Ribarstvo, 61, 2003, (4), 147—174
S. B. Georgiev: The Balkan Peninsula Salmonids

ISSN 1330–061X
CODEN RIBAEG

UDK: 597.553.2(497)
Review article

ON THE ORIGIN OF THE BALKAN PENINSULA SALMONIDS

S. B. Georgiev

Summary

This paper puts forward the knowledge of the immigration itineraries of the ancestors of five extant salmonid species on Balkan Peninsula which are the following: *Acantholingua ohridana* (Steindachner, 1892), *Hucho hucho* (Linnaeus, 1758), *Salmo trutta* Linnaeus, 1758, *Salmothymus obtusirostris* Heckel, 1851 and *Thymallus thymallus* (Linnaeus, 1758). The thesis for the migration itineraries is based on the anatomical, molecular and zoogeographical facts recently published. These latest facts complement or reject the previous thesis that considered the origin of separate species, which in this paper are analyzed together. A new position on the origin of some *S. trutta* populations inhabiting the Mediterranean Sea watershed is proposed. The new thesis is that they did not inhabit it from the west, through the Atlantic Ocean and Gibraltar, but from the North, through the branches of the former Sarmatian Sea, using the continental way. *A. ohridana* and *S. obtusirostris*, the only endemic Balkanean salmonids, have developed here from the mutual ancestor with the extant Siberian *Brachymystax lenok* (Pallas, 1773). This ancestor came first, together with the *S. trutta* lineage known as »marmorata«. Using the same migration way, the *T. thymallus* population of Soča River, the North–West boundary of Balkan Peninsula remained restricted at that corner of Adriatic Sea watershed.

In the Black Sea watershed (the Danube River flow extension on Balkan Peninsula) the distribution of *T. thymallus* coincides with the distribution of *H. hucho*. The thesis which has been proposed for this, largest contemporary Balkan Peninsula salmonid fish was that it came here last, after the connections between the Mediterranean Sea basin and once existent Sarmatian Sea disappeared. This occurred after the end of the last glaciations. This has been concluded on the basis of the exclusion of the areas of the »marmorata« lineage of *S. trutta* (Mediterranean Sea watershed) and *H. hucho* (Black Sea watershed). Their extensions touch just at the water–separation between the Mediterranean Sea and the Black Sea on the Dinarid Mountains. The idea for this thesis originates from the distribution of the small cobitid

Dr. Simo Georgiev, Senior Science Associate, Institute for Animal Science, Ile Ilievski, 92 a, 1000 Skopje, Republic of Macedonia

Cobitis elongata Heckel & Kner, 1858 given in the work of Karaman, S., (1952). The thesis that the endemic salmonids came in the Adriatic Sea watershed through the Adriatic–Pannonian connection is supported by the zoogeographical distribution of some mutual marine, brachic or freshwater fish species for Adriatic Sea itself or the Adriatic Sea watershed and Ponto–Caspian depression (Black Sea and Caspian Lake). These fish belong to the families Acipenseridae and Cobitidae, some endemic Cyprinidae representatives from the Adriatic Sea watershed belong to widely extended genera in the central Europe, mainly in the Danube river flow.

Key words: *Acantholingua ohridana*, *Hucho hucho*, *Salmo trutta*, *Salmothymus obtusirostris*, *Thymallus thymallus*.

INTRODUCTION

The Balkan Peninsula (Fig. 1), covers small area, 4,7 % of Europe or 0,03% of the total land on the Earth. Its freshwaters belong to five sea watersheds (Fig. 2). In spite of the small surface, it is known as a region which is most abundant in salmonid species. Its western part as Adriatic–Mediterranean Province »possesses the highest degree of endemism of species and genera« (Behnke, 1973). In other words »despite its relatively small size, it is the area harboring the most diverse phenotypic diversity among trout populations« (Bernatchez, 2001). In the works of Hadišče (1960), Vuković and Ivanović (1971), Teskeredžić *et al.* (1993) and Kottelat (1997) on the Balkan Peninsula, a total of 21 species of salmonid fish are listed (Tab. 1).

The results of Apostolidis *et al.* (1996, 1997) and Bernatchez (2001), have shown that the *Salmo* genera on the Balkan Peninsula is represented just by one species, *S. trutta*. Therefore, the list of unquestionable salmonid species of the Balkan Peninsula needs to be reduced to five species which belong to five genera and two families (Tab. 2).

In any case, even with such a reduced list, the Balkan keeps the interest as a region that is still the richest one with salmonid species that are phylogenetically distant, and two of them endemic.

This leads to the assumption that some of them have been present on Balkan Peninsula for a long time, after their ancestors had emigrated from distant places. Those ancestors have evolved here in different ecologic (climate) conditions into new taxonomic categories at the level of genus as it is the case with the endemic *Salmothymus* and *Acantholingua*. Since their phylogenetic relationships are clarified, as well as their exact position in systematization, the issue remaining pending is the question on their origin, or more precisely, the itineraries of immigration of their ancestors in the freshwaters of the Balkan Peninsula. The zoogeographical understanding (Karaman, 1924; Ladiges, 1967; Karaman, 1971), related to some of them, is a bit strange

Table 1. List of salmonid species on Balkan Peninsula described in the past (in alphabetic order).
Tablica 1. Popis salmonidnih vrsta na Balkanskom poluotoku, opisanih u prošlosti (po abecednom redu)

1.	*Acantholingua ohridana*	(Steindachner, 1892)
2.	*Hucho hucho*	(Linnaeus, 1758)
3.	*Salmo aphelios*	Kottelat, 1997
4.	*Salmo balcanicus*	(Karaman, 1927)
5.	*Salmo dentex*	Heckel, 1851
6.	*Salmo farioides*	Karaman, 1938
7.	*Salmo labrax*	Pallas, 1814
8.	*Salmo letnica*	(Karaman, 1924)
9.	*Salmo lumi*	Poljakov, Filipi & Basho, 1958
10.	*Salmo macedonicus*	(Karaman, 1924)
11.	*Salmo marmoratus*	Cuvier, 1829
12.	*Salmo montenigrinus*	Karaman, 1933
13.	*Salmo pelagonicus*	Karaman, 1938
14.	*Salmo peristericus*	Karaman, 1938
15.	*Salmo taleri*	(Karaman, 1932)
16.	*Salmo trutta*	Linnaeus, 1758
17.	*Salmo visovacensis*	Taler, 1951
18.	*Salmo zetenzis*	(Hadzisce, 1960)
19.	*Salmo zrmanjensis*	Karaman, 1937
20.	*Salmothymus obtusirostris*	(Heckel, 1852)
21.	*Thymallus thymallus*	(Linnaeus, 1758)

Table 2. List of undisputable salmonid species on Balkan Peninsula according to the newest biochemical researches (in alphabetic order).
Tablica 2. Popis nespornih salmonidnih vrsta na Balkanskom poluotoku prema najnovijim biokemijskim istraživanjima (po abecednom redu)

1.	*Acantholingua ohridana*	(Steindachner, 1892)
2.	*Hucho hucho*	(Linnaeus, 1758)
3.	*Salmo trutta*	Linnaeus, 1758
4.	*Salmothymus obtusirostris*	(Heckel, 1852)
5.	*Thymallus thymallus*	(Linnaeus, 1758)

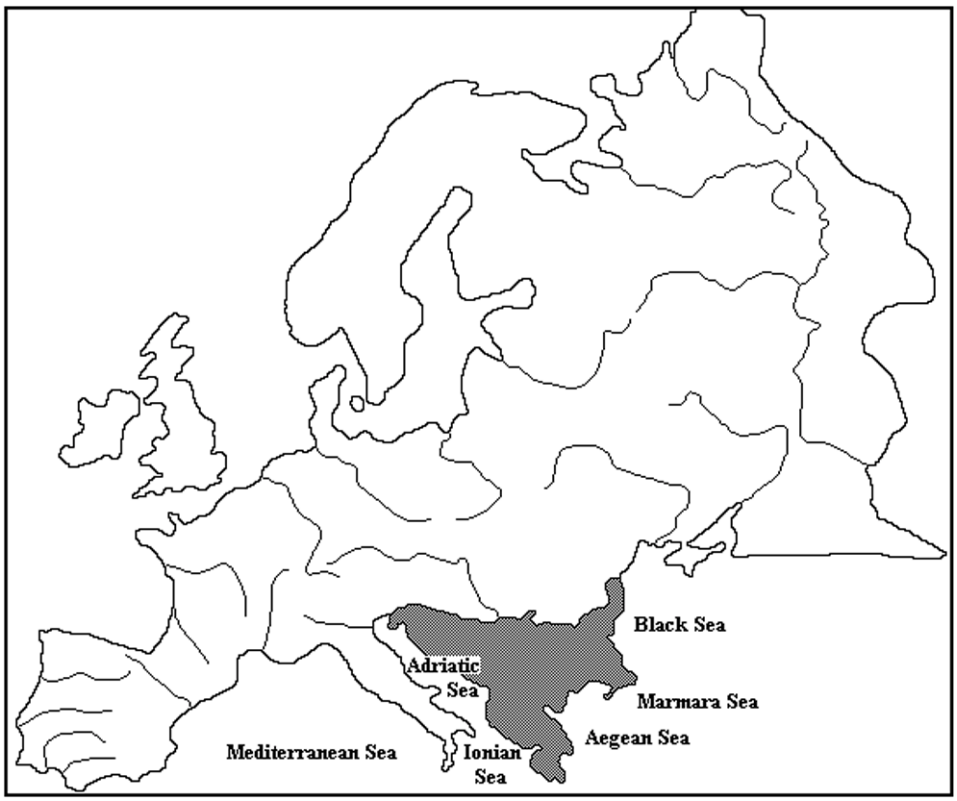

Figure 1. Position of Balkan Peninsula in Europe and the seas surrounding it.
Slika 1. Mjesto Balkanskog poluotoka u Europi i mora koja ga okružuju

and confusing, from the point of view of the commonly accepted position that all the Mediterranean Sea watershed salmonids had entered through the Gibraltar. There are some thesis that attempt to solve the problem of the origin of the Balkan Peninsula salmonid fish, but they usually approach the problem separately, for one (Berrebi *et al.,* 2000), two, or at the most three species (Thaller, 1953; Karaman, 1957). Other works address the issue marginally, discussing the salmonids of other regions: Berg (1948); Sommani (1961); Dorrofeeva (1967); Balon (1968); Stearley and Smith (1993); Guyomard (1989); Bianco (1990); Osinov and Bernatchez (1996); Bernatchez (2001) or for only a part of the Balkan Peninsula (Teskeredzic *et al.,* 1993). Some papers answer the question at the level of genus: Banarescu (1973). The most thorough paper relevant for the issue (Economidis and Banarescu, 1991), mentions some of the Balkan Peninsula salmonid fish as components of the ichthyologic divisions of Balkan Peninsula freshwaters belonging to the surrounding sea watersheds. This

Figure 2. Sea watersheds where the freshwaters of Balkan Peninsula belong.
Slika 2. Morski sljevovi kamo pripadaju slatke vode Balkanskoga poluotoka

paper excludes the ichthyocenose of the main and boundary Balkan Peninsula River, the one of the Danube River.

