Comments on the Classification of the Percoid Fishes[1]

WILLIAM A. GOSLINE[2]

IN TERMS OF DIVERSIFICATION, the Perciformes is by far the most successful of fish orders, maximally represented in the inshore waters of tropical seas. Thus, of the 130 families of native Hawaiian fishes, some 41 belong to the Perciformes, and 18 belong to the single superfamily Percoidae, which forms the subject of the present paper.

From the point of view of classification, the order Perciformes suffers from an overabundance of representation. In fish groups that have undergone extensive extinction the modern members may be unrepresentative, but at least the gaps between them are usually spacious, providing abundant material for the construction of discrete taxonomic pigeonholes. In the Perciformes, however, the results of repeated adaptive radiations seem to be living today. Some of these have led to a relatively high and complex structural reorganization (the "mesoevolution" of Dobzhansky, 1954). Where this has happened, it is comparatively easy to sort lineages. But after the major lines of evolution have been extracted (as separate orders, suborders, or superfamilies), the remaining basal percoids seem to represent a central theme with numerous variations.

Contributions toward our present knowledge of the percoid fishes have been made from a number of viewpoints, all of value. Jordan's classification (1923) is based primarily on external characters, whereas that of Regan (1913) relies heavily on the superb series of skeletons in the British Museum. In recent years more intensive investigations have been undertaken from two viewpoints. One is to trace a particular structure or structural complex through a broad sampling of percoid fishes. This has been done for otoliths by Frost (1927, 1928), for the predorsal bones and subocular shelf by Smith and Bailey (1961 and 1962, respectively), for the caudal skeleton by Gosline (1961), and for the recurrent facial nerve by Freihofer (1963). The other approach is to study as many characters as possible in a particular percoid group, e. g., the Japanese serranids (Katayama, 1959) and carangids (Suzuki, 1962).

The present investigation began as an effort to ascertain the systematic position and relationships of a few percoid genera. It soon became apparent that, except within the narrowest limits, this was impossible without some overview of percoid classification as a whole. This paper is an effort to bring data on the supraoccipital crest and the jaw mechanism to bear on a general percoid classification and to rescue some main outlines of such a classification from the amorphous condition into which they have deteriorated as a result of the widely varied opinions recently expressed on the subject.

MATERIAL AND ACKNOWLEDGMENTS

PERCIFORM ORIGINS

The perciform fishes are generally believed to have arisen among the Beryciformes. Their success, as compared to that of the Beryciformes or indeed of any other order, cannot be attributed to any one major advance, but seems to be the result of an assimilation and integration of a number of minor improvements over beryciform features. Among the characters separating the Perciformes from the Beryciformes, some of the better documented are:

(1) Pelvic fins with no more than 5 soft rays. However, *Channa* (*Ophiocephalus*) has 6 segmented rays, and the flatfishes, presumably derived from the Perciformes, have up to 13 (Norman, 1934).

(2) Pelvic bones extending between and directly attached to the cleithra. The several exceptions to this seem to fall into two categories (Regan, 1909): those groups some or all of which seem never to have attained such an attachment—the Mugiliformes, Anabantidae, Channidae, and *Nannatherina* (Regan, 1940); and those groups in which some or all of the species seem to have secondarily lost such an attachment—Stromateidae, Tetragonuridae, Gempylidae, and Trichiuridae.

(3) Orbitosphenoid, antorbital, and nodules between the pelvic fin rays and the pelvic girdle absent as separate entities. There is no known percoid that retains any of these bones in the adult. Such bones, all present in the beryciform family Holocentridae, have been lost, however, in numerous fishes besides the Perciformes.

(4) Branched caudal rays 15 or fewer. Reduction in the number of branched caudal rays in the percoids is rather commonplace. A few round-tailed forms are known to have more than 15 (Gosline, 1960).

(5) In the percoids, as contrasted with most beryciform fishes, there are basically five circumorbital bones behind the lacrimal, and a subocular shelf, if present, tends to be restricted to the second (but see Katayama, 1959: Figs. 3–5). In the Beryciformes, except Holocentridae, there appear to be only four circumorbitals (Patterson, 1964), and the subocular shelf tends to spread over more than one of them. In this character, as in the generally high degree of ossification, it is the berycoids that seem to be

unusual as compared with other acanthopteran fishes (see below).

That an integration of the above characters did not occur all at once is shown by the groups of modern fishes which seem to have stopped short part way along the path of beryciform-perciform evolution: e. g., the Mugiliformes, anabantoid-channoid group, and apparently *Nannatherina* (see above paragraphs).

