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PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES
FOURTH SERIES

Vol. XXXIII, No. 6, pp. 91-112; 10 figs.; 1 table

January 31, 1966

THE LIMITS OF THE FISH FAMILY
SERRANIDAE, WITH NOTES ON OTHER
LOWER PERCOIDS

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A satisfactory phylogenetic classification of the families of percoid fishes has yet to be worked out. One of the many problems is to determine what characters they inherited from the proto percoid stock. The serranid fishes lie near the heart of this problem. There has been a tendency to place the serranids at the base of the percoids and all basal percoids in the serranids. As a result, Serranidae can only be defined, to misquote slightly a fellow student of the group, as containing all of those percoid fishes that do not belong in some other family. More briefly, it forms a wastebasket for lower percoids.

Here, the family Serranidae is restricted to the subfamilies Serraninae, Epinephelinae, and Anthiinae (except *Callanthias*), of Jordan and Eigenmann (1890). Such limitation greatly improves the coherence and definability of the family. Thus shorn of accretions, Serranidae, together with its specialized offshoot, Grammistidae, comprises, I think, a group of related fishes somewhat specialized in a number of respects.

A major problem, of course, is what to do with the excluded accretions. Some of these, e.g., *Centrogenys* and *Ostracoberyx*, are made up of poorly known fishes that can be at best dubiously allocated. One excluded group, however, contains such well known forms as *Roccus* and *Lateolabrax*. The osteology and relationships of this group, here united under Percichthyidae, will be considered at some length. The importance of the group lies not only in the fame of some of its members but also in the fact that they seem to be among the most generalized of percoids.

MATERIALS AND ACKNOWLEDGMENTS

The opercular spines of serranids and other lower percoids were checked on a rather large number of specimens in the collections of the University of Hawaii, the Stanford Natural History Museum, and the California Academy of Sciences. For courtesies extended at the latter two institutions I wish to thank Drs. G. S. Myers and W. C. Freihofer at Stanford and Mr. W. I. Follett and Mrs. Lillian Dempster at the California Academy. Specimens of the following species have been stained in alizarin and more or less completely skeletonized: from the University of Hawaii collections—*Epinephelus quernus*, *Cephalopholis urodelus*, *Pteranthias longimanus*, and *Caesioperca thompsoni* (all Serranidae), *Apogon snyderi*, *Paramia quinquelineata*, and *Gymnapogon gracilicauda* (Apogonidae); from the U. S. Fish and Wildlife Service—*Howella* sp. (usually placed in the Apogonidae); from the University of Michigan Museum of Zoology—*Centropomus viridis* (Centropomidae); from the Stanford Natural History Museum—*Roccus saxatilis* (Percichthyidae) and *Archoplites interruptus* (Centrarchidae); and from the California Academy of Sciences—*Diplectrum pacificum* (Serranidae), *Percichthys trucha*, *P. melanops*, and *Percilia gillissi* (Percichthyidae). For these specimens I wish to thank Drs. D. W. Strasburg (U. S. Fish and Wildlife Service), R. M. Bailey (University of Michigan), W. C. Freihofer (Stanford), and Mrs. Lillian Dempster and Mr. W. I. Follett (California Academy). I am also indebted to the last named for the photographs of the opercles of *Paralabrax* (fig. 1). Finally I wish to thank W. C. Freihofer, C. L. Smith, and W. I. Follett for advice regarding various aspects of the manuscript.

What will have to pass for drawings were made from wet specimens. As is well known, cartilaginous and membranous areas shrink considerably when such specimens are dried.

DEFINITION OF THE FAMILY SERRANIDAE

The family Serranidae (together with Grammistidae) as here restricted is based on a number of features. One of these—the presence of a (third) lower opercular spine (fig. 1)—appears to be almost unique among percoids and, as its presence is usually though not always verifiable by superficial examination, will be dealt with first.

In the Serranidae and Grammistidae there is, below the main opercular spine and separated from it, a flat opercular point that extends out over the distal end of the subopercle (fig. 3a). (In the serranids and grammistids there is usually, perhaps always, a flat opercular point above the main opercular spine as well.)

One or two opercular spines are quite frequent among percoid fishes. When one is present, it projects from the posterior border of the opercle about at the level of the hyomandibular–opercular articulation. A ridge generally runs along

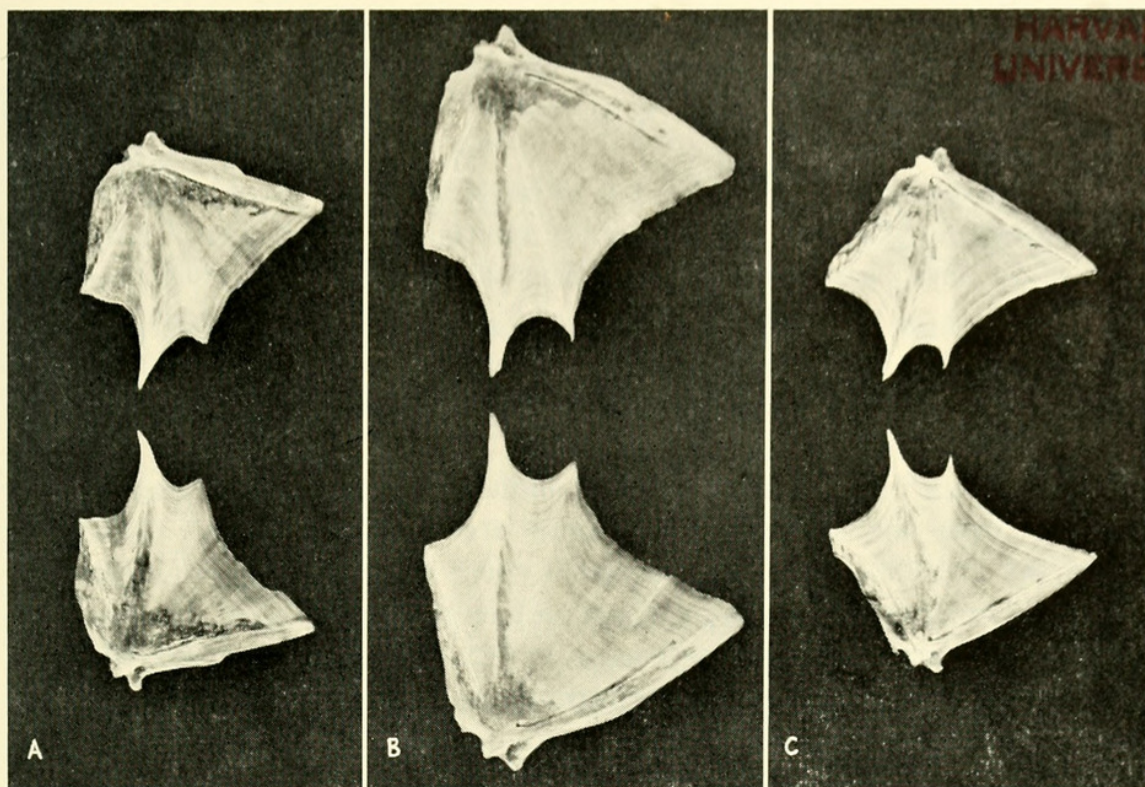


FIGURE 1. Opercles, external view, right above and left below. a. *Paralabrax maculatofasciatus*. b. *P. nebulifer*. c. *P. clathratus*.

the inner surface of the opercle between the spine and the hyomandibular articulation; not only does this add structural support to the spine, but its upper face provides a surface of attachment for the levator operculi muscle.