The work of Thaler (1953) comes nearest to solving this problem: »There is no doubt that the soft muzzled (*Salmothymus obtusirostris*), than the Ohrid whitely (*Salmothymus ohridanus*), the Neretva heady (*Salmo marmoratus*) and some other salmonids of west Balkan area, came by different itineraries, as it has been said, than the salmonids from the northern areas«.

According to the cladogram of relationships of salmonid genera (Stearley and Smith, 1993), the earliest developed extant Balkan Peninsula salmonid fish is *T. thymallus*. The second branching are *A. ohridana* and *S. obtusirostris*. They have originated from their mutual ancestor that appeared soon after the ancestor of Siberian salmonid *B. lenok*, had originated. Therefore, these three fish are phylogenetically close; this had also been concluded by Berg (1948), according to the Hadišče (1961). More advanced than this group is the fourth Balkan salmonid *H. hucho*. The most advanced, at the same phylogenetic distance from *H. hucho,* as *H. hucho* is from two

previous genera, is *S. trutta*. The later one is present in the Balkan Peninsula freshwaters, in four out of the total five lineages stated to exist by Bernatchez (2001): Danubian, Mediterranean, Adriatic and so called »marmorata«.

Here we need to mention a fact which regards some known and unknown supposed implantations of *S. trutta* genetic material from one sea watershed in other on the Balkan Peninsula. We find data on this in Aganović (1958), Niškov and Orešarov (1959), Janković and Raspopović (1960), Georgiev and Cilevski (1991) and Apostolidis *et al.* (1997).

The discover of Bernatchez (2001), that geographic distribution of the lineages Adriatic, Mediterranean and »marmorata« of *S. trutta* overlap a bit the geographic distribution of other two: Danubian and Atlantic, shall be commented upon and the explanation shall be supported by geographic maps 1:100.000 and 1:200.000. The coordinates are given east from Paris.

DIMENSIONS AND BIOLOGY OF BALKAN PENINSULA SALMONID FISHES

There is a lot of data on the Balkan Peninsula salmonids, usually given for one species. Here they are presented synthetic for the fish living together, for two or even three species so closely as nowhere else.

H. hucho is the largest salmonid fish of Balkan Peninsula reaching length up to 1,5 m and weight up to 52 kg (Teskeredzić *et al.,* 1993), 105 kg, data compiled in Holčik (1982). This fish is one typical piscivorous potamian predator occupying the deepest whirls, exclusively lotic (Kosorić *et al.,* 1975). *T. thymallus*, *S. obtusirostris* and *A. ohridana* are medium sized to small fishes regarding the Salmonidae family. The first two inhabit the large full–water fluent habitats of West Balkan, only the last one is the only exclusively limnetic species, (Stefanović, 1948; Thaler, 1953; Stanković, 1957; Basioli, 1958; Janković, 1960, 1961), all of them are macro–invertebrate feeders. In general, their main food is represented by larval stadiums of aquatic Insecta, whereas the other macro–invertebrates: Isopoda and Amphipoda, Molluscs, Vermes, soil Insecta and fish are taken far less in special circumstances. *T. thymallus* and *S. obtusirostris* are benthal–feeders regarding the ecologic features of their most important food. Because of this, their body form, especially their mouth construction is very similar and homologues. For both of those fish the feeding area are the more shallow places after the whirlpools where the river bad broadens (Janković, 1960, 1961; Kaćanski and Kosorić, 1970; Kaćanski *et al.,* 1977; Teskeredžić *et al.,* 1993). *A. ohridana* keeps to the shelf area of Ohrid Lake covered by submersed macrophyts algae *Chara sp.* at the depth of 15–20 m (Stefanović, 1948). Regarding the habitats and dimensions *S. trutta* is the most flexible salmonid fish on the Balkan Peninsula. In the smallest mountainous brooks (Tesk-

eredžić et al., 1993) its average weight is 0,15–0,25 kg, and it also inhabits the largest low–land rivers including Danube as northern boundary of the area (Holčik, 1969; Maletin and Djukić, 1989), although with regard to isolated samples as curiosities, not for a dense continual populations, shallow small glacial lakes (Ćurčić, 1936; Drecun, 1956; Janković, 1963; Vuković and Ivanović, 1971; Drecun *et al.,* 1985), two large tectonic lakes: Skadar Lake and Ohrid Lake (Karaman, 1924, 1957; Stefanović, 1948; Thaller, 1953; Stanković, 1957; Poljakov *et al.,* 1958; Filippi, 1959, 1959 a; Petrovski, 1967; Karaman, M., 1971; Ivanović, 1973; Catsdorakis *et al.,* 1996). Furthermore, it also inhabits one extraordinary travertine limnetic habitat Visovačko Lake (Thaller, 1950) and some habitats without actual surface connection to the other waters in the corresponding watershed: Gacka, Lika, Vrlika, Trebišnjica and Prespa Lake (Karaman, 1924, 1957; Ćurčić, 1936; Thaller, 1953; Stefanec and Bunjevčević, 1982). The average weight in the limnetic habitats is 2–5 kg. The maximal weight of 25 kg is reach in the new, anthropogenic limnetic habitats, reservoirs, (Pažur, 1969), which is the ordinary weight for the »marmorata« lineage, even though there is data about a sample weighting 31 kg (Neresheimer, 1937, cited in Behnke, 1972). The food consumed by this most advanced Balkan Peninsula salmonid fish species, as well as in Europe, is by far with a larger spectrum than the previous four species: aquatic and terrestrial invertebrates, vertebrates and of course Pisces. Here it is unavoidable to mention that the lineage »marmorata« differs from the other lineages in its nutrition manner. It is an invertebrate feeder only when young and small, growing up faster than the others, when it reaches the dimensions large enough to swallow a fish, it becomes a typical piscivorous predator. The proof for the recent geologic appearance of *S. trutta* is the largest extension on the Balkan in continuity of habitats and populations and its plasticity. The alevins implanted in other habitats different than the ones from which their parents originate or the representatives of the stream populations found to in new ecologic conditions, natural or artificial, suddenly change the phenotype and ecology: Sidorovski (1955, 1960, 1971); Apostolski (1976); Pažur (1957); Janković and Raspopović (1960); Orešarov and Niškov (1959).

DISTRIBUTION OF SALMONID FISH ON THE BALKAN PENINSULA

Areas of the five salmonid species on the Balkan Peninsula which are being discussed, among which the four lineages of *S. trutta* (Adriatic, Danubian, Mediterranean and »marmorata«), are reconstructed according the data of Karaman (1924, 1936, 1957); Thaller (1936, 1944, 1950, 1953); Poljakov *et al. (*1958); Orešarov and Niškov (1959); Janković (1960); Aganović (1967); Vuković and Ivanović (1971); Sabiončello *et al.*

(1973); Karapetkova *et al.* (1993); Teskeredžić *et al.* (1993); Karapetkova (1994); Rakaj and Flloko (1995); Apostolidis *et al.* (1996); Kottelat (1997); Georgiev (1998) and Bernatchez (2001).

The narrowest distribution has been noted for *A. ohridana* (Fig. 3) known for the Ohrid Lake only, having an inferior position in the fish assemble when compared to the dominant *S. trutta*, Adriatic lineage.

The area of *S. obtusirostris* is limited only to the Adriatic Sea watershed (Fig. 3), the most northern point being the river Krka, and the most southern, the Bojana/Drim system, the Morača and Zeta confluents of the narrow Bojana river flow (Thaller, 1953). I believe that the discontinuous areal of this fish among Krka, Jadro, Vrlika and Neretva, and its absence in the Cetina river, deserve to be separately considered. First of all, the discontinuous areal shows us that the species is old from geological point of view. Cetina River is a full–water, but very fast running stream that ends with a waterfall, Gubavac (56 m) just in front of the mouth, between the Krka, Jadro and Neretva riverine flows. Both of the other two big rivers (Krka and Neretva) have almost the same ichthyofauna, and with the exception of *S. trutta*, most of the fish are endemic. Perhaps the absence of *S. obtusirostris* is due to ecological reasons, as an inconveniently fast running habitat. Here we should not exclude the possibility that the ichthyofauna of Cetina originates from the source of the neighboring Krka River and not from the mouth, as usually is the case. The division between the flows and streams of Krka and Cetina rivers is very low and according to Cvijić (1989), all the today periodically flooded Dalmatian carstic depressions where the discussed rivers cross, used to represent connected large limnetic systems. The presently independent riverine system of Zrmanja River, the neighboring North–West system of Krka river system, used to be an integral part of the Krka river system. Zrmanja River used to be only a confluent of the Krka river. Perhaps both Zrmanja River and Krka River used to be upper parts of former unit stream Cetina river. (* Split, 1963).