It has generally been postulated, implicitly or expressly, that the Perciformes has had a single origin among the Beryciformes. In 1964, however, Patterson suggested four separate origins for perciform families among the Beryciformes. Specifically these are:

BERYCIFORM ANCESTORS	PERCIFORM DERIVATIVES
Polymixiidae ⟶	Scorpidae, Monodactylidae, and Kyphosidae
Sphenocephalidae ⟶	Serranidae
Aipichthyidae ⟶	Menidae and Carangidae
Pharmacichthyidae ⟶	Acanthuroidei
Pycnosteroididae — ? →	Chaetodontidae
Dinopterygidae — ?? →	Centrarchidae

Thus, according to Patterson's view the basal percoid families would have at least three and possibly five independent derivations from the Beryciformes, and the Acanthuroidei would have evolved from a sixth. Such a viewpoint deserves discussion in considerable detail.

Thanks to Patterson's (1964) excellent redescriptions and figures of the Cretaceous berycoids *Berycopsis, Homonotichthys, Hoplopteryx,* and *Caproberyx,* it is possible to make a detailed comparison between these forms and the better known of modern berycoids (Starks, 1904). They fit together nicely. Thus *Berycopsis* and *Homonotichthys* belong in the same family with the modern *Polymixia* (Starks, 1904); *Hoplopteryx* with the modern *Trachichthys;* and *Caproberyx* with the modern holocentrids. These Cretaceous and modern forms together make up a sort of central core of the known Beryciformes, forming a congruent, easily recognizable, and clearly definable group of fishes. Thus, when Patterson suggests *Berycopsis,* a Cretaceous polymixiid that he has described in detail, as an ancestral type for the percoid families Scorpidae, Monodactylidae, and Kyphosidae, what he is saying is clear. Unfortunately,

both today and in the fossil record, little-known beryciform-like fishes lead out in all morphological directions from the central berycoid core. Patterson's other suggested points of origin for percoids are not core berycoids, but rather are peripheral forms for which little knowledge is available: *Sphenocephalus, Aipichthys,* the Pycnosteroididae, and the Dinopterygidae. What is known about these four groups gives me, at least, no feeling of assurance about even their beryciform affinities. Indeed, the various percoids Patterson suggests as separate derivatives from them (Serranidae, Menidae and Carangidae, Chaetodontidae, Centrarchidae) would seem to me to be a far more close-knit group than the various forms from which they were supposedly derived.

That some of the lesser known, "peripheral" fossil berycoids like *Aipichthys, Sphenocephalus, Dinopteryx,* and *Pycnosteroides* may prove to be nearer the ancestral percoid type than the "core" berycoids seems quite probable, if only because the reduction in ossification which may well have led to the lack of knowledge of the "peripheral" berycoids is also a step in the direction of the percoids. Stated conversely, the "core" berycoids, except possibly the Polymixiidae, seem to be too completely ossified to have been percoid ancestors.

So far the objections to deriving different basal percoids from separate berycoid stocks have been of a general nature. Some discussion of the supraoccipital crest will, I think, provide evidence against certain of the specific derivations postulated by Patterson.

The supraoccipital crest attains extensive development only in the teleosts. Among lower teleosts the supraoccipital tends to be a small bone at the rear of the skull that does not extend forward between the parietals. In general, the size of the supraoccipital bone is quite closely associated with the size of its crest: where the crest is large the supraoccipital is large, and in groups where the crest is low or lacking the supraoccipital may disappear, as in some congrid eels. In the acanthopteran fishes the supraoccipital crest may become very large; here the deeper-bodied fishes tend to have larger crests.

Among deep-bodied fishes, however, there are two quite different types of crest and,

though each has doubtless arisen many times, it seems improbable that one would give rise to the other. In strongly swimming, compressed fishes the body musculature tends to extend far forward over the head. This musculature has its attachment in large part to the supraoccipital crest which extends forward within it. In the berycoid *Homonotichthys* (Patterson, 1964:284, fig. 35) and in numerous percoids the supraoccipital comes forward between the frontals or its crest extends forward over the frontals. In a whole series of percoid families, including the Carangidae, Coryphaenidae, and Priacanthidae, an even greater anterior extension of the supraoccipital crest is brought about by the development of a median ridge on the paired frontals. In all these fishes the crest is buried in musculature and is not broadly exposed on the surface, its upper rim being more or less knife-edged. Finally, the cranial roof below the crest is not especially vaulted or otherwise distended.

A quite different type of supraoccipital crest, constructed in another way and serving another principal function, is that of the acanthuroids, chaetodontids, *Antigonia,* etc. Here, in essentially slow-moving, spinous fishes, the supraoccipital extends up and back over the nape as a sort of protective shell. (This same type of development is found in some of the lower teleosts, e.g., catfishes.) One can envision this construction as arising from the condition in fishes like the modern berycoids *Holocentrus* or *Myripristis.* In these the supraoccipital crest is small and extends directly back from the upper surface of the skull; its upper border has flattened out somewhat. If, in deeper-bodied forms such as the extinct holocentrid *Caproberyx,* this type of supraoccipital crest, along with the whole posterior portion of the cranium, were to be raised up and expanded over the nape, then the development of a posteriorly vaulted skull continued up and back as a rooflike supraoccipital crest would occur. In such a fish as *Chaetodon,* which has this type of construction, there is very little muscle attachment to the high, broad, and strong supraoccipital crest. The vaulting at the rear of its cranium adds structural strength to the crest base (and also has the curious result of leaving the brain resting in the bottom of a high, empty vault).

