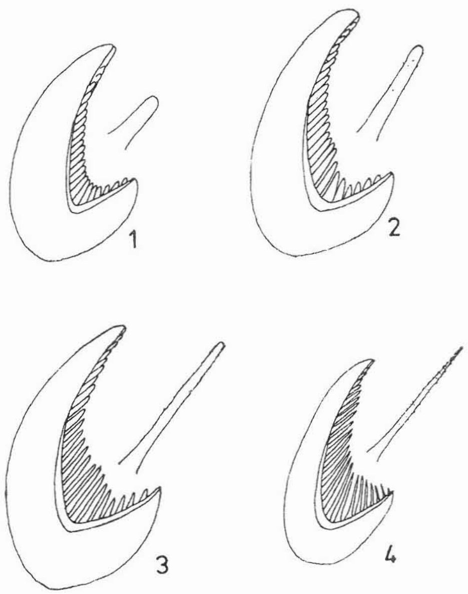
SVETOVIDOV and DOROFEEVA 1963, referring to Jakovlev's work suppose the perch penetrated to North America across Bering land bridge already in late Tertiary and support their opinion by findings that river Kolyma's perch — from the most eastern region, where they have been recently living on Eurasian continent — has transitory position between European and American yellow perch. But the results of my own work in no way support their conclusion what is proved even by the end of preceding chapter.

If we want then to accept the hypothesis that perch and other species of fishes penetrated to North America from East Asia across Beringuiada, we should have to put up with some discrepancies. First of them, particularly cogent objection against "Bering" theory in the case of perch, is the contemporary distribution of this species in palearctic and nonarctic area. It doesn't indicate at all that such a distribution would have been occurring in past time; all over the extensive territory from Kolyma river to the east over Alaska up to Maskenzie system this species doesn't exist at all. Perch is not found in Asia to the east Kolyma and Anadyr mountains, in North America west of Rocky and Mackenzie mountains; those both mountain chains are probably a limit *Perca fluviatilis* never surpassed. Paleontologic discoveries east of Kolyma are situated to the west of those mountains and don't contradict that assertion; they only prove that perch used to exist in Quarter more to the east than today, but they don't confirm the connection of Asian and North-american populations of perch of that period.

6. **Discussion**

It is very probable the perch penetrated to North America from European continent, namely — owing to not very expressive taxonomic differences we can find between Eurasian perch and North-american yellow perch — certainly in time relatively recent, either at the end of Pleistocene or in early Postpleistocene period. And because neither Wegener's older theory nor Lindberg's younger one didn't stand the proof in long-termed discussion about this problem, it is necessary to consider some other possibilities, a new way through which the distribution of perch and other fresh-water fishes from Europe to America in past time occurred.

One of them, in opinion of author of this publication the most probable one, has not been considered yet. It is the **distribution of fishes and their settlement in a new continent in the period of retreat of the last Arctic glaciation (the end of the Pleistocene) along ice masses by the fresh or braskish water through the sea.** (Picture No. 4.)



Picture No. 3

Dependence of length and shape of gill rakers on food factors:

1 — big, predatory perch has the rakers very short and smooth;

2 — perch living on bigger morsels has his rakers relatively short and slightly rugged;

3 — fishes living on subtle morsels have long rakers with many short bumps;

4 — planctofagous perch has very long rakers with many long bumps working together as a filtr of subtler food.

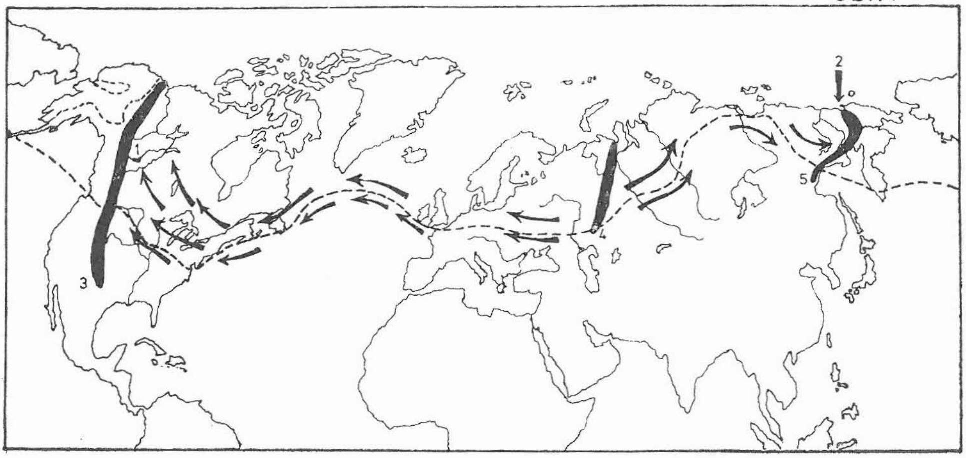
Obr. 3

Picture No. 4

Hypothetical distribution of perch and other species of fishes in holarctic region in Postpleistocene. Bounds of arctic glacial is marked by broken line (after DARLINGTON 1957), arrowheads specifying direction of distribution of perch along the thawing glacial, black spots distinguishing mountain ridges limiting the perch distribution: 3 — Rocky Mountains and Mackenzie Mountains, 4 — Ural, 5 — Kolyma and Anadyr mountains.

1 — Little Slave Lake, most western locality of perch in North America, 2 — Tchaun bay, where the remnants of *Perca fluviatilis* were found in Quarter strata by LEBEDEV, 1960 (the most remote in the east of North Asia).

