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**CONSIDERATIONS REGARDING THE RELATIONSHIPS OF
THE PERCOPSIFORM, CYPRINODONTIFORM, AND
GADIFORM FISHES**

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AMONG modern teleostean fishes above the scopoliform (myctophiform or iniomous) level of structural organization and below that of the Perciformes, there is a chaotic jumble of orders of controversial or unknown affinities. In the present paper I have attempted to work out the interrelationships among certain of these. The fishes dealt with here are those included in the orders Percopsiformes, Cyprinodontiformes, and Gadiformes. The presentation has been divided into three sections. The first takes up a postulated relationship between the Percopsiformes, the Gadiformes, and the suborder Amblyopsoidei of the Cyprinodontiformes. The second discusses the presumed affinity between the suborders Amblyopsoidei and Cyprinodontoidei of the Cyprinodontiformes. The third deals with taxonomic considerations.

Certain points regarding terminology may be advantageously treated here. For purposes of the present paper the names and content of orders and suborders follow Berg (1940), with the following exception. The order Mugiliformes is here considered to contain the polynemid, sphyraenid, mugilid, atherinid, and phallostethid fishes (Gosline, 1962). With regard to vernacular names, the endings *id*, *oid*, and *iform* will be used for family, subordinal, and ordinal groups, respectively. Bone names are from Devillers (1958).

The primary material on which this paper is based consists of alizarin-stained, partly dissected specimens of each of the following species: Clupeiformes; *Umbra pygmaea* (105502) and *Dallia pectoralis* (164848). Beloniformes; *Chriodorus atherinoides* (102192) and *Exocoetus obtusirostris* (176556). Gadiformes; *Microgadus proximus* (106412)

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and *Merluccius productus* (106416). Percopsiformes; *Percopsis omiscomaycus* (56829) and *Aphredoderus sayanus* (128227). Cyprinodontiformes; *Amblyopsis spelaea* (146994), *Chologaster agassizi* (177561), *Aplocheilichthys panchax* (146559), *Rivulus holmiae* (141930), *Profundulus guatemalensis* (166697), *Fundulus majalis* (66865), *Floridichthys carpio* (153586), and *Belonesox belizanus* (159298). Mugiliformes; *Sphyræna argentea* (63644) and *Atherinops affinis* (131818). Perciformes; *Stizostedion vitreum* (from exchange material) and *Centropomus viridis* (172103). Each number in the above paragraph refers to a catalog lot in the University of Michigan Museum of Zoology fish collection from which the specimen was taken. For each species listed a single subadult or adult was stained, except for *Chologaster* which is represented by half-grown material. Wherever in the paper a generic name is used alone, it is the species listed above that is referred to. However, other unstained material from the same and other lots, skeletons, and, in the case of *Chologaster*, stained and cleared materials were also used.

The work reported here was done at the Museum of Zoology of the University of Michigan while on sabbatic leave from the University of Hawaii. For the opportunity to use the space, facilities, and specimens of the Museum of Zoology, I am greatly indebted to the staff of that institution, especially to Dr. R. M. Bailey. I should also like to thank Dr. Warren Freihofer of Stanford University for his comments on the manuscript.

SECTION I. THE RELATIONSHIPS AND SYSTEMATIC POSITION OF PERCOPSIFORM FISHES

The old name Salmopercae indicates well the mosaic nature of percopsiform characteristics. Thus, *Percopsis* has an adipose fin and several more salmon-like features. On the other hand, Hubbs (1919) showed that in branchiostegal-ray structure the percopsiform fishes belong among the higher, "acanthopteran" teleosts, and various other lines of evidence point in the same direction. Presumably then the nearest living relatives of the percopsiform fishes should be sought among the lower "acanthopteran" groups, i.e., those below the perciform level of structural organization. Such are the cyprinodontiform, gadiform, lampridiform, syngnathiform, gasterosteiform, beryciform-stephanoberyciform, zeiform, mugiliform, and possibly the anabantid-ophiocephalid fishes (and some little-known oceanic groups). As the result of a search for similarities among the members of this rather extensive list, it was found that the percopsiform fishes and the first

three of the groups named have two characteristics in common. First, none of the percopsiform, cyprinodontiform, gadoid-macrouroid, or lampridiform fishes have a true pelvic spine, whereas at least some members of all the other groups listed do (Gosline, 1961a, diagram 3; since that diagram was compiled I have discovered that at least some of the centriscoids, notably *Notopogon*, among the Syngnathiformes have a well-developed pelvic spine). Second, the percopsiform, gadiiform, amblyopsoid, and at least some of the lampridiform fishes have, in the caudal skeleton, an intervertebral-like articulation between the base of one of the upper hypurals and the terminal vertebra (see below, also Whitehouse, 1910, pl. 49, figs. 17, 18; Gosline, 1961a, figs. 2, C, D, and 3, A, B, and D).

Whether these similarities provide an indication of interrelationships rather than of convergence is of course a question that can be answered only through an investigation of additional characters. In the case of the Lampridiformes such an inquiry has not been made, though the literature strongly suggests that the Lampridiformes do not belong with the groups dealt with here. However, further work on the percopsiform fishes, gadoids, and amblyopsoids has led to the conclusion that these groups really are related. It is the results of this inquiry that are presented in this section.

The two (or three) living genera of percopsiform fishes, *Percopsis* (of which *Columbia* is sometimes considered a synonym) and *Aphredoderus*, are restricted to the fresh waters of North America. They are quite different, both externally and internally, and have always been placed in separate families. Indeed, *Percopsis* appears to stand somewhat nearer the base of the gadoid stock, while *Aphredoderus* belongs closer to that of the amblyopsoids. Nevertheless, there seems no reason to doubt the generally admitted relationship of *Aphredoderus* and *Percopsis* (see, however, Starks, 1926:212).