Thus *Chaetodon* and *Caranx,* representing the two extreme types of supraoccipital just described, both have high crests, but structurally and functionally they are far apart. Furthermore, the two extremes represent quite different modes of life in the fishes that bear them. Any combination of them seems unlikely. Nor does it appear that one could be developed from the other except by going all the way back through some intermediate form with a relatively small, unspecialized occipital crest. Yet among Patterson's derivations, he has the sharp-crested carangids and menids arising from *Aipichthys,* which according to his illustration (1964: Fig. 83) seems to have a chaetodontid-type (roofed) occipital process. Similarly, *Sphenocephalus,* which Patterson has as a progenitor of the Serranidae, appears (Patterson's Fig. 78) to have the broad-roofed crest of *Chaetodon,* not the cutting edge found in the serranids (Katayama, 1959). If the preceding analysis of supraoccipital crest development is sound, both of these derivations of Patterson's would seem most improbable.

But to belabor Patterson's individual derivations is probably overshooting the mark, for at the present time I see no reason to look nearly as far back as the berycoids for a percoid progenitor. It seems to me, rather, that some one berycoid lineage could have evolved a fairly long way, i.e., could have developed most of the characters listed previously, before branching into the various percoid lineages, or even before giving off such subpercoid groups as the Mugiliformes. In short, I am far more impressed by the differences between the berycoids and the percoids, or among the berycoids themselves, than by those between the various percoids.

THE ARRANGEMENT OF PERCOID FAMILIES

The 50 or so families of fishes included in the superfamily Percoidae have been grouped in various ways. Data on feeding and on jaw structure to be presented below support an arrangement proposed by Regan in 1913. In that paper Regan merely took up the families in serial order. However, in his introductory statement (1913:113) he said: "In the following arrangement a few of the more aberrant fami-

lies are placed last, and the remainder are grouped into those without (Serranidae to Coryphaenidae) and those with a scaly process in the axil of the pelvic fins." The process in question is made up of one to several modified scales that form a pointed projection extending back between the lateral border of the pelvic spine and the body. Among acanthopteran fishes the process occurs in some but not all members of the Beryciformes and Mugiliformes, and in the Perciformes it occurs among the Percoidae, Pomacentroidae, and Labroidae (Table 1). In the Percoidae the axillary process can be postulated as being an independently developed or as an inherited character. Since there is no indication that the axillary processes of the Beryciformes, Mugiliformes, and Perciformes are not homologous, it seems more satisfactory to postulate that the percoid process has been lost one to many times in the families in which it is lacking (Table 1), rather than that a structure found in the Beryciformes and Mugiliformes has been lost and then redeveloped in certain members of the Percoidae. Within percoid families the axillary process, when present, is fairly constant; exceptions are the Centropomidae (Weber and deBeaufort, 1929:393), Sciaenidae (Norman, 1957:219), and Chaetodontidae (Fraser-Brunner 1946:466). Percoid families with and those without axillary scales are listed in Table 1. "Above" the Percoidae axillary processes are found, to the author's knowledge, only among the perciform superfamilies Pomacentroidae and Labroidae.

It would seem that those families without and those with an axillary process are characterized by two rather different modes of feeding. Percoid families without an axillary scaly process generally engulf their food, so to speak. Either the fish simply runs down its prey, merely opening its mouth at the appropriate moment, or food organisms in close enough proximity are sucked into the mouth by sudden expansion of the oral and branchial cavities. In either event the main problem is to get the jaws *open* at the right time, and the chief function of the unspecialized teeth is merely to grasp the prey. By contrast, the perciform families with an axillary process tend to specialize in the direction of selecting their food items with their front teeth. They may pluck it out from its

surroundings, as the chaetodontids and labrids do, or nip it off, as the scarids do. Their main problem is to get the mouth effectively *shut* over the selected item, and their front teeth are often specialized in various ways.

In the above analysis two quite different methods of feeding have been contrasted. However, among the less specialized percoids a fish that habitually feeds in one of these two ways may shift more or less easily to the other, and many percoids are opportunists, eating what they can find in whatever manner they can get it.

The jaw mechanisms in the two groups just differentiated reflect their main feeding habits (or vice versa). Certain general attributes of jaw structure are held in common by all percoid fishes. Among these are the (usual) abilities (1) to bring the maxillary down across the corner of the mouth when the lower jaw is swung open, (2) to protrude the premaxillaries, and (3) to expand the oral cavity laterally as well as vertically.

