MORPHOLOGICAL DISTINCTION OF THE MARBLE TROUT, *SALMO MARMORATUS*, IN COMPARISON TO MARBLED *SALMO TRUTTA* FROM RIVER OTRA, NORWAY

by

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ABSTRACT. - Detailed morphological analysis of 76 specimens of *Salmo marmoratus* from rivers draining to the Adriatic Sea and 295 specimens of other *Salmo* species shows that it is possible to diagnose *S. marmoratus* from remaining *Salmo* species, including a marbled *S. trutta* from the River Otra in Norway, using colour pattern alone. *S. trutta* from the River Otra have pronounced white leading edges followed by black on anal and dorsal fins irrespective of the extensive variation in colour pattern on head and trunk. This pigmentation on the fins, commonly found in Atlantic basin *S. trutta*, is missing in *S. marmoratus*. Except for the marbled colour pattern in some specimens, *S. trutta* from the River Otra resemble Atlantic basin *S. trutta* in morphology. In multivariate statistics the combination of a high number of vertebrae, high proportion of abdominal vs. caudal vertebrae, and few caudal fin procurrent rays, separates *S. marmoratus* from remaining *Salmo* species. The recognition of *S. marmoratus* as a distinct species is also supported by published osteological and molecular data. Morphometry is less informative but *S. marmoratus* is characterised by a less deep but wider body compared to other *Salmo* species. However, the variation and overlap with other *Salmo* species is extensive. *Salmo carpio* and *S. letnica* inhabiting Adriatic drainages, are closer to *S. salar* than to *S. marmoratus* or *S. trutta* in morphometry. Thus, the two-species view, prevailing among fishery biologists and geneticists, only recognising *S. salar* and a polymorphic brown trout, *S. trutta* in *Salmo* is not supported by morphological data and disregards distinct, diagnosable, evolutionary units.

RÉSUMÉ. - Distinction morphologique entre la truite marbrée *Salmo marmoratus* et *Salmo trutta* marbrée originaire du fleuve Otra, Norvège.

Une analyse morphologique détaillée de 76 spécimens de *Salmo marmoratus* originaires du bassin adriatique et de 296 spécimens des autres espèces de *Salmo*, montre qu'il est possible de distinguer *S. marmoratus* des autres espèces de *Salmo*, y compris *S. trutta* marbrée originaire du fleuve Otra en Norvège, en n'utilisant que des détails de coloration. Indépendamment des larges variations de la couleur de la tête et du corps, *Salmo trutta* originaire du fleuve Otra a des bords frontaux blancs prononcés avec les nageoires anale et dorsale noires. Cette pigmentation sur les nageoires, ordinairement trouvée sur la *Salmo trutta* atlantique, manque chez *S. marmoratus*. À l'exception de la couleur marbrée de quelques spécimens, *Salmo trutta* du fleuve Otra ressemble morphologiquement à *Salmo trutta* atlantique. Une analyse multivariée conclut que la combinaison d'un grand nombre de vertèbres, une grande proportion de vertèbres abdominales par rapport aux vertèbres caudales et un petit nombre de rayons sur les nageoires caudales, distinguent *Salmo marmoratus* des autres espèces de *Salmo*. La distinction de *S. marmoratus* comme une vraie espèce est également supportée par des données ostéologiques et moléculaires publiées. L'analyse morphométrique est moins informative mais *S. marmoratus* est caractérisée par un corps moins long mais plus large que chez les autres espèces de *Salmo*. La variation et les similarités avec d'autres espèces de *Salmo* sont pourtant nombreuses. *Salmo carpio* et *S. letnica*, qui habitent également le bassin adriatique sont morphométriquement plus proches de *S. salar* que de *S. marmoratus* ou de *S. trutta*. Ainsi, le point de vue des ichtyologistes et des généticiens, qui affirment qu'il n'y a que deux espèces de *Salmo*, *S. salar* et la truite d'Europe polymorphe, n'est pas confirmé par les données morphologiques et ne tient pas compte des unités distinctes d'évolution.

Key words. - Salmonidae - *Salmo marmoratus* - *Salmo trutta* - Norway - Otra River - Morphometry - Multivariate statistics - Species distinction.

According to recent estimates of *Salmo* diversity, there may be about 25 valid species in Eurasia (Kottelat, 1997). This is in striking contrast to the two-species view of the genus *Salmo* suggested by, e.g., MacCrimmon and Marshall (1968) and Elliott (1989), which recognise only *S. trutta* Linnaeus, 1758 and *S. salar* Linnaeus, 1758. A more sober estimate of six species is found in Dorofeyeva (1998). Studies on genetic diversity (e.g., Giuffra *et al*., 1994; Apostolidis *et al*., 1997; Bernatchez, 2001) also support the recognition of several *Salmo* species. However, among ichthyologists investigating molecular variation in *Salmo*, it is common to reject the formal nomenclature, and instead to lump all *Salmo*, except *S. salar*, in a 'brown trout complex'.

Out of numerous nominal Eurasian *Salmo* species, the marble trout, *Salmo marmoratus* Cuvier, 1829, is one of the most distinct species. Its native distribution includes rivers emptying into the Adriatic Sea from northern Italy (Sommani,

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1960) to Albania (Schöffman, 1994). The most striking and diagnostic feature is the prominent marbled colour pattern (Fig. 1A). Another feature of *S. marmoratus* is its growth potential, reaching at least 24 kg (Povz *et al*., 1996). The validity of *S. marmoratus* has only been questioned indirectly in the way of indecisive statements by adherents of the two-species view. Some authors (e.g., Tortonese 1970; Ielli and Duchi, 1991; Alessio *et al*., 1991) consider it to be a subspecies of *S. trutta* only, whereas others (e.g., Pomini, 1939; Sommani 1948, 1960; Vukovic, 1971; Ocvirk, 1989) treat *S. marmoratus* as a species. Recent comparative studies, both morphological (Dorofeyeva *et al*., 1991) and genetic (Giuffra *et al*. 1994, 1996; Berrebi *et al*., 2000), confirm its distinction from other *Salmo* species.

Salmo marmoratus has experienced introgression from alien stocked *Salmo* species within its entire range of distribution (e.g., Ocvirk, 1989; Ielli and Duchi, 1991; Povz *et al*., 1996). At present it is not possible to tell for sure whether there are any unaffected populations left at all. This uncertainty stems from lack of detailed knowledge of all the introductions that have taken place over the last 100 years. There is also disagreement among ichthyologists whether pure *S. marmoratus* can have red spots typical of *S. trutta* or

not, and whether an *S. marmoratus* population having a typical marbled colour pattern but 'wrong' allele in some of the most informative allozyme loci can be regarded as genetically 'pure' (e.g., Berrebi *et al*., 2000).

The marbled colour pattern in *Salmo* is not restricted to *S. marmoratus*. Skaala (1992) mentioned a trout from the River Otra basin in Norway, which he called 'marmorated trout' (Fig. 2A). Herein I will use the term marbled instead of 'marmorated' as it refers to a colour pattern similar to that of *S. marmoratus*. Skaala and Solberg (1997) concluded that the marbled Otra trout did not differ genetically from adjacent trout populations referred to *S. trutta*, except for high frequencies of the *CK-1** 115 allele, otherwise more common in, e.g., the Lake Vänern basin in Sweden. Hypotheses on a hybrid origin (e.g., *Salmo* x *Salvelinus*) of the marbled pattern in the marbled Otra trout were strongly rejected by Skaala and Solberg (1997) based both on allozyme data and historical facts related to the introduction of brook trout, *Salvelinus fontinalis* (Mitchill, 1814) in Otra. Whereas Adriatic basin *S. marmoratus* populations are rather uniform in their colour pattern, the trout from Otra show large variation, ranging from a typical brown trout spotted phenotype to a marbled pattern (Fig. 2).
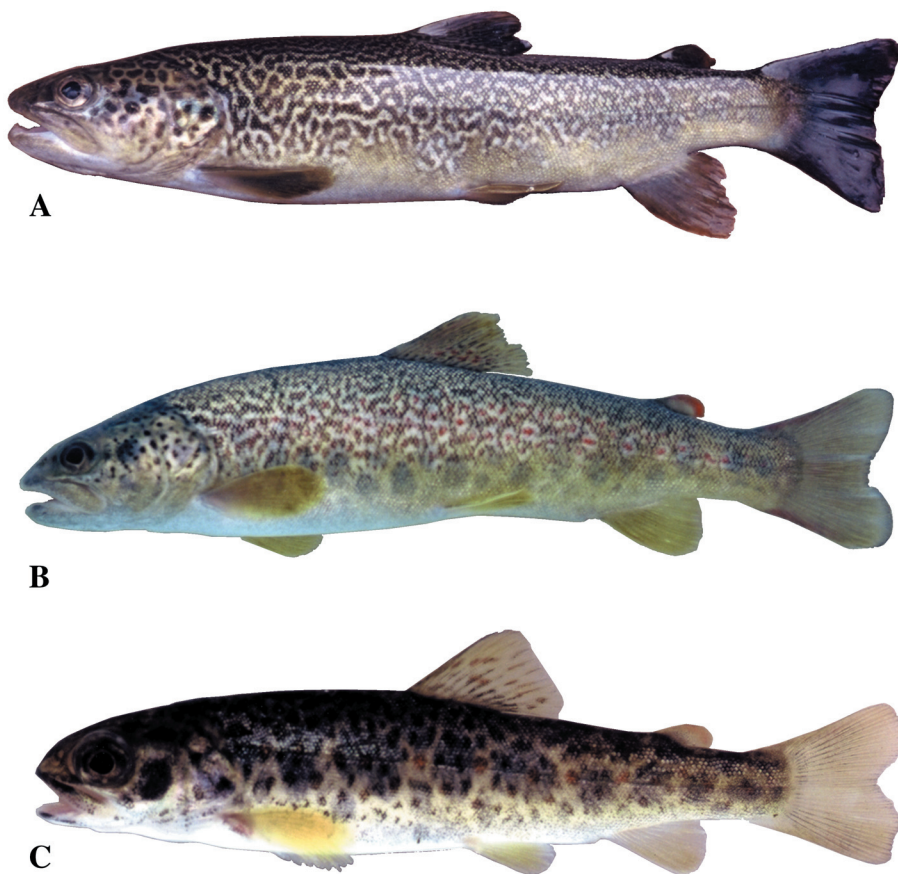

Figure 1. - *Salmo marmoratus* from Soca River basin, Slovenia. **A**: NRM 46229, 265 mm SL, from Zadlascica Stream; **B**: NRM 46230, 183 mm SL, from Trebuscica Stream; **C**: NRM 46231, 65.2 mm SL, from upper Idrijca Stream.