Obr.4



Ice ages always used to have an immense influence on nature of areas arctic ice afflicted with its influence. In time of the last würm glaciation, a continuous arctic ice sheed in Europe extended down to North-german and North-polish lowlands and encroached upon wast areas of northern parts of Asia. In North America, a huge Wisconsin ice was covering almost all Canada and Alaska, penetrated deeply into the today's United States'territory and was of a big importance for a contemporary distribution of North-american ichthyofauna (RYDER, SCOTT, CROSSMAN 1964, Mc PHAIL and LINDSEY 1970). The approximatelly south limit of glaciation in the würm ice age can be seen in picture No. 4.

The ice age passed, climate of north hemisphere begun to grow warmer, ice masses were thawing and receding to the north. At that time, continuous depressions and system of glacial lakes, filled with freshwater, arose in continents along the edges of thawing ice; there, partly water of thawing ice was flowing down, partly all rivers, flowing from the south to the north desembogued there and their waters fused in bulky flow which outflew to oceans (VALENTIN 1957, see picture No. 5).

Picture No. 5
The North Sea area during the maximum of the Würm glaciation (according to VALENTIN 1957):
1 — British ice sheet, 2 — Scandinavian ice sheet, 3 — Glacial lake, 4 — Elbe-"Urstrom", 5 — Channel-"Urstrom".

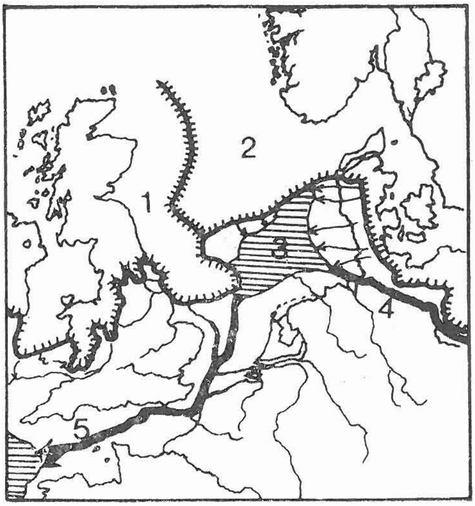


FIG. 5

The main water-shed of Eurasian continent must have been Ural, in North America then Rocky Mountains and Mackenzie Mountains. Through the rivers and glacial lakes along the edges of arctic ice sheed, the freshwater fishes could undoubtedly distribute in land throughout various river systems but the high mountains were obstructing such a distribution. Supposing the distribution of fluvial perch of that time extended from the West Europe up to Siberia (according to OSNOVY PALEONTOLOGII 1964, there are known remnants of fluvial perch of West Europe and Siberia Pliocene), that species could distribute from Ural water-sheed in two directions — westward to Atlantic region, then eastward to East Siberia rivers up to Kolyma and Anadyr mountains, that stopped the species from distributing far to the east.

Similar situation as in continents must have been very likely along the edge of ice in the sea, too. Huge rivers of fresh-water, flowing down off the thawing ices through deep river-beds, not only increased substantially ocean level in ice and after-ice ages but freshed the sea water far from its environs; that can be noticed at arctic icebergs even now, though. Almost all water along the ice must have been less or more brackish; big rivers, flowing down from land to oceans along thawing ice sheets, in all likehood contributed to its freshing. In those times the warm Golf flow probably didn't exist in the form we know it today, but there must have been existing similar warm sea flows that drifted to the north from warm Atlantic region, washed all round the arctic ice and perhaps flowed along it from Europe to the American continent.

Huge ice masses kept in time of glacials a considerable amount of water. Therefore, the area of continents in ice ages and during their receding was bigger than now and distances between them were shorter. For example — according to HEEZEN and THARP (in LÖWE and LÖWE 1963) lowered the sea-level in this time between 105—160 m. (See picture No. 6.) Through that way, along the receding arctic ice, driven probably by sea flows, many species of fresh-water European fishes — perch, pike perch, Umbra and perhaps some other species, too — could have had distributed in those times from Europe to North America.

FIG.6

Picture No. 6

Hypothetical bathymetric chart of the Faeroe — Iceland — Greenland Ridge if sea level were lowered 200 m (black), 300 m (pointed) and 800 m (white). Many botanics believe, that this Ridge occurred in the Late Pleistocene (after HEEZEN and THARP, in LÖWE and LÖWE 1963).

The last ice age finished — from the geological point of view — rather recently, some fifteen to twelve thousand years B. P. If some European fishes entered exactly in that period the North-american continent, they comprehensibly couldn't differentiate taxonomically from their european precursors in such a short period. And this can be a good reason why till now there is no unity as to opinions on taxonomy of some genus and species of European and North-american fishes, fluvial perch and its north-american subspecies icluded.

As far as the intraspecies variability of fluvial perch in Eurasian and North-american continent is concerned, it is stated by the fact the geographical isolation of individual fluvial systems, lakes etc. occurred in geologically younger times (Mc PHAIL and LINDSEY, 1970 — see the picture No. 7). So for instance the North-american yellow perch settled in today's Little Slave Lake (the most western locality in America where it can be found as an original fish) when the Laurentide ice sheet reached the 55th paralell.

Picture No. 7

Postglacial lakes, selected to illustrate drainage patterns that crossed present drainage boundaries during glacial retreat in North America. The lakes shown did not exist all at the same time (after Mc PHAIL and LINDSEY, 1970):

1 — Glacial Dezadeash Lake, 2 — Prince George basin, 3 — Lake Peace, 4 — Miette Lake, 5 — Lake Edmonton, 6 — Glacial Lake Mc Connell, 7 — Lake Tyrrell, 8 — Lake Agassiz, Campbell phase, 9 — Lake Agassiz, Gimli phase, 10 — Lake Barrow — Ojibway. Through the lakes along the edges of Wisconsin ice, the fresh-water fishes could distribute throughout various river systems.