The extension of *T. thymallus* (Fig. 2), is also limited on the west part of Balkan Peninsula. It inhabits the big mountainous confluents of second, third or fourth range of the Danube River (Black Sea watershed) and only one population in the Adriatic Sea watershed, the one of the Soča River. The population of the Soča River distinguish the most from the ones of the Danube river flow (Vrbas river with Pliva river confluent separated by old travertine waterfall, Drina with confluents Luča, Piva, Tara and Čehotina) in the meristic and morphometric characters (Janković, 1960). This is an undisputable confirmation of the old presence and separation between the populations of the two watersheds. I do not believe that the absence of *T. thymallus* in the convenient habitats of Eastern Balkan (the Iskar river which is the oldest Balkan Peninsula river originating down the highest peak on the Balkan Peninsula Mussala–2925 m up of sea level, Orešarov and Niškov, 1959) is due to tectonic reasons (Iron Gate), but due to ecologic ones. The existence

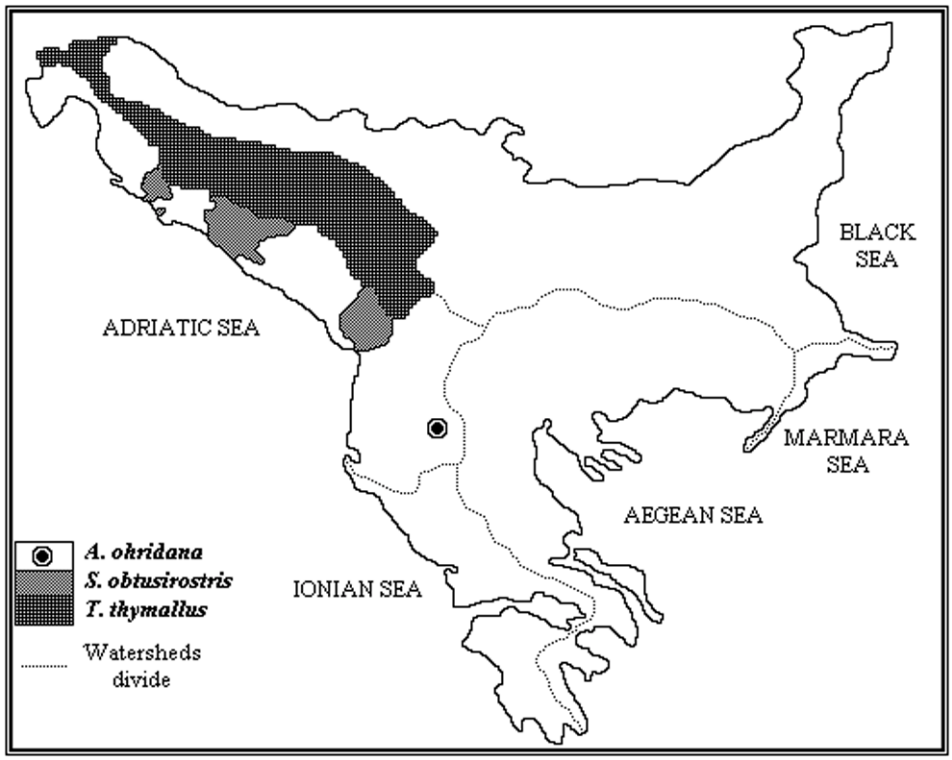

Figure 3. Extension of A. ohridana, S. obtusirostris *and* T. thymallus *on Balkan Peninsula.*
Slika 3. Rasprostranjenost A. ohridana, S. obtusirostris *i* T. thymallus *na Balkanskom poluotoku*

of *T. thymallus* in the Danube River down part left hand confluents out of Balkan Peninsula (Banarescu, 1964), only supports this thesis.

The extension of *H. hucho* (Fig. 4), if we exclude the main Danube river (Banarescu, 1964; Michailowa, 1967; Karapetkova, 1993), where rare samples are caught during the winter time as curiosity, in general corresponds to the extension of *T. thymallus*. This shows that those two species are not in a competition. The extension of *H. hucho* is a bit more flexible than the one of *T. thymallus*. Its distribution is increased during the winter when some samples descend in the downward parts of the Dinarid Danubian confluents (Sava Bohinjka, Sava Dolinka, Kupa, Una, Vrbas, Bosna, Drina, Ibar, Vuković and Ivanović, 1971), even in the Danube itself, and after the spawning they intensively feed themselves on ciprinids, whereas zoo–geographically it is absent only in the river Studenica. The river Studenica is fast running mountainous stream without convenient deep whirls.

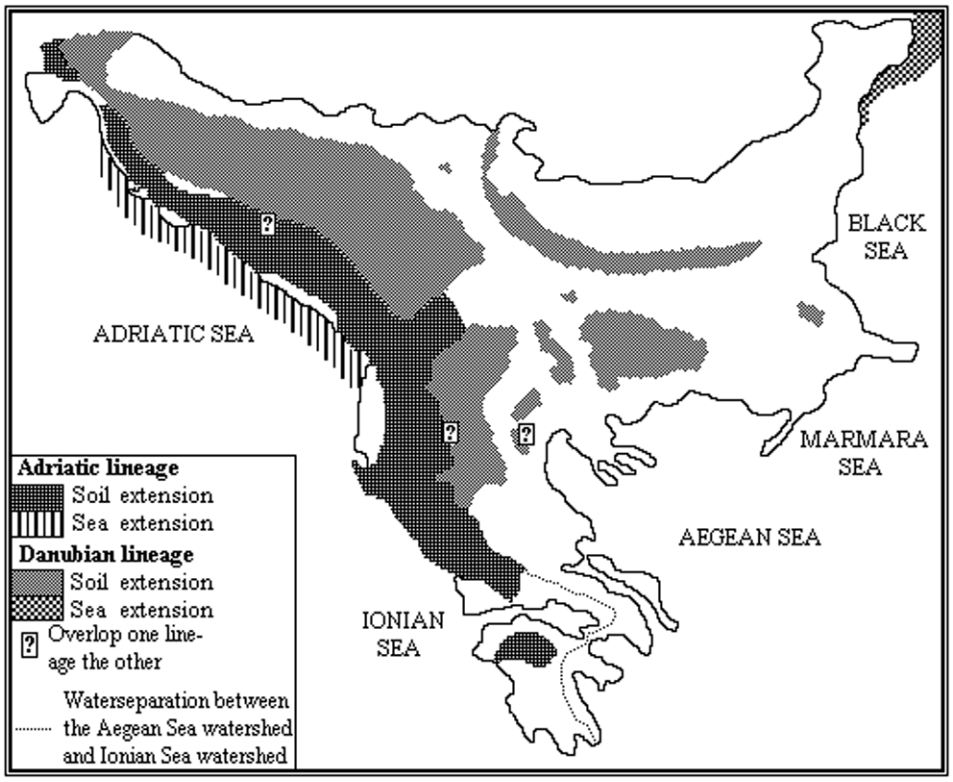

Figure 4. Extension of S. trutta *Danubian and Adriatic lineages on Balkan Peninsula; question marks–disputable parts of surface boundaries between both of the lineages because of incompatibility of the sea watersheds separation and stated biochemical indicators of examined populations distribution.*
Slika 4. Rasprostranjenost S. trutta *dunavske i jadranske linije na Balkanskom poluotoku; upitnici — sporni dijelovi površinskih granica između dviju linija zbog nepodudarnosti vodorazdjela morskih sljevova s utvrđenim biokemijskim pokazateljima rasprostranjenosti istraživanih populacija*

The largest area has *S. trutta*, extended almost over the entire Balkan Peninsula (Fig. 4, Fig. 5), where the ecological conditions are convenient. Two of its lineages are almost equally extended. The Adriatic lineage covers the North West and South West banks of the area, the numerous fluent and some limnetic habitats in continental area (in the meaning of riverine flows bordering each other) of the Adriatic Sea watershed and Ionian Sea watershed. Only the Southern populations on Peloponnesus are discontinued (Ladonas river flow). The Danube lineage is extended on the North, East and central part of Balkan Peninsula (Black Sea watershed and the largest part of Aegean Sea watershed). Some results of Apostolidis *et al.* (1997) regarding the

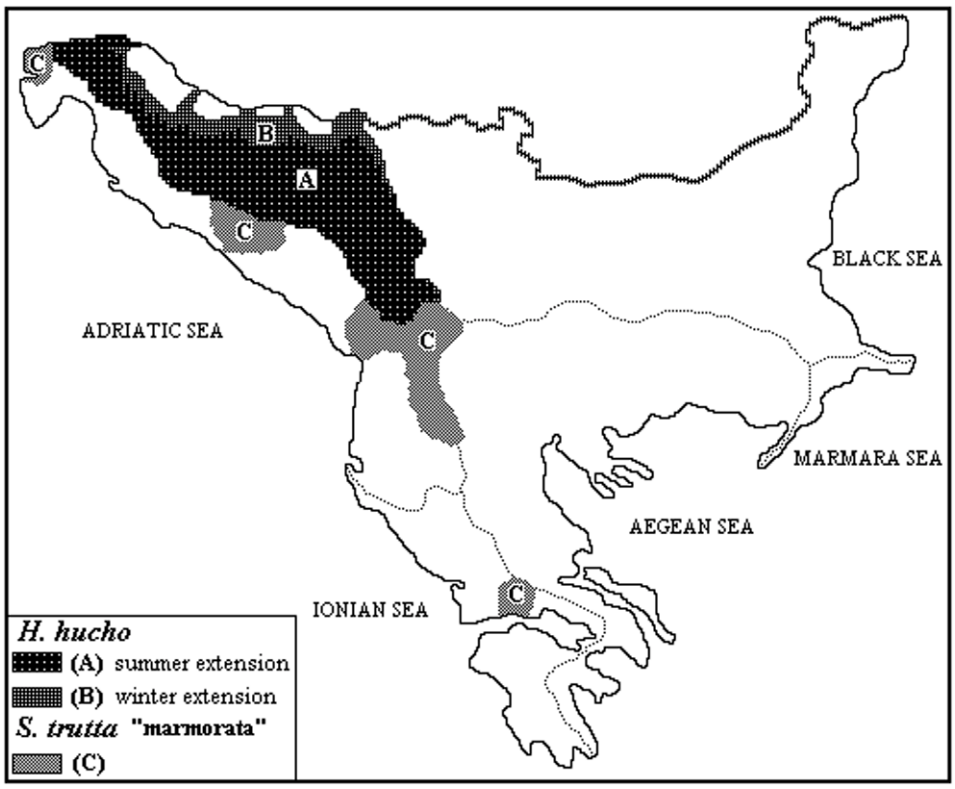

Figure 5. Extension of S. trutta *»marmorata« lineage and* H. hucho *on Balkan Peninsula.*
Slika 5. Rasprostranjenost S. trutta *»marmorata« linije i* H. hucho *na Balkanskom poluotoku*

genetic characteristics are controversial from the point of view of the geographic extension of riverine flows and the corresponding sea watersheds. They point out the possibility of the studied populations not to be indigenous but to originate from implanted material: eggs or alevines (introduced and acclimatized specimens). The »marmorata« lineage (Fig. 4) has the narrowest extension. The data of B e r n a t c h e z (2001) on the Evinos and Mornos rivers are the newest ones, the later habitats have never before been mentioned as »marmorata« biotopes.

It is interesting to mention here that the »marmorata« lineage of *S. trutta* distribution corresponds partly to those of *S. obtusirostris*: both live together near the Danubian lineage of *S. trutta* in Neretva river flow (B e r n a t c h e z, 2001) and the Adriatic lineage in Bojana/Drim system (B e r n a t c h e z, 2001). The Neretva river and Drim river are the largest (the longest and the richest with water) potamian systems belonging to the Balkan Peninsula Adriatic

coast. There are two full water potamian habitats between the Soča River and the Neretva river; the »marmorata« lineage can not be seen there but the Adriatic lineage is there: the Krka River and the Cetina River. The Krka River differs from all the other Adriatic Sea watershed salmonid fluent habitats: the long deep parts of tranquil living conditions are inter–cut by travertine cascades and waterfalls (Basioli, 1958). The ecologic features of Cetina River were cited above. It is obvious that both of those habitats do not correspond to the ecological needs and adaptations of the »marmorata«.