Thus, the presence of a marbled colour pattern similar to that of *S. marmoratus* in a *Salmo* species in northern Europe necessitate morphological comparisons between the marbled Otra trout, *S. marmoratus*, and common Atlantic basin *S. trutta*, to discuss diagnosability and taxonomic status of the different forms. Comparative material, representing *Salmo* species other than *trutta* and *marmoratus* is also included for a discussion on the usage of morphological characters and molecular data in *Salmo* systematics in general.

MATERIALS AND METHODS

Specimens of *S. marmoratus* were collected by electrofishing in four tributaries to the Soca River in Slovenia, viz. the upper Idrijca, Trebuscica, Lipovscek, and Zadlascica. Museum material of *S. marmoratus* from Po and Adige River basins in Italy and a single large specimen from Neretva River in former Yugoslavia were also included. Specimens of *S. trutta* from the Otra River basin were collected by seine in the river and by trap in the Lake Byglandsfjorden. See Skaala and Solberg (1997) for details

on distribution of the marbled phenotype. The entire material from the Otra basin is herein referred to as the 'Otra trout' or *S. trutta* from Otra. All freshly collected specimens were fixed in 10% formalin and later transferred to 75% ethyl alcohol prior to analyses.

For comparison, material of *S. trutta* and *S. salar* from the Atlantic basin and material of non-Atlantic *Salmo* species, usually referred to different species distinct from *S. trutta* and *S. salar*, were included in analysis. For the comparative material nomenclature follows Kottelat (1997) with minor exceptions, e.g., some non-Atlantic specimens are referred to '*Salmo* spp. Mediterranean' only. A complete list of analysed material with a few notes on nomenclature is given in the Appendix.

Institutional abbreviations. - MHNG, Muséum d'Histoire naturelle, Genève; MNHN, Muséum national d'Histoire naturelle, Paris; BMNH, Natural History Museum, London; NRM, Swedish Museum of Natural History, Stockholm; ZMH, Zoologisches Museum, Universität Hamburg, Hamburg; ZISP, Zoological Institute, Russian Academy of Sciences, St. Petersburg. Specimens included in the analysis were selected from lots listed in the Appendix.

All available specimens of *S. marmoratus* larger than

Figure 2. - *Salmo trutta* from Otra River basin, Norway. **A**: NRM 46232, 218 mm SL, from Otra River; **B**: NRM 46233, 216 mm SL, from Otra River; **C**: *Salmo trutta*, NRM 46234, 161 mm SL, from Lake Byglandsfjord.

100 mm SL were included in measurements and counts (75 specimens, 104-280 mm SL). For the single large specimen from Neretva, counts were taken from x-ray only. For the Otra trout all 25 specimens (217-303 mm SL) caught by seine in the River Otra were included. From Lake Byglandfjorden, 20 specimens (152-224 mm SL) were selected out of 114 available; both marbled and spotted specimens were included, but large eyed and meagre specimens were excluded.

Measurements were taken on the left side of the specimen with a digital calliper connected to a data recording computer and rounded to nearest 0.1 mm (Fig. 3). The length of the uppermost gill raker on the lower limb of first gill arch (right side) was measured *in situ* using a pair of dividers. The length and height of three selected vertebrae were taken from radiographs under a binocular dissection microscope equipped with a graded ocular. Measurements were taken in the anterior and dorsal region of the preural centrum. The three selected vertebrae were: the third one from the head (anterior part of the body), the one corresponding to the posteriormost dorsal fin pterygiophore (central part of the body, right below the dorsal fin), and the

ninth one counting forwards from the third (last) upturned vertebra in the caudal skeleton (central part of the caudal peduncle).

Number of pored scales along lateral line to the end of the caudal peduncle (left side), scales in an oblique row from base of adipose fin backwards down to lateral line including lateral line scales (left side), gill rakers, including rudimentary elements, on lower and upper limbs of first gill arch separately (right side), and branchiostegal rays on both sides, were taken under a binocular dissection microscope.

Number of abdominal vertebrae, caudal vertebrae, unbranched and branched rays in dorsal and anal fins, pterygiophores supporting anal and dorsal fins, caudal fin upper and lower procurrent rays, interneurals, expanded neural spines in the caudal skeleton and vertebrae having expanded neural spines were taken from radiographs. Rudimentary vertebrae in the caudal skeleton in addition to the three upturned vertebrae were not included in the counts. In cases of fused centra, number of neural arches or spines were counted. The last abdominal vertebra is herein defined as the last one having ribs (sometimes rudimentary or missing) and/or having the haemal spine much shorter than in the
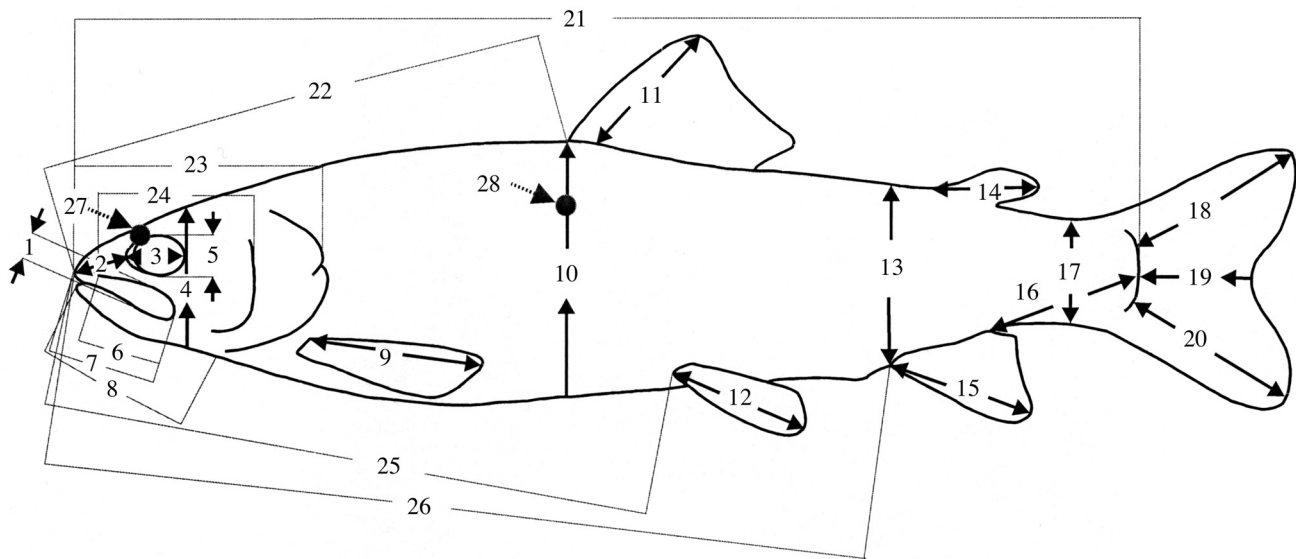

Figure 3. - Measurements taken on *Salmo* specimens. 1: upper jaw depth, as largest depth of the maxilla and supramaxilla; 2: snout length, from symphysis of premaxilla to osseous orbit margin; 3: orbital horizontal diameter, between osseous orbital margin; 4: head depth, just posterior to orbit; 5: orbital vertical diameter, between osseous orbital margin; 6: length of maxilla, from premaxillad end to posterior end of maxilla; 7: upper jaw length, from symphysis of premaxilla to posterior end of maxilla; 8: lower jaw length, from symphysis of dentary to retroarticulare; 9: pectoral fin length, from base of first ray to tip of longest ray; 10: body depth, at level of origin of dorsal fin; 11: dorsal fin length, from base to tip of longest ray; 12: pelvic fin length, from base of first ray to tip of longest ray; 13: body depth, at level of origin of anal fin; 14: adipose fin length, from origin to tip; 15: anal fin length, from base of first ray to tip of longest ray; 16: caudal peduncle length, from end of anal fin to middle base of caudal fin; 17: least depth of caudal peduncle; 18: length of upper caudal fin lobe, from base to tip of longest ray; 19: length of middle caudal fin ray, from base to tip of shortest ray; 20: length of lower caudal fin lobe, from base to tip of longest ray; 21: standard length (SL), from upper jaw symphysis to middle base of caudal fin; 22: predorsal length from upper jaw symphysis to origin of dorsal fin; 23: head length, from upper jaw symphysis to posterior tip of operculum; 24: premaxilla to preoperculum length, from premaxilla end of maxilla to posterior margin of preoperculum; 25: prepelvic length, from upper jaw symphysis to origin of pelvic fin; 26: preanal length, from upper jaw symphysis to origin of anal fin; 27: interorbital width, transverse at narrowest part of skull, 28: body width, transverse at widest part of body at level of dorsal fin origin, above abdominal cavity.

consecutive first caudal vertebra. The position of the dorsal and anal fins were estimated in relation to the vertebral column. The anterior most strongly developped pterygiophore was used as marker of dorsal and anal fin position respectively. Dorsal and anal fin pterygiophores do not articulate with neural and hemal spines respectively, and in uncertain cases I have chosen the lower value. The dorsal and anal fin positions are treated as meristic characters in statistic analyses. Number of expanded neural spines were divided into two characters (see above) because of the common state where one vertebra possesses two spines. A membranous triangular bone sometimes present, located above the neural spine of the first vertebrae was not included in interneural counts. Analysed material from MHNG was not x-rayed.

Specimens of *S. marmoratus* from upper Idrijca, Trebuscica and Zadlascica, were photographed in field prior to, or shortly after fixation in formalin. For the material of Otra trout and *S. marmoratus* from Lipovscec, photographs were taken at NRM after fixation in formalin but prior to transfer to alcohol.