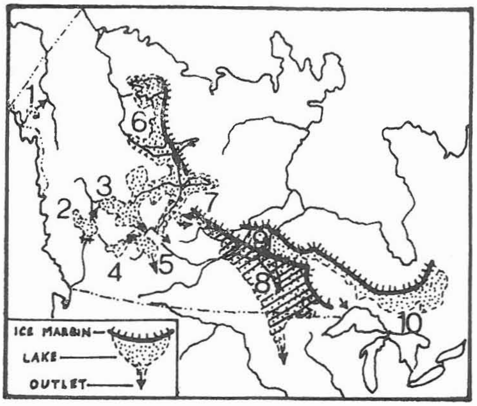


FIG. 7

Dispersal of the perches and other freshwater fishes during glacial retreat in North America explains the Mc PHAIL's and LINDSEY's publication 1970, based on many geological studies of the Wisconsin ice age. (Picture No. 7.)

According to those authors ice did not retreat uniformly to the north — in costal regions fairly rapidly than in inland. Most of Nova Scotia and costal regions of Labrador were ice-free by 10.000 years BP. In the Great Lakes area the great glacial Lake Barlow — Ojibway and Agassiz Lake were formed in this time, drained to the south into Mississippi basin and southeast into the St. Lawrence system.

In the inland the southern edge of the Laurentide ice sheet extended in a northwest direction. Southern Alberta and southwestern Saskatchewan became ice-free relatively early and numerous smaller glacial lakes were formed in southern Alberta, drained south into the Missouri river, and later east into Lake Agassiz. When the ice retreated in the area north of Edmonton, another series of large glacial lakes was formed: Lake Edmonton, Peace and Tyrrell. These lakes, in the same way as the later large Mc Connell Lake, formed in the Great Slave Lake — Great Bear Basin, were connected with the Lake Agassiz.

The salt Champlain Sea what flooded the St. Lawrence lowlands after the Atlantic coast deglaciation, occurred perhaps in the time of the two Creeks interval, about 10 000 BP. Long ago the freshwater fishes from Europe undoubtedly could reach the North American continent.

For the distribution of the perch and some other freshwater fishes, seems as most important the early retreat of ice from coastal atlantic regions and the rapid northeasterly retreat of ice in the inland. At the foot of the northern ice formed coherent system of great glacial lakes; this way the freshwater fishes could comparatively quickly disperse from St. Lawrence "Urstrom" in various river systems of northeastern parts of North America continent, up to the Rocky Mountains ridge.

In conclusion, we shall try to sum up briefly the probable history of distribution of genus *Perca*; we shall keep to the hypothesis that the distribution of fluvial perch had occurred both in continents and across the Atlantic Ocean from Europe to North America, along the thawing and receding arctic glacial (see picture No. 4).

Species *Perca schrenki* isolated the first of all perches, probably during Tertiary, in Balkhash and Alakul Lakes — in refugium, non-influenced by arctic glacial during the whole Pleistocene ice age. Fifteen to twelve thousand years BP., after the end of the last Würm glacial, contemporary yellow perch, *Perca fluviatilis flavescens* penetrated together with some other species of fresh-water fishes from Europe to North America through brackish water along artic ice, perhaps with help of sea flows. Successive separation of individual geographically mutually isolated perch populations in European and North-american continent (in lakes, British isles, in fluvial systems etc.) is of younger data so that today some of them form independent lower taxonomic unities (natio, infraspecies, morpha).

In Eurasian continent, the perch penetrated farthest to the east to Kolyma and Anadyr mountains, mountain ridge that extends approx. from the south to the north-east of Kolyma river, being a water-shed of Arctic Ocean and Bering sea. The finding place of Quarter period perch in Tchaun bay belongs to this area and doesn't contradict the new hypothese at all.

In North America, the perch distributed to the west up to the big massif of Rocky Mountains and Mackenzie Mountains, where it has been living since in Little Slave Lake in system of Mackenzie river.

Taxonomic position of American yellow perch is now, with regard to Eurasian perch, close to the subspecies; it is without doubt, that in the long future its taxonomic dissimilarity will reach such values that it will become an independent species. In fact we are now seeing a new species coming to existence, while the Eurasian and North-american perch natia will be differentiating in the future in taxonomically well distinguishable subspecies; natia will be changed in subspecies, infraspecies will become natia etc.

It is very likely that not only perch settled along the arctic glacial through Atlantic in North America. Contemporary geographical distribution and taxonomic affinity of some other fishes of the first Meyers division in Europe and in North America (*Stizostedion, Esox, Lota, Umbra, Thymallus* etc., for details see BERG 1949) suggest, that at least some of them used the same way in the same period, some of them probably even earlier, in Riss or Mindel ice age.

7. **Conclusions**

This work on zoogeography and history of distribution of some European fishes deals with geographical and ecologic variability of perch and history of its probable distribution in holarctic area. It is based on results got by studying 560 fishes from all kinds of localities throughout the area of species *Perca fluviatilis* distribution. The achieved results can be summed up in the following summary:

1. All over the vast region the fluvial perch lives, its considerable inter-species variability can be noticed.

2. Only one of the investigated signs, number of rays in the first dorsal fin, has in average slightly increasing tendency from the south to the north and from the west to the east. The Canadian and US yellow perch has the least number of rays in D1, followed by fishes of European localities; towards the east number of rays in D1 continues increasing. Kolyma river perch has the biggest number of rays in D1.