Such other spines as may be present on the opercular border appear to be supplementary. The usual secondary spine, *e.g.*, in the Mullidae, is one directed upward and backward toward the upper limit of the gill opening; it corresponds to the uppermost opercular point of the Serranidae. A supplementary spine on the opercle below the main one occurs among percoids, to my knowledge, only in the Serranidae and Grammistidae, and in *Niphon*. (*Niphon*, see below, differs immediately from the Serranidae as recognized here in the presence of a serrated preorbital.) Sometimes, as in the centrarchid *Archoplites* or the apogonidlike *Howella*, the opercle splays out posteriorly into a whole series of small points, but these are all immediately adjacent to one another.

The use of any single, minor character as a marker for a taxon is, of course, a dangerous procedure. In the present instance the danger seems to lie less in creating an artificial assemblage, for the fishes considered here as the serranid group have always been united on other grounds, than in the possible exclusion of fishes which properly belong in the group but which have secondarily lost the usual serranid opercular armature. Boulenger (1895, p. 271), for example, states in the account of his expanded genus *Serranus*: "Opercle with one, two

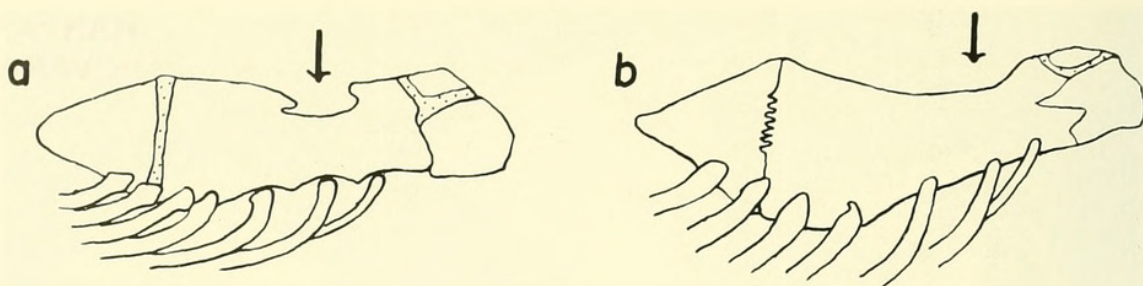
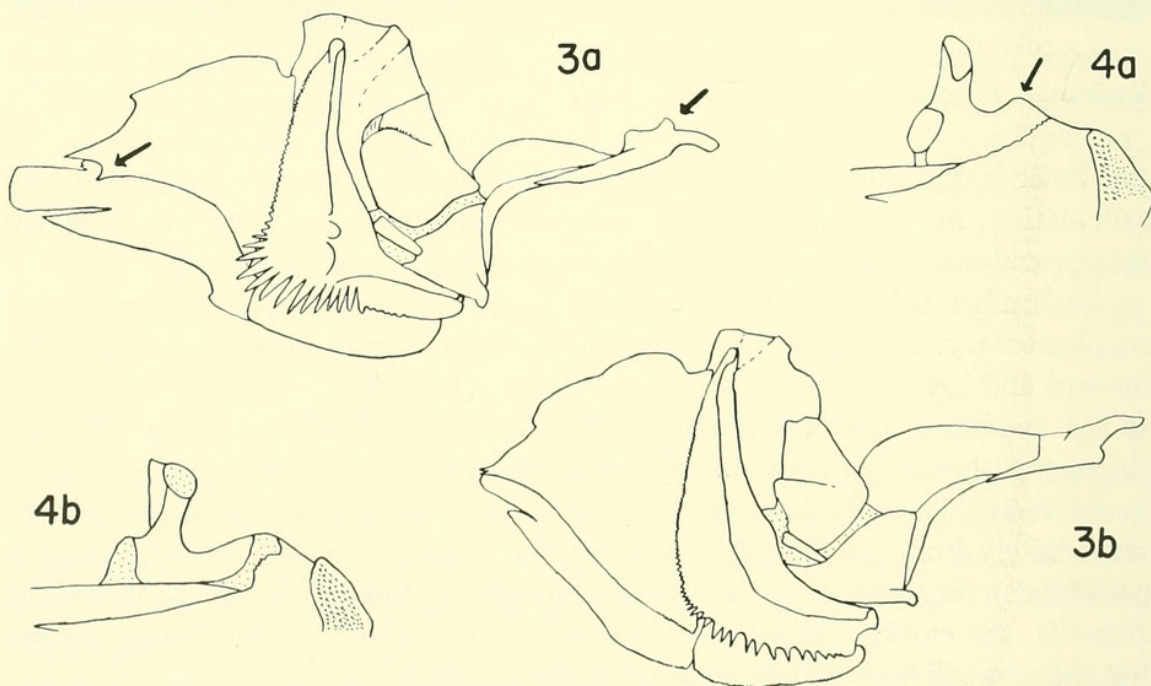


FIGURE 2. Right half of hyoid arch (interhyal not shown) with upper portions of branchiostegal rays, external view. a. *Percichthys trucha*. b. *Diplectrum pacificum*. Dotted areas indicate cartilage. Arrows point to excavated area in a, and to the same region in b.

of three spines." In his description of individual species he frequently says that the upper and lower opercular spines are "small or absent"; indeed, he (1895, pp. 278–280) makes this statement about all three species of *Paralabrax* illustrated in figure 1. Though the distal portion of the bony opercle is sometimes so flimsy that no lower point can be seen or felt, in all instances observed by me one appears with alizarin staining or careful maceration (figs. 1 and 3; see also



FIGURES 3 and 4. Fig. 3. Suspensoria and opercular bones, right side, external view. a. *Diplectrum pacificum*. b. *Percichthys trucha*. Dotted areas represent membrane. On Fig. 3a the left hand arrow points to the lower opercular spine of serranids, the right arrow to the anterior articular facet of the palatine. Fig. 4. Left side of the anterior portion of the cranium, from below. a. *Diplectrum pacificum*. b. *Percichthys trucha*. Dotted areas posterior to the vomerine teeth in 4b represent cartilage (I can find no cartilage in this portion of the cranium of *Diplectrum*). The arrow in 4a points to the anterior lateral ethmoid facet for articulation with the palatine.

Katayama, 1959, p. 115, figs. 6-9 and Gosline, 1960, pp. 32-33, fig. 5). Dr. W. J. Courtenay has, however, clearly demonstrated that the third (lower) opercular spine is consistently absent in a new species of *Rypticus* he will shortly describe.

Using this lower opercular spine as a touchstone, it is possible to exclude from the Serranidae-Grammistidae certain fishes generally included there. Thus the subfamilies of Serranidae recognized by Katayama (1960, pp. 3-5) in his revision of Japanese forms would be allotted as follows:

<i>Included</i>	<i>Excluded</i>
Nipponinae	Acropomatinae
Diploprioninae	Doderleiniinae
Grammistinae	Malakichthyinae
Epinephelinae	Maccullochellinae
Giganthiinae	Polyprioninae
Liopropomatinae	Ostracoberycinae
Serraninae	Callanthiinae
Anthiinae	<i>Symphysanodon</i> (which is not allocated to a subfamily by Katayama)

Of Katayama's subfamilies with a (third) lower opercular spine, only Nipponinae seems, on the basis of a host of other osteological characters described by Katayama (1959), not to belong there. Its systematic allocation will be discussed below.

In addition to Katayama's subfamilies, a number of other groups, sometimes placed in Serranidae, are here excluded. These include Theraponinae and Pseudochromidinae, recognized as serranid subfamilies by Norman (1957); Centrogenysinae of Weber and de Beaufort (1931, p. 86); and Priacanthinae and Latinae of Boulenger (1895). On the other hand Pinguilabrinae of McCully (1961) should apparently be included, though nothing is known about its osteology.

