

Comparative Studies of the Scales in Japanese Freshwater Fishes,
with Special Reference to Phylogeny and Evolution

(Continued from vol. iii, p. 208)

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[IV] Particular Lepidology of Freshwater Fishes

I. Suborder Isospondyli (Continued)

[4] Salmonidae

Scales of Salmonidae are longitudinally ellipsoid; angles are not so conspicuous; focus is situated near center; scales are primitive and simple cycloid having no grooves at all and with ridges only, which may be considered to be scales of Salmonidae type.

When observed more minutely, situation of the focus is various; some nearly central, some basal, or some apical; but it is not situated so far from center as in other families, and within the same species, situated in an almost fixed spot.

Generally young scales are of ellipsoid form with no angles, but as fishes grow older, angles are observed, especially apicolateral angles being somewhat distinct. Ridges are all circular; network formation may be observed in posterior part of lateral ridges, but this is limited within some species of Genus *Oncorhynchus*. Ridges run almost parallel with margin except in *Oncorhynchus*, in which outer ones disappear in the lateral margin and do not run perfect parallel with it.

There are various degrees in the degeneration of apical ridges, which is thought to be a mark when the phylogeny of Salmonidae is discussed, viz., it is believed that the further advanced the degeneration in the apical ridges is, the more evolved the species is, and that the more apical ridges are left behind, the more primitive the group is.

It is not limited to Salmonidae that Salmonids fish scales being so simple, young ones resemble one another so much that they are indistinguishable into genera only by observing young scales. Young scales are of primitive type with ridges all over them, but as they grow up, they gradually come to show the character of the genus or species, the details of which will be reserved for the description of each genus, and this gives us a good example to prove that Haeckel's biogenetic law is also true in lepidology.

There are many which have distinct winter zones or annual rings, and the age and life history of fishes was considered upon this by GILBERT (1912), to begin with, and by native and foreign scholars. In the spawning season, the phenomenon of the absorption of scales takes place, and it is a wonder that in some species they are so much absorbed as to become almost shapeless. It is the characteristic of Salmonids scales, which cannot be seen in another family of freshwater fishes, that the distinct spawning mark is seen in scales of fishes which survive spawning.

When Salmonidae is compared by scale character with a similar family, and their phylogenetic relation is considered, Osmeridae which has ridges all over scales is more primitive than Salmonidae; Salmonidae in which apical ridges are degenerated, and yet a fine network structure is developed in the posterior part of lateral ridges, is much more evolved; Coregonidae comes so close to Salmonidae that it is natural some systematists regard Coregoninae as a subfamily of Salmonidae. Plecoglossidae also comes close to Salmonidae; s. c. p. scales of *Plecoglossus* resemble those of *Oncorhynchus*, telling the close affinity between them; but c. b. s. scales are very different in structure