3. While differences between Eurasian and Nort-american perch are considerable and more than fully justify determination of two subspecies, the differences between perches of various Eurasian localities are substantially minor. In some cases one can speak about natia, more frequently about infraspecies or ecologic forms, morpha.

4. These facts indicate that the geographical isolation of Eurasian and North-american perch had occurred before the isolation of their population on Eurasian and North-american continent.

5. Considerable differences were found during studies of plastic signs on perch body, in individual body proportions. Practically almost each of investigated populations differs distinctly in some signs of other perches in sense of habit. There are small perches with low bodies living in Alpine lakes Mondsee and Lago Maggiore, perch of Scandinavian localities are big and robust.

6. The length of gill rakers taken into consideration at taxonomy by BERG 1949, POKROVSKIJ 1951, etc. turned out to be an unreliable taxonomic sign. It depends considerably both on body length of fish and on ecologic factors (food) of the respective biotop.

7. As to the kind of food received we can divide perches to four categories. Fishes with the longest gill rakers live — according to analysis of their digestive organs — mostly on subtle food (zooplancton etc.), fishes of the 2nd and 3rd group have their rakers medium large or short and their food are bigger morsels (bigger insect larvae, small fishes), perch with the shortest gill rakers lives almost exclusively on fish food.

8. Kolyma subspecies of perch *Perca fluviatilis intermedius,* described by SVETOVIDOV and DOROFEEVA 1963, which according to those authors should be a transient form between Eurasian and North-american perch, is not well founded (according to the results of this work). While it reminds the North-american yellow perch by some signs (the length of the first ray D1), by others (number of rays in D1, number of scales in the lateral line etc.) *Perca fluviatilis flavescens* differs substantially and resemble perch of East Eurasian localities. Kolyma river perch is undoubtedly lower taxonomic unity than subspecies.

9. Although most of newer theories try to prove that the perch penetrated from Eurasia to North-american continent across Tertiary land bridge in place of today's Bering straits, some of cogent reasons don't suggest it. The first reason is the contemporary distribution of *Perca fluviatilis* in North-american territory and in Eurasia. Further reason that gives evidence against such a theory is a contemporary rather small taxonomic diversity of North-american yellow perch and Eurasian perch. It indicates that their geographical indication occurred — from the geological point of view — later than in Tertiary so that it is rather young.

10. Nor the theories applied by some ichthyologues and explaining the penetration of freshwater ichthyofauna from Europe to North America either in period of Mesozoic connection of both continents or newer Lindberg's hypothesis on Miocenous or Pliocenous connection of European and North-american river systems (Paleorhein, Paleohudson) were not accepted by experts because of cogent reasons, in spite of long discussions.

11. This work presents a new work-hypothese: on the basis of all arguments, cited in No. 9 it considers the penetration of perch from Europe to North America in last Pleistocene or early Holocene through the Atlantic freshing or brackish water along the thawing arctic ice. Migration could have been supported both by sea flows, moving on along the ice from Europe towards the American continent, and minor sea extent in glacial and post-glacial ages. The distribution of perch in East Asia to the east was prevented by Kolyma and Anadyr mountains, distribution in North America towards the west by Rocky Mountains and Mackenzie mountains.

12. This hypothese is supported by today's relatively small diversity of Eurasian and North-american yellow perch and some other species of fishes of the 1st Meyers division. According to this "glacial" hypothese the geographical isolation of Europe North-american yellow perch had occurred some fifteen to twelve thousand years ago. The isolation of individual populations in enclosed lake or river systems of both continents than happened in later period. The exception is *Perca schrenki* of Balkhash and Alkul lakes that has been developing isolatedly since Tertiary in refugium, non-interfered by arctic glacial.

REFERENCES

ABDURACHMANOV, J. A. (1962): Ryby presnych vod Azerbajdžana. Izd. Akad. Nauk Azerb. SSR, Baku, 405 p.

BANARESCU, P. (1960): Einige Fragen zur Herkunft und Verbreitung der Süßwasserfischfauna der europäisch-mediterranen Unterregion. Arch. Hydrobiol., **57**, (1/2), 16—134.

BERG, L. S. (1905): Ryby Turkestana. Naučn. rezultaty Aralsk. eksped., VI, Izv. Turk. otd. Russk. geogr. o-va, IV, 261 p.

BERG, L. S. (1949): Očerki po fizičeskoj geografii. Izd. AN SSSR.

BERG, L. S. (1949): Ryby presnych vod SSSR i sopredelnych stran, I—III, Moskva, 1381 p.

BOULENGER, G. A. (1895): Catalogue of the Perciform fishes in the British Museum. 2nd. ed., I, 394 p.

ČIHAŘ, J. (1958): Zametki po systematike karasja (Carassius carassius m. humilis Heckel 1840). Vopr. ichtiol. Vyp. 11, 136—141.

DARLINGTON, P. J. (1957): Zoogeography: the geographical distribution of animals. John Wiley and sons, inc., New York, 675 p.