A diagnosis of the SERRANID-GRAMMISTID GROUP as here restricted, drawn largely from the literature but partly from the subsequent portion of this paper, may be written as follows:

Opercle with a spine or flat point below and separated from the main opercular spine (as well as one above). Preorbital (lacrimal) without serrations. Adults without a single, greatly enlarged preopercular spine. Subocular shelf present. Metapterygoid lamina present (Katayama, 1959). Supraoccipital crest with a low flange extending out along either side of it (fig. 9). Baudelot's ligament (fig. 5) small or lacking, so far as known, the lateral wall of the basioccipital forming a surface of attachment for a portion of the body musculature. Parietal crests, if present, not continued forward onto frontals; body musculature extending forward on top of head about to the level of the front

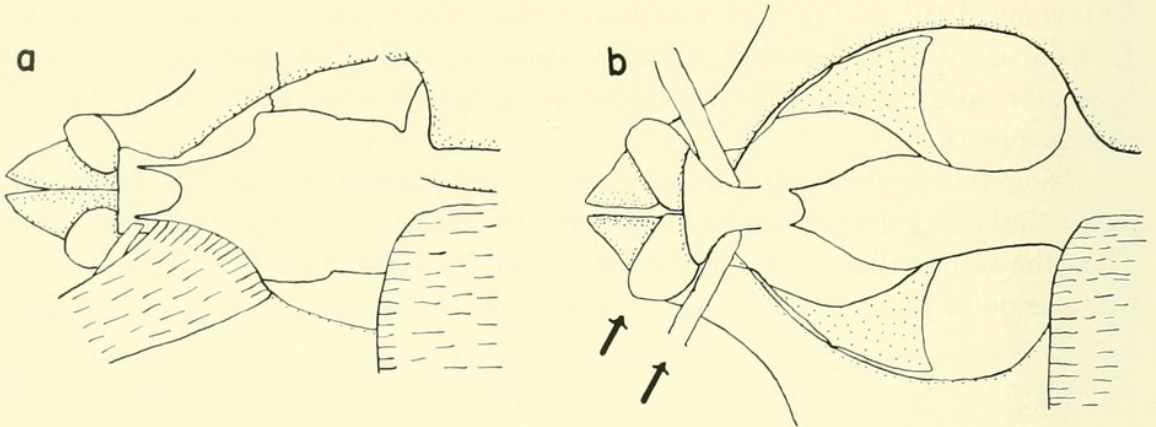


FIGURE 5. Rear of cranium, from below, head of fish to the right. a. *Diplectrum pacificum*. b. *Percichthys trucha*. Evenly dotted areas represent membrane, dashed areas musculature (which has been removed from the right side of the fishes' skulls). The left hand arrow points to the exoccipital condyle for articulation with the first vertebra; the right arrow to Baudelot's ligament (which is shown only on the left side of the fish's skull in 5a).

of the supraoccipital. Upper border of ceratohyal distinctly concave (Katayama, 1959); branchiostegal rays 7. Lateralis accessorius nerve, if present, showing pattern 9 of Freihofer (1963). One and a half or two actinosts borne on the coracoid. Postpelvic process relatively small (Katayama, 1959); pelvic fin with a spine and five soft rays, without a scaly axillary process. Caudal skeleton with autogenous hypurals, and a single uroneural (fig. 10); the caudal fin either rounded or lunate, rarely forked (bilobed). Scales belonging to types II, III, and IV of McCully (1961). Fishes hermaphroditic, though the two sexes usually do not develop synchronously (Smith, 1965).

The serranid-grammistid lineage seems to be represented by three main groupings, represented by the old subfamily categories Serraninae, Anthiinae, and Epinephelinae (*cf.* Jordan and Eigenmann, 1890; Smith, 1965). "Serraninae" appears to be made up mostly of small, large-scaled, functionally hermaphroditic fishes; "Anthiinae" of deeper-water, often reddish or yellowish forms; and "Epinephelinae" of small-scaled, large-mouthed, predaceous forms. The last group can also be characterized by an increased fleshiness of its members, *e.g.*, in the nape region where the number of predorsal bones is reduced (Katayama, 1959), which reaches its epitome in the Grammistidae (Gosline, 1960). This last family contains a series of specialized offshoots of the Epinephelinae that hold in common the following characters by which they may be separated from the Serranidae (Gosline, 1960):

GRAMMISTIDAE. Nasal rosette expanded dorsoventrally (Gosline, 1960, fig. 2b), to an extent that appears highly exceptional if not unique among percoids. Opercle joined to the skull above by a membrane for its full length. Upper portion of preopercular border usually with one or a few spines. Inner pelvic ray attached to the abdomen by a membrane.

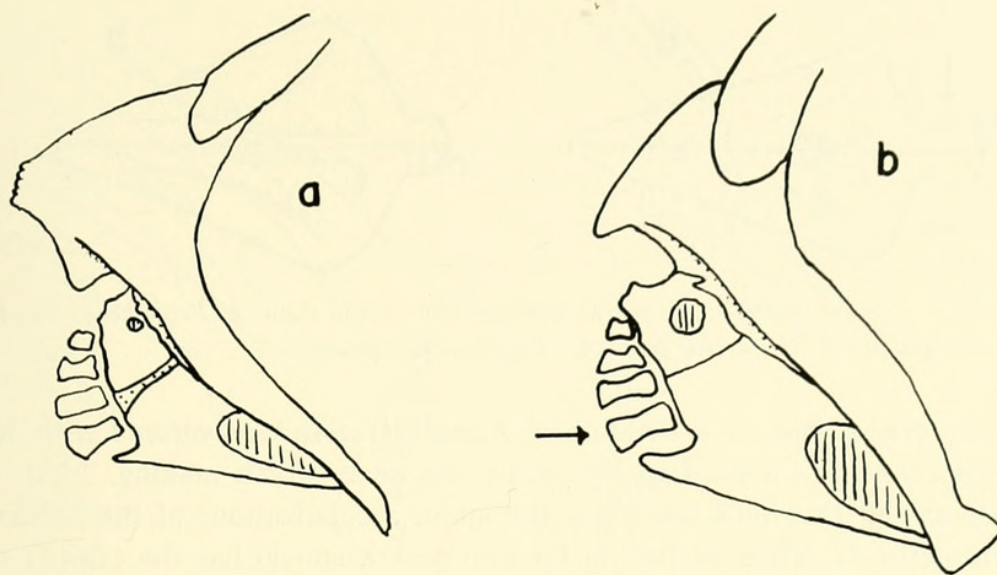


FIGURE 6. Lower portion of the pectoral girdle, right side, external view. a. *Percichthys trucha*. b. *Diplectrum pacificum*. The dashed areas represent open spaces, the dotted area between the scapula and the coracoid in 6a represents cartilage. The arrow points to the lowermost actinost.

Some of the grammistids, e.g., *Pseudogramma*, have an interrupted lateral line. Others, e.g., *Rypticus*, have one anal spine and only three dorsal spines. With the grammistids removed, three anal spines and a continuous and complete lateral line can, I believe, be added to the list of characters held in common by all members of the Serranidae.

GROUPS HERE EXCLUDED FROM SERRANIDAE

The serious problem remains of what to do with the groups usually placed in Serranidae but here excluded from that family. With the exception of the percichthyids, which will be dealt with in some detail below, I have made no thorough study of these, and the suggestions that follow as to their allocation are purely tentative.

Therapon and its relatives are included in the Serranidae by Regan (1913) and Norman (1957), but no intensive study of their systematic position seems ever to have been made. Fraser-Brunner (1945) and Freihofer (1963, p. 147) have pointed out similarities with the Scorpidae.