Although the more generalized percoids are quite similar to one another in jaw structure, rather different trends of development from this basal pattern are discernible in those fishes with, and in those without, an axillary process. In the "engulfing" forms (without an axillary process) the teeth do not become specialized and the jaw structure develops in one of two directions. In such fishes as the carangid *Scomberoides* (or *Chorinemus*), which simply runs down its prey, premaxillary protrusion has been lost and the maxillary has become a simple strut above the premaxillary (Suzuki, 1962: Fig. 15F). In contrast, the serranid fishes of the genus *Epinephelus* perhaps represent the epitome of a trend toward a cavernous mouth opening.

A comparison between *Epinephelus spilotoceps* (without an axillary process) and *Lutjanus vaigiensis* (with an axillary process) may serve to exemplify the differences between the two groups. In specimens of both species 140–155 mm in standard length the width of the gape is about the same when the mouth is closed (14–15 mm), yet when the mouth is opened wide the gape expands laterally only to 18 mm in *Lutjanus* but becomes a yawning chasm 30 mm across in *Epinephelus*. One factor that makes possible the relatively wide gape opening is the

TABLE 1

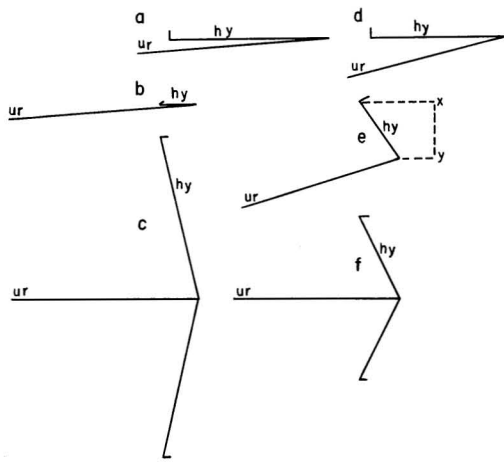| FAMILIES WITH A SCALY PROCESS IN THE AXIL OF THE PELVIC FIN	FAMILIES WITHOUT A SCALY PROCESS IN THE AXIL OF THE PELVIC FIN
Beryciformes	Beryciformes
Polymixiidae	Trachichthyidae
Holocentridae	
Mugiliformes	Mugiliformes
Mugilidae	Sphyraenidae
Atherinidae	
Polynemidae	
	Zeiformes
	Antigoniidae
Perciformes	Perciformes
Percoidei	Percoidei
Percoidae	Percoidae
Centropomidae	Percichthyidae
Bramidae	Serranidae
Pempheridae	Plesiopidae
Arripididae	Acanthoclinidae
Lutjanidae	Kuhliidae
Scorpididae	Centrarchidae
Nemipteridae	Priacanthidae
Pomadasyidae	Cepolidae
Toxotidae	Rainfordiidae
Monodactylidae	Apogonidae
Lobotidae	Percidae
Lethrinidae	Lactariidae
Kyphosidae	Labracoglossidae
Dichistiidae	Bathyclupeidae
Girellidae	Pomatomidae
Sparidae	Rachycentridae
Centracanthidae	Carangidae
Emmelichthyidae	Menidae
Leiognathidae	Coryphaenidae
Sciaenidae	Nandidae
Mullidae	Cichlidae
Chaetodipteridae	Sillaginidae
Drepanidae	Branchiostegidae
Scatophagidae	Cirrhitoidei
Chaetodontidae	Cirrhitidae
Enoplosidae	Cheilodactylidae
Histiopteridae	Trachinoidei
Oplegnathidae	Parapercidae
Pristolepidae	Embiotocoidei
Pomacentroidae	Embiotocidae
Pomacentridae	Notothenioidei
Labroidae	Nototheniidae
Labridae	Acanthuroidei
Scaridae	Acanthuridae
	Zanclidae
	Siganoidei
	Siganidae
	Scombroidei
	Scombridae
	Stromateoidei
	Nomeidae
	Anabantoidei
	Anabantidae

FIG. 1. Movement of the hyoid apparatus in *Epinephelus spilotoceps* (*a–c*) and *Lutjanus vaigiensis* (*d–f*). Diagrammatic side view with the mouth shut (*a, d*) and the mouth open (*b, e*), and top (or bottom) view with the mouth open (*c, f*). Head of fish to the right. *hy*, Hyoid bar; and *ur*, urohyal. The distance *xy* indicates the amount of potential lateral expansion lost in *Lutjanus* by the downward pull of the urohyal.