Statistic analyses were performed using SYSTAT 5.0 (Wilkinson *et al*., 1992). Measurements and counts were subjected to principal component analysis (PCA). The PCA was performed in two steps using a covariance matrix on log-transformed measurements and a correlation matrix on square-rooted counts (Bookstein *et al*., 1985). Analyses were performed both on the total sample, i.e., including the comparative material and with comparative material restricted to Atlantic basin *S. trutta*. The morphological variation was then studied by plotting scores of the most informative principal components in each data set, labelling the specimens according to species, locality, or colour pattern. In the latter analysis, the sample of Otra trout were sorted into two groups, marbled or spotted, to test if the marbled phenotype differs from the spotted phenotype and Atlantic basin *S. trutta*. Soft measurements such as body width and body depth, sensitive to conditions of preservation, were excluded from multivariate statistics. Instead, these characters were studied on a subset of the material restricted to recently collected and preserved specimens.

For vertebrae measurements, indices (proportions) were calculated dividing the height by the length. Thus, a vertebra having the index 1.0 appears as a square on the radiograph. Vertebrae measurements were not included in PCAs.

RESULTS

Colour pattern

In the Otra trout the colour pattern is extremely variable (Fig. 2), especially in number and size of spots on the sides of the body and in the marbled colour pattern when present.

In densely spotted specimens that have large dark spots, there is a tendency for the dark spots and the lighter background to merge into each other, resulting in an irregular mixture of a light vermiculate pattern on a dark background and a spotted pattern (Fig. 2B). The number of light red spots is variable and sometimes such spots are absent (Fig. 2C) or occasionally, when very numerous, spots merge and bright red is the major colour on the sides of the body. The overall colour on head and trunk includes brown, green, and dark red shades on the back and sides, changing to white or yellow on the ventral side, often with a dusky grey tint. Specimens spotted also on the belly are rare (Uleberg, pers. comm.). In marbled specimens (Fig. 2A) the light portion of the marbled pattern merges with the light rings enclosing the red spots along lateral line, usually resulting in a light stripe along the lateral line. This light stripe is also present in three comparatively large marbled specimens lacking red spots. These specimens (NRM 42544) were caught in Otra, and kept in captivity (Syrveit fiskeanlaegg) as part of a feeding experiment. They were not included in measurements and counts. Both marbled and spotted specimens often have the caudal fin marbled or spotted. The dorsal fin has distinct black spots, rarely a few red spots. Some specimens have a red spot on the adipose fin (Fig. 2B). White leading edges followed by black on the anal and dorsal fin (Fig. 2) are present in all specimens. On the dorsal fin, the black and white markings are most intense at the tip.

In *S. marmoratus* small juvenile specimens have a densely spotted or speckled colour pattern (Fig. 1C) on the head and sides of the body, that later on, as specimens get larger, develops into a marbled pattern. However, some specimens retain a spotted pattern on the sides of the head when growing larger (Fig. 1B). One specimen from Zavjaska Grappa, a small stream previously void of fish, but stocked with *S. marmoratus* of Zadlascica origin, have two distinct black spots on the sides of the head. This specimen was photographed alive in field and not preserved. The same specimen has a prominent marbled pattern made up of yellowish white and a comparatively pale greenish-brown colour. The overall colour on head and trunk in *S. marmoratus* includes brown, green, and dark red shades on the back and sides, changing to white on the ventral side, often with a dusky grey tint.

In *S. marmoratus* from Soca River, considerable variation in colour pattern is found between the four headwater streams. The Zadlascica population have the most prominent marbled colour pattern (Fig. 1A) followed by the Lipovscek population. The Zadlascica population usually lacks red spots on the sides of the body. The Trebuscica, Idrijca and Lipovscek populations have a less prominent marbled pattern and numerous red spots on the sides of the body, however, usually less common in larger specimens

and absent in specimens larger than 300 mm from Lipovscek (Jesensek, pers. comm.). The red spots are mainly found along the lateral line and larger spots are often enclosed by a light ring. The light ring, when present, merges with the marbled pattern (Fig. 1B). The old faded museum specimens from Po and Adige River basins all seem to have had a pronounced marbled pattern similar to that of the Zadlascica population.

Salmo marmoratus sometimes shows four broad transverse dark bars on the side of the body. The bars, when present in *S. marmoratus*, are most easily seen on live fish in water, especially in smaller specimens. The bars are located right behind the head, below the dorsal fin, above the anal fin, and on the caudal peduncle close to the base of caudal fin [barely traceable as in figure 1A and in Povz *et al.* (1996), figure on page 5]. In the four included samples of *S. marmoratus*, I have found bars in those from Zadlascica and upper Idrijca. Bars were also present in marbled trout inhabiting a small stream (Gorska Grappa), previously void of fish, but stocked with *S. marmoratus* of Zadlascica origin. Some hybrid trout from various localities in the Soca river also had bars. The background colour of the rayed fins ranges from yellow to dark olive green. Larger specimens sometimes have a marbled pattern on dorsal, adipose and caudal fin. The dorsal fin has distinct dark spots and occasionally numerous red spots. The adipose fin or its margin is occasionally red. The upper and lower margins of the caudal fin are occasionally red, most frequently in specimens from Trebuscica.

In both *S. marmoratus* and the marbled Otra trout, the marbled pattern is most prominent on the back and down to the lateral line, often extending halfway below the lateral line on the sides of the body. If the marbled pattern extends below the lateral line, it is most often interrupted by a light stripe along the lateral line merging with the marbled pattern in the marbled Otra trout (Fig. 2A). In *S. marmoratus* there is no such interruption (Fig. 1A, B). In general, *S. marmoratus* have its fins less pigmented compared to the Otra trout. Often the Otra trout, both marbled and spotted, have a red spot on the adipose fin (Fig. 2B). In *S. marmoratus*, the entire adipose fin or its margin is sometimes red, ranging in intensity from just a tint in the Zadlascica population to very bright in some of the others, but never in the form of a distinct spot. However, the most striking difference is presence and absence of the black and white leading edges of dorsal and anal fins in Otra trout and *S. marmoratus* respectively. Some specimens of *S. marmoratus* (Fig. 1B, C) have leading edges with a pale but not truly white tint, but the contrasting black is absent. Black and white leading edges are usually present in, e.g., Atlantic basin *S. trutta*.

Measurements and counts

Results from PCA performed on the total sample places

S. marmoratus distinctly separate from remaining *Salmo* specimens as a closely connected cluster (Fig. 4), however, not fully separated from the comparative material. The Otra trout are found together with Atlantic basin *S. trutta*. Some of the non-Atlantic *Salmo* species, i.e., *S. carpio* and *S. letnica* are more close to Atlantic salmon than to Atlantic *S. trutta* in morphometry. Character loadings (Tab. I, II) indicate that measurements related to jaws, caudal peduncle and caudal fin are important for separation along the morphometric axes, whereas number of abdominal vertebrae, dorsal and anal fin positions and number of expanded neural spines receive the highest loadings for the meristics. Examination of meristics, character by character, also shows that, e.g., the number of caudal fin procurrent rays is important for the distinctiveness of *S. marmoratus*. On the contrary, high loadings for number of lateral line scales and branchiostegal rays (Tab. II) reflect extensive variation in *Salmo*, but variation in these characters is mainly to be found within species. The most informative meristic characters are summarised in tables III-V. Specimens overlapping with, or located close to *S. marmoratus* in figure 4 are of both Atlantic and Mediterranean origin.

Excluding *S. salar* and non-Atlantic trout species except *S. marmoratus* from the PCA, labelling the marbled Otra
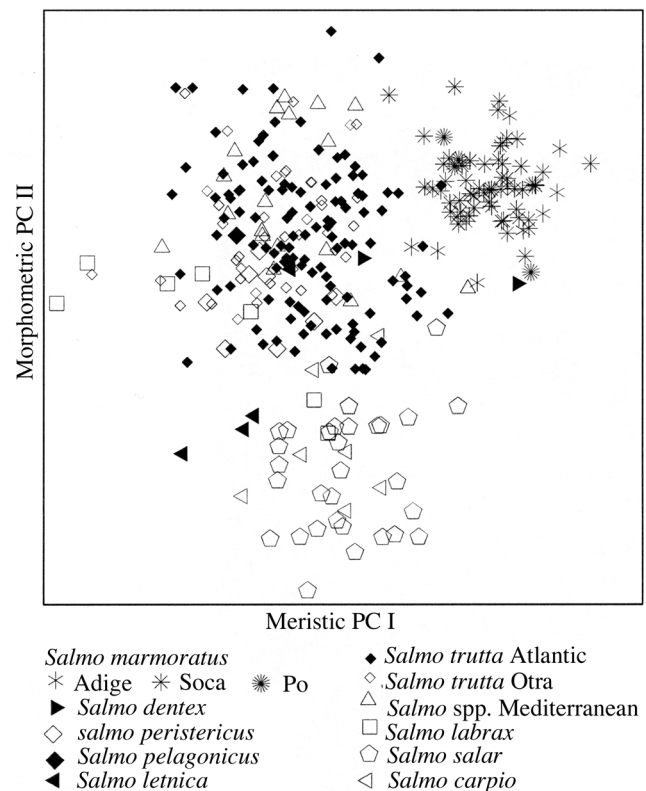

Figure 4. - Plots of scores of first meristic principal component on second morphometric principal component for the total sample of *Salmo*.

