

Relationships among Some Relatively Deep-Bodied Percoid Fish Groups

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Abstract The nominal families considered here are the Kyphosidae, Scorpididae, Girellidae, Labracoglossidae, Oplegnathidae, Scatophagidae, Pomacanthidae, Chaetodontidae, Monodactylidae, Ephippidae and Drepanidae. All of these except the Pomacanthidae were recognized as families by Regan (1913) though the taxonomic status of some of them has been downgraded since. On the basis of morphological features these nominal families are divided into three groups: (1) the Ephippidae and Drepanidae, (2) the Monodactylidae, and (3) a series containing the remaining nominal families. It is postulated that the Ephippidae, probably the Monodactylidae, and the kyphosid-chaetodontid series developed their deep body-forms independently and that many of their similarities are the result of secondary developments functionally associated with such a body-form.

The fifty or so families of percoid fishes present one of the most perplexing problems of ichthyology. The aspect of this problem of particular concern here is that of family relationships. The interpretation of interrelationships among percoid families is particularly complex because these families appear to stand at the base of a very extensive adaptive radiation. They appear to have evolved similar specializations repeatedly, e.g., the deep body form with concomitant attributes (see below). The question thus arises in an acute form of which of these specializations indicate relationships and which are the result of parallel or convergent evolution. If this had been an easy question to answer, the problem of interrelationships among percoid families would have been solved long ago.

In the past, percoid families have been arranged in various ways. The groups into which they were segregated by earlier authors, e.g., Jordan (1923), have proved in large part to be artificial assemblages. Today, most classifications of percoid families follow the arrangement of Regan (1913), which merely treats the percoid families consecutively, starting with the more generalized groups and ending with the more aberrant families. It appears that a better knowledge of interrelationships among individual percoid groups will have to precede any meaningful subdivision of percoid fishes as a whole.

The present paper deals with relationships among certain of the families usually placed toward the last in arrangements of percoid families. A large proportion of them have recently been dealt with by Mok and Shen (1983; see Addendum). Most of the fishes included are marine, tropical, small-mouthed and relatively deep-bodied. Because of superficial similarities, deep-bodied perciform fishes of quite different lineages have frequently been included in the same taxonomic unit, e.g., the Chaetodontidae of Weber and de Beaufort (1936). Many such similarities seem to be functionally associated with the deep body form, which has evolved repeatedly. A few resemblances of this type may be noted here. Basic to several of these is the inability of such fishes to attain a rapid swimming speed. Fishes with a body depth greater than that of *Caranx* have given up the generalized percoid feeding habit of out-swimming relatively large prey. All of the fishes considered here are small-mouthed and, like other such percoids, have lost the supramaxillary. They seem to feed by various systems of nipping, scraping, plucking or/and plankton picking, and many of them have highly specialized dentitions of different types.

One specialization associated with feeding that has evolved two, perhaps three, times among the fishes considered here is probably related to the increased declivity of the anterior profile in deep-bodied forms. The usual pre-

maxillary protrusion in percoid fishes involves the anteroventral sliding of the ascending premaxillary processes along an ethmovomerine ridge that forms the anterior rim of the skull. This type of structural organization in deep-bodied fishes with an anterior profile that is nearly vertical results in an upper jaw that is protruded downward. Some of the groups considered here have reconstituted a more forward type of jaw protrusion by developing a cavity in the front of the skull over the floor of which the ascending premaxillary processes slide.

Another set of morphological adjustments in deep-bodied fishes associated with forward locomotion has to do with the vertical fins. With increasing body depth in compressed fishes, the relative surface of the posterior parts of the body increases compared to that of the caudal fin. The soft dorsal and anal fins of such fishes are frequently large and the caudal fin small. Some chaetodontids, for example, have a small brush-like caudal fin that does not even extend beyond the dorsal and anal, and their attempts to move rapidly consist of swinging the whole posterior end of the body from side to side. In such movements the soft dorsal and anal fins act as a posterior extension of the body, and the scales of the body are continued out on the fin bases (as they are in all but *Girella* among the fishes discussed here).