THE CRANIUM

The skull of percopsiform, gadoid, and amblyopsoid fishes tends to be low and broad. The eye sockets do not reach the midline, with the result that the orbital boundaries are well separated from one another. Associated with this, the olfactory nerves pass forward between the orbits rather than through them (see below). Also, the basisphenoid has been lost. In *Percopsis* and *Aphredoderus* the pleurospenoids (alisphenoids, pterosphenoids) abut below against the prootics (Figs. 1 and 2); however, in *Chologaster* (Fig. 3), which has a very flat head, the

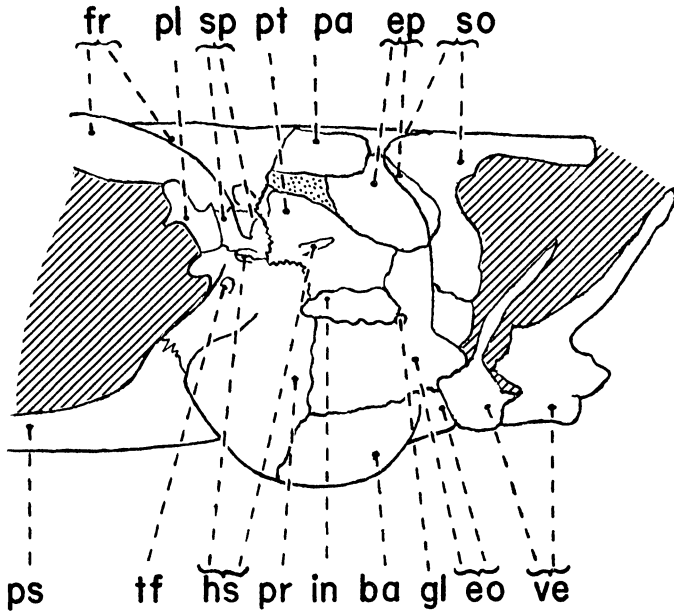


FIG. 1. Posterior portion of the skull and the first two vertebrae of *Percopsis omiscomaycus*, left lateral view. Cartilaginous area stippled; interorbital opening and intervertebral spaces cross-hatched: *ba*, basioccipital; *eo*, exoccipital; *ep*, epiotic; *fr*, frontal; *gl*, glossopharyngeal foramen; *hs*, hyomandibular socket; *in*, intercalar; *pa*, parietal; *pl*, pleurospenoid; *pr*, prootic; *ps*, parasphenoid; *pt*, pterotic; *so*, supraoccipital; *sp*, sphenotic; *tf*, trigeminal foramen; *ve*, vertebra.

pleurospenoids extend down from the skull roof well ahead of the prootics to an anterolateral expansion of the parasphenoid.

Of other cranial characters it only seems necessary to mention here that the orbitospenoid is invariably absent, that the intercalar (opisthotic) has a large surface area, and that the exoccipital condyles are well separated from one another in all three groups.

NASAL STRUCTURE AND BRAIN

The two nostrils on each side are close together in *Percopsis*, with the narrow fleshy bridge between the two forming a baffle, presumably for deflecting water into the anterior when the fish moves forward. In *Aphredoderus* the two nostrils of the same side are separated by a fleshy bridge that is wider than the nostrils; the posterior nostril is a round hole and the anterior one is in a short, projecting tube.

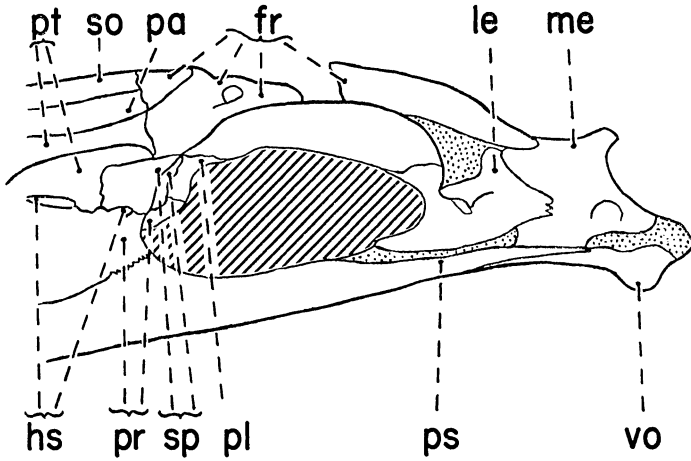


FIG. 2. Anterior portion of the skull of *Aphredoderus sayanus*, right lateral view. Cartilaginous areas stippled; interorbital opening cross-hatched: *fr*, frontal; *hs*, hyomandibular socket; *le*, lateral ethmoid; *me*, mesethmoid; *pa*, parietal; *pl*, pleurospenoid; *pr*, prootic; *ps*, parasphenoid; *pt*, pterotic; *so*, supraoccipital; *sp*, sphenotic; *vo*, vomer.