DAY, F. (1880—1884): The fishes of Great Britain and Ireland. I, London, p. 3.
DIANOV, P. A. (1955): Okuň ozera Zajsan. Avtoref. diss., Inst. zool. AN Kaz. SSR.
EDDY, S., SURBER, T. (1947): Northern fishes, with special reference to the Upper Mississippi valey. Univ. Minnesota Press, 276 p.
GÜNTHER, A. (1859): Catalogue of the Acanthopterygien Fishes, I, p. 60.
HOLČÍK, J., SKOŘEPA, V. (1971): Revision of the roach [Rutilus rutilus (Linnaeus, 1758)], with regard to its subspecies. Annot. zool. et bot., Bratislava.
HUBBS, C. L., LAGLER, K. F. (1958): Fishes of the Great Lakes region. Cranbrook Inst. Sci., Bull. **26**, 207 p.
JAKOVLEV, V. N. (1961): Rasprostranenie presnovodnych ryb neogena goloarktiki i zoogeografičeskoe rajonirovanije. Vopr. ichtiol., **1**, vyp. 2.
KIRILLOV, F. N. (1972): Ryby Jakutii. Izd. Nauka, Moskva, 360 p.
LEBEDĚV, V. D. (1959): Neogenovaja fauna presnovodnych ryb Zajsanskoj vpadiny i Zapadno-Sibirskoj nizmennosti. Vopr. ichtiol., Vyp. 12, 45—47.
LEBEDĚV, V. D. (1960): Ostatki okunja Perca fluviatilis L. v četvertičnych otloženijach severo-vostoka Sibiri. Vopr. ichtiol. Vyp. 14, 164, 245.
LINDBERG, G. U. (1961): Svjaz evropejskich rek s rekami Ameŕiki i severoatlantičeskij razryv. Zool. žurnal XL, 5, p. 662.
LINDBERG, G. U. (1962): O svjazi kontinentov Evropy i Ameriky. Sb.: Sovetsk. rybochozj. issled. v sev.-zap. časti Atlant. okeana. Izd. Rybnoje chozjajstvo, p. 81.
LÖWE, A., LÖWE, D. (1963): North Atlantic Biota and their History. Pergamon Press, Oxford — London — New York — Paris, 430 p.
Mc PHAIL, J. D., LINDSEY, C. C. (1970): Freshwater fishes of North-western Canada and Alaska. Fish. Res. Board of Canada, Bull 173, Ottawa, pp. 7—14.
NICHOLS, J. T. (1928): Fishes from the White Nile... (With table of "world's freshwater fish faunae"). Amer. Mus. Novitates, No. 319.
NIKOLSKIJ, G. V. (1951): Ryby bassejna Amura. Izd. AN. SSSR, Moscow, 551 p.
OSNOVY PALEONTOLOGII (1944): Izd. Nauka, Moskva, Bd. 11.
POKROVSKIJ, V. V. (1951): Materialy po issledovaniju vnutrevidovoj izmenčivosti okunja (Perca fluviatilis L.). Tr. Kar.-Finsk. otd. Vsesoj. naučn. inst. ozer. i reč. rybn. chozjajstva, T. III, pp. 95—149.
RYDER, R. A., SCOTT, W. B., CROSSMAN, E. J. (1964): Fishes of Northern Ontario, North of the Albany river. Royal Ont. Mus., Toronto, pp. 1—30.
SCOTT, W. B., CROSSMAN, E. J. (1969): Checklist of Canadian Freshwater Fishes with Keys for Identification. Royal Ont. Mus., Toronto, Contr. 66, pp. 1—106.
SCOTT, W. B., CROSSMAN, E. J. (1973): Freshwater fishes of Canada. Fish. res. Board of Canada, Bull. 184, Ottawa.
SIMPSON, G. G. (1947): Holarctic mammalia faunas and continental relationships durin Cenozaic. Bull. Geol. Soc. Amer., **58** (7), p. 656, 686.
STEINDACHNER, F. (1878): Ichthyologische Beiträge (VII.). X. Perca fluviatilis, Lin. Sitzungsber. Akad. Wissensch. Wien, LXXVIII, 1, p. 398.
STERBA, G. (1959): Süßwasserfische aus aller Welt. Urania-Verlag, Leipzig, Jena, p. 502.
SUVOROV, N. A. (1948): Osnovy ichtiologii. Sovetskaja nauka, Moskva.
SVETOVIDOV, A. N., DOROFEEVA, E. A. (1963): Sistematičeskije otnošenija, proischožděnije i istorija rasselenija evropejsko-aziatskich i severoamerikanskich okuněj i sudakov (Rody Perca, Lucioperca i Stizostedion). Vopr. ichtiol., **3**, Vyp. 4 (29), pp. 625—651.
SYČEVSKAJA, E. K., DEVJATKIN, E. V. (1962): Pervyje nachodky ryb iz neogenovych i nižně četvertičnych otloženij Gornogo Altaja. Dokl. AN SSSR, **142** (Vyp. 1), p. 175.
VALENTIN, H. (1957): Glazialmorphologische Untersuchungen in Ost-England. Abh. d. Geogr. Inst. d. freien Univ. Berlin, pp. 1—86.
WEGENER, A. (1915): Die Entstehung der Kontinente und Ozeane. Brunswick, Friedr. Vieweg und Sohn.

JIŘÍ ČIHAŘ

GEOGRAFICKÁ A EKOLOGICKÁ VARIABILITA OKOUNA ŘÍČNÍHO (PERCA FLUVIATILIS) A HISTORIE JEHO ROZŠÍŘENÍ Z EURASIE DO SEVERNÍ AMERIKY

Práce se zabývá taxonomií a morfologií 560 exemplářů okouna říčního (*Perca fluviatilis*) z 29 lokalit po celém areálu rozšíření tohoto druhu od USA a Kanady po řeku Kolymu v severovýchodní oblasti SSSR. Bylo zjištěno, že okoun tvoří na tomto obrovském území celou řadu místních ekologických a geografických forem, které odpovídají nižším taxonomickým jednotkám (*natio, infraspecies, morpha*). Z řeky Kolymy SVETOVIDOVEM a DOROFEEVOU popsaný poddruh *Perca fluviatilis intermedius*, stejně jako jejich předpoklad, že kolymský okoun tvoří přechodnou formu mezi evropskými a severoamerickými populacemi a tak naznačuje i směr šíření okounů v minulých dobách z Eurasie do Severní Ameriky, nebyly autorem tohoto sdělení potvrzeny.