The continuation of body movements into the vertical fins of these fishes also seems to be reflected in their dorsal fin configurations. In deep-bodied forms in which the soft dorsal moves primarily or entirely with the body, as does the spinous dorsal, the two dorsal fins are continuous. This is not true of deep-bodied forms in which the soft dorsal moves independently of the body, e.g., most zeiform and plecognath fishes; here the spinous and soft dorsal fins may be completely separate. Nor do the soft dorsal fins of such fishes have a basal sheath of scales.

Material examined

The primary material examined for this paper, all of it in the University of Michigan fish collections, is listed below alphabetically by nominal families.

Kyphosidae: *Kyphosus cinerascens* (183097, 1 spec., 118 mm.), Japan; *Kyphosus sectatrix* (187001-

s) skeleton, Florida.

Scorpididae: *Medialuna californiensis* (130678, 1 spec., 116 mm), California; (177368-s) skeleton, California; *Microcanthus strigatus* (56739, 1 spec., 88 mm), Hawaii.

Girellidae: *Girella nigricans* (92628, 2 specs., 135 and 147 mm), California; (176307-s) skeletons from aquarium discards; *Girella punctata* (183078, 2 specs., 114 and 160 mm), Japan.

Labracoglossidae: *Labracoglossa argentiventris* (142717, 2 specs., 143 and 146 mm), Japan.

Oplegnathidae: *Oplegnathus fasciatus* (185129, 5 specs., 67–118 mm), Japan; *Oplegnathus punctatus* (176817, 1 spec., 92 mm), Japan.

Scatophagidae: *Scatophagus argus* (3 specs., 22–58 mm) uncataloged aquarium specimens; (177347-s) skeleton of aquarium specimen; *Scatophagus tetracanthus* (209045, 2 specs., 22 and 26 mm), Philippines.

Pomacanthidae: *Centropyge bispinosus* (185891, 5 specs., 32–65 mm), Madagascar; *Centropyge potteri* (196203-s) skeleton of aquarium specimen; *Holacanthus passer* (190204, 2 specs., 110 and 113 mm), Costa Rica; *Holacanthus tricolor* (194994-s) skeleton, Florida; *Pomacanthus arcuatus* (172867, 1 spec. 69 mm), Puerto Rico; (187016-s) skeleton, Florida.

Chaetodontidae: Skeletons from aquarium specimens of *Chaetodon falcula*, *Chelmon rostratus*, *Forcipiger longirostris* and *Heniochus acuminatus*.

Monodactylidae: *Monodactylus argenteus* (198067, 3 specs., 63–77 mm), Mariana Islands; *Psettias sebae* (187909, 5 specs., 50–67 mm), Sierra Leone.

Ephippidae: *Chaetodipterus faber* (145905, 6 specs., 76–85 mm), Texas; (187015-s) skeleton, Florida; *Ephippus orbis* (176576, 1 spec., 82 mm), Java; *Platax pinnatus* (189535-s) skeleton of aquarium specimen.

Drepanidae: *Drepane punctata* (3 specs., 88–100 mm), uncataloged material without data.

Relationships

Gregory (1933), following an earlier proposal by Boulenger (1910), postulated the derivation of the most deep-bodied of the groups considered here, i.e., the Monodactylidae, the Ephippidae and the Chaetodontidae from the family Scorpididae. This postulate is only supported by characteristics of a rather general nature. Two morphological features: posterior projections from the epiotics (Fig. 1) and ventral extensions of the coracoids that meet the tip of the cleithra (Fig. 2A, B) suggest (1) the validity of such a series but (2) the exclusion from it of the Ephip-

pidae and (3) the inclusion in it of certain families not mentioned by Gregory. Different grounds suggest at least the provisional exclusion of the Monodactylidae from the scorpidid-chaetodontid series.

A synopsis of the three main groups considered here, with their included nominal families, is given below.

1a. Epiotics with posteriorly-extending body projections; coracoids reaching the ventral ends of the cleithra (except *Scatophagus*).