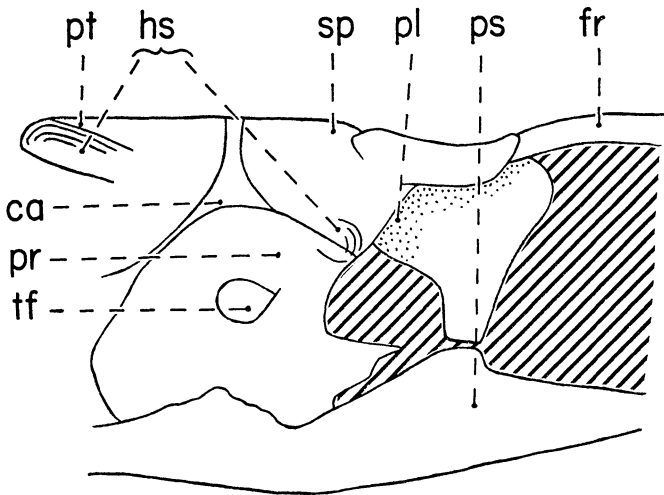


FIG. 3. Middle portion of skull of *Chologaster agassizi*, right lateral view. Interorbital opening cross-hatched: *ca*, cartilage; *fr*, frontal; *hs*, hyomandibular socket; *pl*, pleurospenoid; *pr*, prootic; *ps*, parasphenoid; *pt*, pterotic; *sp*, sphenotic; *tf*, trigeminal foramen.

The olfactory organ is in the form of a rather typical rosette in *Percopsis* (Fig. 4, B), *Aphredoderus*, *Amblyopsis* and the cod (cf., Burne, 1909:614, fig. 188, B). The nasal sac has no accessory diverticulum in *Percopsis*, *Aphredoderus*, the amblyopsoids, or most cods; however, one is present in *Merluccius* (Burne, 1909:617, fig. 191).

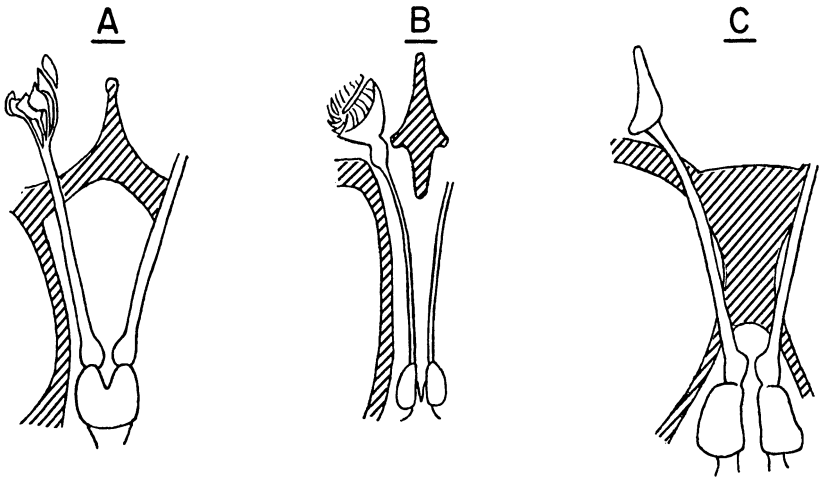


FIG. 4. Diagram of the cranial wall, olfactory lobes, nerves, tracts, and epithelium, as though the cranium were cut away just above these structures: A, *Aphredoderus sayanus*; B, *Percopsis omiscomaycus*; C, *Mollienesia sphenops*. Walls of cranium cross-hatched.

The nerve connecting the olfactory organ with the brain is quite different in *Percopsis* and *Aphredoderus*. In *Aphredoderus* (Fig. 4, A), the amblyopsoid genus *Chologaster*, and all cyprinodontoids (Fig. 4, C) examined, the olfactory bulb lies close to the forebrain and the olfactory nerve passes through the cranial wall far forward. In *Percopsis* (Fig. 4, B), the olfactory nerve tract is never strictly enclosed by the cranial wall but rather passes through a broad cavity in the lateral ethmoid to enter the nasal capsule; the olfactory bulb lies just behind the olfactory rosette. The same forward position of the olfactory bulb occurs in cods and certain other fishes (see Dietz, 1921:436, fig. 1; Svetovidov, 1953).

THE SENSORY CANALS AND RELATED BONES

The lateral line of the body is present and complete in *Percopsis* and usually in the cods (Svetovidov, 1948), present and incomplete in *Aphredoderus*, and absent in amblyopsoids.

On the head the sensory canals of all three groups are enlarged and are not bone-enclosed except frequently for the section of the supraorbital canal that passes through the rear of the frontals; elsewhere they lie in flesh-covered troughs. In *Aphredoderus* and *Percopsis* the sensory canals of the head have the usual configuration—the infraorbital canal is complete, the preopercular-mandibular canal joins the rest of the main system somewhat ahead of the incomplete supratemporal commissure, there is a frontal or supraorbital commissure, and the main head canal passes back on to the body from the pterotic via a tabular, the posttemporal and thence the supracleithrum; spaced along the whole system is a series of primary pores to the exterior. In the gadids (see Cole, 1898) the preopercular canal ends blindly above rather than joining the rest of the system, and frequently there are no primary pores between the primary canals and the exterior. In *Amblyopsis* and *Chologaster* the entire head is covered with loose, scaleless flesh; the sensory canals enclosed in this flesh are not conspicuous; they seem, however, to differ from the percopsiform configuration chiefly in the absence of frontal and supratemporal cross-commissures.

Of the sensory canal bones it seems necessary only to call attention to the circumorbital series. In *Percopsis*, apparently alone among the fishes under consideration, there is a separate antorbital bone (Gosline, 1961a:30). Aside from the antorbital, the percopsiform, gadiform, and amblyopsoid fishes all appear to have a complete series of circumorbital bones.

JAW MECHANISM AND ASSOCIATED STRUCTURES

In the percopsiform, gadiform, and amblyopsoid fishes, the ascending process of the premaxillary is usually rather low (Fig. 5, A–C). Laterally, the maxillary extends well beyond the tip of the premaxillary. There is no supramaxillary. In the percopsiform and gadiform fishes the upper lip overlaps the lower as usual, but in the amblyopsoids the lower lip folds out over the upper laterally as it does in the cyprinodontoids.