much longer jaws. In *E. spilotoceps* 140–150 mm long the length of the upper jaw to the end of the maxillary is 32 mm and that of the lower jaw is 40 mm; these same dimensions for *L. vaigiensis* are only 21 and 23 mm. If the longer jaws of *Epinephelus* create the possibility of greater gape expansion they do not ensure it per se. (Fishes with the longest jaws quite frequently have a rather narrow gape, e.g., *Lepisosteus, Belone.*) In *Epinephelus* there are three ways in which gape expansion is actually accomplished. First, the lower rims of the suspensoria may be swung out from the cranium by contraction of the levator hyomandibularis et arcus palatini (van Dobben, 1935:7, 8). Second, contraction of the sternohyoideus pulls the urohyal backward (Fig. 1) and in so doing forces the posterior portions of the epihyals out laterally (van Dobben, 1935:8). Finally, a twisting of the maxillary shaft rolls its lower border, and with it the lateral end of the premaxillary, somewhat outward away from the head in *Epinephelus,* as in *Perca* (van Dobben, 1935:11).

Epinephelus and *Lutjanus* show differences in all three of these processes. That having to

do with the spreading of the suspensoria by way of contraction of the levator hyomandibularis et arcus palatini is merely one of degree: in *Epinephelus* this muscle appears to be much broader and more powerful than in *Lutjanus.* (The dilatator operculi, which is instrumental in expanding the gill cavity, is also much larger in *Epinephelus* than in *Lutjanus.*)

So far as the hyoid bar method of gape expansion is concerned, there are differences both in degree and in the direction of the forces. In the first place, *Lutjanus* has hyoid bars that are only two-thirds as long as those of *Epinephelus,* so that the potentiality for lateral expansion is only two-thirds as great. But even allowing for this difference, the hyoid bars are not forced out to their maximum lateral expansion in *Lutjanus* when the mouth is opened. In *Epinephelus* (Fig. 1*a–c*) contraction of the sternohyoideus pulls the urohyal (Fig. 1, *ur*) almost straight back, forcing the posterior ends of the hyoid bars directly outward. In *Lutjanus* (Fig. 1*d–f*), however, as in most deep-bodied fishes, contraction pulls the front of the hyoid bars backward and *downward,* and some of the potential lateral thrust is lost in the downward motion (the amount equal to *xy* in Fig. 1*e*).

Though the hyoid bar factors just mentioned would seem to play the greatest quantitative role in the difference in lateral gape expansion between *Epinephelus* and *Lutjanus,* the feature showing the largest qualitative difference is the twisting or nontwisting of the maxillary shaft when the mouth is opened. In both *Lutjanus* and *Epinephelus* a ligament from the adductor mandibulae and the lower jaw runs to an attachment on the outer surface of the maxillary shaft anteriorly (Fig. 2, *L*). In narrowmouthed fishes, when the adductor contracts this ligament helps to pull the maxillary up and back to the closed-mouth position. In widemouthed fishes it has a different function when the gape is widely opened: as the posterior end of the maxillary swings laterally with gape expansion, the ligament comes to pull across it, causing the maxillary to rotate on its shaft (Fig. 2). This rotation at the anterior end of the maxillary causes protrusion of the premaxillaries; posteriorly it rolls the lower border of the maxillary outward, and with it to some extent the lateral ends of the premaxillary, thus

expanding the already broad gape even farther.

The tremendous expansion of the open gape of *Epinephelus* seems to be at the end of one trend of jaw development. However, almost the same jaw construction and capabilities occur in the Beryciformes (e.g., *Holotrachys*), Scorpaeniformes (e.g., *Scorpaenopsis*), etc. A fish with this type of jaw construction would seem well adapted to engulfing nearby objects of moderate to large size, especially those close to the bottom. There are, however, a number of things such a fish will not be able to do well. It has no method of selecting one particular food item from its immediate surroundings. Nor can it bite off a part of anything, e.g., a fisherman's bait. Finally, such a fish probably cannot bite down on anything with much force; the length of the jaws militates against this, especially since the partly rotated maxillaries do not form a very firm support for the

FIG. 2. Maxillary and associated features in *Epinephelus* with the mouth open, superior view. *A*, Adductor mandibulae muscle; *L*, ligamentum maxillomandibulare posterius of van Dobben (1935:FIG. 5): anteriorly it joins a ligament to the inner surface of the maxillary, above it is joined by a sheath to the adductor mandibulae, and posteriorly it is attached to the lower jaw (not shown); *mx*, maxillary; and *sm*, supramaxillary.

lateral ends of the premaxillaries when the mouth is open.