Callanthias, to which *Grammatonotus* seems closely related (Gilbert, 1905), has generally been placed in the Serranidae, but Katayama (1959) has pointed out its many distinctive characters, and Böhlke (1960, p. 5) has suggested a possible affinity with the pseudochromid-plesiopid-acanthoclinid group of families. This area of percoid classification has generally been treated as a sort of trailing appendage to the family Serranidae (e.g., Regan, 1913; Gosline, 1960). Much remains to be done with this series of families. However, on the

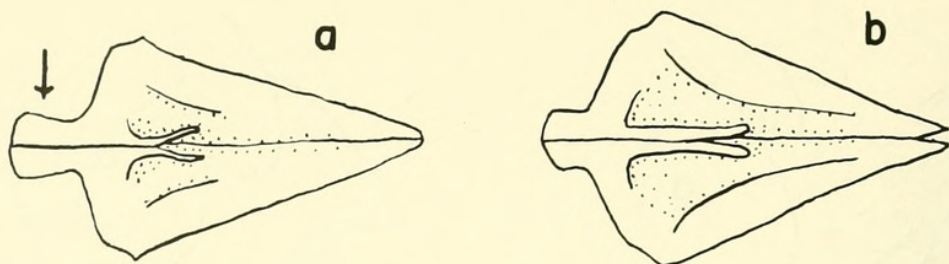


FIGURE 7. Pelvic girdle, from below, head of fish to the right. a. *Percichthys trucha*. b. *Diplectrum pacificum*. The arrow points to the postpelvic process.

basis of a comparison of a skeleton of *Pseudochromis tapeinosoma* with Katayama's account of *Callanthias*, two comments seem worth making. First, both *Callanthias* and *Pseudochromis* lack the major specializations of the Serranidae (as here defined). Thus, neither of the two genera named has the (third) lower opercular spine; *Pseudochromis* has Baudelot's ligament well developed but no body musculature attaching to the basioccipital; there is no metapterygoid lamina (Katayama, 1959); the postpelvic process is short; and some of the dorsal and anal pterygiophores have three sections in *Pseudochromis*. It seems impossible therefore to treat at least *Callanthias* and *Pseudochromis* as direct serranid derivatives. Second, if *Callanthias* and *Pseudochromis* are any criteria, the fishes in this whole general area are quite diverse (at least by percoid

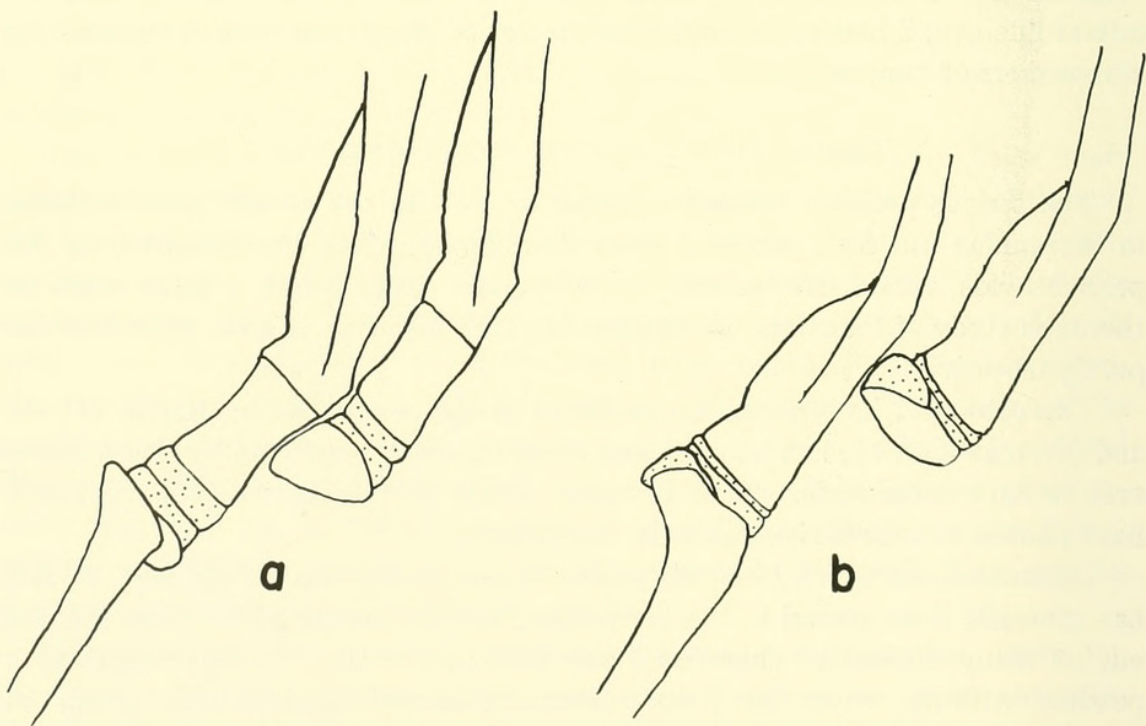
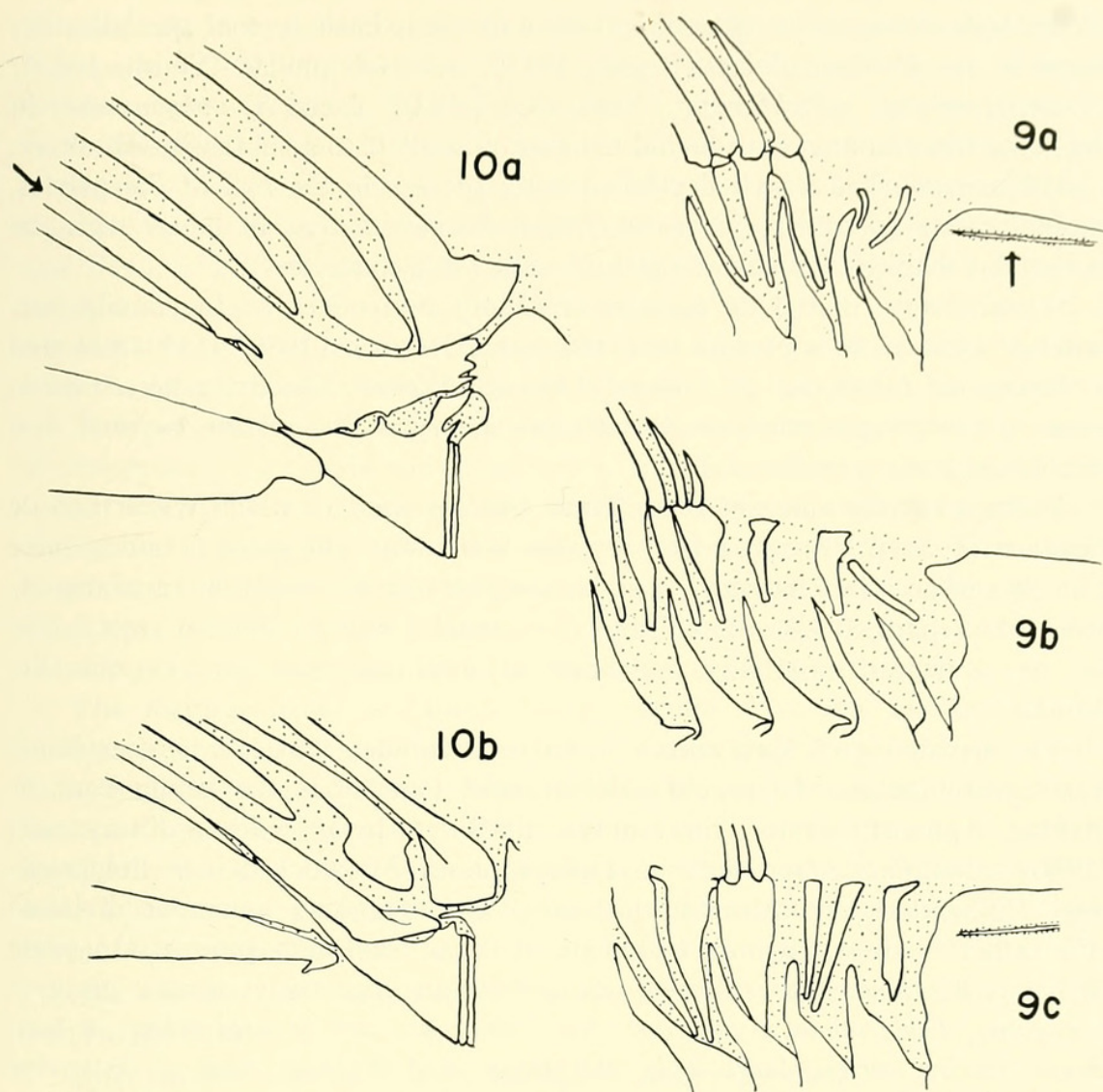