In the percopsiform and amblyopsoid fishes the upper jaw is more or less firmly attached to the cranium; in the gadids it seems to be at least moderately protrusile. Quite possibly related to this difference is the presence in the cods of crossed ethmoid-maxillary and premaxillary-palatine ligaments (see Burne, 1909:615, fig. 189; Dietz, 1921:445, fig. 7; 447, fig. 9). In certain cods, however, part of the premaxillary-palatine ligament has been figured as attached to that running from

the ethmoid to the maxillary (Burne, 1909, fig. 190; Schaeffer and Rosen, 1961, fig. 5, B). In the percopsiform and amblyopoid fishes, the crossed ligaments are present, but that from the ethmoid has developed a broad additional attachment to the palatine bone (Fig. 5, A, B).

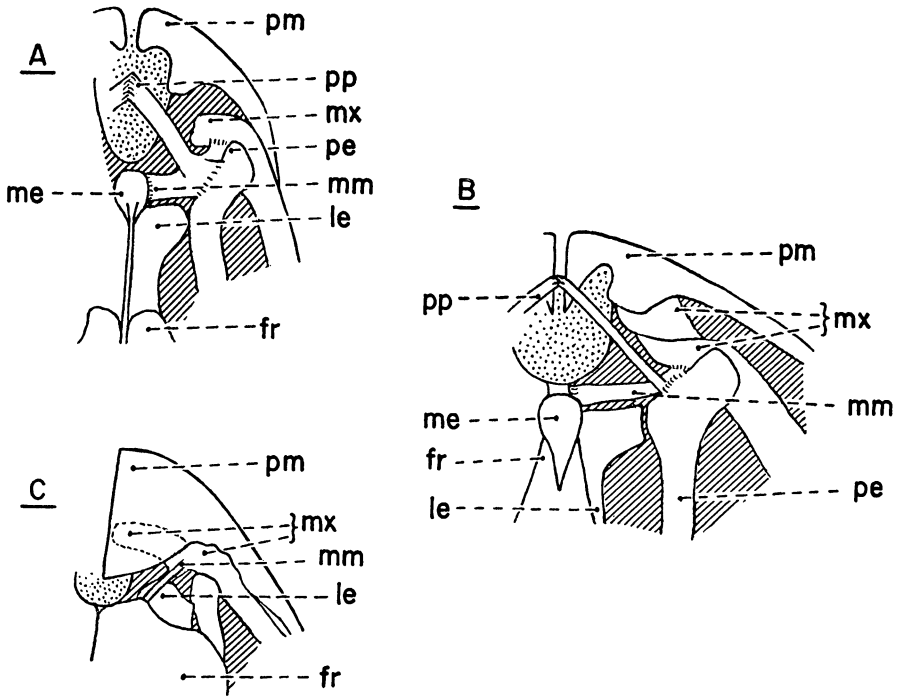


FIG. 5. Anterior portion of head, from above and with nasal bones removed, rostral cartilage stippled: A, *Aphredoderus sayanus*; B, *Amblyopsis spelaea*; C, *Aplocheilus panchax*; fr, frontal; le, lateral ethmoid; me, mesethmoid; mm, ethmoid-maxillary ligament; mx, maxillary; pe, palatine; pm, premaxillary; pp, premaxillary-palatine ligament.

Among cyprinodontoids, *Aplocheilus* (Fig. 5, C) and *Rivulus* appear to have only the pair of ligaments running from the ethmoid to the maxillary, and among other genera examined even these were not found.

That the crossed ligaments to the upper jaw vary elsewhere than in the cyprinodontiforms is easily demonstrated. Thus, among mugiliform fishes *Polydactylus* has the normal, crossed configuration, though the premaxillary-palatine ligament appears to be partly attached to

the ethmoid-maxillary ligament. In *Mugil* there seems to be only a fine ethmoid-maxillary ligament, as in *Aplocheilus* and *Rivulus*. In the atherinids *Atherinops* and *Chirostoma*, the ethmoid-maxillary ligament passes mainly to the palatine and only secondarily to the maxillary somewhat as in the amblyopsoids and percopsiform fishes.

In other subperciform groups the crossed ligaments appear to be just as variable. In the berycoid *Polymixia* both ligaments are present and cross one another, but in contrast to the situation in the amblyopsoid and percopsiform fishes both attach to the maxillary, and the tip of the palatine seems to have become entirely cartilaginous. In the berycoid family Holocentridae, and in the Gasterosteiformes, neither of the crossed ligaments was found; it appears that in both of these groups the protrusile premaxillaries are held down by the nasals which overlap them and are rigidly joined to the cranium.

Eaton (1935:164-66) stressed the similarity in jaw musculature between *Aphredoderus* and the gadids. Dietz (1921:444-53) used the same set of muscles as part of his demonstration of a supposed relationship between the gadids and *Liparis* and *Cyclopterus*. I am not sufficiently acquainted with jaw musculature to be able to evaluate its possibilities as an indicator of relationships.

In one aspect of jaw structure *Percopsis* and the gadoid *Merluccius* differ from *Aphredoderus* and *Gadus*. In *Percopsis* and *Merluccius* the toothless palatine is flexibly attached to the rest of the suspensorium by cartilage and articulates with the cranium in a cartilaginous area. In *Aphredoderus* and *Gadus* the palatine is firmly attached to the rest of the suspensorium by an interdigitating basal suture and articulates with a bony area of the cranium. In *Amblyopsis* and *Chologaster* the palatine is firmly attached to the rest of the suspensorium as in *Aphredoderus* and *Gadus*.