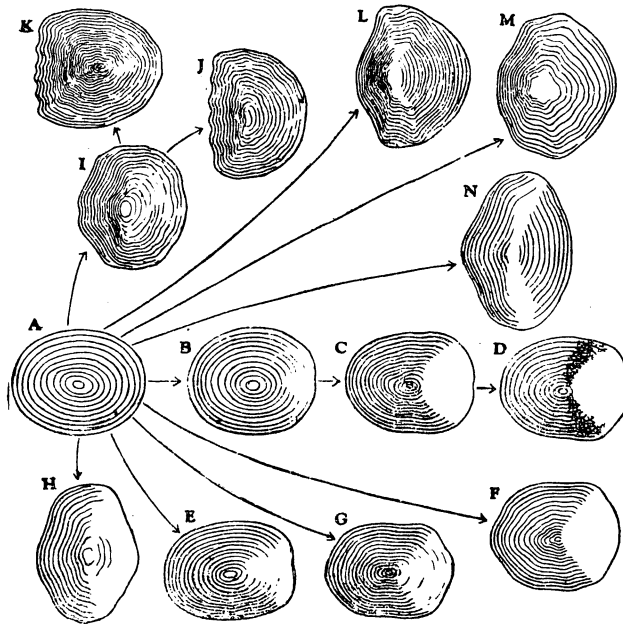
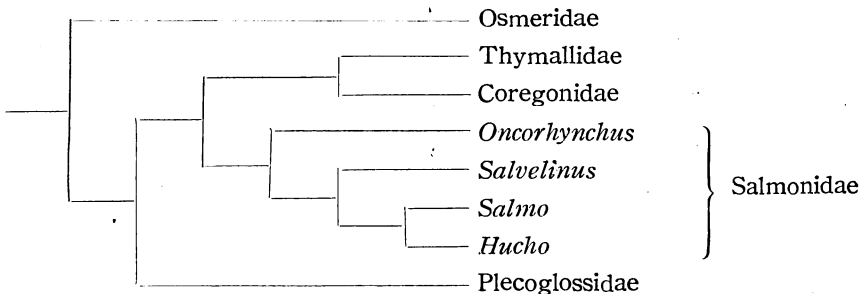


Fig. 19. Phylogenetical relation of salmonoid scales. A. Suggested ancestral salmonoid scale, B-D. *Oncorhynchus*, E. *Salvelinus*, F. *Salmo*, G. *Hucho*, H. *Plecoglossus*, I. *Coregonus*, J. *Brachymystax*, K. *Thymallus*, L. *Osmerus*, M. *Spirinchus*, N. *Hypomesus*.

from those of Salmonidae, and when compared with those of Coregonidae, they seem to be a little distinct in affinity. Then Thymallidae also comes close to this family, but it is much more primitive than Salmonidae, and as was stated already, *Thymallus* has its origin in *Brachymystax* of Coregonidae. These systematic relations will be illustrated as follows:

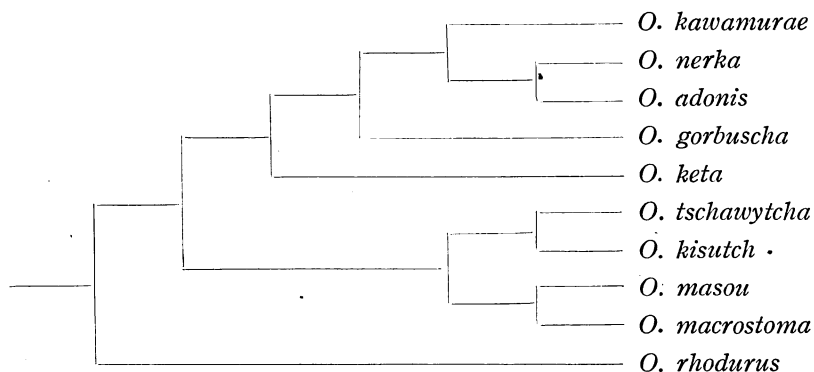


(1) Genus *Oncorhynchus*

Scales of *Oncorhynchus* are the simplest cycloid with a primitive structure, and though in adult scales the characteristic as a species is shown, every species shows such a similar structure in young scales that it cannot possibly be hoped to distinguish them.

When young scales are observed, it is known that all the present *Oncorhynchus* has a single line, and was separated through *Salvelinus*, *Hucho*, *Salmo* in Salmonidae comparatively in recent times. The early stage of ontogeny in these scales of Salmonidae shows the ancestral form which has ridges forming complete circles—in which apical ridges are not degenerated —, and thus Haeckel's law is considered to be applicable also to lepidology.