	Total sample of *Salmo*			*Salmo marmoratus* and Atlantic basin *S. trutta*		
	PCI	PCII	PCIII	PCI	PCII	PCIII
Standard length	0.290	-0.045	-0.004	0.280	0.028	-0.016
Preanal length	0.297	-0.037	-0.002	0.285	0.027	-0.014
Prepelvic length	0.301	-0.028	0.002	0.291	0.020	-0.012
Predorsal length	0.295	-0.017	0.003	0.282	0.011	-0.013
Head length	0.284	0.011	0.010	0.275	-0.012	0.003
Premaxilla to preoperculum length	0.299	0.013	0.016	0.289	-0.013	0.012
Caudal peduncle length	0.261	-0.079	-0.013	0.252	0.047	-0.031
Caudal peduncle depth	0.274	0.015	-0.025	0.254	0.004	-0.023
Length of upper caudal fin lobe	0.267	-0.072	0.000	0.259	0.050	0.013
Length of lower caudal fin lobe	0.271	-0.073	0.001	0.259	0.048	0.020
Length of middle caudal fin ray	0.282	0.022	0.004	0.268	0.008	0.011
Pectoral fin length	0.254	-0.046	-0.003	0.245	0.014	0.017
Pelvic fin length	0.275	-0.030	-0.007	0.264	0.020	0.007
Adipose fin length	0.270	0.062	-0.091	0.254	-0.064	-0.060
Anal fin length	0.295	0.005	-0.001	0.282	0.010	0.016
Head depth	0.277	0.009	0.002	0.264	-0.002	0.002
Horizontal orbit diameter	0.203	0.012	0.035	0.199	-0.022	0.045
Vertical orbit diameter	0.192	-0.004	0.043	0.190	-0.015	0.060
Interorbital width	0.312	-0.002	-0.019	0.298	0.005	-0.028
Snout length	0.316	0.022	-0.003	0.303	-0.023	-0.018
Upper jaw length	0.310	0.065	0.012	0.298	-0.035	0.003
Length of maxilla	0.315	0.070	0.018	0.300	-0.032	0.009
Height of maxilla	0.257	0.051	0.022	0.253	-0.044	0.023
Lower jaw length	0.314	0.050	0.015	0.301	-0.029	0.006
Variance explained (%)	94.437	2.186	0.702	95.535	1.121	0.799

Table I. - Character loadings on principal component I-III for 24 measurements taken on 371 *Salmo* specimens (total sample) and for a restricted sample (n = 266).

	Total sample of *Salmo*			*Salmo marmoratus* and Atlantic basin *S. trutta*		
	PCI	PCII	PCIII	PCI	PCII	PCIII
Lateral line scales	0.476	-0.010	0.228	0.404	0.230	0.019
Scales from adipose fin to lateral line	-0.182	0.655	-0.118	-0.319	0.340	0.279
Left side branchiostegal rays	0.346	0.330	0.436	0.190	0.587	0.153
Right side branchiostegal rays	0.449	0.363	0.410	0.344	0.567	0.215
Gill rakers on lower arch	-0.113	-0.301	0.417	-0.122	0.338	0.398
Gill rakers on upper arch	-0.227	-0.477	0.474	-0.278	0.400	0.136
Abdominal vertbrae	0.897	-0.082	-0.131	0.905	-0.047	-0.041
Caudal vertebrae	-0.365	-0.104	0.339	-0.394	0.254	0.005
Dorsal fin position	0.758	-0.230	-0.060	0.796	-0.005	-0.001
Anal fin position	0.815	-0.145	-0.059	0.812	-0.021	0.033
Dorsal fin rays	0.217	0.260	0.539	0.092	0.513	-0.363
Dorsal fin pterygiophores	0.267	0.173	0.558	0.158	0.515	-0.260
Interneurals	0.541	0.005	0.027	0.523	-0.007	0.049
Anal fin rays	0.020	0.135	0.503	-0.031	0.432	-0.661
Anal fin pterygiophores	-0.078	0.096	0.432	-0.100	0.302	-0.734
Caudal fin upper procurrent rays	-0.376	0.762	-0.074	-0.655	0.289	0.225
Caudal fin lower procurrent rays	-0.130	0.840	-0.030	-0.453	0.476	0.301
Expanded neural spines	0.608	0.255	-0.247	0.704	0.214	0.234
Vertebrae having expanded neural spine	0.569	0.305	-0.199	0.664	0.296	0.228
Variance explained (%)	21.532	13.944	11.117	24.565	12.771	9.230

Table II. - Character loadings on principal component I-III for 24 meristic characters taken on 371 *Salmo* specimens (total sample) and for a restricted sample (n = 266).
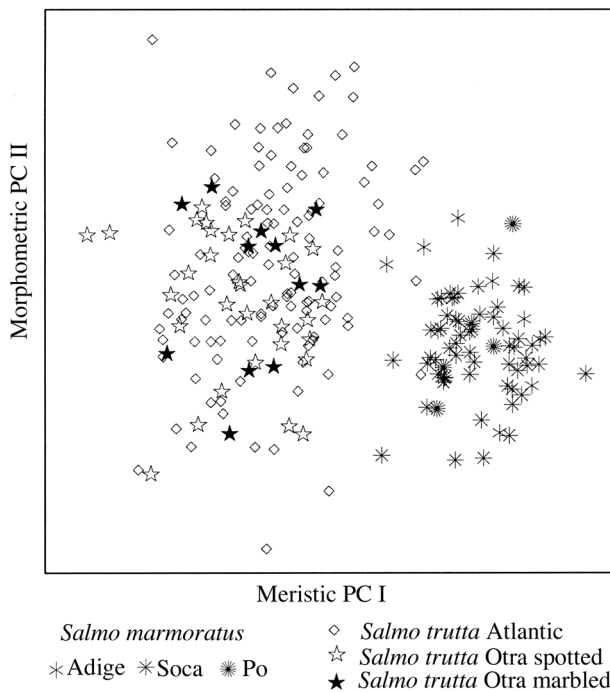
Figure 5. - Plots of scores of first meristic principal component on second morphometric principal component for a sample of *Salmo* restricted to *S. marmoratus*, Atlantic basin *S. trutta* and Otra trout.

trout separately, shows that the marbled Otra trout does not differ from the spotted phenotype in Otra or from Atlantic basin *S. trutta* in general (Fig. 5). However, the exclusion of body width and the two body depth measurements left very little information in the morphometric data set. Character loadings (Tab. I, II) resemble those of the previous analyses for the total sample. Some specimens of Atlantic basin *S. trutta* are still to be found within the *S. marmoratus* cluster.

Shape indices for the anteriormost vertebra are summarised in box plots (Fig. 6). Within sample regressions of shape indices on SL indicate a slight negative correlation related to size and contribute to about 0.1 for the range of variation for some samples (not shown). *Salmo marmoratus* differs from remaining *Salmo* species. For a majority of the Atlantic basin *S. trutta* and other included *Salmo* species the index is smaller than 1.4, whereas samples of *S. marmoratus* have median values around 1.5 and only a few specimens below 1.4. However, the sample of *S. marmoratus* from Po differ in having somewhat lower index. The lowest indices in *Salmo* are found in *S. carpio*. The shape index for the vertebra situated below the dorsal fin varies in a similar way, but the variation within samples is larger (not shown). In the caudal region of the vertebral column, the within sample variation in shape index overshadows variation between samples and/or species. The specimens (NRM
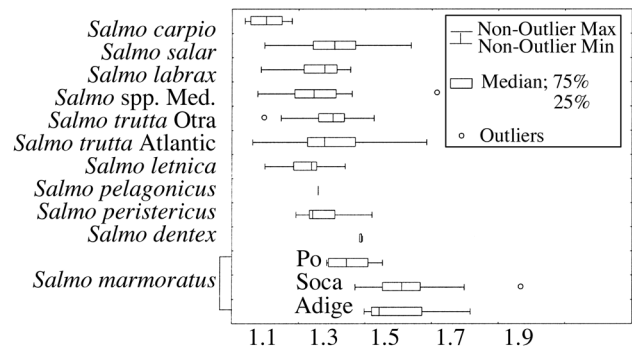

Figure 6. - Variation in shape index for the third vertebra from head for the total sample of *Salmo*. Subsamples are the same as in figure 4.
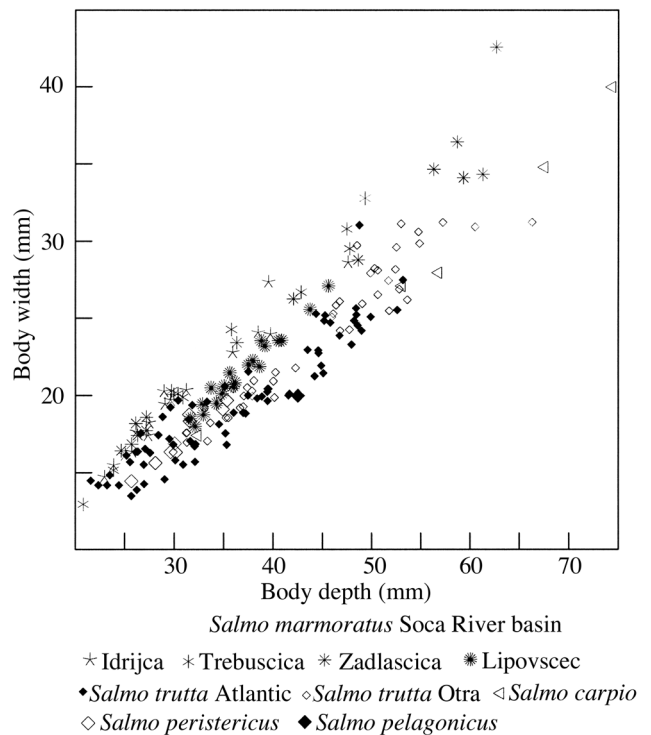

Figure 7. - Body width plotted on body depth at origin of dorsal fin for a sample of *Salmo* restricted to recently collected and well preserved specimens.