For an account of the jaw mechanism of these same groups of fishes, written from a somewhat different angle and stressing musculature, see Rosen (1962).

GILL ARCHES

In *Percopsis* the upper and lateral surfaces of the gill arches are covered with patches of small teeth resembling those on the pharyngeal bones. Besides the ones that represent the usual gill rakers (which are absent) there are two median crescent-shaped patches covering the basibranchial area; one of these lies approximately between the bases of the third and the other between the bases of the second pair of gill arches. On the fourth ceratobranchial the tooth patches are somewhat

more nearly continuous than on the preceding gill arches but otherwise do not seem to differ from them. The upper pharyngeal teeth are in three patches on each side, and the lower pharyngeal patches of the two sides seem to be firmly united but not completely fused to one another. *Aphredoderus* (Fig. 6) differs in that the two basibranchial tooth patches are continuous or subcontinuous and that the fourth ceratobranchials bear a single distinctive tooth patch on either side.

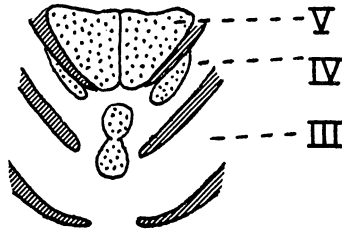


FIG. 6. *Aphredoderus sayanus*; lower portions of gill arches viewed from above. Gill slits cross-hatched; tooth-bearing portions stippled.

Amblyopsis resembles *Aphredoderus* except that the two basibranchial tooth patches are distinct and the lower pharyngeals are separate. *Chologaster* more closely resembles *Percopsis*, but it appears that there are only two upper pharyngeal tooth patches on either side.

Among cyprinodontoid fishes there are generally lath-like gill rakers on the first arch and no basibranchial tooth patches. However, the presence of pharyngeal-like teeth on the fourth and sometimes (e.g., *Fundulus majalis*) also on the third ceratobranchials seems to be at least widespread.

The percoids seem to have evolved in a somewhat different direction from the percopsisiform-amblyopsoid-cyprinodontoid fishes in regard to gill arch dentition (and indeed in regard to epibranchial construction). The ceratobranchials do not function as supplementary pharyngeals but, instead, the upper portions of the third epibranchials are often toothed, their dentition frequently becoming more or less contiguous with the third upper pharyngeal patches.

In the gadoids *Merluccius* and *Microgadus* and in the atherinid *Atherinops* there are no dental patches on either the epibranchials or ceratobranchials.

PECTORAL GIRDLE

The pectoral girdle of the amblyopsoids, gadoids, and percopsisiform fishes has no mesocoracoid arch. In *Amblyopsis* the postcleithra are

also (usually) missing and in *Chologaster* a fine strut that lies free in the flesh appears to represent the postcleithrum. In *Microgadus* there seems to be a single long postcleithrum that runs down to a point, above and behind the pectoral girdle. The postcleithrum of *Percopsis* is also apparently single, with a posterior lamina above and forming a strut below that ends above the middle of the pelvic girdle with which it has no connection. In *Aphredoderus* the postcleithrum forms a strong strut, the tip of which has a strong ligamentous attachment to the outside of the pelvic girdle alongside the base of the outer pelvic ray.

In *Aphredoderus*, *Percopsis* and *Amblyopsis* (Rosen, 1962:23, fig. 15) the scapular foramen lies high in the scapula. In the gadoids it usually lies between the scapula and the coracoid (cf., Starks, 1930).

PELVIC FINS AND GIRDLE

At least some gadoids, amblyopsoids, and percopsiform fishes have more than 5 soft pelvic rays, but there is never a true pelvic spine. *Aphredoderus* and *Percopsis* do, however, have a bony splint at the outside of each pelvic fin. In an earlier paper (Gosline, 1961a), the history of this splint was traced from the lower teleostean fishes. Here, it may be appropriate to compare it with the splint-like structure at the outer edge of the pelvic fins in some higher forms.

In general, the pelvic fins of higher teleostean fishes consist of an outer spine and five soft rays on each side. This count is only rarely exceeded, but frequently there is a reduction or complete loss of the pelvics. The usual pelvic spine may undergo reduction concomitantly with or separately from that of the soft rays, and in some instances remains only as a small splint. Thus in the mugiliform series the pelvic spine is fairly stout in those forms in which the pelvic girdle has a postcleithral abutment (*Polydactylus*, *Mugil*, *Sphyraena barracuda*) and relatively thin and splint-like where there is no such support (*Sphyraena argentea* and Atherinidae). Throughout these fishes, however, the pelvic spine retains a double-winged base articulating with the pelvic girdle, thus differing from the pelvic splint found in *Percopsis*, *Salmo*, etc. When, as in *Sphyraena argentea*, the base is asymmetrical, it is the lower wing that is the larger. Similarly, the pelvic spine of the flatfish *Psettodes* has a bifid base; flatfishes such as *Psettichthys*, however, have no pelvic spine and have six articulated rays. In the anabantoid-ophiocephaloid series, *Anabas* and *Helostoma* have strong, sharp pelvic spines with bifid bases; in *Trichogaster* the pelvic "spine" forms a short cap, still with a forked base, over the

outside of the base of the first filamentous soft ray. The outer pelvic ray of *Channa* [= *Ophiocephalus*] *gachua* is made up of two completely distinct "halves," the lower of which is much shorter than the upper; neither half has any articulations, thereby differing strongly from the five inner pelvic rays. Finally, in many salariform blennies, e.g., *Cirripectus*, there is no trace of the pelvic spine, which presumably has disappeared, though well-developed soft rays remain. In brief, the pelvic spine may be reduced or disappear (as in *Cirripectus*), or it may be transformed into a soft ray (as apparently happens in most flatfishes), but it never seems to be represented by a structure that could be confused with the outer splint of *Percopsis*, *Aphredoderus*, and many lower teleosts. In amblyopsoids and gadoids there appears to be no trace of either the percopsiform splint or of a spine in the pelvic fin.