REASONS ABOUT THE ACTUAL DISTRIBUTION OF THE BALKAN PENINSULA SALMONIDS AND PLACES WHERE THE MOST UPPER STREAMS IN DINARIDS COULD HAVE CHANGE THE CAPTURES/FLOWS

Bianco (1990) analyzes the reasons for the distribution of the Euro–Mediterranean freshwater fish in the Plio–Pleistocene period. He lists also the ice dams as a cause for inversion of river flows, pointing out to the Dinarids, and also the *Salmo* genus. I believe that for today's distribution of salmonids on Balkan Peninsula this opinion may be accepted with a dose of reserve, but not categorically discarded. The Dinarids are by far lower than the two other mentioned mountain chains: Pyrenees and Alps. They are about 1000 m lower than Pyrenees and about 2000 m lower than the Alps. Therefore, the effect of the glaciations on them could not be as strong. The present geomorphologic feature of Dinarids and the hydrologic features of the Dinarian waters confirm this. If we ignore the small isolated glacial lakes on the Dinarids, far less numerous than the ones on Rila or Pyrin Rodopian mass, the two highest Balkan Peninsula mountains (Orešarov and Niškov, 1959), really, there is only one limnetic habitat convenient for the salmonids, the Plavsko Lake (Drecun, 1956; Janković, 1963; Vuković and Ivanović, 1971), exist in the Dinarid chain. However it is far smaller than the glacial lakes surrounding the Alps. Also, the boundary of the »eternal« snow on the Dinarids has character of discontinuity and no such large glaciers have ever been formed, as it was case and still is today with the Pyrenees and the Alps.

Furthermore, we are going to present another opinion on the freshwater fish fauna migrations related to the Balkan Peninsula, more exactly the Dinarids. Stanković (1957) claims (p. 296) that the mountains chains of Dinarids and Heleneids present a unsurpassable barrier for West Balkan fauna (focused to a fish migrations). I think this statement should be accepted with a dose of reservation and hesitation. This is valid for most of the cyprinids ecologically adapted to quiet and warm lowland and still waters. The style of the life of the salmonids is quite different. *S. trutta* as ecologically very plastic fish penetrates in the smallest, high–mountainous brooks, so high that it can conquer the waterfalls by making upward leaps. The presence of *S. trutta* in

the Indian Ocean watershed, Euphrates River, is indicative. The flow of this river is separated today from the watershed of the Black Sea by mountain chains which at an average are 1000 m higher than the Dinarids. This suggests that some populations of *S. trutta* that inhabit the brooks which used to belonged to the Black Sea watershed later could have become ichthyofaunistic compounds of the Adriatic Sea watershed (or *vice versa*) thanks to the seismic/tectonic activities. According to H e r a k (1985) there are two distinctive phases in the tectonic consolidation between the Adriatic and Dinarid structures, one in Paleogen, and the second one in Neogen. Both of these seismic phases have caused the sub–ducting of the complexes one under the other along a 600 km long line Tolmin–Budva. The consequences were differentiated elevations, regressions, inclinations, dislocations, so some structural units became disintegrated. This causes the present ornamental contacts on the surface, the difficulties in their definition, and even local deviations from the canons in the regional relationships. If it is determined that these irregularities exist in the geography of the Dinarid chain where this line incises the division between the Black Sea and the Adriatic Sea, we can accept this to be valid for the fish distribution as well. More precisely, that the influence stated caused the irregularities in the dispersion of the Danubian and Adriatic lineages of *S. trutta*.

Below are listed the places where the barriers between the Black Sea watershed and Adriatic Sea watershed are the lowest, but where the streams of the neighboring brooks belonging to the both different sea watersheds lie in the same flexure.

Vrbas, left confluent Dragučina/Rama–nameless confluent near the village Mejnik (43° 50':15° 20'), less than 100 m of height distance, bellow the isohypse 900 (* T r a v n i k, 1963). Neretva left nameless confluent of Sutjeska distinct 2 km isohypse 1000, Gredelj Pass 1227, difference 250 m (43° 16':16° 40') (*Dubrovnik, 1963). Zrmanja/Una nameless pass between the villages Velika Popina/Kupinovo, 700 m isohypses (44° 18':13° 45'), the sources of the streams 200–300 m lower of the pass. Krka (Batušnica confluent)/Una (Krka right hand confluent) 15 km distanced, the pass between is 700 m lower than the absolute sea level, the rivers' sources lie less than 200 m below the pass (Una–Krka), less than 100 m below the pass (Krka–Batušnica), the pass is in the triangle between the villages Dugo Polje–Osredci–Trubar (44° 21':13° 52', *Split, 1963). Ivan Saddle among Tresanica right hand Neretva river confluent/nameless confluent of Bioča–Bosna river flow, less than 200 m at the highest isohypse of 1000 m (* S a r a j e v o, 1963=43° 45':15° 43').

The lowest point between the Adriatic Sea watershed and Black Sea watershed on the Dinarids is situated at the North West part of Dinarids, Lika river+Gacka river depressions/Korana river, Pass Babin Potok, at 828 m (* S e n j, 1971, 44°50':13°12'). Korana River appear from the famous travertine Plitvička Lakes, about 300 m lower than the pass. Nevertheless we need to bear on thing in mind, unlike the Lika River and Gacka River, both of them

underground disappearing streams, the Plitvička Lakes *S. trutta* populations are not indigenous (Bogdanović, 1961).

Bellow are listed and shortly described the salmonid habitats by specific characteristics, different from the other standard ones and having salmonid fish assemble but with a slightly illogical composition.

Among the many of the *S. trutta* populations which live in the habitats without actual surface communication with the sea, hydrographically belonging to the Adriatic Sea watershed, four of them deserve to be elaborated upon. Three of them are fluent and lie in Dalmatia close to the sea coast: Lika, Gacka and Trebišnjica. They have a lot of water throughout the year, along the entire stream (Lika and Gacka) or at least near the source (Trebišnjica). Their inclination is insignificant, appears suddenly by strong sources and disappears suddenly in caves (Lika and Gacka always, and Trebišnjica in winter and in spring) or gradually in the porous bottom (Trebišnjica during the summer and autumn). Their water lost underground appears just below the surface of the sea level (Gacka and Lika) or some meters above of the sea level (Trebišnjica). The fields where they run are separated from the Adriatic Sea coast by orograph mass extended parallel to the coast, with sharp fall down to the Adriatic Sea synclinal, distancing the streams from the coast for about 15–20 km. The highest point between the Lika River and the coast is the peak V. Kozjak, 1620 m. North of the peak is the pass Oltare at the height of about 900 m, which is higher than the water separation between the Adriatic Sea watershed and Black Sea watershed, above mentioned pass Babin Potok 828 m. The water disappears at 500 m absolute height. Gacka River looses the water in Brlog (479 m), appears in Sv. Juraj at the coast on 0 m, it is separated from the coast by a nameless peak 1417 m high. Finally, it is difficult to say how the limnetic population of *S. trutta* inhabiting the outletless Prespa Lake in Epirus, has in fact inhabited it (Karaman, 1924; Petrovski, 1967).

The famous Neretva River, the largest Dalmatian fluent salmonid habitat also deserves a separate elaborate explanation. The uppermost point where *S. obtusirostris* and »marmorata« lineage of *S. trutta* climb, is the waterfall named Stolački Pad (Ćurčić, 1936) or Krupačke Stijene (Kosorić, 1969). The Danubian lineage of *S. trutta* living above the waterfalls, possibly originates from the neighboring Sutjeska River, belonging to the Black Sea watershed, a case analogue to the Euphratus river that has been mentioned above.

The results of Apostolidis *et al.* (1996) for the genotype of *S. trutta* stated for the Tripotamos brook population (Aliakmon river confluent, Aegean Sea watershed) deviates a bit from the others, from the Danubian lineage and shows that it belong to the Adriatic lineage. Unlike this one, the trout from Venetikos, also Aliakmon river confluent, together with the *S. trutta* samples from the Voidomatis River, are more similar to the Atlantic lineage–Garonne (Apostolidis *et al.,* 1997). This warns us that this might be another case

when the Neretva River *S. trutta* population deviation repeats: the stock does not originate from the Aegean Sea flow where the habitats geographically belong, but from Adriatic Sea watershed through the upper branch of Devoli River. This is easily acceptable and explainable, due to the very low water separation of 50 m only in the plate area among the Adriatic Sea watershed and Aegean Sea watershed. The aerial distance between the Devoli River, Adriatic Sea watershed, and the Korereka brook, Aliakmon river confluent, Aegean Sea watershed, at that level of height distance of 50 m is 3 km only (40º 32': 18º 39' *Prespa). The endemic genera for both Adriatic Sea watershed and Aegean Sea watershed *Pachychylon* leads to the possibility of exchange of ichthyofaunistic material. This genus consists of two endemic species: *Pachychylon pictus* Heckel & Kner, 1843 in Adriatic Sea watershed and *Pachychylon macedonicus* (Steindachner, 1892) in Aegean Sea watershed (Fig. 6), Economidis and Banarescu (1991). Even the divides between the Adriatic Sea watershed and Black Sea watershed (Danube river flow) on one side and Aegean Sea watershed and Black Sea watershed (the same Danube river flow) on the other side, are far lower and seem »easier« for the fish to pass them, the genus *Pachychilon* is not to be met in the Danube river flow (Black Sea watershed). Another thing pointing out that the hypothetical communication of the Devoli–Aliakmon river flows was a possible way of exchange of ichthyologic material, is the presence of another endemic cyprinid species, *Chalcalburnus belvica* Karaman, 1924, in the Prespa Lake. The Prespa Lake lies just near the sources of both of the rivers. The presence of another species of the genus *Chalcalburnus* in the limnetic habitat Volvi Lake, near Aliakmon river entrance, lying in the same flexure where the down stream of Aliakmon river lies (Economidis and Banarescu, 1991) can help to explain the possible fish migration ways at this part of the Balkan. This flexure might be a deformed remnant from the large flexure that had extended in Miocene from Tethys to Parathetys as »Transaegean channel« (Bianco, 1990; Cvijić, 1991).

Not only some *S. trutta* species populations show illogicality in their extension contrary to some commonly known genetic and zoogeographic laws in the biology. Truly, they do help us to understand and explain the geological past of the Balkan Peninsula.