Rozdíly mezi severoamerickými a eurasijskými okouny jsou relativně malé a potvrzují, že jde o dva poddruhy téhož rodu, nikoli o dva samostatné druhy.

Současné rozšíření okounů v Eurasii a v Severní Americe, relativně malé taxonomické rozdíly mezi *Perca fluviatilis fluviatilis* a *Perca fluviatilis flavescens* ani paleontologické argumenty nepotvrzují teorii, zastávanou dnes většinou autorů, tj. že okoun z Eurasie do severní Ameriky pronikl přes severopacifický pevninský most (Beringiádu). Spíše naznačují, stejně jako v případě některých jiných sladkovodních ryb, že se jejich šíření do Severní Ameriky dálo z Evropy.

Autor předkládá novou pracovní hypotézu: okoun a některé jiné sladkovodní druhy ryb pronikly do Severní Ameriky z Evropy v postglaciálním období, tj. asi před třinácti až patnácti tisíci léty mořem, proslazenou mořskou vodou podél tajícího a ustupujícího severského ledovce. Migraci snad podporovaly mořské proudy a větší rozsah pevnin v té době.

Rozšíření okounů po různých říčních systémech těchto dvou pevnin bylo pak umožněno spojením řek a jezer při úpatí ustupujícího ledovce. V severovýchodní Asii tvořilo přirozenou hranici, zabraňující šíření okouna směrem na východ, Kolymské a Anadyrské pohoří, v Severní Americe bylo jeho šíření směrem na západ zabráněno hřebenem Skalnatých hor a Mackenziho pohoří. K izolaci populací v jednotlivých říčních systémech a jezerech na obou pevninách došlo později než k izolaci severoamerického poddruhu.

Balkašský a alakulský druh *Perca schrenki* se vyvíjel izolovaně už od terciéru v refugiu, kde ledové doby na jeho vývoj neměly podstatný vliv.

РЕЗЮМЕ

В своей работе автор занимается проблемами таксономии и морфологии 560 экземпляров окуня речного (*Perca fluviatilis*) из 29 мест распространения этого вида по всей территории от США и Канады до реки Колымы в северо-восточной части СССР. Было установлено, что на всей обширной территории окунь образует многочисленные местные экологические и географические формы, соответствующие низшим таксономическим единицам (natio, infraspecies, morpha). Подвид *Perca fluviatilis intermedius* описанный Световидовым и Дорофеевой на примере окуня из реки Колымы, автором этой статьи подтвержден не был. Не было подтверждено также и их предположение, что колымский окунь образует переходную форму между евразийскими и североамериканскими популяциями, что должно таким образом демонстрировать, какими путями шло расселение окуней из Евразии в Северную Америку в прошлом.

Различия между североамериканскими и евразийскими окунями сравнительно невелики и подтверждают, что это не самостоятельные виды, а два подвида того же самого вида.

Ни распространение окуня в Евразии и в Северной Америке в настоящие время, ни относительно мелкие таксономические различия между *Perca fluviatilis fluviatilis* и *Perca fluviatilis flavescens*, ни палеонтологические аргументы не подтверждают теории, которую выдвигает сегодня большая часть авторов, а именно: что из Евразии в Северную Америку окунь проник через северопацифическую континентальную связь (Берингиада). Они скорее предполагают, что, подобно некоторым другим видам пресноводных рыб, окунь проник в Северную Америку из Европы.

Автор предполагагет новую гипотезу: окунь и некоторые другие пресноводные виды рыб проникли в Северную Америку из Европы в постглациальный период, в конце Плейстоцена, то есть приблизительно 13—15 тысяч лет тому назад, морским путем, а именно в опресненых водах, образовавшихся вдоль тающего и отступающего арктического ледника. Миграции способствовали, можеть быть, морские течения и гораздо большие массивы материков в то время.

Расселение окуней по различным системам рек этих двух материков стало возможным благодаря соединению рек и озер у подножья отступающего ледника. В северовосточной Азии Колымские и Анадырские горы препятствовали расселению окуня в восточном направлении, а в Северной Америке его расселение в западные области материка ограничивал хребет Скалистых гор и гор Маккензи. Изоляция популяций в отдельных речных системах и озерах евразийского и американского материков произошла намного позже, чем изоляция североамериканского подвида.

Вид *Perca schrenki* из озера Балхаш и Ала-Кул развивался изолированно, начиная уже терциером в рефугию, когда ледяной период уже не оказал значительного влияния на его развитие.