In the amblyopsoid and percopsiform fishes each half of the pelvic girdle has a median projection which overlaps and is ligamentously attached to its fellow from the other side. Among the cods, *Microgadus* has each half of the pelvic girdle with a median strut, but these do not reach each other or the midline; in *Merluccius* there are no such projections.

In *Percopsis* and in those amblyopsoids in which it is present, the pelvic girdle lies free in the abdominal wall. In *Aphredoderus* it is attached by a strong ligament to the tips of the postcleithra; anteriorly the pelvic girdle does not seem to have any special ligamentous attachment to the cleithra. The gadoids generally have the pelvics farther forward and in some sort of association with the cleithra. In *Microgadus* there are special ligaments (rather long and weak) running from the anterior ends of the two halves of the pelvic girdle to the cleithra. In *Merluccius* the anterior ends of the two halves are tightly bound to one another by ligamentous tissue and fit between the wings of the cleithra to which they are firmly attached about as in the percoids.

One last point about the pelvic fin and girdle is that in *Aphredoderus* and *Percopsis* there are two or three small, separate bony nodules (actinosts) between the base of the pelvic rays and the pelvic girdle (Gosline, 1961a). These are absent in *Microgadus*.

VERTICAL FINS AND FIN SUPPORTS

Percopsis retains an adipose fin, but none of the other fishes under consideration do. The percopsiform and cyprinodontiform fishes all have a single, undivided, rayed dorsal fin inserted over the middle

or posterior third of the body. This fin may have from one to four spines anteriorly in *Aphredoderus*, *Percopsis*, and the cyprinodontid *Jordanella floridae*. In *Aphredoderus* the first dorsal pterygiophore interdigitates between the third and fourth neural spines, and that of *Percopsis* between the fourth and fifth; in both of these genera there is one predorsal bone. Among the cyprinodontiform fishes, *Floridichthys* has the first dorsal pterygiophore interdigitating between neural spines three and four, that of *Chologaster* over the 17th, and in some cyprinodontoids like *Anableps* undoubtedly farther back still; no member of the order examined has predorsal bones. Among the Gadiformes, there are usually two and frequently three separate, spineless dorsal fins. The anteriormost ray, though variable in position, usually originates near the rear of the head. Thus, the first dorsal pterygiophore of *Merluccius* extends between the second and third vertebrae, and that of *Microgadus* between the fourth and fifth.

In the caudal fin and caudal skeleton the cods, as is well known, differ quite markedly from the other fishes dealt with here (see Whitehouse, 1910, figs. 17, 18). Nevertheless, Barrington (1937), and for that matter Agassiz (1878) long before, showed that the parts of the gadid caudal skeleton could be easily and logically homologized with the more typical structure found in such fishes as the plaice (*Pleuronectes platessa*). In discussing the major difference between the caudal skeleton of the cod and that of the plaice Barrington (1937:466) stated: "The effect is as though the terminal vertebra in *Pleuronectes* included the penultimate as well as the terminal vertebra of *Gadus*, and this may well be so, for the evolution of the homocercal fin has been accompanied by a reduction and fusion of the vertebrae which primitively (e.g., *Salmo*) extend to the tip of the notochord along the upturned axis. It thus becomes possible to argue that the tail of *Gadus* was derived from a homocercal tail of a type less specialized than that of *Pleuronectes*; from a type, in other words, in which the terminal vertebrae were less reduced than they are in this genus."

I have no quarrel whatever with Barrington's statements. I would like to point out in addition (1) that *Anguilla* (Fig. 7, A), along with the osteoglossids and mormyrids, seems to represent one stage earlier than the cod, and (2) that the gadid caudal skeleton is essentially that of the percopsiform (Fig. 7, B), amblyopsoid (Gosline, 1961a, figs. 3, A,B) and at least some lampridiform fishes (*Ibid.*, fig. 3 D).

The caudal skeleton of the lampridiform, percopsiform, gadiform, and amblyopsoid fishes appears to be of a highly unusual, if not unique, nature. To follow a line of previous speculation (*Ibid.*: 4-6),