Pliva is a full water river originating from and crossing the limestone area. It belongs to the Black Sea watershed and enters the Vrbas River, Danube river confluent of second range with a waterfall. Its salmonid fish assemble, if we ignore the *S. trutta* population as unimportant for this case, contains the *T. thymallus* species but the *H. hucho* is not to be met, although both of the species live in the Vrbas river (Ćurčić, 1936; Aganović, 1967). The travertine waterfall as barrier for the upward migration of *H. hucho* in the Pliva river according to Matoničkin and Pavletić (1960) is fossil and an old one. This leads us to the conclusion that *T. thymallus* is an old salmonid species that had inhabited the Pliva River long before *H. hucho* has entered the today's Danube river flow. On the other side, in the Krivaja and

Figure 6. Areals of Pachychylon *and* Chalcalburnus *cyprind gens in the central part of Balkan Peninsula.*
Slika 6. Areali ciprinidnih rodova Pachychylon *i* Chalcalburnus *na središnjem dijelu Balkanskog poluotoka*

Spreča River, confluents of Bosna River, which is neighboring confluent of Danube river by second range of Vrbas River, exists *H. hucho* but not *T. thymallus* (Janković, 1960). Both *H. hucho* and *T. thymallus* live together in the main Bosna River, Krivaja River does not have any natural barrier impeding the movement of the fish (Ćurčić, 1936; Janković, 1960).

CENTERS OF FORMING, WAYS AND TIME OF SUCCESSIVE IMMIGRATION OF BALKAN PENINSULA BY SALMONID FISH

The idea exposed in this work originates from the lucid consideration of Karaman, (1952) on the dispersion of cobitid *C. elongata*. He came to the discovery that this fish is extended in both watersheds in contact–Adriatic Sea and Black Sea where the narrower flows of Soča River and Sava River touch. It also lives in the confluent of Sava Kupa river, whose flow is in contact with

the flow of the Soča River, but is not present in the neighboring riverine flows. There is a phenomenon here; the underground disappearing stream Postojna whose flow contact the flows of all the three above mentioned riverine flows, the ones of Soča, Sava and Kupa. Here is the lowest point between the Adriatic Sea watershed and Black Sea watershed. Karaman (1952), considered that the narrow distribution of *C. elongata* in two sea watersheds, but only at the lowest point where the two watersheds touch, is strange and illogical. He concluded that the only logic explanation is the existing »pocket«, a gulf touching the former Sarmatian Sea as part of the large Tethys and former sea covering the actual Mediterranean Sea basin.

Having in mind the distribution of salmonids on Balkan Peninsula it is clear that *A. ohridana* evolved in the Ohrid Lake from the same ancestor as the ancestor of *S. obtusirostris*. When such questions are debated, one should not discard the thesis that *A. ohridana* shows more redundant characteristics due to the slower evolution, and is closer to the mutual ancestor having in mind the more stable ecological conditions present in Ohrid Lake (Stanković, 1957), whereas *S. obtusirostris* and *B. lenok* have advanced in their evolution caused by the more changeable ecological conditions of the fluent habitats in which they live (with one exception of *B. lenok* population in the Baikal Lake, which is connected with the fluent habitats entering and going out from the lake). In any case I think this question deserves to be separately elaborated upon. These two species are indisputably the oldest Balkan Peninsula salmonid settlers, perhaps even from Pliocene, when according Dumurđanov and Stojanov (1992), the Ohrid Lake had started to appear, 3–4 million years before, far before the first phase of glaciations had started. Hence, this geologic event that the older authors have accepted as a convenient and favorable period for extension of the salmonids and their occupation of new areas should to be further discussed. Starting from the fact that the areas of *S. obtusirostris* and »marmorata« lineage of *S. trutta* partly correspond, and also *A. ohridana* area and »marmorata« lineage of *S. trutta* (the Bojana–Drim system), it appear that the logical conclusion is that all these three fish have inhabited West Balkan, Adriatic Sea watershed, in the same, praediluvial time during warm climate. However, the limited dispersion of »marmorata« is a bit strange, its absence in the convenient tributaries entering the west coast of Adriatic Sea South of river Po, and the discontinued area between the Bojana–Drim system and Evinos+Mornos habitats far South. According Povž *et al.* (1996) and Berrebi *et al.* (2000), all the riverine systems of the middle and north Adriatic Sea which are independent now, in praediluvial time used to be members of the same riverine system, more precisely confluents of the river Po. The largest of them (Potenza, Pescara, Sangro) are ecologically convenient for »marmorata«. Between the Bojana–Drim system and Evinos+Mornos there are other convenient riverine systems for »marmorata« ecological needs (Shqumba, Semeni, Viosa, Kalamas, Louros, Alphios). Because of the narrower areal than the one of the »marmorata« only

to the East coast tributaries of Adriatic Sea, all the facts show that the center of forming of *S. obtusirostris* is the Adriatic Sea basin. More precisely, it is Dalmatia and its extraordinary, short but full water carstic streams. As far as the »marmorata« lineage is regarded, as part of the species with a by far larger area than the Adriatic Sea watershed (Vuković and Ivanović, 1971; Povž *et al.,* 1996), it seems that the center of forming is out from Adriatic Sea basin, perhaps in the today's Ponto–Caspian depression when the fresh-water phase and warm climate conditions used to exist. Consequently, together with the *A. ohridana* and *S. obtusirostris* ancestor, *T. thymallus* already formed, *C. elongata*, old *Acipenser stellatus* Pallas, 1771, and *Huso huso* (Linnaeus, 1758), if we ignore the endemic Adriatic Sea *Acipenser nacarii* (Bonaparte, 1834–1841) the only acipenserid living both in Adriatic Sea and Ponto–Sarmatian region (Jardas, 1983), probably some large European or even Eurasian cyprinids: *Alburnus alburnus* (Linnaeus, 1758), *Leuciscus cephalus* (Linnaeus, 1758), *Scardinius erythrophthalmus* Linnaeus, 1758, *Tinca tinca* Linnaeus, 1758 (Vuković and Ivanović, 1971) and ancestors of today's exclusively Adriatic Sea watershed endemic cyprinids belonging to larger European genera: *Chondrostoma genei* (Bonaparte, 1839), *Chondrostoma kneri* Heckel, 1843, *Chondrostoma phoxinus* Heckel, 1843 *Chondrostoma soetta* Heckel, 1843, *Leuciscus illiricus* (Heckel & Kner, 1858), *Leuciscus microlepis* (Heckel, 1843), *Leuciscus montenigrinus* Vuković, 1963, *Leuciscus svalize* (Heckel & Kner, 1843), *Leuciscus turskyi* (Heckel, 1843), *Leuciscus ukliva* (Heckel, 1843), *Leuciscus zrmanjae* (Karaman, 1928), *Rutilus aula* (Bonaparte, 1848), *Rutilus basak* (Heckel, 1843), *Rutilus ohridanus* (Karaman, 1924), *Rutilus rubilio* (Bonaparte, 1837), *Scardinius scardafa* (Bonaparte, 1837), according to Vuković and Ivanović (1971); Bianco and Taraborelli (1985); Kottelat (1997), have inhabited the Adriatic Sea basin.

Commonly exploited thesis which is accepted as a fact is that all the Mediterranean Sea watershed salmonids have inhabited it through Gibraltar (Geldiay, 1971; Tortonese, 1954, cited in Geldiay, 1971).

The results of Bernatchez (2001), and the analysis of salmonid distribution on Balkan Peninsula presented above, most of which are logical, but some illogic and unexplained by the point of view of known laws of geography and biology, throw a new light on the knowledge of their origin. The distribution of the Atlantic lineage of *S. trutta*, and its center of re–colonization toward northern Atlantic at the outer side of Gibraltar (Bernatchez, 2001) but different of other lineages (Danubian, Mediterranean, Adriatic and »marmorata«) on one side and the bigger similarity with the Mediterranean lineages (Adriatic lineage and »marmorata« lineage) to the Danubian lineage, shows that the Mediterranean lineages lead their origin not through the Gibraltar from the Atlantic Ocean (water route), but from Ponto–Caspian. Conditionally it is a »continental« route. These three lines that invaded the Mediterranean basin through the connections that existed in the different phases of the Ponto–Caspian and Mediterranean basin evolution

(transgressions) show that such connections used to happen very often in this seismically active zone where the unique Tethys used to exist (Bianco, 1990, Fig. 7).

The area of *H. hucho* continuously extends in six riverine flows in Siberia. Three of them (Lena, Yenissey, Ob) are very large, ranged among the biggest rivers on the planet. From its Siberian center of forming, (Nikolsky, 1956; Holčik, 1982), it has inhabited the Balkan Peninsula waters through the continental, northern way. Differently from the East part of the area, in central and west part: the flow of Ob, Ural, Pečora, Volga and Danube inhabits only the parts of the flows as more or less discontinued habitats. This old species that had appeared in the circumstances of warm climate, is absent in the other convenient habitats in Europe at west from the Danube river flow or in the Adriatic Sea watershed where there is a fish with the same position in the fish assemble (»marmorata«). It is not to be found in some Balkan Peninsula habitats where in the Danube river flow lives the accompanying salmonid species *T. thymallus* (Pliva River) or Soča river in the Adriatic Sea watershed. This speaks in favor of the conclusion that this fish even though geologically relatively old, having in mind the salmonids, was the last one to inhabit the Balkan Peninsula waters. This had happened in the post–diluvia time, across the Volga River and Dniepr River flows, although presently it is missing in the later one. It is also not present in the main stream of the Volga River flow, where it inhabits only its confluent the Kama River. The flow of this confluent makes a contact with the flows where this species live in continuity with the center of formation: Pechora and Ob. I do not agree with Holčik (1982) that the contemporary Danubians huchen represent the ancient relic form, whose range »has periodically been reduced and/or enlarged mostly vertically according to the climatic and hydrologic conditions occurring here and there in particular periods of time«. If *H. hucho* had been so long in Europe, it is illogic not to spread out at North. Scandinavia is one area at the same geographic distance as Pečora River flow, and many Baltic Sea confluents are with convenient ecologic conditions. The Gulf stream makes the ecological conditions of Scandinavian rivers more convenient than the closed and half year frozen Barentz Sea where Pechora enters. Other streams with convenient ecologic conditions for *H. hucho* more at west than Danube are Dunajec River one confluent of Visla River, the independent: Rhine, Loire, Gironde or even to South in the Mediterranean Sea watershed: Ebro, Rhone, Tiberius, Po, Neretva, Drim. The old salmonid *T. thymallus* lives in all of the listed West Europe streams, accompanying salmonid species of *H. hucho* in the Danube river flow at the Balkan Peninsula. The other old salmonids *A. ohridana*, *S. obtusirostris* or the advanced *S. trutta* live in many listed or missed streams convenient for *H. hucho* which belong to the Adriatic Sea watershed. Finally the habitats where the »marmorata« lineage of *S. trutta* lives should be most convenient for *H. hucho*.