Then when the phylogenetic relation between species of Genus *Oncorhynchus* is imagined by scale character, *O. rhodurus*, to begin with, is a line which was separated earlier than any other line, and the rest, after the separation of *O. rhodurus*, were divided into 2 lines, of which the one is *nerka* line; and from this line, *O. keta* and *O. gorbuscha* were separated on the way, *O. kawamurae*, much later than they, and *O. adonis*, comparatively recently; and *O. kawamurae* has already come to make a species, but *O. adonis* is not considered to be so isolated. Next, the *kisutch* line is supposed to have been separated together with the *nerka* line; this line generated *O. tschawyscha* on one hand, and *O. masou*, on the other; and *masou* generated landlocked *O. macrostoma*, which should be considered to be about to 'make a variety. Now it was formerly disputed whether *rhodurus* (Amago) and *macrostoma* (Yamame) were of the same species or not, but when they are observed by scale character, it is out of question that they are different in line; OSHIMA (1930) and OHNO & ANDO (1931) already admitted the difference of their scale character. These relations will be shown with a genealogical tree as follows;



Discussion

(1) OSHIMA, after considering scale character, closely examined other morphological characters, and reaches the strained conclusion that *O. kawamurae* is "closest to *O. nerka* in morphological structures other than scale structure, and that it is not a landlocked form of *nerka*, though it resembles *rhodurus* in scale character, and it cannot be

identified with *rhodurus* because of the said morphological characters." As to the scale character, the author confirms OSHIMA's conclusion, but when scales of the 3 species of *nerka* — *adonis* — *kawamurae*, are compared with one another, apical ridges, passing through *adonis*, are most developed in *kawamurae*, giving the reason why *kawamurae* is more primitive than *adonis*. From this, the author, after putting together other morphological characters than scale character, thinks that though *kawamurae* has its origin in *nerka*, it was separated from *nerka* in the age much earlier than *adonis*, so that its scales preserve a primitive structure. As *kawamurae* is a landlocked form and the phenomenon of Neoteny is seen in it as in *adonis*, the author believes that it is not mistaken to think like that, but to solve this problem, there is nothing but to study from another point of view — e. g., cytological.

(2) The scale character of *O. gorbusha* resembles that of *nerka* or *keta* very much, and shows really that the former belongs to the same line as the latter; above all they resemble each other in the condition of network formation of ridges, and it resembles *nerka* in the intensity of the phenomenon of absorption, more than *keta*, and in this respect it differs a little from *keta*. In short, *gorbusha* represents a median type between *nerka* and *keta*, and no fundamental difference seems to be found in the scale character of these 3 species.

(3) Scales of *O. keta* closely resemble those of *nerka*, but judging from the fact that the number of focal ridges forming perfect circles is small, and from the outline of scales, the author agrees with systematists who regard it as entirely another species related to *gorbusha* as well as to *nerka*. It shows its primitive character and similarity to Coregonidae that scales of *keta* is sometimes broader than long and that scales in the early stage of their development are all broader than long. It is worth noticing that in scales of *keta*, absorption does not take place even in the spawning season, and consequently no spawning mark is formed.

(4) The scale character of *O. kisutsch* closely resembles that of *tschawytcha* in the position of the focus and the inconspicuousness of the network ridges, but both are different in the following point, viz., it is the characteristic of this species that upper and lower lateral margins are swelled out in posterior part. In short, when observed by scale character, the species is together with *tschawytcha*, considered to be a line separated earlier than *nerka*, *gorbusha*, *keta*, etc.

(5) The principal scale characters of *O. tschawytcha* are as follows: (1) focus is comparatively apical, and accordingly apical area is small, (2) network formation of ridges is indistinct, (3) spawning mark is sometimes observed, etc. In short, this species resembles *kisutsch* and is in a close affinity with it. It is different from the *nerka* line also in other morphological points, and seems to be a line separated from *kisutsch*; it may be in a distant relationship with the *nerka* line.