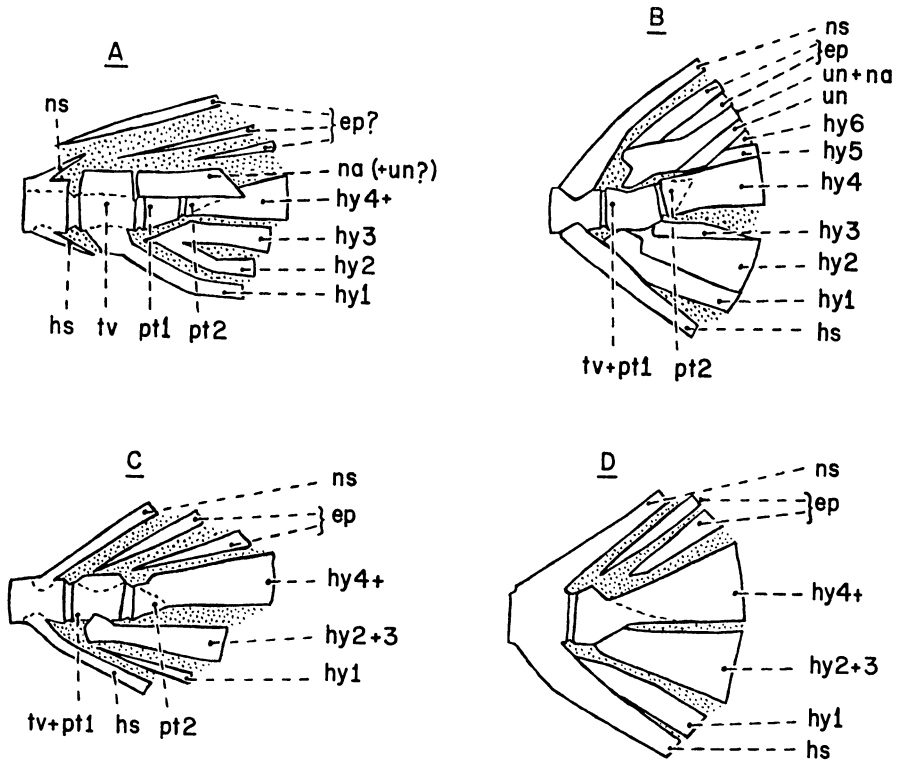


FIG. 7. Diagrams of caudal skeletons: *A*, young *Anguilla vulgaris* (based on Whitehouse, 1910, fig. 10); *B*, *Percopsis* sp. (based on Gosline, 1961a, fig. 2, C); *C*, *Molva vulgaris* (based on Whitehouse, 1910, fig. 17); *D*, *Pleuronectes platessa* (based on Barrington, 1937, fig. 1); *ep*, epural; *hs*, hemal spine; *hy*, hypural; *na*, neural arch; *ns*, neural spine; *pt*, postterminal centrum; *tv*, terminal vertebra; *un*, uroneural.

it would seem that the groups under consideration represent a rather different lineage of sequential fusion of parts (or at least a different stage of arrested development in such a sequence) from that which has led to the type of caudal skeleton found in the plaice (Fig. 7, D) and most other higher teleosts. The usual sequence would seem to be a fusion of postterminal centra 1 and 2 with the terminal vertebra to form the urostyle (Gosline, 1961*b*), frequently followed by more or less fusion of the hypurals to this urostylar vertebra. In the fishes under consideration, however, postterminal centrum 1 would seem to have fused with the terminal vertebra, but postterminal centrum 2 has apparently become fused with one or more upper hypurals while

TABLE 1

COMPARISON OF PERCOPSIFORM, GADIFORM, AND AMBLYOPSOID FISHES WITH BERYCIFORM FISHES

Character	Percopsiform, Gadiform, and Amblyopsoid Fishes	Beryciform Fishes
Caudal skeleton	With an intervertebral-like articulation between the base of an upper hypural plate and the terminal centrum; epurals 2, 1, or 0	Without an intervertebral-like articulation between the base of an upper hypural and the terminal centrum; epurals 3
Pelvic fin	Without a true spine, but with an outer splint in the percopsiform fishes	With a true spine except in <i>Polymixia</i>
Exoccipital condyles	Widely separated	Forming, with the basioccipital, a single articular surface for the first vertebra (Starks, 1904a)
Orbits	Bounded dorsomedially by membranes, between which the brain extends forward from the cranial cavity; olfactory nerve not traversing orbit; pleurospenoids widely separated from one another; no orbitosphenoid or basisphenoid	Bounded dorsomedially by bone; olfactory nerve traversing orbit; pleurospenoids meeting one another on the midline; orbitosphenoid and basisphenoid present
Subocular shelf	Absent	Present (in Berycoidei)
Supramaxillary bone	Absent	Present
Nasals	Not attached to the cranium by suture	Attached to the cranium by suture
Predorsal bones	Single or absent	Two or three in the few species investigated

TABLE 2
 APPARENT DIFFERENCES AMONG AMBLYOPSOID, PERCOPSIFORM, AND GADIFORM FISHES

Character	Amblyopsoids	Percopsiform Fishes	Gadiform Fishes
Adipose fin	Absent	Present in <i>Percopsis</i> , absent in <i>Aphredoderus</i>	Absent
Antorbital bone	Absent	Present in <i>Percopsis</i> , absent in <i>Aphredoderus</i>	Absent
Splint at outside of pelvic fin	Absent	Present	Absent
Bony nodules at base of pelvic rays	Absent	Present	Absent
Vent position in adults	Forward of pelvics	Forward of pelvics in <i>Aphredoderus</i> , normal in <i>Percopsis</i>	Normal
Olfactory bulb	Near forebrain	Near forebrain in <i>Aphredoderus</i> , near olfactory organ in <i>Percopsis</i>	Near olfactory organ
Ethmoid-maxillary ligament	With a palatine attachment	With a palatine attachment	Without a palatine attachment

TABLE 2 (Continued)
 APPARENT DIFFERENCES AMONG AMBLYOPSOID, PERCOPSIFORM, AND GADIFORM FISHES

Character	Amblyopsoids	Percopsiform Fishes	Gadiform Fishes
Pharyngeal-like teeth on the fourth ceratobranchials	Present	Present	Absent
Scapular foramen	High in the scapula	High in the scapula	Between scapula and coracoid
Pelvic girdle	Not attached to cleithra	Not attached to cleithra	Attached to cleithra by ligament
Each half of pelvic girdle	With a median prong that overlaps its fellow on midline	With a median prong that overlaps its fellow on midline	With median prong, if present, not reaching midline
Epipleurals	From the 1st vertebra	From the 1st vertebra	From the 3rd vertebra
Epurals	1	2	2(?)

retaining its intervertebral articulation with the fused postterminal centrum 1 plus the terminal vertebral element ahead of it.