24885 from White Sea basin) overlapping with *S. marmoratus* in figure 5, all have a shape index of the anterior vertebra smaller than any specimen of *S. marmoratus*, including the sample from Po. Among the non-Atlantic *Salmo* species, the two specimens referred to *S. dentex* have high shape indices (Fig. 6). A single specimen (MNHN 0000-2575) from the Rhône River basin also have a high index (outlier of '*Salmo* spp. Mediterranean' in figure 6).
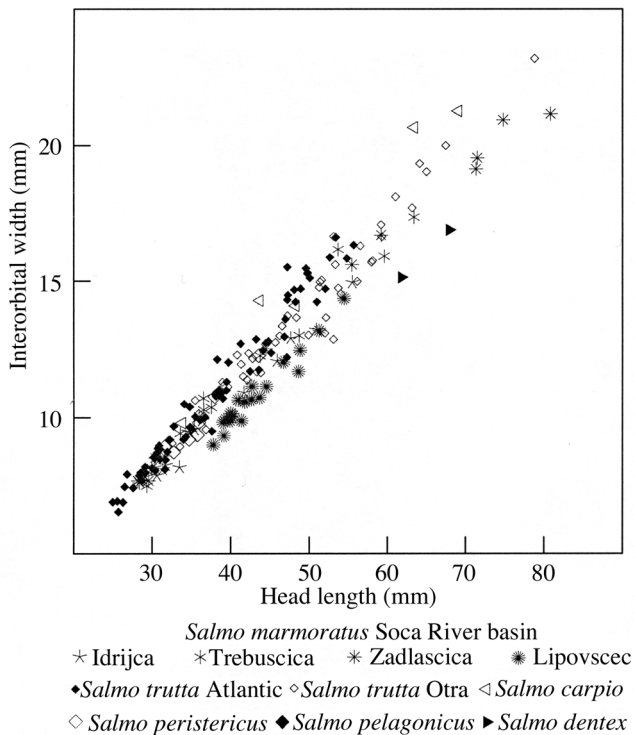
Regarding the body measurements excluded from PCA,

Figure 8. - Interorbital width plotted on head length for a sample of *Salmo* restricted to recently collected and well preserved specimens and two older specimens of *S. dentex*.

a bi-plot (body width vs. body depth at origin of dorsal fin, figure 7) for a subset restricted to recently collected specimens, shows that *S. marmoratus* in general has a wider and less deep body than Atlantic basin *S. trutta*. There is also a pronounced difference between certain *S. marmoratus* populations within the Soca River basin. A bi-plot of interorbital width on head length (Fig. 8) also confirms earlier statements (se below) of a comparatively narrow cranium in *S. marmoratus*. In figure 8 the two specimens referred to *S. dentex* are also included.

DISCUSSION

Characters

Results from principal component analyses (Fig. 4, 5; Tab. I, II) and comparison character by character (Tab. III-V; Fig. 6-8), show that *S. marmoratus* and the marbled Otra trout only share a marbled colour pattern. *Salmo marmoratus* also possess low gill raker counts similar to Atlantic basin *S. trutta*, however, not restricted to these taxa only (Tab. V). Thus, neither allozymes (Skaala and Solberg, 1997), morphometry, or meristics suggest any closer relationship between the two forms, and the most probable

explanation is that a marbled colour pattern has evolved twice. Whether the dark and light parts of the marbled colour pattern are homologous with the dark spots and their lighter rings in Atlantic *S. trutta*, remains elusive. Some observations, i.e., merging dark spots in trout from Otra (Fig. 2B), and that the light rings of the red spots tend to merge with the light portion of the marbled pattern (Fig. 2A and to a certain degree in Fig. 1B) support homology. In the typical *S. trutta* spotted colour pattern, spots are black or very dark. In both *S. marmoratus* and the marbled Otra trout, basic colours on head and body varies including different nuances of red, brown, and green but never black. Large Atlantic salmon males have a marbled pattern made up of light windings on a dark red background on the sides of the head during spawning season. However, they still have distinct black spots and a speckled dark red colour on the sides of the body. Further, at least some *S. marmoratus* specimens, otherwise rather pale but distinctly marbled, have truly black spots on the sides of the head. This suggests that the lighter windings in the marbled pattern might be homologous to the pale rings enclosing black and red spots in *S. trutta*, whereas the darker portion of the pattern is the overall background colour of the body.

Differences in the marbled pattern and pigmentation on the fins are diagnostic for *S. marmoratus* in comparison to the Otra trout. Previous morphological studies on *S. marmoratus* have not revealed any single diagnostic character, besides the colour pattern, and some osteological characters studied in *S. marmoratus* from Neretva River in Bosnia Herzegovina (Dorofeyeva *et al.*, 1991), that with 100% accuracy diagnose the species. A well developed hypethmoid (endochondral ossification in the ethmoid cartilage) rarely found in other *Salmo* species was found in all studied specimens from Neretva (ibid). A narrow neurocranium, quantified by three width measurements, is the most diagnostic osteological character for *S. marmoratus* and the relative width of the cranium in the pterotic region is diagnostic in comparison to other *Salmo* species (ibid). Plotting interorbital width on head length for some of my material (Fig. 8) confirms a relatively narrow head in *S. marmoratus*. This difference is most pronounced in larger specimens. Dorofeyeva (1998) also describes several additional osteological character, e.g., shape of the premaxilla, which for *S. marmoratus* differs from her comparative material of *S. trutta*, *S. letnica*, *S. ischchan*, *S. carpio*, and *S. salar*.

Some distinctive characters responsible for separation in PCA in the present study, such as high vertebral counts agrees with earlier studies (e.g., Tortonese, 1970). Other characters, i.e., proportions of abdominal *vs.* caudal vertebral counts, procurrent caudal fin ray counts, number of expanded neural spines in the caudal region, and vertebra shape have not been described earlier and reinforce the distinctiveness of *S. marmoratus*.

	Abdominal vertebrae								Caudal vertebrae					
	32	33	34	35	36	37	38	39	21	22	23	24	25	26
Salmo marmoratus					3	27	37	10		10	42	24	1	
Soca					1	22	29	9		6	34	20	1	
Po					1	3	2			1	4	1		
Adige						2	6	1		3	4	2		
Neretva					1							1		
Otra trout		3	19	20	3					1	13	26	5	
Salmo trutta Atlantic		5	31	49	38	16	2		1	6	31	76	25	3
Salmo spp. Med.		1	7	10	4	1				4	6	9	2	
Salmo carpio				3	5						1	5	2	
Salmo dentex					1		1				2			
Salmo peristericus			5	4							2	3	4	
Salmo pelagonicus		1											1	
Salmo letnica		2	2	2						1	1	4		
Salmo labrax	3	4	1	3								7	4	
Salmo salar			1	18	11	2					4	19	7	2

Table III. - Frequency distribution of abdominal and caudal vertebrae in *Salmo* species, subdivided per drainage in *S. marmoratus*.

	Caudal fin upper procurrent rays								Expanded neural spines			
	10	11	12	13	14	15	16	17	3	4	5	6
Salmo marmoratus		1	30	32	10	4				1	29	46
Soca		1	25	22	9	4				1	23	36
Po			2	4							2	4
Adige			3	5	1						3	6
Neretva				1							1	
Otra trout			1	15	13	15	1			28	16	1
Salmo trutta Atlantic			3	13	41	56	27		1	52	78	
Salmo spp. Med.			3	9	7	2				3	17	3
Salmo carpio				5	3					1	7	
Salmo dentex			1		1						1	
Salmo peristericus			4	5							6	3
Salmo pelagonicus				1							1	
Salmo letnica			1	5						1	5	
Salmo labrax				3	2	3	2			3	7	1
Salmo salar	1	7	24								21	11

Table IV. - Frequency distribution of caudal fin upper procurrent rays and expanded neural spines in the caudal peduncle *Salmo* species, subdivided per drainage in *S. marmoratus*.

	Total number of gill rakers											
	13	14	15	16	17	18	19	20	21	22	23	24
Salmo marmoratus	1	4	12	18	28	13						
Soca	1	4	11	17	18	10						
Po			1	1	3	1						
Adige				7	2							
Otra trout			1	9	27	15	2					
Salmo trutta Atlantic		1	13	35	56	24	10	1				
Salmo spp. Med.				4	11	5	3	1	1			
Salmo carpio				1	2	4						
Salmo dentex						1	1					
Salmo peristericus				3	5	1						
Salmo pelagonicus									1			
Salmo letnica							2	5		1		1
Salmo labrax					2	1	5	2				
Salmo salar						4	10	15	2	1		

Table V. - Frequency distribution of gill rakers in *Salmo* species, subdivided per drainage in *S. marmoratus*.

Compared to the other *Salmo* species studied by me so far, *S. marmoratus* is diagnosable by its colour pattern alone. It is also evident from analyses of measurements and counts (Fig. 4-8) that *S. marmoratus* differs from a majority of included *Salmo* species even if colour pattern is excluded. Whether the four broad bars on the sides of the body indicates any closer relationship between *S. marmoratus* and the Doubs trout from the Rhône basin awaits morphological analysis, but published pictures of Doubs trout (fig. 1E in Guyomard,1989; fig. 1A in Largiadèr and Scholl, 1996 and fig. 15 in Lundberg *et al*., 2000) show trout with large head, strong jaws, and slender body thus in some respects looking similar to *S. marmoratus*. The Doubs trout was tentatively referred to *Salmo rhodanensis* Fowler, 1974 by Kottelat (1997)

Morphometry proved to be of limited use in diagnosing *S. marmoratus vs*. Atlantic *S. trutta*. However, for other species, i.e., *S. carpio* and *S. letnica*, the result is promising despite small samples (Fig. 4). The four recently collected specimens of *S. carpio* included in the PCA are two males and two females. One of each gender has swollen gonads and was close to spawning, and at a first glance the four specimens look rather different. Another specimen (the neotype, NRM 28000), not included in the PCA due to missing data for some characters, descends from a wild-caught stock grown at a fish farm. Despite small size (138 mm SL) and artificial growth conditions, this specimen looks like a miniature of a large *S. carpio*, characterised by slender caudal peduncle and short head. The distinction of *S. carpio* from *S. trutta* is of the same magnitude as the distinction between *S. salar* and *S. trutta* (Fig. 4).

Most progress during the last 20 years to understand *Salmo* diversity has been made at the molecular level (e.g., Ferguson and Taggart, 1991; Bernatchez and Osinov, 1995; Apostolidis *et al.*, 1996). These studies show that the 'brown trout complex', most often all *Salmo* except for *salar* and sometimes even '*S. obtusirostris*' listed among *Salmo* species (Laikre *et al.*,1999) [apparently referring to *Salmothymus obtusirostris* (Heckel, 1852)], is very variable and that a large portion of this variation is found between major and minor basins and sometimes between sympatric populations or species. Some species such as *S. marmoratus* has almost diagnostic allozyme alleles and mtDNA haplotypes (Giuffra *et al.*, 1994, 1996; Berrebi *et al.*, 2000). In several more recent publications on *Salmo*, mainly molecular, but also some morphological studies, one finds a rather negative attitude towards morphology, referring to direct phenotypic response to environment and characters that are supposed to respond quickly to selective forces, e.g., those related to feeding.