2a. Supraoccipital crest not extending to the preorbital area of the head; pelvic fins normally developed; swim bladder not extending much, if any, behind body cavity. Kyphosidae, Scorpididae, Labracoglossidae, Girellidae, Oplegnathidae, Scatophagidae, Pomacanthidae and Chaetodontidae.

2b. Supraoccipital crest extending forward on to the preorbital part of the head; pelvic fins rudimentary; swim bladder extending well behind body cavity. Monodactylidae.

1b. No posterior projections on the epiotics; coracoids not reaching the ventral ends of the cleithra. Ehippididae and Drepanidae.

Neither epiotic projections nor ventrally-extended coracoid bones are unique to the groups of fishes indicated above. Epiotic projections (Fig. 1; for an illustration of these in *Chaetodon*, see Motta, 1982: fig. 2) occur elsewhere among percoids in such fishes as the percichthyid genus *Lateolabrax* (Katayama, 1959, fig. 16) and in teraponids. The coracoid extensions are even less diagnostic, for they occur in a number of unrelated deep-bodied fishes. Perhaps the most notable aspect of such extensions in the fishes under consideration is that they occur in the rather fusiform *Labracoglossa* but are not present in the deep-bodied ehippids. The shape of the space between the coracoid and cleithrum in the scorpidid-chaetodontid series is rather distinctive. It is usually rather elongate and broadens below the middle (Fig. 2A). Its width may be restricted in the central region, and in chaetodontids (Fig. 2B), also in *Monodactylus*, the central area is completely closed, leaving openings above and below.

In the following accounts of individual groups, the members of the scorpidid-chaetodontid series are dealt with first. Among these, the nominal

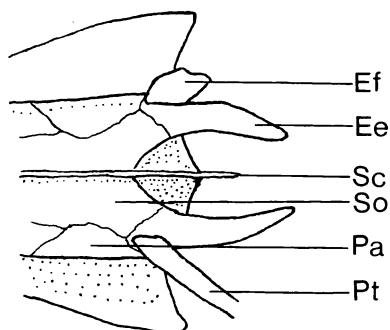


Fig. 1. Dorsal view of the posterior part of the skull of *Kyphosus sectatrix*, with the left posttemporal included. Ee, posterior extension of the epiotic; Ef, epiotic facet for the posttemporal articulation; Pa, parietal; Pt, posttemporal; Sc, supraoccipital crest; and So, supraoccipital.

families Kyphosidae, Scorpididae, Girellidae and Labracoglossidae are taken up together, the other families separately. The monodactylid and ehippid groups are discussed at the end of the paper.

The nominal families Kyphosidae, Scorpididae, Girellidae and Labracoglossidae. Concepts concerning these four nominal families, which I think can at least provisionally be combined under the name Kyphosidae, have changed considerably. In the Scorpididae Norman (1966) included six genera. Of these, the large-mouthed *Parascorpis* was removed to its own separate family by Smith (1949). (I have not seen *Parascorpis*, which is omitted from further consideration here.) Conversely, *Microcanthus*, formerly placed in the Chaetodontidae, was transferred to the Scorpididae by Fraser-Brunner (1945).

At the family level of classification, the Kyphosidae, Scorpididae, Girellidae and Labracoglossidae were all considered as separate by Regan (1913), followed by Norman (1966). However, at least as far back as Jordan and Evermann (1898), American kyphosids, scorpidids and girellids were all included in the single family Kyphosidae. In Regan's (1913) account of percoid families, the Labracoglossidae were widely separated from the other three groups, presumably because of the absence of a pelvic axillary process. However, I cannot see that the axillary process of *Labracoglossa* is