Among perciform fishes with an axillary scaly process there are some basal families, e.g., Centropomidae, Pempheridae, Bramidae, and perhaps Sciaenidae, in which no particular jaw specialization is apparent. But in the other families there is a notable trend toward a single row of specialized teeth. Sometimes, as in the chaetodonts, these teeth are hairlike and are used for such purposes as separating the eggs of other fishes from the rocks on which they have been laid. In other families the teeth may be incisiform (Kyphosidae, Pomacentridae), molariform (Sparidae), or fused into a beak (Oplegnathidae, Scaridae). Whatever the type of teeth, there are several features of head structure held in common by the more advanced perciform fishes with axillary scales. One is that the mouth is always relatively small, with comparatively little lateral expansion. The maxillary is more or less restricted to a single plane of movement, sliding up and down directly above the lateral ends of the premaxillary; it often forms a sort of cap fitting over the tip of the premaxillary, and in its most extreme development, i.e., in the Scaridae, the maxillary becomes rigidly united to the premaxillary. With the restriction of the lateral expansion of the gape, the lacrimal (preorbital) frequently extends down over the maxillary and premaxillary, completely covering them when the mouth is closed, e.g., as in *Lutjanus*. This lacrimal expansion helps restrict the maxillary below it to a single plane of movement and inhibits rotation of the maxillary; it also carries openings of the lateral line canal down to just alongside the mouth (along the lower border of the expanded lacrimal). Finally, as the fishes in this group become smaller-mouthed, the mouth tends to move downward and forward and the eye up and back on the head. Sometimes, as in the labrid *Gomphosus*, the mouth seems to operate somewhat on the principle of long-handled forceps, or again, as in the labrid *Epibulus*, on the principle of a bellows.

The jaw differences between the two main types of percoid fishes discussed in the preceding paragraphs are summarized in Table 2.

In this paper an association has been postulated between certain aspects of feeding and an
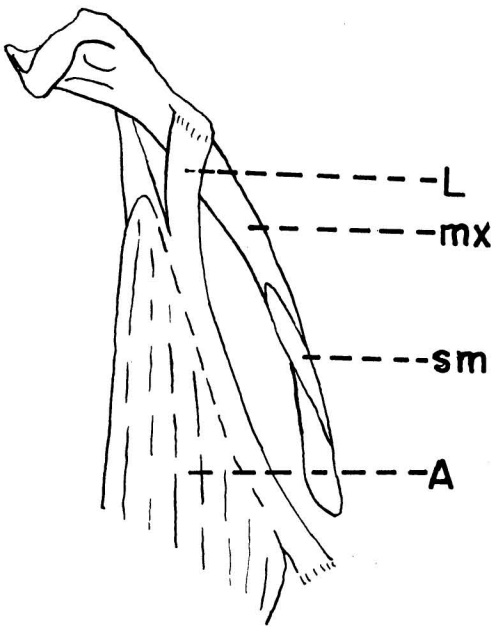
arrangement of families proposed by Regan ostensibly on the basis of the axillary scaly process. This postulate requires amplification and clarification in several respects.

In the first place, it has been hypothesized that the presence of an axillary process is an inherited character and that its loss in the percoids has been secondary. On the other hand, those fishes that have retained the process include the forms which have developed much the most specialized jaw structure. I can see no causal explanation for this divergence of evolutionary direction and must fall back on the fact that functionally independent and nonpleiotropically controlled characters evolve independently. It may be instructive, therefore, to discuss separately the assumed evolutionary sequence in axillary process loss and jaw structure specialization.

Axillary processes, if inherited in percoids as here believed, would seem to have been lost many times under varied circumstances. Among the Beryciformes a minute-scaled *Paratrachichthys* lacks axillary processes, as do all other groups known to me that have very small scales or none at all. Among the Mugiliformes *Sphyraena* lacks axillary processes; and, whether there is a causal relationship or not, all fast-swimming fishes except the Bramidae and Pempheridae lack processes, e.g., Carangidae, Coryphaenidae, Scombroidei. Again, all fishes that prop themselves off the bottom by the pelvic fins lack axillary scales, e.g., Blenniidae, Cirrhitidae as well as all fishes that have modified

or reduced pelvics, e.g., Gobioidei, Ophidioidei. Indeed, since apparently all families above the Percoidae except the Pomacentroidae and Labroidae lack axillary processes, the major problem is perhaps that of why so many percoid families have them. To this question there is, to my knowledge, no answer worth writing.

A related matter for which I know no solution is why Regan (1913) excluded "a few of the more aberrant families" from his division between those percoids with, and those without, an axillary process. The families so excluded are apparently the Cepolidae, Cichlidae, Oplegnathidae, Nandidae, and Pristolepidae (with all of which I have very little familiarity).