Direct phenotypic response is obviously the case for the variation in certain characters, such as growth (Alm, 1939). However, there are also several studies showing a genetic basis for morphological traits in *Salmo*, e.g., vertebral counts (Schmidt, 1919), black and white leading edges on fins (Alm, 1939), fine spotted colour pattern and lack of parr marks (Skaala and Jørstad, 1987). Direct phenotypic response to the environment is of course not unique to *Salmo* and within all fields of systematics and taxonomy, one has to keep this possibility in mind, and the variation in characters used for species descriptions, diagnosis, and phylogenetic studies shall preferably not overlap between species (but see below).

Compared to genetics where, e.g., an A (the base Adenine) is an A, notwithstanding problems with homology due to conflicting alignment options and gene duplications, morphological characters are more problematic to evaluate as the phenotype is the result of both genes and environment. However, when a character within a genus varies in a distinct and non-clinal fashion, e.g., high abdominal vertebral count in *S. marmoratus* compared to adjacent *Salmo* species, it is most reasonable to assume that the observation has a genetic background. In this particular case the conclusion is also strengthened by the fact that a sample of supposed hybrids (59 specimens from one locality in Slovenia) between native *S. marmoratus*, introduced Atlantic *S. trutta* and introduced Danubian and/or Mediterranean *Salmo* sp. possess more variation in abdominal vertebral count (34-38) (Delling *et al.*, 2000), than my entire sample of *S. marmoratus* from several different localities (Tab. III).

Genetically *S. marmoratus* is characterised by a set of specific mtDNA haplotypes, 'Ma1-Ma3' (Bernatchez *et al.*, 1992), however, also to be found in some specimens of *S. carpio* (Giuffra *et al.*, 1994) and probably in some Greece *Salmo* populations (cf. Bernatchez, 2001 and Apostolidis *et al*., 1997) outside *S. marmoratus*. The most informative allozyme locus is the *LDH-5**, where *S. marmoratus* populations usually are fixed for the autapomorphic 120 allele. Non-Atlantic basin *Salmo* and 12 other salmonids have a plesiomorphic 100 allele only, whereas an apomorphic 90 allele usually dominates over the 100 allele in the Atlantic basin *S. trutta* (Hamilton *et al.*, 1989). The *S. marmoratus* populations from Soca River basin studied herein are all classified as 'genetically pure' even though the Zadlascica population is almost fixed for the 100 allele (Berrebi *et al.*, 2000). Thus, neither mtDNA, nor allozymes, provides a 100% diagnosis of *S. marmoratus*. Ocvirk (1989) thought that the Zadlascica population was the only pure *S. marmoratus* population within the Soca River, as it has the most prominent marbled colour pattern and very few red spots. Ielli and Duchi, (1991) have used the presence of red spots as an indication of introgression in Italian populations of *S. marmoratus*. The absence or near-absence of alien allozyme alleles in the red spotted populations and the high frequency of the 100 allele in the most prominent marbled population led Povz *et al.* (1996) and Berrebi *et al.* (2000)

to the conclusion that pure *S. marmoratus* sometimes have red spots and that the 100 allele in the Zadlascica population is a rare case of ancient introgression and fixation of the ancestral allele in an otherwise pure population. To me this reasoning is circular, i.e., 'wrong' colour pattern is justified by pure allozymes and vice versa. It is possible that the conclusion is correct but the observed pattern of variation does not give strong support and other explanations could be offered, e.g., introgression due to stocking. Neither genetic data nor morphology can resolve this dilemma and even if every single specimen from the entire range of the distribution was analysed in detail we can never know for sure whether the presence of rare alleles in *S. marmoratus* is the result of introgression due to stocking or represents natural variation within the species. However, the remoteness and inaccessibility for migrating fish to these headwater streams in Soca speak in favour of purity. So does morphological distinctiveness and homogeneity of *S. marmoratus* presented herein, and as both the 100 allele and red spots are plesiomorphic in Salmonidae it is not unlikely to find them also in some populations of *S. marmoratus*.

Species recognition

The phylogenetic species concept defines a species as an irreducible cluster of organisms diagnosably distinct from other such clusters, within which there is a parental history of ancestry and descent (Cracraft, 1989 and citations therein). The exact meaning of 'diagnosably distinct' presents some problems of both theoretical and practical nature. Most characters used in descriptions and diagnoses of salmonid fishes are variable and the degree of overlap among species largely depends on sample size and amount of included comparative material. In a species rich, variable, and widely distributed genus such as *Salmo*, this problem is partly solved by using characters in combination, i.e., the diagnosis of *S. marmoratus* only requires a detailed comparison with other marbled *Salmo* species. The character in combination approach solves this particular problem. However, if we find an *S. marmoratus* populations also having black and white leading edges on the fins, what to do then? One desirable way is to include additional diagnostic characters. Based on the present day knowledge *S. marmoratus* can be diagnosed by the combination of, e.g., the 'Ma' haplotype, *LDH-5** (120), a marbled colour pattern, a well developed hypethmoid, few or no red spots, multivariate morphology, fins without black and white leading edges etc. However, none of these characters alone provide a 100% diagnosis and it is impossible to set a threshold for how much a population can deviate from the diagnosis and still be regarded as a pure *S. marmoratus*. However, deviation in a single or a few characters, e.g., *LDH-5** (100) in the Zadlascica population, or numerous red spots and a slightly paler marbled colour pattern in the Trebuscica

population is better explained as variation within the species *S. marmoratus*, than introgression or variation within single polymorphic species, i.e., a brown trout complex.

Theoretically one can also argue against 100% diagnosability. Baum (1998) discusses the individuality and existence of species through time, using the term 'fuzziness' to describe the lack of sharp boundaries between entities, making it impossible to always place an organism inside or outside a given species. The reasoning by Baum (1998) seems logic but is hard to extend further and implement into rigid rules for the practising taxonomist. My interpretation is that the species category is best understood in terms of homogeneity and uniqueness instead of levels of diagnosability as exemplified above with *S. marmoratus*. The uniqueness of a species is ultimately supported by numerous (100%) diagnostic characters for the studied sample. But if that is not the case, character in combination in a simple fashion or by means of multivariate ordination methods is sufficient to recognise species and by that describe unique entities.

There is also some discussion (e.g., Carvalho and Hauser, 1999; Turner, 1999) how to make use of the molecular data for species recognition. In the case of *S. marmoratus* it would be possible to distinguish, e.g., the Zadlascica population as a separate species based on the unique combination of a marbled colour pattern and the *LDH-5** (100) allele close to fixation. This hypothesis might be correct but any splitting of *S. marmoratus*, requires a more detailed understanding of the variation among its populations. The latter part of the phylogenetic species definition, i.e., parental history of ancestry and descent, prevents recognition of phenotypically similar populations with presumed different history, e.g., *S. fario* for all small sized spotted resident brook dwelling populations of *Salmo*. There are numerous examples among fishes, where genetic markers indicate closer relationship between different 'species' within the same drainage for so called 'species pairs', than between populations having similar phenotype from different drainages. See Taylor (1999) for a review. In Atlantic basin *S. trutta* - if regarded as a single generalistic species, diversification such as anadromous and resident populations within the same drainage is not linked to any pronounced morphological differences and I see no problem in treating them as conspecific. However, molecular markers are supposed to be selectively neutral and a seemingly close relationship between sympatric species pairs might be a result of introgression.

Thus, the molecular markers widely applied in salmonid biology has a potential to falsify recognisable species. I have no prompt solution to this problem but when molecules support multiple origins of supposed genetically determined diagnostic morphological characters, I suggest to consider the alternative hypothesis, depreciate the molecular 'evi-

dences', especially when constituted only of statistical differences in allozyme or mtDNA haplotype frequencies. However, when a molecular marker, e.g., *LDH-5** (120) in *S. marmoratus* is apomorphic, not necessarily fixed in all populations, it is a strong support of monophyly. The highly diagnostic marble trout mtDNA, however, also present in *S. carpio* and some other *Salmo* sp. is most interesting in a phylogenetic context to test for common ancestry or introgression of the species involved.

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APPENDIX

Salmo marmoratus **Cuvier, 1829**

Slovenia, *Soca River basin*. - NRM 41516; 6 (5, 152.4-201.7 mm SL); NRM 41519; 18 (11, 106.2-136.3 mm SL); NRM 46231; 1 (65.2 mm SL); Idrijca Stream, upstream dam near Idridske Klavske; Jun. 1998; B. Delling *et al*. NRM 41522; (4, 166.1-220.1 mm SL); NRM 41523; 12 (5, 104.0-143.7 mm SL); NRM 46230; 1 (183.0 mm SL); Trebuscica Stream, just above water fall upstream old bridge; Jun. 1998; B. Delling *et al*. NRM 41528; 13 (9, 106.2-180.0 mm SL); NRM 41529; (5, 212.3-280.0 mm SL); NRM 46229; 1 (265.0 mm SL); Zadlascica Stream, upstream hydroelectric power station near Zadlab-Zabce village; Jun. 1998; B. Delling *et al*. NRM 44701; (6, 149.7-180.4 mm SL); NRM 44702; (6, 139.0-181.0 mm SL); NRM 44703; (8, 149.6-215.0 mm SL); Lipovscec Stream; Sep. 1999; A.J. Crivelli *et al*.

Italy, *Po River basin*. - MNHN 0000-3635; 1 (260.0 mm SL); MNHN 0000-3636; 1 (258.0 mm SL); MNHN 0000-4920; 1 (305.0 mm SL); Syntypes of *Salar Ausonii* Valenciennes *in* Cuvier and Valenciennes, 1848; Po River; 1823; M. Savigny. MNHN B-1139; 3 (198.5-236.0 mm SL); [No locality data except Italy, tentatively referred to Po basin, possibly Lago Maggiore, based on collector (cf. Valenciennes *in* Cuvier and Valenciennes, 1848, p. 327)]; M. Savigny.

Italy, *Adige River basin*. - BMHN 1924.3.14:7-10; 4 (2, 144.8-169.2 mm SL); BMHN 1924.3.14:4-6; 3 (146.9-216.5 mm SL); 'Antholzer Lake'; Howell. BMHN 1924.3.14:11-13; 3 (112.4-184.9 mm SL); 'Passer River, Isonzo [= Soca] River system'[sic]; Howell. BMHN 1924.3.14:2-3; 2 (1, 200.6 mm SL); 'Rienz'; Howell.