(6) Scales of *O. masou* are almost longitudinally ellipsoid, length being $\times 1-1.6$ the breadth; lateral margin is swelled out, apicolateral angles being sometimes observed. Focus is inclined a little from center toward base, and situated anterior $1/2.2-2.5$ of

scales in fish from River Yodo, 25.3cm. Focal ridges are comparatively dense, 4-9 of which form complete circles; network formation appears at end of the second year, and increases in number as fish grows up, but it is comparatively small in breadth and does not reach margin. In young scales, apical ridges are finely formed, but in adult ones, there is none of them, and only a few ridges are seen to run into the apical area. Absorption during the spawning season is intense in apical margin, and pressing against the focus, disappears almost in a straight line, but in basal and lateral margins it disappears almost in parallel with them. Annual zones or winter bands are observed in ridges.

Scales of *O. macrostoma* are just the same as those of *masou* mentioned above, but in s. c. p. scales, apicolateral angles are extremely protruded, and number of focal ridges forming complete circles is great. Position of focus is especially basal in s. c. p. scales. Scales of 'Saramaomasu' are just the same as those of 'Yamame' found in Japan.

Macrostoma is comparatively small-sized in body, and phenomenon of Neoteny takes place in it, so its scales often show character of a young fish and many complete apical ridges are found. When this grows up to be a large-sized 'Yamame', it also stops apical ridge formation as *masou* does. The author has not observed a network structure in 'Yamame' or 'Saramaomasu' as yet, but as it is a landlocked form, this difference need not be regarded as of importance. According to OSHIMA & ANDO, however, *macrostoma* is said to form a slight network after the 4th year. As this fish lives on after spawning, spawning mark is often formed on surface of scales.

As will be mentioned later, *macrostoma* and *rhodurus* are different in line, and it is worthy of special mention that in considering the difference between them, scale character is of great use.

(7) Few fishes have been discussed so much on the difference of species as *O. rhodurus* and *macrostoma*, while there are few examples which differ so definitely in scale character as these 2 species once the scale character of both are known, they can be identified at first sight through a microscope, the author believes. This is what was formerly remarked by OHNO & ANDO (1931) and by OSHIMA M. (1930, 1940), and the author hereupon confirms their view, which is true and worthy of special mention. Both fishes, in spite of their likeness in external form and coloration, when considered by scale character, are so distant in affinity that they must rather be said to belong to different lines. Now important points of difference between *rhodurus* ('Amago') and *macrostoma* ('Yamame') will be picked out as follows:- In scales of *rhodurus* (1) focus is remarkably basal, (2) apical ridge formation does not stop even in adult scales.

Rhodurus is much more primitive than *macrostoma*; but it should be noticed here that cannot be distinguished from each other in young scales, which is a common phenomenon not only to these fishes but to all Salmonids fishes.

Now when the line of *rhodurus* is considered, it is supposed to be a line separated from the *nerka* line earlier than *macrostoma* and *masou*, viz. the *kisutsch* line.

An interesting phenomenon, however, is that according to OSHIMA M. (1940), in

the hybrid between *macrostoma* and *rhodurus*, the scale character of both is closer to *rhodurus* than to that of their medium type, and OSHIMA describes that the F_1 scale character shows a complete *rhodurus* type, and that the *rhodurus* type is dominant over the *macrostoma* type, but when the author observes his photo (Fish, p. 254, fig. 289), he can not but regard it as the medium type, for though apical ridges exist, they are broken as well as small in number. When the author, thinking of the fact that the intergeneric hybrid of *Carassius* and *Cyprinus* shows the medium type of both, observes this photo, it appears to be the medium type. As a hybrid is generated even between *Carassius* and *Cyprinus* which belong to different genera, it is no wonder that a hybrid should be generated between these fishes, though they are different in line, and this does not always offer the reason why both fishes are considered to be close in affinity, the author believes.

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(2) Genus *Salvelinus*

The scale character of *Salvelinus* closely resembles that of *Oncorhynchus*, scales being primitive cycloid ones. In Salmonidae they resembles those of *Hucho* or *Salmo*, which will be mentioned later, more closely than those of *Oncorhynchus*; and it can be clearly said by scale character that the fishes of these 4 genera are close in affinity with one another.