With regard to the jaws and teeth, those of *Roccus* and *Perca* (without axillary processes) and those of *Lates* and *Pempheris* (with axillary scales) would seem to be very similar and about equally generalized. There appears to be no morphological reason why the jaw structure of any of the four genera should not have developed on the one hand the specializations of *Epinephelus* (without axillary processes) or on the other the peculiarities of *Kyphosus* or *Chaetodon* (with axillary processes). What does seem clear is that the jaw structure of *Epinephelus* could not directly have given rise to that of *Kyphosus,* or vice versa. Therefore it is somewhat disconcerting to find certain families with the jaw specializations of those families with an axillary process to be without such a process. Among such families would appear

TABLE 2

TRENDS OF DEVELOPMENT IN TWO CATEGORIES OF PERCOID FAMILIES

AXILLARY PROCESS PRESENT	AXILLARY PROCESS ABSENT
Narrow-headed fishes, with the eye set well up and back on the head	Broad-headed fishes, with the eye set relatively far forward on the head
Feeding usually accomplished by nipping off or plucking out individual items from their surroundings	Feeding usually accomplished by engulfing whole animals
Carnivores, herbivores, or omnivores	Carnivores
Mouth relatively small	Mouth often large
Jaw teeth often reduced to a single specialized row, conical, incisiform, molariform, or fused	Teeth conical, usually in bands, used for grasping prey
Jaws capable of relatively slight lateral expansion	Jaws capable of relatively great lateral expansion
Maxillary shaft with little rotation when the mouth is opened, forming a supporting cap over the lateral end of the premaxillary	Maxillary shaft with considerable rotation when the mouth is opened, giving slight support to the lateral end of the premaxillary

to be the Sillaginidae (which I have not seen) and the Branchiostegidae (Table 1). No explanation for these apparent anomalies will be attempted here.

The remaining question to be discussed is how Regan's arrangement (1913) of percoid families agrees with other proposed classifications. Since Patterson's views (1964) are much the most radical (see above), they will be considered first. Patterson, as previously noted, has suggested five independent origins for different percoid families. Only one point with regard to these percoid derivations will be added here. Patterson (1964:470, and elsewhere) stressed the primitiveness among percoids of the Scorpidae, Monodactylidae, and Kyphosidae as being "the only perciform families which retain both a toothed endopterygoid and a separate foramen for the hyomandibular trunk of the facial nerve in the lateral wall of the pars jugularis." Although the "primitiveness" of these particular features is not in dispute, it would seem that the dentition and jaw structure of at least *Kyphosus* in the Kyphosidae and of *Microcanthus* in the Scorpidae (Scorpididae) are highly specialized and have evolved a long way from that of *Berycopsis,* from which Patterson would derive them. If, in fact, one were to use jaw structure as a basis for postulating lineages, *Berycopsis* would seem to provide a much more appropriate ancestor for either *Epinephelus* or *Lates* than for *Kyphosus* or *Microcanthus.*

Freihofer (1963) surveyed the various pathways followed by the ramus lateralis accessorius of the facial nerve in teleostean fishes with particular reference to the percoids. These different pathways were then grouped into patterns. Freihofer's Patterns 8, 9, 10, and 13 occur among the percoids, though 13 is restricted to the family Mullidae; it should also be added that a rather large number of species distributed through various percoid families have the ramus lateralis accessorius absent or reduced. An arrangement of percoid families based solely on the patterns worked out by Freihofer would cut across that of Regan (1913), for Patterns 8, 9, and 10 all occur among families with an axillary process and again among families without an axillary process. Thus, the two methods of arrangement would divide percoid families in quite different

ways, although neither one is for that reason necessarily an incorrect indicator of relationships.

The last arrangement of percoid families that will be discussed is that of Matsubara (1955a,b, 1963). Matsubara raises the divisions (superfamilies) of Regan (1913) and of Norman (1957) to subordinal status. But more pertinent to the present discussion, he places the families accepted here as members of the Percoidae under four different suborders. The family Coryphaenidae he places in the Scombrina (equals Scombroidei). The Carangidae, Formiidae, Leiognathidae, Lactariidae, Menidae, and Rachycentridae comprise Matsubara's (1955a:ix) Carangina. The Monodactylidae, Toxotidae, Drepanidae, Ephippidae, Platacidae, Scorpididae, Antigoniidae, Chaetodontidae, Scatophagidae, Zanclidae, and Acanthuridae make up his (Matsubara, 1955b:i) Chaetodontina. In the Percina Matsubara (1955a:ix–x) includes the remainder of the families considered here as percoids, and adds the Cirrhitidae. His serial arrangement of families, though not his groupings, seem to follow rather closely Jordan's (1923) "Classification of Fishes." (Perhaps Matsubara has stated the historical background for his classifications of 1955 and 1963, but both these works are in Japanese and I have been able to get only parts of them translated.) Actually, the relationships of the groups excluded from his Percina have been moot points for a long time (Gregory, 1933). The difficulty, if the carangoids and chaetodontoids are set up as separate groupings from the percoids, is to know what to include in them and on what basis. No two authors are agreed on these matters. If and when carangoid and chaetodontoid groups can be satisfactorily defined, they should undoubtedly be recognized; meanwhile, however, more confusion than clarification would seem to result from such recognition.