Neretva River basin. - ZISP 48210; 1 (520 mm SL); 1985.

Otra trout

Otra River basin, *Norway*. - NRM 42540; 6 (192.5-222.0 mm SL); NRM 42541; 5 (195.2-232.0 mm SL); NRM 42542; 6 (198.2-226.8 mm SL); NRM 42543; 3 (210.4-221.3 mm SL); NRM 42539; 3 (229.2-264.6 mm SL); NRM 46232; 1 (218.0 mm SL); NRM 46233; 1 (216 mm SL); Otra River S of Byglandsfjord village between Vassend and Syrveitfossen; Oct. 1998; B. Delling *et al*. NRM 42544; 3 (285.5-323.7 mm SL); Hatchery at Syrveit; Oct. 1998; B. Delling *et al*. NRM 42548; 9 (6, 137.1-167.2 mm SL); NRM 42551; 15 (6, 142.4-198.3 mm SL); NRM 42549; 13 (7, 134.6-173.4 mm SL); NRM 46234; 1 (161.0 mm SL); Lake Byglandsfjorden at Grendi; Oct. 1998; B. Delling *et al*.

Salmo trutta **Linnaeus, 1758**

Norway. - NRM 42558; 5 (155.7-190.1 mm SL); NRM 42559; 5 (203.0-223.0 mm SL); Tovdalselva River, upstream Bås; Oct. 1998; B. Delling *et al*. NRM 41373; 1 (183.4 mm SL); Etne River; Jun. 1998; T. Odsjö *et. al*. NRM 36996; 1 (148.5 mm SL); Todalselva River at Todal; Aug. 1997: A. Johnels. NRM 44780; 2 (199.9-219.0 mm SL); Etne River; Jul. 1999; T. Odsjö *et al*. MNHN 0000-2909; 2 (213.0-216.0 mm SL); Paralectotypes of *Salar bailloni* Valenciennes *in* Cuvier and Valenciennes, 1848; de la Moriniere. MNHN A-5532; 1 (165.6 mm SL); MNHN A-5533; 1 (146.9 mm SL); 'swartiselv' [= probably a river close to Svartisen glacier]; 1882; Rabot.

Sweden. - NRM 24849; 1 (244.0 mm SL); Umeälven River basin, Lake Gäutan Tärnaby; Aug. 1879; F. Trybom. NRM 24866; 1 (272.3 mm SL); [Dalälven River], Älvkarleby; Oct. 1879; F. Trybom. NRM 24357; 1 (169.1 mm SL); Ljusnan River basin, Mittån Stream 1 km downstream Lake Messlingen; Sep. 1974; K.J. Gustafsson. NRM 24903; 3 (2, 211.0-226.5 mm SL); Lake Norra Dellen; Oct. 1882; Wiström. NRM 23661; 1 (153.0 mm SL); Igelbäcken stream at Sörentop; Sep. 1993; S.O. Kullander and F. Fang. NRM 24847; 1 (226.0 mm SL); Lake Vättern at efluent of stream at Djurkälla; Dec. 1861; H. Widegren. NRM 24895; 2 (235.0-246.8 mm SL); Lake Vättern, Motala; 1879; Holmerz. NRM 43978; 4 (123.2-137.6 mm SL); Ålebäcken Stream close to effluent in Lake Vättern; Jul. 1999; B. Delling and S.O. Kullander. NRM 24841; 1 (193.7 mm SL); [Motala Ström River or Lake Vättern] Motala; 1879; Holmertz. NRM 24894; 1 (230.8 mm SL); [Motala Ström River or Lake Vättern] Motala; Oct. 1861; C. Sundevall. NRM 23404; 4 (3, 1498.5-196.9 mm SL); Råne Älv River basin, Kvarnbäcken Stream at Mårdsel; Jul. 1993; B. Rånby. NRM 23406; 5 (4, 118,5-138.7 mm SL); Råne Älv River basin, Blåkölsbäcken Stream where crossed by road Grundträsk-Risappi; Jul. 1993; B. Rånby. NRM 24343; 24 (4, 156.4-187.3 mm SL); Verkaån River near Andrarum; Jul. 1998; Å. Strömberg and T. Calberg. NRM 24345; 22 (4, 105.1-127.4 mm SL); Verkaån River 2 km NW of Eljaröd, below fall; Jul. 1998; Å. Strömberg and T. Calberg. NRM 24344; 2 (179.5-194.4 mm SL); Verkaån River 2 km NW of Eljaröd, above fall; Jul. 1998; Å. Strömberg and T. Calberg. NRM 24361; 4 (113.3-189.3 mm SL); Gallån River 1 km E of Brinkamåla; Jul. 1988: Å. Strömberg and T. Calberg. NRM 41781; 3 (2, 119.8-162.1 mm SL); Lake Mälaren basin, Svartån River system, Stenarstugebäcken Creek where crossed by road Kil-Mogetorp; Jun. 1998; U. Pettersson. NRM 41793; 7 (4, 105.5-147.0 mm SL); Lake Mälaren basin, Svartån River system, Damsjöbäcken Creek (emptying in Frösividalsån River); Jun. 1998; U. Pettersson. NRM 41794; 1 (123.2 mm SL); Lake Mälaren basin, Svartån River system, Ånnabobäcken Creek; Jun. 1998; U.

Pettersson. NRM 41790; 6 (3, 110.9-123.0 mm SL); Lake Mälaren basin, Svartån River system, Gölgebäcken Creek; Jun. 1998; U. Pettersson. NRM 41791; 6 (1,112.4 mm SL); Lake Mälaren basin, Svartån River system, Damsjöbäcken Creek (emptying in Frösividalsån River); Jun. 1998; U. Pettersson. NRM 41789; 4 (93.2-109.9 mm SL); Lake Mälaren basin, Svartån River system, Gårdsjöbäcken Creek (emptying in Frösividalsån River); Jun. 1998; U. Pettersson. NRM 41785; 6 (96.1-137.9 mm SL); Lake Mälaren basin, Arbågaån River system, Rangelbäcken Creek; Jun. 1998; U. Pettersson. NRM 41783; 4 (1,108.6 mm SL); Lake Mälaren basin, Arbågaån River system, Stenbrobäcken Creek near Hålahult; Jun. 1998; U. Pettersson. NRM 44775; 10 (165.2-227.0 mm SL); Lake Stora Bävervattnet; Aug 1999; S. Palm. NRM 44037; 3 (149.4-163.4 mm SL); Borkhultsån Stream between Lake Borken and Lake Yxningen; Oct. 1998; U. Pettersson.

Russia. - NRM 24885; 5 (229.4-293.0 mm SL); White Sea basin, Archangelsk; 1876-1879; H. Sandeberg.

Germany. - ZMH 10734; 1 (165.3 mm SL); Holstein, Brockstedt, 'Fischerei-Austellung, Altona…1905', L. Conze 1905. ZMH 10736; 1 (268.0 mm SL); Holstein, Brockstedt, 'Fischerei-Austellung, Altona …1905. ZMH 10721; 8 (81.7-127.5 mm SL); 'Au bei Lockstedt, Südliche Schleiswig-Holstein'; Jun.-Jul. 1928. ZMH 10733; 2 (119.4-132.7 mm SL); 'Zucht Sarlhuse, Brockstedt, Holstein'. ZMH 10712; 1 (188.5 mm SL); 'Zucht Sarlhuse, Brockstedt, Holstein'. ZMH 10732; 1 (218.0 mm SL); Aumühle, 'Fischerei-Austellung, 1905. ZMH 10718; 1 (305.0 mm SL); 'Zucht Hohenbuche, Alster, gezüehtet in Hohenbuchen bei Potepen Uttel'. Oct. 1903; E. Lippert. Note: The above listed lots from ZMH come from the 'Fischerei-Austellung, Altona 1905' and some specimens have been caught in the wild and kept and fed in captivity for a certain time. The material is herein regarded as Atlantic basin *S. trutta* from northern Germany. ZMH 10731; 1 (205.7 mm SL); Hohenwestedt; May 1905. ZMH 1206; 1 (193.8 mm SL); [Elbe or Weser River basin] Breitenhees, Uelzen (Schwartzstorchnest); Jul. 1960. P. Kaiser. ZMH 5672; 2 (189.3-217.0 mm SL); Unterelbe River, Lühe-Mündung, Aug. 1975, H. Wilkens. ZMH 5735; 1 (137.4 mm SL); Unterelbe River; Apr. 1979; Oesman. ZMH 10738; 1 (128.5 mm SL); Eider River basin, 'Nord-Ostsee-Kanal, Borgstedter Enge, at Rendsburg'; May 1936; Peters. ZMH 6346; 2 (142.6-193.9 mm SL); Cuxhaven, Aussen-Kante, Bauhafen; Apr. 1958; Krefft. ZMH 6344; 2 (99.4-102.8 mm SL); [Weser River basin], artificial pool at Lauterthal; Harz; Jul. 1959; MNHN 0000-3649; 1 (278.0 mm SL); MNHN 0000-3650; 1 (277.0 mm SL); MNHN 0000-3651; 1 (294.0 mm SL); Syntypes of *Salar Ausonii* Valenciennes *in* Cuvier and Valenciennes, 1848; Rhine River basin, Nidda, Frankfurt;

1827; M.A. Valenciennes. MNHN 0000-3634; 1 (228.0 mm SL); Syntypes of *Salar Ausonii* Valenciennes *in* Cuvier and Valenciennes, 1848; 'Marche d' Berlin', 1827; M.A. Valenciennes.

Scotland. - NRM 20125; 5 (143.3-191.8 mm SL); River Brora basin, Loch Bad an t-Sean-tighe; May 1993; K. Dalarud and A. Brew. NRM 20126; 2(184.4-197.4 mm SL); River Helmsdale upstream bridge in Helmsdale; May 1993; T. Johansson. MNHN 0000-3638; 1 (208.9 mm SL); MNHN 0000-3639; 2 (157.4-194.5 mm SL); MNHN 0000-3640; 2 (162.8-167.0 mm SL); MNHN 0000-3641; 1 (239.0 mm SL); MNHN 0000-3642; 1 (228.0 mm SL); MNHN 0000-3643; 1 (179.2 mm SL); Syntypes of *Salar Ausonii* Valenciennes *in* Cuvier and Valenciennes, 1848; 'Lacs d'Écosse'; Mac Cullock.