Tab. 9 — Proportional measurements of *Perca fluviatilis*

	U. S. A.	Canada	England	Italy	Norway	GFR	GDR	Austria	Czechosl.	Sweden	Poland	Rumania	Ladoga L.	USSR (river Ob)	USSR (Kolyma)	Average *Perca fluviatilis*	
																ssp. fluviatilis	*ssp. flavesc.*
In % long. corporis:																	
long. capitis	33,3 (31—36)	31,4 (29—33)	30,4 (29—32)	30,6 (29—33)	31,2 (29—32)	33,5 (32—35)	32,8 (32—34)	31,0 (30—32)	32,6 (31—34)	33,0 (32—34)	31,0 (30—32)	33,2 (33—35)	31,8 (31—33)	32,3 (30—34)	30,0 (29—34)	31,8 (29—35)	32,4 (29—36)
dist. praedorsalis	35,8 (33—38)	35,8 (34—37)	29,6 (28—32)	30,3 (28—32)	31,0 (28—33)	31,5 (30—34)	30,4 (29—32)	31,8 (30—34)	30,9 (30—32)	31,3 (30—35)	30,4 (29—32)	33,1 (32—35)	30,2 (29—31)	30,7 (28—34)	31,7 (30—34)	32,6 (28—35)	35,8 (33—38)
dist. praeventralis	37,6 (33—40)	36,2 (35—38)	35,1 (33—36)	32,8 (30—35)	33,8 (32—36)	36,0 (35—37)	36,3 (32—39)	34,0 (32—36)	36,0 (34—38)	34,6 (33—37)	33,6 (32—35)	36,7 (35—38)	35,0 (34—36)	34,6 (33—37)	34,3 (33—36)	34,9 (30—39)	36,9 (33—40)
dist. praeanalis	69,4 (67—72)	72,7 (70—75)	69,3 (68—71)	68,3 (66—73)	69,3 (68—72)	69,3 (66—71)	69,8 (68—74)	67,4 (63—70)	68,0 (65—70)	69,1 (66—72)	67,7 (65—69)	68,8 (67—70)	71,2 (69—75)	66,9 (65—73)	70,0 (67—73)	68,9 (63—75)	71,1 (67—72)
alt. corporis	26,7 (24—29)	30,1 (28—32)	27,3 (25—29)	28,2 (27—30)	32,2 (29—35)	29,7 (26—32)	28,9 (27—30)	25,0 (23—27)	27,9 (27—29)	30,8 (27—35)	26,1 (24—29)	29,5 (27—33)	28,0 (27—30)	29,9 (27—30)	32,3 (29—34)	28,9 (23—35)	28,4 (24—32)
lat. corporis	14,2 (13—16)	15,7 (14—17)	12,6 (11—14)	14,7 (13—18)	16,5 (15—18)	17,9 (15—20)	17,6 (15—21)	14,3 (13—16)	15,6 (15—16)	15,8 (14—18)	11,7 (11—13)	16,3 (14—19)	14,8 (12—25)	13,1 (12—14)	16,6 (15—18)	15,2 (11—25)	15,0 (13—17)
long. ped. caudae	22,1 (20—23)	21,6 (18—27)	22,2 (20—24)	22,1 (19—25)	20,5 (19—22)	21,9 (20—24)	21,2 (19—22)	21,2 (20—23)	22,2 (20—23)	21,1 (19—23)	23,7 (20—26)	21,1 (19—23)	20,8 (21—25)	20,9 (16—24)	20,8 (19—23)	21,3 (16—26)	21,9 (18—27)
long. D1	30,9 (30—33)	28,4 (26—31)	35,9 (33—39)	37,0 (35—40)	36,2 (33—38)	33,7 (30—37)	37,1 (36—39)	34,0 (31—36)	34,7 (34—37)	38,3 (36—43)	33,4 (31—36)	33,1 (32—36)	36,2 (31—39)	31,9 (28—34)	37,3 (35—42)	35,3 (28—43)	29,7 (26—33)
long. D2	18,9 (17—23)	18,0 (16—19)	19,1 (18—21)	17,7 (17—19)	20,7 (18—22)	19,9 (18—21)	20,4 (19—22)	18,9 (18—20)	19,3 (17—22)	18,8 (16—22)	16,7 (18—22)	19,2 (18—20)	18,4 (18—19)	18,7 (17—25)	19,6 (17—22)	19,0 (16—25)	18,5 (16—23)
long. A	11,5 (10—13)	10,2 (10—11)	11,1 (11—12)	11,2 (10—12)	11,7 (11—13)	12,6 (11—14)	11,7 (10—13)	11,4 (10—14)	12,3 (11—13)	12,1 (9—21)	10,7 (10—12)	11,4 (10—13)	11,5 (10—14)	12,1 (10—14)	11,4 (10—15)	11,6 (9—21)	10,9 (10—13)
long. C	21,0 (19—24)	18,1 (17—21)	18,1 (17—20)	18,4 (17—20)	18,2 (16—20)	16,6 (14—18)	18,3 (17—20)	16,6 (13—18)	19,1 (18—20)	20,0 (17—22)	17,5 (16—19)	18,7 (17—20)	18,6 (17—20)	16,6 (15—21)	19,0 (18—21)	18,4 (13—22)	19,6 (17—24)
long. P	19,5 (18—21)	18,1 (16—21)	15,9 (15—18)	17,6 (17—18)	17,7 (16—19)	16,9 (15—19)	17,2 (16—19)	16,2 (15—18)	18,1 (17—20)	17,5 (15—19)	16,8 (15—18)	17,6 (16—19)	17,7 (16—19)	18,6 (16—21)	18,1 (17—19)	17,2 (15—21)	18,8 (16—21)
long. V	19,9 (19—21)	19,5 (18—21)	18,5 (18—19)	18,8 (17—20)	20,0 (19—21)	19,0 (18—20)	18,4 (16—19)	19,6 (18—20)	20,7 (19—22)	19,6 (18—22)	18,3 (17—20)	20,0 (19—21)	19,4 (18—21)	20,1 (18—23)	20,4 (19—22)	20,1 (16—23)	19,7 (18—21)
alt. D1	15,8 (14—17)	14,6 (12—17)	15,1 (13—16)	14,5 (13—16)	14,8 (13—16)	14,8 (14—17)	14,0 (13—16)	14,0 (12—16)	16,1 (14—19)	15,1 (14—17)	13,9 (13—15)	14,9 (13—16)	15,5 (14—16)	17,3 (13—18)	15,7 (14—17)	15,1 (12—19)	15,2 (12—17)
alt. D2	12,8 (11—15)	13,5 (13—15)	12,6 (11—14)	12,5 (11—14)	11,3 (10—15)	12,5 (9—20)	12,6 (11—15)	12,4 (10—15)	13,5 (12—14)	13,0 (12—14)	11,4 (10—13)	13,2 (12—14)	12,9 (11—14)	12,6 (11—14)	12,7 (12—14)	12,7 (9—20)	13,2 (11—15)
alt. A	16,1 (15—17)	14,5 (12—17)	14,2 (14—15)	15,4 (14—17)	14,2 (14—15)	15,1 (13—17)	14,1 (13—15)	15,5 (14—17)	15,9 (15—17)	14,9 (14—17)	14,2 (13—15)	15,1 (14—16)	14,4 (13—15)	13,8 (11—17)	15,5 (14—17)	14,8 (11—17)	15,3 (12—17)