SUMMARY AND CONCLUSIONS

The various percoid fishes (Superfamily Percoidae) are considered to represent a single structural theme with numerous variations. There seems no need to consider the group to be of polyphyletic origin, and data on the

supraoccipital crest and on the jaw structure are offered as evidence against certain of Patterson's (1964) specific polyphyletic derivations.

The limits of the superfamily Percoidae adopted by Regan (1913) and Norman (1957) are accepted here, not because they are definitive but because at present they seem to be more concretely based than others yet proposed.

Data on feeding habits, dentition, and jaw structure are brought out in support of an arrangement of percoid families proposed by Regan (1913). That much remains unsatisfactory in this or any other arrangement has been clearly indicated, it is hoped.

REFERENCES

DOBZHANSKY, T. 1954. Evolution as a creative process. Atti del IX Congresso Internazionale di Genetica, pp. 435–449.

FRASER-BRUNNER, A. 1946. On the systematic position of a fish, *Microcanthus strigatus* (C. & V.). Ann. Mag. Nat. Hist., ser. 11, 12:462–468, 3 figs.

FREIHOFER, W. C. 1963. Patterns of the ramus lateralis accessorius and their systematic significance in teleostean fishes. Stanford Ichthyol. Bull. 8:80–189, 29 figs.

FROST, G. A. 1927. A comparative study of the otoliths of neopterygian fishes (*continued*). XVIII. Percomorphi. Ann. Mag. Nat. Hist., ser. 9, 20:298–305, pl. 5.

――― 1928. A comparative study of the otoliths of neopterygian fishes (*continued*). XVIII. Percomorphi (*continued*). Ibid. ser. 10, 1:451–456, pl. 17.

GOSLINE, W. A. 1960. A new Hawaiian percoid fish, *Suttonia lineata,* with a discussion of its relationships and a definition of the family Grammistidae. Pacific Sci. 14:28–38, 8 figs.

――― 1961. The perciform caudal skeleton. Copeia, 1961: 265–270, 3 figs.

GREGORY, W. K. 1933. Fish skulls: a study of the evolution of natural mechanisms. Trans. Am. Philosoph. Soc., new ser., 23:75–481, 302 figs.

JORDAN, D. S. 1923. A classification of fishes. Stanford Univer. Publ., Biol. Sci. 3:79–243.

KATAYAMA, M. 1959. Studies on the serranid fishes of Japan (1). Bull. Faculty Educ., Yamaguchi University 8:103–180, 39 figs.

MATSUBARA, K. 1955a. Fish Morphology and Hierarchy. Part I. [In Japanese.] Ishizaki-shoten, Tokyo: xi + 789 pp., 289 figs.

――― 1955b. Fish Morphology and Hierarchy. Part II. [In Japanese.] Ishizaki-shoten, Tokyo: v + 790–1605, figs. 290–536.

――― 1963. Animal Systematic Taxonomy. Vol. 9, Part 2, Vertebrates (Ib), Fishes. [In Japanese.] Tokyo. Pp. 197–531, figs. 195–657.

NORMAN, J. R. 1934. A Systematic Monograph of Flatfishes (Heterosomata). Vol. 1. British Museum, London. viii + 459 pp., 317 figs.

PATTERSON, C. 1964. A review of Mesozoic acanthopterygian fishes, with special reference to the English Chalk. Philosoph. Trans. Roy. Soc. London, ser. B, 247:313–482, pls. 2–5, 103 text figs.

REGAN, C. T. 1909. On the anatomy and classification of the scombroid fishes. Ann. Mag. Nat. Hist., ser. 8, 3:66–75.

――― 1913. The classification of the percoid fishes. Ibid. 12:111–145.

――― 1940. The perciform genera *Gymnapogon* and *Nannatherina*. Copeia, 1940:173–175.

SMITH, C. L., and R. M. BAILEY. 1961. Evolution of the dorsal-fin supports of percoid fishes. Papers Michigan Acad. Sci., Arts, and Letters 46:345–362, 1 pl., 1 text fig.

――― 1962. The subocular shelf of fishes. J. Morphol. 110:1–10, pls. 1–3.

STARKS, E. C. 1904. The osteology of some berycoid fishes. Proc. U. S. Natl. Mus. 27:601-619, 10 figs.

SUZUKI, K. 1962. Anatomical and taxonomical studies of the carangid fishes of Japan. Rept. Faculty of Fisheries, Prefectural Univ. of Mie 4:43–232, 61 figs.

VAN DOBBEN, W. H. 1935. Über den Kiefermechanismus der Knochenfische. Archives Néerlandaises de Zoologie 2:1–72, 50 figs.

WEBER, M., and L. F. DE BEAUFORT. 1929. The Fishes of the Indo-Australian Archipelago. Vol. V. Brill, Leiden. xiv + 458 pp., 98 figs.