FIGURE 8. Pterygiophores of the penultimate and antepenultimate anal rays, with the base of the penultimate ray shown, lateral view, head of fish to the right. a. *Percichthys trucha*. b. *Diplectrum pacificum*. Dotted areas indicate cartilage.



FIGURES 9 and 10. Fig. 9. Posterior portion of supraoccipital, predorsal bones, and anterior neural spines, dorsal pterygiophores and dorsal spines, lateral view, head of fish to right. a. *Cephalopholus urodelus*. b. *Roccus saxatilis*. c. *Pseudanthias* (? = *Zalanthias*) *kelloggi*. Dotting indicates interspaces between bony areas. Arrow points to ridge running along each side of the supraoccipital. Fig. 10. Upper portion of caudal skeleton, only the upper hypurals shown, lateral view, head of fish to the right. a. *Percichthys melanops*. b. *Diplectrum pacificum*. Dotting indicates interspaces between bony areas. Arrow points to the second uroneural in 10a.

standards). *Callanthias* has very long supraoccipital-frontal and parietal crests on the top of the head. *Pseudochromis* has a very short, low supraoccipital crest and no parietal crest. It, however, has at least two areas of specialization. One is the increased number of branched caudal rays (17) and the rather highly fused caudal skeleton (with only 2 epurals and 3 or 4 hypurals). The other is in the very curious jaw structure, with the palatine far more firmly attached to the lateral ethmoid by ligaments than to the rest of the suspensorium (Gosline,

1960). Indeed this jaw structure represents the same basic type of specialization found in the Congrogadidae (Regan, 1912) and Haliophidae (Smith, 1952).

Apparently as an addendum, Katayama (1960) placed *Symphysanodon* in the Serranidae; in any event he did not even allocate it to a subfamily. However, *Symphysanodon* has a well developed scaly process in the axil of the pelvics, parietal crests (personal observation), and fin counts that fit better with the Lutjanidae than the Serranidae (as do the other two characters).

Ostracoberyx, placed by Katayama (1960) and others in the family Serranidae, seems to be a percoid fish *sui generis*. Norman (1939, p. 57), followed by Katayama (1959, fig. 39), placed it next to *Nippon*. The two genera have in common the greatly enlarged preopercular spine and the serrate lacrimal, but that would seem to be about all.

Perhaps equally aberrant is the genus *Centrogenys*, for which Weber and de Beaufort (1931, p. 87) recognize a separate subfamily. The genus is said to have a number of peculiar characters, *e.g.*, "lower pharyngeals united into a triangular bone, but separated by suture," and the caudal "with 12 divided rays." The fish has a fringed nasal flap, and bears a superficial resemblance to the Cirrhitidae.

The remaining of Katayama's (1960) subfamilies that are here excluded from Serranidae may be provisionally grouped together in the family Percichthyidae.¹ As here understood this family comprises, of Japanese forms, Katayama's (1960) subfamilies Acropomatinae, Doderleiniinae, Malakichthyinae, Polyprioninae, Nipponinae, and Maccullochellinae. As Katayama's numerous divisions of a rather small family would indicate, it is far from homogeneous. In mode of life it contains three different categories: an apparently oceanic group—*Acropoma*, *Doderleinia*, *Synagrops*, *Neoscombrops*, and *Malakichthys*; a benthonic marine series—*Stereolepis*, *Polyprion*, and *Nippon*; and an estuarine and freshwater lot. This last seems to have representatives in most of the temperate and subtropical regions of the world (in the tropics it is to some extent replaced by the Centropomidae, including *Lates*): *Roccus* in North America, Europe, and North Africa; *Percichthys* and *Percilia* in South America; *Coreoperca*, *Siniperca*, and *Lateolabrax* in Asia; and *Percalates*, *Ctenolates*, *Macquaria*, and *Maccullochella* (*Oligorus*) in Australia. The relationships of these genera to one another would seem to require rather intensive investigation on a world-wide basis; at least, the American genera examined by me—*Roccus*, *Percichthys*,

¹ The family name here used for this group of fishes is based on the assumption that Jordan and Eigenmann's (1890, p. 330) subfamily term Percichthyinae represents the oldest available name for this family. Jordan and Eigenmann (1890, p. 335) place *Roccus* and *Kuhlia* with *Lates* in the subfamily Latinae, but various authors have since shown that *Lates*, of which Jordan and Eigenmann had no specimen, belongs in a family quite different from *Roccus* or, for that matter, from *Kuhlia*. According to Katayama (1960, p. 6), the oldest available name should be Acropomidae Gill (1872), but I have not been able to find any such name in Gill's 1872 paper, and Gill (1893, p. 134) attributes the name "Acropomidae" to "Gill, 1891."

Percilia—do not seem to fit into the subfamily framework supplied by Katayama (1960) on the basis of Japanese material. Furthermore, there are certain forms included herewith in the Percichthyidae whose pertinence to that family is subject at least to question. One of the more aberrant members is certainly *Acropoma* (Acropomatinae), which has frequently been allotted a separate family principally because of the forward position of the anus (Goode and Bean, 1895) and the light-organs. Again *Niphon* (Niphoninae) in certain respects, e.g., opercular spines, is more like a serranid than a percichthyid. In the great majority of features (Katayama, 1959), however, it appears to belong with the latter. Finally, Katayama (1959 and 1960) has based his account of the Polyprioninae on *Coreoperca* and *Stereolepis ischinagi*; however, figures of *Polyprion*, e.g., Goode and Bean, 1895, fig. 236, indicate a rather different sort of fish. With the above caveats, the Percichthyidae, comprising, in Japan, Katayama's subfamilies mentioned above, will be accepted here. This family, based upon Katayama's (1959) account of Japanese forms, plus my own dissections of *Percichthys trucha*, *P. melanops*, *Percilia gillissi*, and *Roccus saxatilis*, may be contrasted with the Serranidae as shown in table 1.

The features listed in table 1 differ greatly from one another in their biological significance and in the extent to which they have been investigated in the serranid and percichthyid fishes. By far the most thoroughly tested characters are those which Katayama (1959) has checked in some 8 genera of Japanese Percichthyidae and 20 of Serranidae. My own work with the features listed in table 1 has for the most part been limited to three serranid genera (*Diplectrum*, *Pteranthias*, and *Caesioperca*) and three percichthyid genera (*Percichthys*, *Percilia*, and *Roccus*) not available to Katayama; it is thus essentially a supplement to his work.

Brief comments on each of the characters seem warranted.