Tab. 10 — Proportional measurements of *Perca fluviatilis*

	U. S. A.	Canada	England	Italy	Norway	GFR	GDR	Austria	Czechosl.	Sweden	Poland	Rumania	Ladoga L.	USSR (river Ob)	USSR (Kolyma)	Average *Perca fluviatilis* *ssp. fluviatilis*	Average *Perca fluviatilis* *ssp. flavesc.*
In % long. capitis:																	
dist. praeorbitalis	26,3 (24—29)	26,3 (24—28)	26,3 (25—28)	26,6 (24—29)	29,3 (28—30)	28,4 (26—32)	25,6 (25—27)	26,4 (23—29)	30,2 (27—35)	27,0 (25—29)	25,2 (24—28)	27,1 (24—31)	26,9 (25—28)	25,7 (24—27)	27,4 (27—28)	27,1 (23—35)	26,3 (24—29)
long. maxillae	35,4 (34—37)	36,3 (33—44)	37,4 (35—40)	37,5 (37—40)	43,5 (41—44)	40,3 (38—43)	38,9 (37—40)	36,5 (33—42)	36,7 (32—40)	40,5 (38—43)	36,9 (34—40)	39,4 (37—42)	40,1 (38—42)	39,1 (35—50)	38,3 (35—41)	38,9 (32—50)	35,9 (33—44)
dist. internasalis	14,2 (13—16)	14,3 (12—17)	14,9 (13—18)	15,6 (14—17)	17,0 (15—19)	15,7 (15—17)	14,0 (12—16)	16,2 (11—20)	14,8 (12—16)	15,7 (14—17)	14,8 (11—18)	15,5 (13—18)	15,5 (14—18)	16,8 (12—20)	15,2 (12—18)	15,5 (11—20)	14,3 (12—17)
diameter oculi	22,9 (19—27)	17,8 (15—20)	20,9 (18—23)	19,1 (18—20)	16,0 (15—18)	16,7 (14—19)	19,7 (17—22)	23,5 (21—27)	20,4 (18—23)	18,1 (15—21)	23,5 (20—25)	21,0 (19—24)	18,6 (18—20)	19,8 (16—23)	16,2 (15—18)	19,5 (14—27)	20,4 (15—27)
dist. interocularis	22,9 (21—26)	25,5 (24—27)	25,8 (24—29)	27,3 (25—29)	28,7 (26—31)	26,9 (25—29)	26,2 (25—29)	27,1 (25—28)	25,8 (23—28)	25,7 (24—27)	23,9 (22—26)	24,9 (22—27)	25,7 (23—28)	25,4 (23—29)	26,8 (26—29)	26,2 (22—31)	24,2 (21—27)
dist. postorbitalis	53,0 (52—57)	54,4 (52—57)	53,2 (50—55)	55,8 (54—57)	56,2 (54—58)	55,0 (53—57)	54,6 (53—57)	54,1 (48—57)	52,7 (51—55)	54,5 (51—57)	52,8 (49—57)	53,6 (51—55)	54,8 (54—57)	54,6 (51—59)	57,6 (55—61)	54,6 (48—61)	53,7 (52—57)
altitudo capitis	58,4 (52—66)	61,7 (57—70)	64,7 (57—68)	61,5 (56—70)	64,8 (62—69)	62,6 (59—67)	61,5 (59—64)	61,5 (58—63)	63,0 (61—65)	61,8 (58—67)	58,7 (53—63)	59,3 (57—67)	60,4 (55—63)	63,4 (56—70)	62,2 (57—67)	62,0 (53—70)	60,1 (52—70)
latitudo capitis	43,8 (40—49)	43,3 (40—47)	42,4 (39—45)	43,0 (40—47)	47,8 (45—49)	50,4 (47—58)	45,5 (41—51)	41,0 (38—47)	45,9 (41—51)	44,7 (39—53)	37,8 (33—43)	46,1 (44—52)	38,7 (36—41)	36,5 (33—41)	44,6 (39—50)	43,4 (33—58)	43,6 (40—49)
In % long. ped. caudae:																	
alt. ped. caudae	58,5 (50—65)	60,2 (51—69)	54,3 (46—60)	57,3 (54—61)	71,3 (68—77)	59,2 (53—67)	57,8 (56—70)	56,0 (50—61)	57,8 (53—61)	67,9 (60—81)	55,3 (46—63)	63,4 (58—72)	57,8 53—65)	53,4 (45—65)	67,6 (53—80)	59,9 (45—81)	59,4 (50—69)
min. alt. dorporis	39,5 (33—45)	39,0 (37—50)	33,4 (31—36)	36,7 (33—43)	41,2 (38—44)	38,7 (35—41)	39,5 (36—45)	36,4 (33—40)	35,8 (33—39)	40,7 (35—50)	33,5 (29—37)	38,8 (35—46)	37,9 (31—44)	38,6 (31—50)	45,7 (40—52)	38,2 (29—52)	39,3 (33—50)