The principal points where *Salvelinus* differs from *Oncorhynchus* are as follows (in c. b. s. scales): (1) No focus is situated forward from the geometrical center of scales. (2) No fine network structure is seen in ridges. (3) Ridges are comparatively thick and widely spaced. (4) Number of regenerated scales is so great, probably in correlation with its living condition, that it is sometimes difficult to find out ordinary ones.

(6) *S. fontinalis* is not a native species of Japan, but it does not differ much from the species belonging to *Salvelinus* found in Japan and its neighbourhood, and no doubt it is of the same line as the species found in this country. This is understood from the fact that the same species of *Oncorhynchus* is commonly distributed both in Japan and along the west coast of North America.

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(3) Genus *Salmo*

Scales of *Salmo* so closely resemble those of *Salvelinus* that there is almost no need of making a distinction between these genera. Scales of this genus resemble those of *Salvelinus* as follows: (1) No network is observed in scales. (2) Ridges run almost parallel with margin. The species can be considered according to the degree of degeneration in the apical ridges, the author believes, but having no specimen from foreign lands, and there being introduced one found in this country, he will not touch this point.

Discussion

Salmo shasta is a single *Salmo* fish in this country introduced from U. S. A., and its principal characteristic is that the degeneration in the apical ridges of scales is imperfect. And then a structure like growth lines is observed in the apical area, being mistaken for apical ridges at first sight. When the BAHATIA's figure (1931) of *Salmo irideus* is observed, in *irideus*, focus is rather apical, and yet important apical area is covered with epidermis, and besides, no detailed description being made, it cannot be said for certain, but it is similar to *shasta* on the whole. Accordingly the author can not declare whether what is stated above is the character of the genus.

When imagined through the scale character of the single species, *shasta*, it is in a close affinity with *Oncorhynchus* and *Salvelinus*, or *Hucho*, especially being so similar to *Salvelinus* that may be said to be of the same genus. The difference between this species and *Salvelinus* is that in c. b. s. scales of the former, the focus is basal from the center. This is considered to be separated from *Salvelinus*.

According to the excellent photos seen in the papers by JARVI & MANZIES (1936), and by HUTTON (1909)—though with no description—in *Salmo trutta* and *S. t.* var. *fario*, 5 apical ridges are seen and most conspicuous annual zones observed. In *Salmo salar*, no apical ridges are observable at all, and no fine network ridges are observed in any scale.

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(4) Genus *Hucho*

In this genus, a specimen of one species from this country and another from a foreign land were used, and though enough consideration cannot be given with these few materials, scales of *Hucho* resemble those of *Salmo* and also of *Oncorhynchus*.

(1) Ridges run almost parallel with margin, (2) No network ridges are seen. These two characteristics are just the same as those of *Salmo* or *Salvelinus*, and some of *Oncorhynchus*. It is a species separated earlier from *Oncorhynchus* and later from *Salvelinus* and *Salmo*. Annual zones are distinctly seen, but spawning mark is not observed as yet.

Discussion

Scales of *H. taimen* are distinguished from those of *H. perryi* by the situation of the focus and the number of the focal ridges forming complete circles.

A¹ Focus apical, several of focal ridges form complete circles *H. perryi*.

A² Focus basal, more than 10 of focal ridges form complete circles.....*H. taimen*.

Judging from this fact, 2 species are fairly distinct species in scale character and never to be mixed together.