I. *The number of opercular spines* (figs. 1 and 3). This feature has already been discussed.

II. *The upper border of the ceratohyal* (fig. 2). A nerve runs forward in the epi- and ceratohyal. The degree to which it is bone-enclosed in the percichthyid-serranid fishes varies greatly. In some percichthyids (Katayama, 1959, fig. 10) there is merely a window in the upper part of the ceratohyal; in this area the nerve runs along without bony protection; in others (fig. 2a and Katayama, 1959, fig. 11) the window breaks through more or less narrowly to the upper surface of the ceratohyal. In the Serranidae this break has broadened out to form a broad-bottomed indentation in the upper surface of the ceratohyal (fig. 2b and Katayama, 1959, figs. 12-13).

III. *The lateral ledge along the supraoccipital crest* (fig. 9). In *Percichthys* and *Percilia* the front of the supraoccipital crest is somewhat expanded above into a roof which lies just under the skin of the nape, but there are no lateral flanges below this. In *Roccus* the supraoccipital crest forms a simple flat

TABLE 1

Percichthyidae	Serranidae
I. Opercle without a spine or point below the main spine (except <i>Nippon</i>) (fig. 3b).	Opercle with a spine or flat point below the main spine (figs. 1, 3a).
II. Upper border of ceratohyal either approximately straight or with an oblong hollow excavated in it (fig. 2a).	Upper border of ceratohyal smoothly concave (fig. 2b).
III. Supraoccipital crest without a longitudinal ridge extending laterally along its mid-sides (except Polyprioninae) (fig. 9b).	Supraoccipital crest with a longitudinal ridge running along its mid-sides for most or all of its length (fig. 9a, c).
IV. Lower surface of lateral ethmoid with only two articular facets, one for the lacrimal and one for the palatine (fig. 4b).	Lower surface of the lateral ethmoid with three articular facets, one for the lacrimal and two for the palatine (fig. 4a).
V. Exoccipital facets for articulation with the first vertebra adjacent or nearly so (fig. 5b).	Exoccipital facets for articulation with the first vertebra well separated from one another (fig. 5a).
VI. No body musculature running forward below Baudelot's ligament to an attachment along the lateral walls of the basioccipital (fig. 5b).	Baudelot's ligament small, body musculature extending forward below and around it to an attachment along the lateral walls of the basioccipital (fig. 5a).
VII. Usually $\frac{1}{2}$ or 1 actinost articulating with the coracoid (fig. 6a).	$1\frac{1}{2}$ or 2 actinosts articulating with the coracoid (fig. 6b).
VIII. Postpelvic process relatively long (fig. 7a).	Postpelvic process relatively short (fig. 7b).
IX. Vertebrae 25, frequently more.	Vertebrae 24 in most, more in some Anthiinae.
X. Some of the dorsal and anal soft ray pterygiophores divided into three parts (fig. 8a).	None of the dorsal and anal soft ray pterygiophores divided into three parts (fig. 8b).
XI. Three or four predorsal bones (except <i>Nippon</i>), the last interdigitating behind the second neural spine (fig. 9b).	One to three predorsal bones, the last, except in Serraninae (fig. 9c), interdigitating between the first and second neural spines (fig. 9b).
XII. Caudal skeleton with two uroneurals (fig. 10a).	Caudal skeleton with a single uroneural (fig. 10b).
XIII. Caudal fin usually forked.	Caudal fin rounded, truncate, or lunate, rarely forked (<i>i.e.</i> , bilobed).
XIV. Gas bladder tending to produce a pair of anterior lobes and/or a posterior projection into the first interhemal spine.	Gas bladder rounded at both ends.
XV. Fishes belong to McCully's (1961) scale group I.	Fishes belonging to McCully's (1961) scales groups II or III.
XVI. Fishes belonging to Freihofer's (1963) ramus lateralis accessorius patterns 8 or 9, or the ramus absent.	Fishes belonging to Freihofer's (1963) ramus lateralis accessorius pattern 9, or the ramus absent.
XVII. Fishes not hermaphroditic (Smith, 1965).	Fishes hermaphroditic, though the two sexes are usually not developed synchronously (Smith, 1965).

vertical lamina throughout. *Epinephelus*, *Cephalopholis* (fig. 9a), *Diplectrum*, *Pseudogramma*, *Pteranthias*, *Caesioperca*, and *Pseudanthias* (fig. 9c), among Hawaiian serranids all have a low ridge running along either side of the supra-occipital crest well below its top. Judging from Katayama's illustrations (1959, figs. 15–23), all serranids have this type of lateral ridge developed to some extent, but so also do certain other lower percoids including apparently some percichthyids (*Coreoperca*, *Stereolepis*; Katayama, 1959, fig. 17).

IV. *The palatine-lateral ethmoid articulation* (figs. 3, 4). In *Diplectrum* and *Epinephelus*, and less markedly in *Pteranthias*, the palatine and lateral ethmoid articulate with one another at two distinct points. The posterior of these is the usual one located just inside the lacrimal-lateral ethmoid facet on the lower surface of the front bony border to the orbit. Additionally, there is anteriorly a distinct knob on the palatine (fig. 3a) which articulates with a marked lateral flange on the lateral ethmoid (fig. 4a). In the percichthyids *Percichthys*, *Percilia*, and *Roccus*, the usual posterior articular facet is present; anterior to this the palatine extends along under and in close association with the lateral ethmoid, but has no particular point of articulation with it.

V. *The exoccipital-vertebral column articulation* (fig. 5). This character is discussed and illustrated by Katayama (1959). Among the percichthyids (fig. 5b and Katayama, 1959, figs. 15–17) the surfaces of vertebral articulation on the two exoccipitals either adjoin one another or are narrowly separated. In the Serranidae (fig. 5a) these two articular surfaces are well separated. Katayama's illustrations and my own observations on *Percilia* and *Epinephelus* suggest that, although this differentiation is valid in general, there is so much gradation between Katayama's described types as to make them of little value as criteria for distinguishing families.

VI. *Muscle and ligament attachment to the basioccipital* (fig. 5). Since this character lies in an area of the fish that is quite difficult to investigate without damaging the specimen, the account here is based largely on *Epinephelus*, *Diplectrum*, *Pteranthias*, *Percichthys*, and *Percilia*. In *Percichthys* (fig. 5b) and *Percilia* there is a strong ligament (Baudelot's) running from the top of the cleithrum to the lateral wall of the basioccipital just ahead of the basioccipital-vertebral articulation. In *Diplectrum* (fig. 5a) Baudelot's ligament is very slight and a portion of the body musculature runs forward below it to an attachment along the whole lateral surface of the basioccipital. *Epinephelus merra* duplicates *Diplectrum* in the above respects. *Pteranthias* seems to differ in that at least part of the musculature to the basioccipital appears to come from the cleithrum.

VII. *The primary pectoral girdle* (fig. 6). Katayama (1959, p. 155, figs. 29, 30) has described and figured two (probably associated) features in the primary pectoral girdle that would seem to separate the Percichthyidae from the Serranidae. Of these the relationship between the actinosts and the coracoid

would seem to be the more reliable and easier to use, even though the percichthyid genus *Percilia* seems to have $1\frac{1}{2}$ actinosts on the coracoid.

VIII. *The postpelvic process* (fig. 7). The postpelvic process, according to Katayama's account and illustration (1959, pp. 161–163, fig. 3) forms a more or less graded series—from long in the Percichthyidae to short in most Serranidae.

IX. *Number of vertebrae*. Vertebral counts in the Serranidae and Percichthyidae have been given by Boulenger (1895, p. 115) and Katayama (1959, pp. 146, 147). Among the genera of Percichthyidae for which they give counts six have 25 vertebrae and eight have more. Among the genera of Serranidae, thirteen have 24 vertebrae and fourteen have more; within the Serranidae the Epinephelinae and Serraninae have 24 vertebrae, whereas the Anthiinae tend to have 26.