Switzerland. - MHNG 816.8; 1 (198.9 mm SL); Rhine River basin, Lake Neuchâtel; 1843; E. Galopin. MHNG 642.70; 1 (243.3 mm SL); Rhine River basin, Lake Neuchâtel; Dec. 1896; E. Galopin.

France. - MNHN 0000-6321; 1 (312.0 mm SL); Lectotype of *Salar bailloni* Valenciennes *in* Cuvier and Valenciennes, 1848; Somme River, Abbeville; Valenciennes. MNHN 1923-0215; 1 (265.0 mm SL); MNHN 1923-0216; 1 (188.9 mm SL); Gironde River basin, Lake Oo; 'Gadeau de Kerville'. MNHN 0000-2898; 1 (248.0 mm SL); Loire River; Le Clerc. MNHN 1939-0017; 1 (148.3 mm SL); Loire River basin, fishing village; 1939; Le Clerc.

Spain. - MNHN 1982-0480; 1 (250.0 mm SL); Tazone (marine); 1979.

Salmo salar Linnaeus, 1758
Sweden. - NRM 24914; 1 (208.3 mm SL); Norrköping; Aug 1863; Widegren. NRM 21142; 1 (234.0 mm SL); Gullspångsälven River; Nov. 1882; Trybom and Wåhlen.

Norway. - NRM 41372; 1 (181.2 mm SL); Etne River; Jun. 1998; T. Odsjö *et al*. NRM 46136; 1 (109.5 mm SL); Etne River; Jul. 1999; T. Odsjö *et al*. NRM 42545; 9 (196.1-239.3 mm SL); NRM 42546; 8 (186.1-206.0 mm SL); NRM 42547; 7 (132.3-158.7 mm SL); Lake Byglandsfjorda at Grendi; Oct. 1998; B. Delling *et al*.

Germany. - ZMH 10727; 2 (130.5-133.0 mm SL); Elbe River at Entenwerder; Nov. 1904. ZMH 10714; 2 (112.6-117.3 mm SL); Schleswig-Holstein, Brockstedt [Hatchery]; May 1905.

France. - MNHN 0000-1441; 2 (156.7-198.6 mm SL); Hatchery. MNHN 1898-0143; 1 (196.3 mm SL); Loire River, Nevers; Moreau. MNHN 1894-0004; 2 (122.6-125.3 mm SL); MNHN 1894-0005; 2 (99.3-115.2 mm SL); Loire

River Basin, Allier River, Brioude; Ferry. MNHN 1939-0016; 1 (115.2 mm SL); Quimperle (marine); 1939; Roulé.

Salmo labrax **Pallas, 1814**

Material listed below comprise *Salmo* specimens from the Black Sea basin without any further consideration on the taxonomic status of *S. labrax*. ZMH 10717; 1 (334.0 mm SL); Austria, Danube River, Vienna; 1856. ZMH 4223; 2 (125.0-141.9 mm SL); Turkey, Kuzey Anadolu mountains, 'Surmene-Trabzon'[Black Sea or stream between Trabzon (41°00'00"N - 39°43'00"E) and Sürmene (40°55'00"N - 40°07'00"E); 1967. MNHN A-7594; 1 (222.0 mm SL); Romania; Danube River; Fitzinger. ZISP 48330; 7 (5, 99.2-128.0 mm SL); Russia, Lake Mtszi, close to Lake Ritsa in Georgia; 1962. ZIPS 27005; 1 (x-ray only); Russia, Anapa; May 1902; Slastenenko.

Salmo letnica **(Karaman, 1924)**

Salmo letnica, endemic to Lake Ohrid (Albania and FYROM) is often divided in several distinct species and/or races (e.g., Stankovic, 1960; Kottelat, 1997). Trout from Lake Ohrid have been introduced to Lake Megali Prespa (Albania, FYROM, and Greece) (Crivelli *et al*., 1997). See ZMH 9182 - a previously uncatalogued lot holding one specimen of *Acantholingua ohridana* (Steindachner, 1892) (also endemic to Lake Ohrid), now ZMH 9183, and two *Salmo* species, looking like *S. letnica*. MHNG 2573.92; 3 (1, 248.2 mm SL); Albania, Lake Ohrid; May 1995; P. Klein. MNHN 1977-0262; 2 (228.0-270.0 mm SL); Albania, Lake Ohrid; 1929; Petit. ZMH 791; 2(140.1-203.7 mm SL); Macedonija, Lake Ohrid; Aug. 1958. ZISP 39456; 2 (368.0-372.0 mm SL); Lake Ohrid, Nov. 1969. ZMH 9182; 2 (246.0-270.0 mm SL); 'Presper-See Exk. Hamburg IV 1961' and [field label] 'Prespa-See 18.4.61' [= Lake (Megali?) Prespa; Apr. 1961; Excursion from Hamburg].

Salmo carpio **Linnaeus, 1758**

Salmo carpio is endemic to Lago di Garda in Italy and material listed below, except the neotype, comes from Lago di Garda. NRM 28000; 1 (138.1 mm SL); NEOTYPE; Italy, Istituto Sperimentale San Michele al Adige; Aug. 1996; M. Kottelat. NRM 41539; 4 (204.5-317.2 mm SL); Gargnano; Jun. 1998; B. Delling. ZISP 48207; 1 (276.0 mm SL); May 1966. ZISP 40513; 1 (219.0 mm SL); Vigillio; Dec. 1969. ZISP 40514; 1 (228.0 mm SL); Cassone; Jul. 1971.

Salmo peristericus **Karaman, 1938**

NRM 42538; 10 (9, 128.2-164.7 mm SL); Greece, Agios Germanos Stream (emptying in Lake Megali Prespa); Sep. 1998; A.J. Crivelli.

Salmo pelagonicus **Karaman, 1938**

NRM 44877; 1 (148.6 mm SL); Aljakmon River basin,

Tripotamos Stream near Tripotamos; Nov. 1999; C. Triantaphyllidis and S. Palm. Note: Species designation based on locality in accordance with Karakousis *et al*. (1991).

Salmo dentex **(Heckel, 1852)**

NRM 25000; 1 (271.0 mm SL); Syntype; 'Dalmatia', received from NMW, Wien. NRM 9631; 1 (230.0 mm SL); Italy, Venezia; Oct. 1856; O. Sandahl.

Salmo spp. **Mediterranean**

Spain. - MNHN 1920-0228; 1 (203.4 mm SL): Spain, Lake Sarrade 2052 m a. s. l., Lerida; Aug. 1920; Delamarre. MNHN 1920-0229; 1 (178.0 mm SL): Spain, Lake Sarrade; Delamarre.

France. - MNHN 0000-3644; 1 (261.0 mm SL); MNHN 0000-3645; 1 (219.0 mm SL); MNHN 0000-3646;1 (178.8 mm SL); MNHN 0000-3647; 1 (235.0 mm SL); Syntypes of *Salar Ausonii* Valenciennes *in* Cuvier and Valenciennes, 1848; Argens River basin, Soignes River, Draguignan; 1821; Chevalier. MNHN 0000-0002; 1 (147.2 mm SL); Syntype of *Salar Ausonii* Valenciennes *in* Cuvier and Valenciennes, 1848; Nice; Laurillard. MNHN 0000-3648; 1 (239.0 mm SL); Syntype of *Salar Ausonii* Valenciennes *in* Cuvier and Valenciennes, 1848; Mont Cenis [= Po River basin, Lake mont Cenis]; M. Pentland. MNHN A-7584; 2 (259.0-265.0 mm SL); Val d'Ajol [located close to water shed between Rhine River basin (Mosel River) and Rhône River basin (Ognon River)]; Turck. MNHN 1912-0164; 1 (145.8 mm SL); Thonon [= Thonon-les-Bains],(fish farm); Crettiez.

Italy. - MNHN A-7588; 1 (350.0 mm SL); Lago di Garda. MNHN 0000-3637; 1 (245.0 mm SL); Syntype of *Salar Ausonii* Valenciennes *in* Cuvier and Valenciennes, 1848; Po River basin, Lago Maggiore; M. Major. MNHN A-9702; 1 (326.0 mm SL); Syntype of *Salar Ausonii* Valenciennes *in* Cuvier and Valenciennes, 1848; Po River basin, Lago Maggiore; 1823; Savigny. MNHN 0000-3652; 1 (184.1 mm SL); MNHN 0000-3653; 1 (194.7 mm SL); MNHN 0000-3654; 1 (202.2 mm SL); Syntypes of *Salar Ausonii* Valenciennes *in* Cuvier and Valenciennes, 1848; 'Colfionto' [Probably Colfiorito in the Perugia province. Nearest water course is River Chienti (Bianco, pers. comm.)]; M. Canali.

Switzerland. - MHNG 52.86; 1 (207.4 mm SL); Canton du Tessin, Lac Majeur (Lago Maggiore).

Rhône River basin. - MNHN 1986-0939;1 (213.0 mm SL); France, Doubs River, 'Vaire' [= Vaire le Grand]; Jun. 1975; Vernaux. MNHN 1960-0370; 1 (238.0 mm SL); France, Les Usses Stream; Spillman. MNHN B-0719; 1

(214.0 mm SL); France, Plombières; Turck. MNHN 1960-0347; 1 (160.5 mm SL); France, Donzere-Mondragon. MHNG 2512.72; 1 (209.0 mm SL); Switzerland, Geneva, Rhône River, 'sous le Pont de Sous-Terre, au Quai du Seujet, à St. Jean'; Jul. 1990. P.J. Haymoz. MNHN 0000-2575; 1 (200.8 mm SL): Lac Leman; Major.

Former Yugoslavia. - MNHN A-7591; 1 (193.3 mm SL);

'Cattina, Yugoslavia' according to catalogue and 'Dalmatie' on label [= Cetina River in Dalmatia]. NRM 36425; 1 (198.0 mm SL); Croatia, 'Fiume' [= Rijeka] 'aus der Save'(Heckel and Kneer, 1858) [= Sava River], received from NMW, specimen studied for the redescription of *Salar Ausonii* by Heckel and Kner (1858) according to Smitt (1886).