(5) Plecoglossidae

This family contains only one genus, one species, i. e., *Plecoglossus altivelis*. Scales of this fish are broad; apical ridges run transverse; basal and lateral ridges also show a more or less similar tendency. Except focal apical ridges, there is no apical ridges at all, and in this point they are distinguished from scales of Salmonidae, but among s. c. p. scales there remain Salmonidae type scales. No network formation is seen in ridges, but *Plecoglossus altivelis* in second year shows a conspicuous annual ring a spawning mark like structure (NOMURA, 1921; KOBAYASI, 1938). It resembles Salmonidae in scale character, but entirely differs from it, and also from Osmeridae and Thymallidae, showing the structure by which it is sufficiently qualified as an independent family. As above stated, however, s. c. p. scales show a certain degree of affinity with Salmonidae, and also show some similarity to Thymallidae and Osmeridae. In short, as above stated in the introduction to Salmonidae, it was separated from the line of Salmonidae or Osmeridae, or that of Thymallidae or Coregonidae, etc. and became independent almost in the same age, and did not make so much development keeping independence as one species and one genus, and yet the fish itself seems to have been considerably evolved, for the degeneration in the apical ridges is advanced to no small degree.

Plecoglossus is in such a close relation with Salmonidae that it was formerly considered, as *Coregonus* was to be Coregoninae, to be Plecoglossinae, a subfamily can be emphasized to be much more appropriate, who regarded it as an independent family, Plecoglossidae.

As the author pointed out (1936, '38), scales of *Plecoglossus altivelis* show similarity to those of *Aplocheilichthys lalipes*, and this is not altogether phylogenetically meaningless, though there seems to be no direct relation between them.

Discussion

It was already described that though *Plecoglossus* resembles Salmonidae in scale character, it is a species separated early from the latter and developed independently.

It was often studied that scales of *Plecoglossus* strikingly reflect the influence of environment. When the body length measures ca 6 cm and the animal food is changed into the vegetable, the arrangement of ridges becomes widely spaced, making one ring here, and when the fish grows to be an adult one, here it makes another indistinct ring, which seems to be caused by the physiological change of its coming to sexual maturity. Of these two rings, YASUDA (1941) regards the type in which ridges forming the outer ring do not run parallel, as A type, and the type in which they run parallel, as B type.

Influenced by floods and feeding, however, more rings are sometimes added to these, so that JORDAN & MCGREGOR (1925) mistook these for annual rings and explained that *Plecoglossus* lived as many as 3 or 4 years. Such rings may be called "Pseudo-annual rings."

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(6) Thymallidae

No species of this family is found in this country; one species, *Thymallus jaluensis*, which was obtained as a material for comparative study with Salmonidae and its related family, was observed. It is an interesting fact that scales of *Thymallus* resemble those of *Brachymystax* in Coregonidae, and yet it has a stronger tendency of degeneration in the apical ridges than *Brachymystax*, but it is doubtlessly known also by scale character that it has its origin in the latter.

Discussion

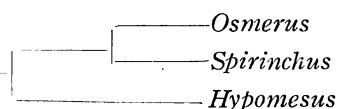
Scales of *Thymallus jaluensis* are at first sight cycloid scales which are different in form from Salmonids scales, but they fundamentally resemble the latter, in that they are primitive scales with no grooves at all and with ridges only. It was already stated that this species has, in scale character, its origin in *Brachymystax* in Coregonidae; as to the relation with other families, it is imagined to be more distant from Salmonidae than from Plecoglossidae and nearer to Osmeridae than to Plecoglossidae.

It was necessary to observe this exotic species is particular in order to prove that scales of this species are nearer to those of Osmeridae than to those of Salmonidae or Plecoglossidae.

(7) Osmeridae

Though scales of the fishes belonging to this family have a certain degree of similarity to those of Salmonidae, Plecoglossidae or Tymallidae, they are considerably different and distinguishable from these as they have scales whose focus is so basal that they have an apical area larger than any other area. The focus is situated anterior $\frac{1}{4}$ of scales, just on the level with upper and lower basilateral angles; but scales are cycloid scales with no grooves at all, and having a primitive structure; they resemble those of the above mentioned families, of which they seem to be closest to those of Tymallidae.