X. *Dorsal and anal soft ray pterygiophores* (fig. 8). Bridge (1895) has shown that the normal dorsal and anal pterygiophore of lower teleosts consists of three parts, and that this condition is retained in a few of the lower percoids, though in most the two lower portions have fused. In the serranids, *Diplectrum* and *Epinephelus* at least have the two-part pterygiophores of higher percoids. In *Percichthys*, *Percilia*, and *Roccus*, however, at least some of the pterygiophores retain the three-part structure.

XI. *The number and position of predorsal bones* (fig. 9). This character has been described for serranid and percichthyid fishes in somewhat different ways by Katayama (1959, pp. 148, 149, figs. 25–28) and by Smith and Bailey (1961). In the Percichthyidae (fig. 9b) there are usually three predorsal bones (two in *Nippon* according to Katayama, 1959, p. 149, and four in *Percilia* and *Percichthys trucha*). Except for *Nippon*, which has both predorsals before the first neural spine, the percichthyids have the last predorsal bone ending behind the second (in *Percilia* and *Percichthys trucha* behind the third) neural arch. The first pterygiophore bears two spines wherever investigated. In the Serranidae the number and configuration of the predorsal bones and first pterygiophore differ according to subfamilies. In the Epinephelinae (fig. 9a) there are one or two predorsal bones the last of which interdigitates ahead of the second neural spine, and the first pterygiophore bears a single spine (Smith and Bailey, 1961, p. 358). In the Anthiinae (fig. 9c) there are three predorsals; the last interdigitates ahead of the second neural spine; and the first pterygiophore seems to bear two spines. Finally, in the Serraninae there are usually three, but sometimes two, predorsals, the last interdigitating between the second and third neural arches so far as known; the first pterygiophore bears two spines. Thus, *Nippon* in this character seems to resemble the serranid Epinephelinae. Among the Serranidae the Epinephelinae and Anthiinae can apparently be distinguished from the Percichthyidae, but the Serraninae cannot.

XII. *Caudal skeleton* (fig. 10). As with the three-part pterygiophore, two separate uroneurals would seem to represent the primitive condition in percoid fishes (Gosline, 1961). Among the percichthyids available, *Roccus* and *Percichthys* (fig. 10a) definitely have two separate uroneurals; *Percilia*, in which the single specimen examined shows a rather large amount of fusion elsewhere in the caudal skeleton, has only a single uroneural. In the Serranidae investigated (fig. 10b) only one uroneural is present.

XIII. *Caudal fin*. There can be no doubt that a forked caudal is basic to the teleosts in general and the percoids in particular. One finds it in almost all strong swimmers. Nevertheless, various other tail shapes have been adopted especially by those fishes that habitually maneuver in rather close quarters, *e.g.*, around a coral reef. At all events the caudal fin of the percichthyids is often more or less forked whereas among the serranids it may be of various shapes, *e.g.*, rounded or lunate, but is rarely if ever forked (bilobed).

XIV. *Gas bladder*. Katayama (1959, pp. 164–166, figs. 33–35) has shown that whereas the gas bladder of the Japanese Serranidae is rather normally shaped, that of the Percichthyidae tends to have a pair of projections anteriorly or to extend posteriorly into the first interhemal. The anterior extensions are most pronounced in *Doderleinia* and *Synagrops* (Katayama, 1952), where they project into a basioccipital fossa of the skull. Genera in which the gas bladder enters the first interhemal are *Acropoma*, *Lateolabrax*, and *Malakichthys*. Though my gas bladder dissections are so inadequate as to make the following observation quite unreliable, I have been unable to find either forward prongs or a backward extension of the gas bladder into the interhemal in *Roccus*, *Percichthys*, or *Percilia*.

XV–XVII. For a discussion of these characters, the reader can best be referred to the papers cited.

DISCUSSION OF PERCICHTHYID–SERRANID DIFFERENCES

Of the various differences between the Serranidae and the Percichthyidae that have been discussed in the preceding paragraphs several strongly suggest evolutionary advances in the Serranidae. Some of these serranid features represent losses as compared to the generalized teleostean or percoid type, *e.g.*, the disappearance of the tripartate pterygiophore (X) and of the posterior uroneural (XII). Another group of characters, *e.g.*, the separation of the exoccipital condyles (V), the pectoral actinost articulations (VII), and the length of the postpelvic process (VIII), represent slight shifts in position or shape for which transitional stages between the serranid and percichthyid condition are either known or can be expected. Still other characters, in varying degrees of certainty, represent specializations. In this category fall the rounded or lunate caudal of the serranids (XIII) and the lower spine on the opercle (I). Indeed,

as already noted, this lower opercular spine seems to be developed among the percoids only in the serranids and grammistids.

Of the seventeen listed differences between the serranids and percichthyids, I think the working hypothesis might be suggested that in all, the serranids are either the more specialized or that they and the percichthyids have both evolved in different directions from a proto percoid ancestor. Stated negatively, this hypothesis would postulate that in no one of the seventeen characters listed have the percichthyids evolved from the serranid condition. Some discussion of this idea is needed.

It is generally considered that 24 is a basal number of vertebrae in the percoid fishes. The reason for such a belief is that in a fairly large number of the lower percoid families 24 is at least a frequently recurring and in some families constant figure. An alternate possibility that would seem worth considering is that percoids have no fixed basal number of vertebrae. Circumstantial evidence for such a suggestion can be marshalled from several sources. One is that certain of the more generalized percoid families seem to have no basal number of vertebrae at all, *e.g.*, the Centrarchidae (Boulenger, 1895, p. 5) and Percidae (Bailey and Gosline, 1955). Another is that even in many of the families that have a frequently repeated vertebral number, *e.g.*, the Serranidae, there are often members with other counts. Finally, there are lower percoid families with other basal numbers, *e.g.*, the Percichthyidae, with 25, or the Priacanthidae with 22–23 (Boulenger, 1895, p. 352). Perhaps with the trend toward reduction and specialization of vertebrae (Williston's law) brought pretty well to completion in the percoids, some groups settled on one number in the general vicinity of 24 and others on another.

A second feature that requires comment is the gas bladder peculiarities in many Percichthyidae. There can be no doubt that the tendency for the gas bladder to extend backward into a hollow interhemal (*Acropoma*, *Lateolabrax*, and *Malakichthys* according to Katayama, 1959, p. 164, fig. 34) or forward as a pair of prongs to the wall of the internal ear (*Doderleinia* and *Synagrops*) is a departure from the normal gas bladder type and must be considered a specialization in the percichthyids. Nevertheless, both of the features mentioned occur time and again in the percoid fishes. The extension of the gas bladder into an interhemal, for example, occurs in the Gerreidae (Gerridae) and Sparidae. The connection between the gas bladder and the cranium in some percichthyids deserves somewhat more discussion.

Among the berycoid and lower percoid fishes a gas bladder-ear connection occurs at least three times: in the berycoid family Holocentridae (*cf.* Nelson, 1955) and in the percoid families Kuhliidae (*Kuhlia*, personal observation) and Percichthyidae (Katayama, 1952 and 1959). In *Kuhlia* the anterior prongs of the gas bladder pass forward above Baudelot's ligament whereas in the Holocentridae they pass below it. In *Doderleinia* and *Synagrops* Katayama

(1952) does not mention (at least in the English resumé) the relationship between the prongs of the gas bladder and Baudelot's ligament, but he does describe and figure for these fishes (1952, fig. 1) a pair of basioccipital fossae for the accommodation of the anterior prongs of the gas bladder. These fossae seem to be somewhat different from the gas bladder-auditory bulla association of either the Holocentridae or Kuhliidae. The implication is that a connection between the gas bladder and the cranium has occurred independently at least three times: in the Holocentridae, Kuhliidae, and Percichthyidae.