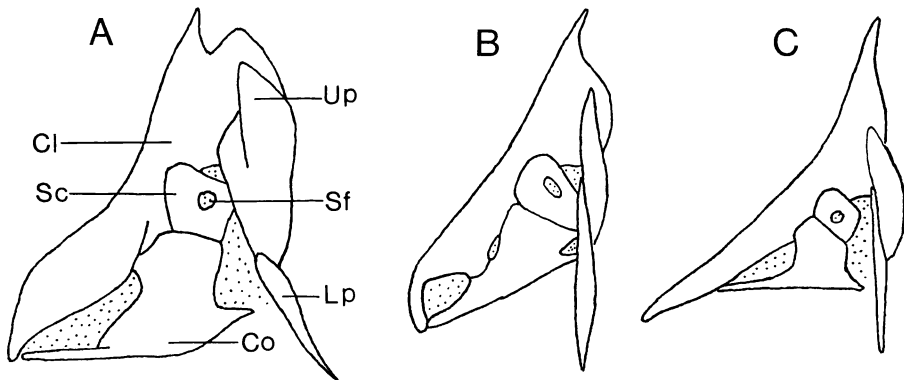


Fig. 2. Internal view of the lower parts of the pectoral girdle and postcleithra of A, the kyphosid (sensu lato) *Girella nigricans*; B, the chaetodontid *Heniochus acuminatus*; and C, the ephippid *Chaetodipterus faber*. Cl, cleithrum; Co, coracoid; Lp, lower postcleithrum; Sc, scapula; Sf, scapular foramen; and Up, upper postcleithrum.

much different from that in the other three nominal families. Regan (1913) also stated that labracoglossids lack a subocular shelf, but one is present and well-developed, at least in *Labracoglossa* (Smith and Bailey, 1962). In 1980, Johnson (p. 9) included *Labracoglossa argentiventris* in the Scorpididae without comment, but he also listed, again without comment, the Girellidae, Kyphosidae, Microcanthidae and Scorpididae as separate families.

Though members of all four nominal families are available, the representation is inadequate for defining or delimiting subgroups. Available members suggest a single, rather coherent group of fishes of a rather generalized percoid nature. Among characters suggesting basal percoid affinities is the serrated lacrimal of *Kyphosus*. This feature occurs again in two, more specialized components of the scorpidid-chaetodontid lineage, namely the Scatophagidae and Pomacanthidae, but in these the serrated lacrimal may have evolved independently.

Available members range from the apparently nektonic *Labracoglossa* to more or less strictly benthonic forms like *Microcanthus* and *Girella*. The plankton-feeding *Labracoglossa*, at one extreme, is a fusiform fish with a deeply-forked tail, projecting jaws, abundant and generalized dentition, and gill openings that extend far forward under the throat. At the other extreme, *Microcanthus* and *Girella* are two quite different fishes that hold in common a deep body-form, slightly indented caudal fin outlines,

and restricted dentition and gill openings.

The principal specializations of these four nominal families, as compared to basal percoid groups, are the epiotic and coracoid extensions and the small mouths. A number of characteristics seem to be associated with their small gapes. The presence of a fatty-fibrous layer between the skin and the skull in the area over the front of the eye may belong here. There is also considerable variation and specialization of dentition within the group. The jaw teeth may be villiform and conical (*Labracoglossa*), at least partly incisiform (*Medialuna*, *Kyphosus*, *Girella*), or setiform (*Microcanthus*). There are granular teeth on the tongue, vomer, palatines and mesopterygoids in *Labracoglossa*, *Kyphosus* and *Medialuna*, but not in *Girella* and *Microcanthus*. *Labracoglossa* also has median tooth plates on the basibranchials. In *Kyphosus* and *Medialuna* there are long, needle-like teeth on the pharyngeals and, sparingly, on the posterior gill arches; the other genera do not have such teeth.

In a number of morphological features *Girella* is the most distinctive of available members of the group. Externally, the heavy scaly sheaths on the soft dorsal and anal fins of other members of the group are greatly reduced. Osteologically, the mesopterygoid is a very small bone that has only a slight medial projection over the roof of the mouth and barely meets the metapterygoid posteriorly. The urohyal has an anterior, upright projection

(Kusaka, 1974). The upper postcleithrum is broadly expanded (Fig. 2B). The vertebrae (said to be 27 or 28 by Jordan and Evermann, 1898) are more numerous than in any other members of the whole series. *Girella* also has two specializations in head musculature. The upper part of the *M. levator arcus palatini*, at least in the adult, extends forward over the dermosphenotic ossicle, and a part of the *M. adductor mandibulae* is directly attached to the posterior rim of the mandible. These peculiarities of *Girella*, if they occur in the other, unavailable genera related to it, might justify family recognition for the Girellidae.