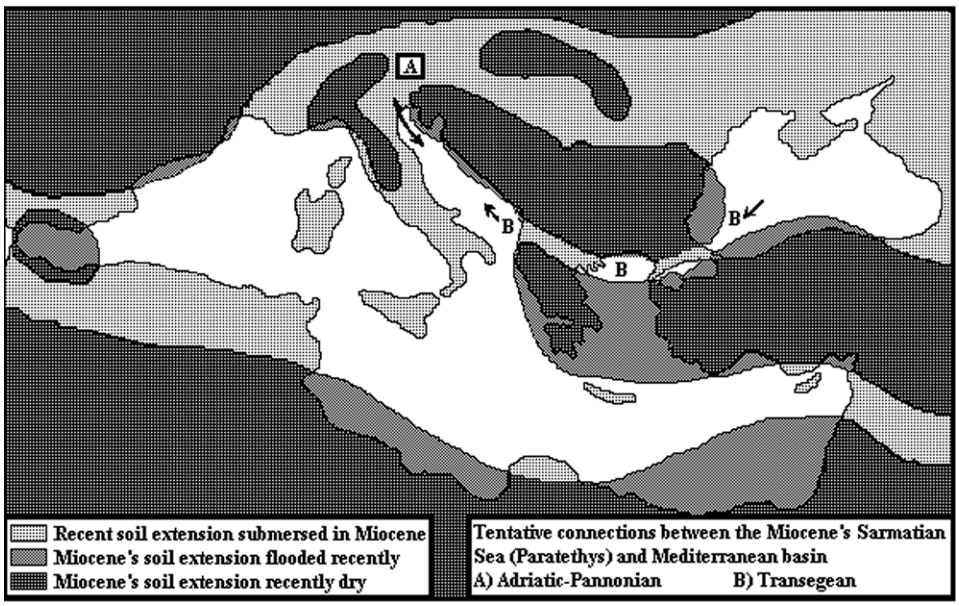

Figure 7. Stated connections between the former Sarmation Sea (Paratethys) and today's Mediterranean Sea basin from where the salmonids of West Balkan could immigrate; adaptation of Hsü, 1978 (cited Fig. 3 A) of Bianco (1990).
Slika 7. Utvrđene veze između negdašnjeg Sarmatskog mora (Paratetis) i današnjeg bazena Sredozemnog mora, odakle su salmonidi zapadnog Balkana mogli doseliti; prilagođeno prema Hsü, 1978 (prema Sl. 3 A) Bianco (1990)

Here we will present another comprehension on the laws for the composition of the fish assemble. The area of *S. obtusirostris* excludes the area of *T. thymallus* from one side and the area of *S. trutta* »marmorata« lineage exclude the area of *H. hucho* on the other side. Both of the »pairs« live almost together in both of the neighboring regions at the western side of the Balkan Peninsula (Dalmatia and Bosnia) where Adriatic Sea watershed and Black Sea watershed touch. Having in mind that the close relative fish with the same ecological needs do not support one another, one thing can be supposed, that the invasion of *Th. thymallus* and latter of the *H. hucho* in the Balkan Peninsula freshwaters, might have destroyed the supposed ancestors of *S. obtusirostris* and *S. trutta* »marmorata« in the Ponto–caspian depression, even the reason might be the cruel climate conditions of the Ice Period.

CONCLUSIONS

1. Salmoniformes ordo on Balkan Peninsula is represented by two families: Thymallidae and Salmonidae. A total of five gens belong there, which are as follows: Thymallidae consist one gen only, this of *Thymallus*, whereas

Salmonidae has four: *Acantholingua*, *Salmothymus*, *Hucho* and *Salmo*. Every genus consists of one species only: *T. thymallus*, *A. ohridana*, *S. obtusirostris*, *H. hucho* and *S. trutta*.

2. *Acantholingua* and *Salmothymus* genera and the corresponding species have their centers of formation right on the Balkan Peninsula in the Adriatic Sea watershed. They have mutual ancestor with the extant Siberian *Brachymystax* genus. Gens and belonging species *Thymallus*, *Hucho* and *Salmo* have their centers of forming out of Balkan Peninsula. Here they are invaders as already formed gens and species.
3. The Ancestors of *A. ohridana* and *S. obtusirostris*, *T. thymallus* and *S. trutta*–«marmorata« lineage already formed, together with some other fish of the families Acipenseridae, Cyprinidae and Cobitidae, anadromous or exclusively freshwater, have inhabited the freshwaters of Balkan Peninsula belonging to the Mediterranean Sea watershed through the water connections between the Mediterranean Sea and the former Sarmatian Sea. The Danubian lineage of *S. trutta* extended on the North, East and central parts of Balkan Peninsula (Black Sea and Aegean Sea watersheds) has immigrated from a refugee in Ponto–Caspian region in the inter–glacials.
4. *H. hucho* was the last one to inhabit the Balkan Peninsula freshwaters last, in the Quaternary, when the ice period was over, the climate became warmer again but the connections among the Mediterranean Sea and former Sarmatian Sea were over. Also, the connections between the big western and northern European rivers with the Danube river were terminated. It even does not use them to extend the artificial anthropogenic creatures, channels as many other fish do, especially when introduced from far away.
5. The existing opinion that Gibraltar is the door for invasion of Mediterranean salmonids is wrong, these fish have never used it to enter in the Mediterranean basin from Atlantic. If it does happen, such behavior is recent, just starting now, in »our« geological time.
6. Some determined lineages of *S. trutta* outside corresponding sea watersheds, if we abstract the registered and unknown supposed introductions in recent time, might be a consequence of the catastrophic tectonic events.

ACKNOWLEDGEMENT

The author dedicates this paper to the memory of his friend, mountain–climber Krasen Andonovski who lost his life trying to climb the Maunt Blanc on 7 of August 2003, some days after the manuscript was accepted. Krasen has been accompanying the author in the last ten years when collecting the *S. trutta* in the Došnica River, Kožuf Mountain.

Proofread by Ms Mirjana Makedonska.

Sažetak

O PORIJEKLU PASTRVA BALKANSKOG POLUOTOKA

S. B. Georgiev

Ovaj rad iznosi spoznaje o putovima doseljavanja predaka pet postojećih pastrvskih vrsta na Balkanskom poluotoku, a to su: *Acantholingua ohridana* (Steindachner, 1892), *Hucho hucho* (Linnaeus, 1758), *Salmo trutta* Linnaeus, 1758, *Salmothymus obtusirostris* Heckel, 1851 te *Thymallus thymallus* (Linnaeus, 1758). Teza o putovima doseljavanja zasnovana je na anatomskim, molekularnim i zoogeografskim čimbenicima objavljenima nedavno. Ti najnoviji čimbenici dopunjuju ili odbacuju prijašnje teze što su razmatrale porijeklo odjelitih vrsta, koje se u ovome radu razmatraju zajedno. Predloženo je novo stajalište o porijeklu nekih populacija *S. trutta* što nastavaju vodoskup Sredozemnog mora. Nova je teza ta da se one nisu doselile sa zapada, preko Atlantskog oceana i Gibraltara, nego sa sjevera, preko ogranaka prijašnjeg Sarmatskog mora, koristeći se kopnenim putem. *A. ohridana* i *S. obtusirostris*, jedine endemske balkanske pastrve, razvile su se ovdje od skupnoga pretka s postojećim sibirskim *Brachymystax lenok* (Pallas, 1773). Taj je predak došao prvi, zajedno s linijom *S. trutta* poznatom kao »marmorata«. Koristeći se istim putem doseljavanja, populacija *T. thymallus* iz rijeke Soče, sjeverozapadna granica Balkanskog poluotoka ostala je izolirana u tom kutu vodoskupa Jadranskoga mora.

U vodoskupu Crnog mora (protezanje slijeva rijeke Dunava na Balkanskom poluotoku) rasprostranjenost *T. thymallus* poklapa se s rasprostranjenošću *H. hucho*. Teza koja je predložena za ovu, najveću suvremenu pastrvnsku ribu Balkanskog poluotoka jest da je ona došla zadnja, nakon što su veze između bazena Sredozemnog mora i jednom postojećeg Sarmatskog mora nestale. To se dogodilo nakon završetka zadnje oledbe. Ovo je zaključeno na osnovi isključivosti areala linije »marmorata« *S. trutta* (vodoskup Sredozemnog mora) i *H. hucho* (vodoskup Crnog mora). Njihova protezanja dotiču se na vodorazdjelu izmedu Sredozemnog i Crnog mora na dinarskim planinama. Ideja o ovoj tezi nastala je na osnovi podataka o rasprostranjenosti malenog kobitida *Cobitis elongata* Heckel & Kner, 1858. iznesenih u radu K a r a m a n (1952). Teza da su endemski salmonidi došli u vodoskup Jadranskog mora preko jadransko–panonske veze potkrijepljena je zoogeografskom rasprostranjenošću nekoliko skupnih morskih, bočatih ili slatkovodnih ribljih vrsta za sam vodoskup Jadranskog mora ili vodoskup Jadranskog mora i ponto–kaspijske depresije (Crno more i Kaspijsko jezero). Te ribe pripadaju porodicama *Acipenseridae* i *Cobitidae*, neki endemski pretstavnici *Cyprinidae* iz vodoskupa

Dr. Simo Georgiev, viši znanstveni suradnik, Institut za stočarske znanosti, Ile Ilievski, 92 a, 1000 Skoplje, Makedonija

Jadranskog mora pripadaju šire rasprostranjenim rodovima u srednjoj Europi, uglavno u slijevu rijeke Dunava.

Ključne riječi: *Acantholingua ohridana*, *Hucho hucho*, *Salmo trutta*, *Salmothymus obtusirostris*, *Thymallus thymallus*.

REFERENCES

Aganović, M. (1967): Uzrasna struktura populacija riba Velikog i Malog Plivskog jezera. *Ribarstvo, 22, (1), 1–6.* (Croatian).

Aganović, M. (1958): Poribljavanje otvorenih voda u NR Bosni i Hercegovini. *Ribarstvo, 13, (1/2), 14–16.* (Croatian).