As to the phylogenetical relation between the 3 genera in Osmeridae, *Osmerus* and *Spirinchus* are so closely related that they are supposed to be of the same genus, but *Hypomesus* seems to be considerably distant from these.



While Plecoglossidae is a simple family with only one genus, one species, Osmeridae has developed into 3 genera in this country alone, and it is known that Genus *Mallotus* is found in the vicinity of Japan. Scales of *Mallotus* could not be obtained after all. It is noticeable that in spite of such development, when seen from scale character, they are the same in the fundamental structure, having what is called the Osmeridae type scales with a very basal focus.

(1) Genus *Osmerus*

This is a possessor of primitive cycloid scales with no grooves at all, and with ridges in all the areas; one genus, one species is found in Japan. When seen from scale character, *Osmerus* most closely resembles *Spirinchus* mentioned below, and shows similarity also to *Hypomesus*. The most important scale character of *Osmerus* is, like that of *Spirinchus*, that the focus is very basal, and in this respect it is distinguishable from that of Tymallidae.

Discussion

The scale character of *O. dentex* most closely resembles that of *Spirinchus lanceolata* and is deeply related to it. And Osmeridae, considered as a whole also shows more similarity to *Spirinchus* than to *Hypomesus*. When the scale character of *Osmerus* is compared with that of *Spirinchus*, it shows such similarity that the 2 may be regarded as one and the same genus. It resembles Tymallidae to a certain degree, but the position of the focus is quite different; and it also resembles Plecoglossidae in that focal and apical ridges run transverse, but differs from it in that it has great many ridges forming complete circles.

(2) Genus *Spirinchus*

The scales closely resemble those of *Osmerus*, being just the same in principle, which shows their close affinity. They show a certain degree of similarity to those of *Hypomesus*, but the degree is much weaker than to those of *Osmerus*.

Discussion

Scales of *O. lanceolatus* so closely resemble those of *Osmerus dentex*, that in scale character, it is hardly necessary to divide them into genera, but it differs from *Osmerus* in that apical ridges in the early stage do not make transverse ridges, but form complete circles. When s. c. p. scales in both are compared, they are so similar as if they were of the same species. According to ASAYAMA (1948), this species also makes the spawning mark like Salmonidae or Plecoglossidae, showing in this respect that it is not so distant from Salmonidae.

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(3) Genus *Hypomesus*

In Japan one genus, one species seems to be found. It has the so-called *Osmerus* type scales like the preceding 2 genera, but when compared with *Osmerus* and *Spirinchus*, it shows its proper characteristic. The affinity between them already considered.

Discussion

The principal characteristic of scales *H. olidus* is that basal and lateral ridges are hardly connected with apical ridges, but are curved facing each other, while apical ridges run more or less transverse. And though as a whole, the scales resemble those of *Osmerus* or *Spirinchus*, they are more or less different in outline, being greater in breadth. The position of the focus being very basal, it closely resembles that of *Osmerus*.

Accordingly *Hypomesus*, though it belongs to the same line as *Osmerus* or *Spirinchus*, is considered to be a single species which had been separated from this line earlier than *Osmerus* and *Spirinchus* were separated from it. There are systematists who admit a different species, *Hypomesus japonicus*, but the author finds it difficult, in scale character, to regard it as a species.

The author was once surprised to find the close affinity between this species and *Spirinchus* by observing that one of the scales of this fish found in Lake Unagi-ike, South Kyūsyū, strikingly resembled that of *Spirinchus*. Thus having a distinct character as Genus *Hypomesus*, it still keeps an evidence which shows its close affinity with *Osmerus* or *Spirinchus*.

FUZITA (1926), comparing scales of the fish found in Lake Suwa with those found in Lake Kasumigaura, discusses that both differ in the number of ridges and position of the focus, and it seems to be true that in scales of fishes found in a mild climate, basal ridges are smaller in number, and the focus is more basal.

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