Family Oplegnathidae. Largely because of the highly specialized, beak-like jaws of its only genus, the Oplegnathidae (Hoplegnathidae auctorum) have always held an ambiguous position among percoid families. They have not previously been placed with the scorpidid-chaetodontid series. However, they have the epiotic and coracoid extensions used here to define the series, and their more general features appear to agree with such a placement. The small, beak-like jaws seem to be still another type of the various tooth and jaw specializations represented in the series. Unlike the Scaridae, which have similar beak-like jaws, the Oplegnathidae have the usual percoid type of pharyngeal dentition.

Family Scatophagidae. *Scatophagus*, the only genus in its family, has, along with the Pomacanthidae, often been included in the Chaetodontidae, e.g., by Weber and de Beaufort (1936). All three of these groups contain high-bodied, strong-spined, shell-headed fishes with the upper rim of the supraoccipital crest laterally expanded over the nape. All three groups have small mouths with more or less setiform teeth, some of them tricuspid in *Scatophagus*, the lower arm of the posttemporal short, and, except *Pomacanthus*, the lower extrascapular bone expanded. The differences between the three groups are, however, extensive.

Scatophagus differs from both the Pomacanthidae and Chaetodontidae in having the usual percoid type of premaxillary protrusion with the ascending premaxillary processes sliding over an ethmovomerine ridge, the gill covers attached to one another across the isthmus, and the anterior part of the interopercle concealed

under the preopercle. *Scatophagus* differs not only from the Pomacanthidae and Chaetodontidae but from all other members of the scorpidid-chaetodontid series in several features. The coracoid does not reach the lower end of the cleithrum. The lacrimal is fused with the following circumorbital bone (Smith and Bailey, 1962), and the anterior rim of the lacrimal is supported by a strong lateral ridge on the palatine. There are only 23 vertebrae and 14 branched caudal rays (Regan, 1913).

These characters indicate a wide morphological separation between *Scatophagus* and other families. Furthermore, its morphological indicators of relationship point in various directions. *Scatophagus* passes through a larval stage of development (Weber and de Beaufort, 1936) that greatly resembles the tholichthys phase of chaetodontids, but not pomacanthids (Burgess, 1974). In postcleithral and rib structure *Scatophagus* resembles the pomacanthids rather than the chaetodontids. Finally, the coracoid structure of *Scatophagus* is more nearly that of the ephippids than of other members of the scorpidid-chaetodontid series.

Family Pomacanthidae. The Pomacanthidae have usually been considered a subfamily of the Chaetodontidae, e.g., by Fraser-Brunner (1933). However, Burgess (1974) not only pointed out a number of differences between the two groups but questioned whether they were closely related to one another, a question that seems well worth raising. The most striking similarity between the two groups is in their mouth structures. Both have setiform teeth and ascending premaxillary processes that extend into a cavity in the front of the skull. However, this same specialization occurs in *Drepane* of the ephippid group and may have developed independently in the pomacanthids and in the chaetodontids.

The pomacanthids, unlike any other groups discussed, have become specialists in head spines. Spines on the preopercle are always large, and in some genera may also be present on the interopercle and lacrimal. Perhaps the closest approach, in other members of the scorpidid-chaetodontid series, to the spiny-headed condition in the Pomacanthidae, is the serrated preopercle of *Microcanthus* or *Oplegnathus*. The scales of pomacanthids (Burgess, 1974) also resemble those of *Oplegnathus*.

Family Chaetodontidae. The chaetodontids are in many ways the most specialized family of percoid fishes, not least in the tholichthys-stage of larval development. This rather large family of highly conspicuous fishes has recently been treated by Burgess (1978) and needs no further comment here.

Some notes are appended regarding two groups of fishes included by Gregory (1933) in the scorpidid-chaetodontid lineage but here excluded, the Monodactylidae provisionally.