Apostolidis, A., Karakousis, Y., Triantaphyllidis, C. (1996): Genetic divergence and phylogenetic relationships among *Salmo trutta* L. (brown trout) populations from Greece and other European countries. *Heredity, 76, 551–560.*

Apostolidis, A. P., Triantaphyllidis, C., Kouvatsi, A., Economidis, P. S. (1997): Mitochondrial DNA sequence variation and phylogeography among *Salmo trutta* L. (Greek brown trout) populations. *Molecular Ecology, 6, 531–542.*

Apostolski, K. (1976): Establishment of Brown Trout in impondment Mavrovsko Ezero. *Ichthyologia, 8, (1), 9–20.*

Balon, E. (1968): Notes to the origin and evolution of trouts and salmons with special reference to the Danubian trouts. *Acta soc. Zool. Bohem. Brno, 32, (1), 1–21.*

Banarescu, P. (1964): Fauna Republici Populare Romine. Pisces–Osteichthyes. *Academia Republicii Populare Romine, Bucuresti. p. 959.* (Rumanian).

Banarescu, P. (1973): Origin and affinities of fresh water fish fauna of Europe. *Ichthyologia, 5, (1), 1–8.*

Basioli, J. (1958): Ribarstvo rijeke Krke. *Ribarstvo, 13, (5), 105–107.* (Croatian).

Behnke, R. (1968): A new Subgenus and Species of Trout, *Salmo (Platysalmo) platycephalus* Behnke, 1968, from Southcentral Turkey, with comments on the Classification of the Subfamily Salmoninae. *Mitt. Hamburg. Zool. Mus. Inst., 66, 1–15.*

Behnke, R. (1973): Systematic problems of the Salmonidae fishes endemic to the Adriatic–Mediterranean province and the potential for developing new information from new techniques. *I Congr. Eur. Ichth. Pap. Abstr., Sarajevo, 19–21.*

Behnke, R. (1972): The Systematics of Salmonid Fishes of Recently Glaciated Lakes. *J. Fish. Res. Bd. Canada, 29, 639–671.*

Bernatchez, L. (2001): The evolutionary history of Brown trout (*Salmo trutta* L.) inferred from phylogeographic, nested clade, and mismatch analyses of mitochondrial DNA variation. *Evolution, 55, (2), 351–379.*

Bernatchez, L., Guyomard, R., Bonhome, F. (1992): DNA sequence variation of the mitochondrial control region among geographically and morphologically remote European brown trout *Salmo trutta* populations. *Molecular Ecology, 1, 161–173.*

Berrebi, P., Povž, M., Jesensek, D., Catta neo–Berrebi, G., Crivelli, A. J. (2000): The genetic diversity of native, stocked and hybrid populations of marble trout in the Soca river, Slovenia. *Heredity, 85, 277–287.*

Bianco, P. G., Taraborelli, T. (1985): Contributto alla conoscenza del genere *Rutilus* Rafinesque in Italia e nei Balcani occidentali (Pisces, Cyprinidae). *Mus. Reg. Sc. Nat. Torino, 3, (1), 131–172.* (Italian, English Summary)

Bianco, P. G. (1990): Potential role of the paleohistory of the Mediterranean and Paratethys basins on the early dispersal of Euro–Mediterranean freshwater fishes. *Ichthyol. Explor. Freshwat., 1, 167–184.*

Bogdanović, I. (1961): Prvi ozbiljni koraci u poribljavanju Plitvičkih Jezera. *Ribarstvo, 16, (2), 44–48.* (Croatian).

Catsadorakis, G., Malakou, M., Crivelli, A. J. (1996): The Prespa barbell, *Barbus prespensis*, Karaman, 1924, in the Prespa lakes basin, north–western Greece. *Tour du Valat, Arles, 79 p.*

Cerović, D., Ivanović, B. (1968): Some morphological characteristics of *Salmo trutta* m. *fario* from the river Čehotina. *Poljoprivreda i šumarstvo, 14, (3), 221–225.* (Serbian, English Summary).

Cvijić, J. (1989): Morfološki tipovi karstnih terena. *in*: Geografija karsta. Collect. Works. *SANU, Beograd, 7, 225–270.* (Serbian).

Cvijić, J. (1991): Geološka hronologija. *in*: Geografija karsta. Collect. Works. *SANU, Beograd, 6, 33–48.* (Serbian).

Ćurčić, V. (1938): Neretva i njene pastrve (Salmonidae). *Sep. Pres., Sarajevo. 89 p.* (Croatian).

Debeljak, Lj., Fašaić, K. (1985): Ishrana potočne pastrve (*Salmo trutta m. fario* L.) u akumulacijskom jezeru Bajer i potoku Lepenica. *Ichthyos, 3, 1–6.* (Croatian, English Summary).

Drecun, Đ. (1956): Pastrmka »Blatnjača« iz Plavskog Jezera. *Naša Poljopr., 2, (1), 63–70.* (Serbian).

Drecun, Đ., Knežević, B., Filipović., Petković, S., Petković, S., Nedić, D. (1985): Biološko–ribarstvena istraživanja rijeke Morača, njenih pritoka i Rikavačkog Jezera. *Agrosaznanje, 4.* (Serbian, English Summary).

Drobnjaković, B. (1934): Ribolov na Drini. *Mus. Ethn. Beograd, Sp. Ed., 4, 56 p.* (Serbian, French Summary).

Dumurđanov, N., Stojanov, R. (1992): The Geology of the Vicinity of Ohrid Lake. *in*: The Conditions and Perspectives for Protection of the Ohrid Lake and its Surroundings. *DEM, 113–120.* (Macedonian, English Summary).

Economidis, P. (1991): Check List of Freshwater Fishes of Greece. *Hell. Soc. Prot. Nat., Athens, 48 p.*

Economidis, P. S., Banarescu, P. (1991): The distribution and origins of freshwater fishes in the Balkan Peninsula, especially in Greece. *Int. Revue Ges. Hydrobiol., 76, (2), 257–283.*

Filippi, N. (1959): L'ichtyofaune du lac de Shkoder. *Bull. Stat. Rech. Sci. Ecc. Pech., Tirane, 1, 135–165.* (Albanian, French Summary).

Filippi, N. (1959 a): L'ichtyofaune du lac de Pogradec et de ses affluants. *Bull. Stat. Rech. Sci. Ecc. Pech., 1, 166–204.* (Albanian, French Summary).

Geldiay, R. (1972): Trout (*Salmo trutta* L.) populations inhabiting the streams of Kazdagi Range. *Verh. Internat. Verein. Limnol., 1212–1221.*

Georgiev, S. (1978): Rastenje i razmnožavanje potočne pastrmke (*Salmo trutta m. fario* L.) iz nekih tekućica u SR Makedoniji. *Arch. Agr. Sc., 31, (115), 121–135.* (Serbian, English Summary).

Georgiev, S. (1992): Ribolovot na Ohridskoto Ezero, specijalizacija ili vraćanje kon vekovnite tradicii. *Compil. Sci. Works. Symp. Ohrid, DEM, 88–94.* (Macedonian, English Summary).

Georgiev, S., Cilevski, A. (1991): Aquaculture and tourism: a case study. *Europ. Aquacult. Soc. Spec. Publ., Gent, 16, 489–495.*

Guiffra, E., Bernatchez, L., Guyomard, R. (1994): Mitochondrial control region and protein coding genes sequence variation among phenotypic forms of Brown trout *Salmo trutta* from northern Italy. *Molecular Ecology, 3, 161–171.*

Hadišče, S. (1962): Zur Kenntnis der Gattung *Salmothymus* Berg–zugleich ein Beitrag zur Systematik des Familie der Salmoniden (Pisces). *Izdanija. Inst. Pisc. Maced., 3, (2), 39–50.* (German, Serbian Summary).

Herak, M. (1985): On the relation of Adriatic and Dinaric structures. *Dissert., ASAS, Ljubljana, 26, 401–414.* (Croatian, English and Slovenian Summary).

Holčik, J. (1969): A note on the occurence and taxonomy of Brown Trout—*Salmo trutta* Linnaeus, 1758 in the Danube river. *Vest. čs. spol. zool., 23, (3), 223–228.*

Holčik, J. (1981): Towards the characteristics of the genera *Hucho* and *Brachymystax* (Pisces, Salmonidae). *Fol. Zool., 31, (4), 369–380.*

Holčik, J. (1982): Review and Evolution of *Hucho* (Salmonidae). *Acta Sc. Nat. Brno, 16, (3), 1–29.*

Ivanović, B. (1973): Ichthyofauna of Skadar Lake. *Inst. Biol. Med. Res., 146 pp.*

Janković, D. (1960): Sistematika i ekologija lipljena (*Thymallus thymallus* L.) u Jugoslaviji. *Biol. Inst. Spec. Iss., 7, 1–145.* (Serbian, English Summary).

Janković, D. (1961): Taksonomska i ekološka istraživanja na mekousnoj pastrmci (*Salmo obtusirostris oxyrhynchus* S.) iz reke Bune. *Inst. Biol. Rec. Trav., 5, (4–5), 1–31.* (Serbian, English Summary).

Janković, D. (1963): Pastrmka iz Plavskog jezera. *Arch. Sc. Biol., 15, (1–2), 25–34.* (Serbian, English Summary).

Janković, D. (1965): Die ursache der nase (*Chondrostoma nasus L.)* verbreitung in dem flusse Studenica. *Arh. Biol. Sci., 17, (3), 173–185.*

Janković, D., Raspopović, S. (1960): Pokušaj nasadivanja Vlasinske akumulacije ohridskom pastrmkom. *Ribarstvo, 15, (4), 78–80.* (Croatian).

Jardas, I. (1983): An analytical account of the Adriatic ichthyofauna. *Ichthyologia, 15, (1), 15–35.* (Croatian, English Summary).

Kačanski, D., Kosorić, Đ. (1970): O ishrani potočne pastrmke (*Salmo trutta* m. *fario* L.) iz nekih bosanskih i hercegovačkih pritoka Jadrana. *Ichthyologia, 2, (1), 63–71.* (Croatian, English Summary).

Kačanski, D., Kosorić, Dj., Ćepić, V. (1977): O ishrani nekih ribljih vrsta u slivu reke Neretve (od Uloga do Mostara). *Ichthyologia, 9, (1), 31–45.* (Croatian, English Summary).

Karakousis, Y., Triantaphyllidis, C. D. (1988): Genetic relationship among Greek Brown Trout (*Salmo trutta* L.) populations. *Pol. Arch. Hydrobiol., 35, (3–4) 279–285.*

Karaman, M. (1971): Zoogeografski odnosi izmedu Prespanskog Jezera i Ohridskog Jezera. *Izdanija, Inst. Pisc. SRM, 4, (5).* (Croatian, German Summary).

Karaman, S. (1924): Pisces macedoniae. *Hrvatska štamparija. Split. Author's edition, 89 p.* (German).

Karaman, S. (1928): Prilozi ihtiologiji Jugoslavije. *Bull. Skop. Sci. Soc., 6, 147–176.* (Serbian, German Summary).