In the Serranidae examined, as previously noted (VI), Baudelot's ligament is small or has completely disappeared and a portion of the body muscle extends forward to an attachment along the lateral walls of the basioccipital. Part of this muscular attachment is on that forward portion of the basioccipital which forms a part of the wall of the auditory bulla. Under such circumstances the lateral basioccipital walls necessarily form a strong, rigid structural support. It would seem that a firm muscle-supporting basioccipital would preclude the development of a gas bladder-inner ear connection (which to be functionally successful would seem to require a highly flexible intervening wall between these two structures). In short, with regard to this character the serranids appear to have evolved in one direction while the percichthyids show at least tendencies to develop in a quite different one.

PERCICHTHYID RELATIONSHIPS

The serranids as here defined have certain specializations, especially the presence of a lower opercular spine, that will distinguish them from other basal percoid families. By contrast the Percichthyidae has, as a group, only the gas bladder tendencies that I am aware of in this category of characters. The question thus arises of how to distinguish the Percichthyidae from other lower percoid groups. For the moment at least, this must be done by a process of elimination. The remainder of the present paper will be devoted to this matter. The percoid families to be considered are Centropomidae, Percidae, Kuhliidae, Centrarchidae, Scorpionidae, and Apogonidae.

As with the Serranidae, it would seem that at least some of these last-named families have peculiarities (perhaps markers would be a more appropriate word) by which they may be distinguished. Thus the PERCIDAE, in addition to the characters usually used to define the family (see Collette, 1963, pp. 620-621), seem to have dropped out the normal connection between the preopercular and temporal sensory canals of the head (Hubbs and Cannon, 1935, p. 10; Disler, 1950). This, however, is a by no means unusual feature.

In the CENTRARCHIDAE, judging from an examination of *Archoplites*, *Pomoxis*, and *Micropterus*, the largely bone-enclosed supraorbital commissure of the lateral line forms a cross-ridge on the frontals. The posterior face of this ridge provides the anteriormost surface of attachment for the body musculature running forward over the skull.

Among the CENTROPOMIDAE, *Centropomus* (personal observation) and *Lates* (Katayama, 1956) have the second neural spine anteroposteriorly expanded into a somewhat bladelike structure. Unlike the other groups mentioned previously they also have a well developed scaly process in the axil of the pelvics.

At this point, a brief discussion of this scaly process in the pelvic axils of many percoids seems advantageous. It is on the basis of the presence or absence of this feature that Regan (1913) and Norman (1957) made their primary division of percoid families. There can be no doubt that the character forms a convenient and valid marker for certain groups. On the other hand, it is an open question, to say the least, whether it will bear the weight that Regan and Norman have placed on it. There are two problems here.

One is whether the percoid families without an axillary process form one phylogenetic group and those with it another. I do not have enough information on this topic to discuss the matter intelligently. The other regards the consistency of the presence or absence of an axillary scale within percoid families. Certainly in some well known families the consistency breaks down. According to Norman (1957, p. 219) this happens in the Sciaenidae. In the Chaetodontidae (*vide* Fraser-Brunner, 1945, p. 466), the Chaetodontinae possess a well developed axillary process but the Pomacanthinae do not. Part of the difficulty lies in the fact that the axillary process is not an all or none character; it can be and frequently is rudimentary or practically transitional between a ridge and a process.

Nevertheless in the great majority of percoid families the scaly axillary process in the pelvics is either consistently absent or consistently present. Consequently the presence of a well developed axillary scale in *Symphysanodon* would argue rather strongly against its inclusion in the serranid-percichthyid group. Similarly, the well developed axillary process shown in Starks' (1899) figure of *Dinolestes* would indicate that this fish is not a member of the Apogonidae, despite its almost invariable allocation to that family.

Among the generalized percoids, *i.e.*, those with the characters listed for the Percichthyidae in table 1, but with an axillary scale, I have dissected only two—*Microcanthus* and *Centropomus*. *Microcanthus*, a scorpidid, differs further from the Percichthyidae in the small mouth and twisted maxillary that usually goes with it; also the premaxillary has only one ascending process. *Centropomus* has already been mentioned.

The two remaining basal percoid families to be differentiated from the Percichthyidae present more difficulty.

KUHLIIDAE, according to Norman (1957, p. 249) contains the Pacific-wide *Kuhlia* and two poorly known Australian freshwater genera—*Nannatherina* and *Nannoperca*. Regan (1940, p. 174), in assigning *Nannatherina* to Kuhlidae, stated: "In *Nannatherina* the pelvic bones are remote from the

cleithra and connected to them by a rather long ligament." If Regan's allocation and statement are correct, Kuhliidae is a very primitive percoid family indeed. Until more is known about *Nannatherina* and *Nannoperca*, a comparison of the Kuhliidae with other families must be based largely on *Kuhlia*. For the present, suffice it to say that *Kuhlia* is very like the percichthyids, differing only in such minor osteological characters as the absence of a subocular shelf.

The final family to be compared with the Percichthyidae is APOGONIDAE. This is another lower percoid family that has been stretched into almost protean form. The absence of information on the internal characters of many apogonid genera makes any final attempt to define the family premature. However, two peculiarities of *Apogon* are worth noting as a possible basis of family definition. One is that the intercalar is included in the convex wall of the greatly expanded auditory bulla; hence the lower prong of the posttemporal is attached to the bulla wall. Second, the single uroneural is reduced to a single weak splint without the anterior expansion usual in percoids.

In light of the foregoing discussion, an attempt can be made to define the basically generalized Percichthyidae in such a way as to exclude at least those other families that have been considered in this paper.

PERCICHTHYIDAE. Percoid fishes with the lateral line canals of head at least partially enclosed in bone; preopercular sensory canal usually joining the temporal canal; supraorbital commissure not enclosed in a raised ridge of bone that forms the anterior level of attachment for the body musculature; lateral line of the body complete and continuous. Premaxillary with two ascending processes; maxillary expanded posteriorly. Opercle with two rounded protrusions or spines (three in *Nippon*), the main one below. A subocular shelf. Expanded auditory bulla, if present, not including the intercalar. Vertebrae 25 or more; 2nd neural spine not anteroposteriorly expanded. Three predorsal bones. No scaly process in the axil of the pelvics; pelvics thoracic, of a spine and five soft rays, the outer the longest. Two uroneurals, the larger expanded anteriorly.

SUMMARY

A preliminary attempt has here been made to unravel the taxonomic confusion that has accumulated around certain of the lower percoid families. Lower percoid groups with a scaly process in the pelvic axis—the Centropomidae, *Symphysanodon*, *Dinolestes*—have barely been mentioned; they do not seem to belong with the serranids and their associates dealt with here. The family Serranidae itself has been restricted and redefined. As here restricted, the Serranidae form a somewhat specialized offshoot of the basal percoid stock. In addition to the Grammistidae, which have been treated previously (Gosline, 1960), the groups here removed from the Serranidae of older authors fall into two categories. One is made up of apparently specialized fishes of dubious affinities—the Callanthiinae and Ostracoberycinae of Katayama (1960); the

Centrogenysinae of Weber and de Beaufort (1931); and the pseudochromids, etc., of Regan (1913). The other category—formed by the Acropomatinae, Doderleiniinae, Malakichthyinae, Maccullochellinae, Polyprioninae, and Nipho-
ninae of Katayama (1960)—is here provisionally considered as a single, separate family of basal percoid fishes. This family, Percichthyidae, is briefly compared with a number of other lower percoid groups and provisionally defined.

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