Group 1. Family Monodactylidae. The two available genera of the family, *Monodactylus* and *Psettias*, possess, in reduced form, the epiotic extensions used to characterize the scorpidid-chaetodontid lineage. They also have the coracoid extensions, and in *Monodactylus* the space between the coracoid and cleithrum is divided into two parts as in chaetodontids (Fig. 2B).

Monodactylus and *Psettias* possess, however, a number of features that do not occur elsewhere among the fishes under consideration. As noted in the synopsis above, their pelvic fins are rudimentary, the swim bladder extends well beyond the body cavity, and the supraoccipital is continued forward on to the preorbital part of the head. In addition, both genera have a palatine attachment to the ethmoid-maxillary ligament.

In several features these two genera resemble the carangid-like *Apolectis* (*Parastromateus* auctorum). However, the third genus, *Schuetzia* (*Bramichthys* auctorum), included in the Monodactylidae by Regan (1913) and Norman (1966) is a much less deep-bodied fish with normally-developed pelvic fins. Internal characteristics of *Schuetzia* appear to be unrecorded. If *Schuetzia* is indeed a monodactylid, it may provide better indications of the derivation of the family than the two specialized genera available, and any final evaluation of monodactylid relations seems best deferred until *Schuetzia* is reinvestigated.

Group 2. The nominal families Ehippidae and Drepanidae. Of the six genera assigned to the Ehippidae by Norman (1966) only *Chaetodipterus*, *Ehippus* and *Platax* are available. *Drepane*, the only genus in the Drepanidae, has been examined.

The ehippid-*Drepane* group has usually been placed close to the Chaetodontidae, which it

resembles in a number of respects, e.g., the deep body, scaled fins, small mouth with setiform teeth and, in *Drepane*, the ascending premaxillary processes that slide over the base of a cavity in the front of the skull (Starks, 1926). Furthermore, *Platax* of the Ehippidae and *Heniochus* both have long membranous extensions from the front of the dorsal fin and large pelvic fins. However, I think these similarities are the results of secondary convergence associated with the development of a deep body-form. In skull characteristics the ehippid-*Drepane* group and the chaetodontids are very different. Chaetodontids have a shell-like cranium with numerous specialized features, none of which are present in ehippids or *Drepane*. As to the two features used to characterize the scorpidid-chaetodontid series, the ehippids and *Drepane* lack them and show no indication that they ever had them. The ehippids appear to be deep-bodied basal percoids, but I have been unable to find characteristics that would suggest a relationship with any particular basal percoid group.

Drepane seems clearly related to the ehippids but differs in a number of features, the most notable of which is the system of jaw protrusion previously noted. *Drepane* has frequently been included in the Ehippidae, and there seems no reason to object to such an allocation.

Addendum

The present article, written before Mok and Shen's (1983) paper became available, has been left essentially unchanged inasmuch as it takes up partly different fish groups, deals with different morphological characters, and approaches the subject matter differently. Suffice it to say that the conclusions reached here agree in part and disagree in part with those of Mok and Shen.

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スズキ亜目の体高の高いグループ間の類縁関係

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イスズミ科, カゴカキダイ科, メジナ科, タカベ科, イシダイ科, クロホシマンジュウダイ科, キンチャクダイ科, チョウチョウウオ科, ヒメツバメウオ科, ツバメウオ科およびスダレダイ科の類縁関係を考察した。これらのうちキンチャクダイ科を除くグループは Regan (1913) によって科として認められた。しかし、その後、これらのいくつかは下位の分類群として扱われるようになった。形態学上の特徴により、これらの科は3グループに分けられる。(1) ツバメウオ科とスダレダイ科, (2) ヒメツバメウオ科および (3) 残りの科。ツバメウオ科, 恐らくヒメツバメウオ科も、そして残りの他の科の3グループは、別個に体高の高い体形を発達させたのであり、これらのグループ間の多くの類似性は体高の高い体形にもなって発達した機能上の二次的な結果と考えられる。