Karaman, S. (1928 a): Salmonidi Balkana. *Bull. Skop. Sci. Soc., Skopje, 2.*

Karaman, S. (1931): Zoološki odnosi Skopske kotline. *Bull. Skop. Sci. Soc., 9, 219–222.* (Serbian, German Summary).

Karaman, S. (1936): Prilog poznavanju slatkovodnih riba Jugoslavije. *Bull. Skop. Sci. Soc., 17, 55–64.* (Serbian, German Summary).

Karaman, S. (1937): Beitrag zur Kenntnis der Susswasserfishe Jugoslaviens (Salmoniden, 1. teil). *Bull. Skop. Sci. Soc., 18, 131–139.* (German).

Karaman, S. (1952): Prilog poznavanju slatkovidnih riba Jugoslavije. *Jugosl. Akad. Znan. Umj., 25, 117–125.* (Croatian, German Summary).

Karaman, S. (1957): Pastrmke reke Radike. *Fol. Balc., Inst. Pisc. Maced., 1, (10), 57–70.* (Serbian, English Summary).

Karapetkova, M., Živkov, M., Aleksandrova–Kolemanova, K. (1993): National Strategy for Protection of Biological Difference. *Sofia, 515–546.*

Karapetkova, M. (1994): Vertebrate Animals. in: Limnology of the Bulgarian Danubian Confluents. *Zool. Inst. BAS, Sofia, 175–186.*

Korovina, V. M., Vuković, T. K. (1972): Anatomical–hystological Characteristics of the Middle Intestine *Salmothymus obtusirostris oxyrchynchus* (Steindachner). *Ichthyologia, 4, (1), 41–58.*

Kosorić, Đ. (1969): Neki podaci o rasprostranjenju i migracijama *Salmo marmoratus* Cuv. u pritokama Neretve. *Bull. Land Mus. Nat. Sc., 8, 79–82.* (Croatian).

Kosorić, Đ. (1974): Ribe rijeke Rame. *Ichthyologia, 6, (1), 69–78.* (Croatian, English Summary).

Kosorić, Đ., Kapetanović, N., Veledar, I. (1975): Ribe Velikog Zlatarskog Jezera. *Ann. Biol. Inst. Univ., Sarajevo, 28, 133–141.* (Croatian).

Kosorić, Đ., Vuković, T. (1966): Ribe rijeke Bune. *Bul. Land. Mus. Nat. Sc., 5, 179–190.* (Croatian, German Summary).

Kosorić, Đ., Vuković, T. (1969): A Research of the Possibilities of Hybridisation of Salmonidae Species of the Neretva River Confluence. *Ichthyologia, 1, (1), 57–67.*

Kottelat, M. (1997): European freshwater fishes. An heuristic checklist of the freshwater fishes of Europe (exclusive of Former USSR), with an introduction for non–systematists and comments on nomenclature and conservation. *Biologia, Bratislava, 52, (5).*

Ladiges, W. (1967): Pisces. *in*: Limnofauna Europea. *Gustav Fisher Verlag. Stuttgart, 429–439.*

Maletin, S., Đukić, N. (1989): Nalaz potočne pastrmke (*Salmo trutta m. fario:* Pisces) u Dunavu. *Biosistematika, 15, (2), 169–173.* (Serbian, English Abstract).

Marić, D. (1980): Prilog poznavanju *Paraphoxinus alepidotus* (Heckel, 1843) u vodama Jugoslavije. *Bull. Inst. Prot. Nat. Mus. Nat. Hist. Titograd, 13, 101–105.* (Croatian, English Summary).

Matoničkin, I., Pavletić, Z. (1960): Učešće jednostaničnih životinja i biljnih grupa u stvaranju životnih zajednica na travertinskim i erozivnim slapovima u Bosni i Hercegovini. *Ann. Inst. Biol. Univ. Sarajevo, 13, (1–2), 41–62.* (Croatian, English Summary).

Michajlowa, L. (1967): Seltene Fischarten aus der Suswasserfauna Bulgariens. *Zeitsch. Fisch., Radebeul Berlin, 15, (1/2) 153–160.* (German, English and Russian Summary).

Nikolsky. G. V. (1956) Lenok–*Brachymystax lenok* (Pallas). *in* Ribi basseina Amura. *Acad. Sc. SSSR, Moskow, 59–70.* (Russian).

Orešarov, P., Niškov, M. (1959) P'tevoditel na ribolovcite. *Drž. Izd. Medic. Fizcult., Sofia. 177 p.* (Bulgarian).

Osinov, A. G., Bernatchez, L. (1996): »Atlantic« and »Danubian« Phylogenetic Groupings of Brown trout *Salmo trutta* Complex: Genetic Divergence, Evolution, and Conservation. *Journ. Icht., 36, (9), 723–746.*

Petrovski, N. (1967): Biometrika na Prespanskiot krap (*Cyprinus carpio* L.). *Izdanija. Inst. Pisc. Maced., 4, (1), 3–27.* (Macedonian, French Summary)

Pintar, Z. (1964): Ribe porječja Kupe. *Bull. City Mus., Karlovac, 1, 219–255.* (Croatian, German Summary).

Poljakov, G. D., Filipi, Nd., Bacho, K., Hysenaj, A. (1958): Peshqit e Shqiperise. *Univ. Popul., Tirane, 281 p.* (Albanian).

Popovska–Stanković, O., Georgiev, S. (1973): Prvi soopštenija za ishranata na potočnata pastrmka (*Salmo farioides* Kar.) od Mavrovskata Akumulacija. *Izdanija. Inst. Pisc. Maced., 4, 9.* (Macedonian, English Summary).

Povž, M., Jesensek, D., Berrebi, P., Crivelli, A. J. (1996): The Marble Trout *Salmo trutta marmoratus*, Cuvier 1817 In the Soča River basin, Slovenia. *Tour du Valat Publication, 65 p.*

Rakaj, N., Flloko, A. (1995): Conservation Status of Freshwater Fish of Albania. *Biol. Conserv., 72, 195–199.*

Sabioncelo, J., Marko, S., Pažur, K. (1973): Bioekološka istraživanja na salmonidima u Hrvatskoj. *Inst. Freshw. Fish. Sell. Sc. Proff. Works, Jub. Ed., Zagreb, 106–120.* (Croatian, English Summary).

Sidorovski, M. (1955): Uber einige Morphologishe Charactere der Forellen aus dem See fon Mavrovo und dem Radika–Flusse. *Izdanija, Inst. Pisc. Maced., 1, (5), 135–147.* (German).

Sidorovski, M. (1960): Plodnost pastrmki iz Mavrovske Akumulacije i reke Radike. *Publ. Proff. Ass. Fish. Jugosl. Dev., 1/60.* (Serbian).

Sidorovski, M. (1971): Vozrast i rastenje na pastrmkata (*Salmo farioides* Kar.) od Mavrovskata Akumulacija. *Izdanija, Inst. Pisc. Maced., 1, 4.* (Macedonian).

Simonović, P. D., Nikolić, V. P. (1995): Ichthyofauna of the Vlasinsko Jezero Rezervoir. *Arch. Biol. Sc. Belgrade, 47, (1–2), 71–74.*

Sommani, E. (1961): Il *Salmo marmoratus* Cuv.: sua origine e distribuzione nell'Italia settentrionale. *Boll. Idrol. Pesca, 15, 40–47.* (Italian, French and English Summary).

Stanković, S. (1957): Ohridsko Jezero i njegov živi svet. *Kultura, Skopje.* (Serbian).

Stearley, R. F., Smith, G. R. (1993): Phylogeny of the Pacific Trouts and Salmons (*Oncorhynchus*) and Genera of the Family Salmonidae. *Trans. Amer. Fish. Soc., 122, 1–33.*

Stefanec, M., Bunjevčević, Z. (1982): Contribution to the knowledge of the morphological characters of Brown Trout of the river Gacka. *Ribarstvo, 37, (2), 30–32.*

Stefanović, D. (1948): Rasna i ekološka istraživanja na ohridskim salmonidima. *SANU. Separ. Publ., Beograd, 139/38, 1–207.* (Serbian).

Šorić, V. (1990): Salmonids in the Ohrid–Drim–Skadar System. *Acta Sc. Zool. Bohemoslov., Bratislava, 54, 305–319.*

Šorić, V. (1990 a): Ichthyofauna of the Ohrid–Drim–Skadar System. *Ichthyologia, 22, (1), 31–43.*

Thaller, Z. (1936): Glavatica i mladica. *Priroda, 26, (8), 230–235*. (Croatian, German Summary).

Thaller, Z. (1944): Lipljen *Thymallus thymallus* (Linne) njegov životni prostor u Hrvatskoj i na Balkanu i gospodarska vrijednost. *Ribar, 2, 5–82*. (Croatian, German Summary).

Thaller, Z. (1950): Visovačka jezerska pastrva (*Salmo visovacensis* n. sp.). *Period. Biol. Soc. Sc. Nat. Cro., 2/B, (2/3)–1948, 1949, 118–158*. (Croatian, German Summary).

Thaller, Z. (1953): Rasprostranjenje i popis slatkovodnih riba Jugoslavije. *Bull. Mus. Hist. Nat. Serb. B (5–6), 425–455.* (Croatian).

Teskeredžić, E., Teskeredžić, Z., McLean, E., Tomec, M. (1993): Occurrence, Distribution, and Potential Future of Yugoslavian Salmonids. *In: Genetic Conservation of Salmonid Fishes, Edit., J. G. Cloud and G. H. Thorgaard, Plenum Press, New York,* 314 pp.

Vovk, J. (1979): Ichthyofauna of the Planinsko Polje (Slovenia, Yugoslavia). *Nat. Cons., 12, 61–64.*

Vuković, T., Ivanović, B. (1971): Slatkovodne ribe Jugoslavije. *Zemaljski muzej, Sarajevo*. (Croatian).

Zaplata, R., Thaller, R. (1933): Ribe Sarajeva i okoline. *St. Pres., Sarajevo, 1–31.* (Croatian).

* Dubrovnik (1963): 1: 200. 000, *Ed. Armygeog. Inst., Belgrade*

* Prespa (1949): 1:100.000, *Ed. Armygeog. Inst., Belgrade*

* Sarajevo (1963): 1:200.000, *Ed. Armygeog. Inst., Belgrade*

* Senj (1971): 1:200.000, *Ed. Armygeog. Inst., Belgrade.*

* Split (1963): 1:200.000, *Ed. Armygeog. Inst., Belgrade*

* Travnik (1963): 1:200.000, *Ed. Armygeog. Inst., Belgrade*

Received: 3. 3. 2003.
Accepted after correction: 13. 11. 2003.