VERTEBRAL COLUMN AND RIBS

In the amblyopoid and percopsiform fishes there are epipleural ribs from the first and pleural ribs from the third vertebra. The gadoids have both epipleural and pleural ribs commencing on the 3rd vertebra.

DIGESTIVE SYSTEM

In *Percopsis*, *Aphredoderus*, *Chologaster*, and *Microgadus* there is a series of finger-like pyloric caeca extending out from either side of the anterior portion of the intestine. No such projections were found in *Amblyopsis*, *Profundulus*, or *Aplocheilus*; in these forms there is indeed little differentiation between stomach and intestine.

DISCUSSION AND SUMMARY

The percopsiform fishes, especially *Percopsis*, retain a number of "lower" teleostean traits—an adipose fin, an antorbital bone, a splint-like strut at the outside of the pelvic fins and the presence of bony nodules between the fin rays and the pelvic girdle (Gosline, 1961a). If, however, *Percopsis* and *Aphredoderus* are compared with the Clupeiformes on the one hand and with the Scopeliformes on the other, they prove to have all the characteristics that distinguish the latter from the former (Gosline, Marshall, and Mead, in press), i.e., the maxillaries are toothless and excluded from the gape, the palatine heads extend over the maxillaries far forward on the latter bones, there is an interorbital (frontal) commissure between the supraorbital canals, and the base of the innermost pelvic ray forms a knob that extends under the bases of the adjacent rays. Unless one hypothesizes that the percopsiform fishes have developed these features from the clupeiform fishes independently of the Scopeliformes, the Percopsiformes would seem to be a scopeliform derivative (Gosline, 1961a:39, diagram 4). Since the "primitive" percopsiform features—the adipose fin, antorbital bone, and pelvic splint and "actinosts"—are all held in common by both the clupeiform and scopeliform fishes, they cause no objection to such an allocation.

The reasons for assigning the Percopsiformes to the "acanthopteran" fishes are more indefinite (or at least less definitive). There are spines in the dorsal and anal; the branchiostegals have the advanced teleost configuration and number (Hubbs, 1919); the pelvics are subabdominal and, in the case of *Aphredoderus*, abut against the postcleithra;

the mesocoracoid and orbitosphenoid are absent; the scales are ctenoid; and the pleural ribs start from the third vertebra and the epipleurals from the first. A probable reason for the rather indefinite nature of the characters on this list is that no recent writer, including the present author, has ever really questioned (and investigated) the pertinence of the Percopsiformes to the "acanthopteran" series.

The Percopsiformes have been associated here with the cods and the amblyopsoids (and provisionally with the Lampridiformes). So far as I have been able to determine there is only one character diagnostic for the three groups. This is the perhaps unique specialization in the caudal skeleton (see above). The other features held in common have either been retained from ancestral forms (e.g., the spineless, often many-rayed pelvics) or have also evolved in other groups of higher teleosts, e.g., the absence of mesocoracoid, orbitosphenoid, and of a bony covering for the sensory canals of the head. Nevertheless, the sum of the resemblances among the three groups (and many of them such as the peculiar shape of the mesethmoid are undefinable) is rather impressive. They can perhaps best be marshalled by drawing up a comparison between these groups and what would appear to be a fairly closely related order, the Beryciformes (Table 1). (As with the Percopsiformes, some members at least of the Beryciformes and apparently no other "acanthopterans" retain an antorbital bone and bony nodules in the bases of the pelvic rays.)

The major apparent differences among the amblyopsoid, percopsiform and gadiform fishes are listed in Table 2.

SECTION II. THE RELATIONSHIPS AND SYSTEMATIC POSITION OF THE CYPRINODONTOID FISHES

To the aquarist or experimental zoologist, the cyprinodontoids include some of the best known fishes: guppies, mollies, swordtails, *Gambusia*, *Poeciliopsis*, *Fundulus*, etc. Nevertheless, their systematic position has never been securely established; the group has been associated at one time or another with various teleosts from pikes to spiny-rayed fishes. To mention some of the taxonomic treatments of the present century, Starks (1904*b*) divided the Order Haplomi into three superfamilies—Esocoidea, Poecilioidea (Cyprinodontoidea or Cyprinodontoidei of many later authors), and Amblyopsoidea. Of the three divisions, Starks said (1904*b*:254): "The families of the Haplomi have either widely diverged from each other or are not of the same line of descent. The order is not held together by any important character,

though some very peculiar characters may be used to rather widely separate three groups."

Regan (1911b) removed the amblyopsoids and poecilioids (=cyprinodontoids) from the haplomous fishes as a separate order Microcyprini (=Cyprinodontiformes). Of the relationships between the Amblyopsoidea and Poeciliodea he stated (1911b:321): "These two groups resemble each other in the absence of a mesocoracoid and an orbitosphenoid, the separation of the parietals by the supraoccipital, &c., but they differ widely in other respects and do not seem to be closely related." It may be added here that, so far as taxonomic treatment is concerned, all but Rosen (1962) of subsequent authors, e.g., Hubbs (1924), Myers (1931), Berg (1940), Woods and Inger (1957), and Sethi (1960), have followed Regan in placing the amblyopsoids and poecilioids (cyprinodontoids) in the same order.

Regan said (1911b:321), concerning the systematic position of this order: "Whereas the Haplomi show relationships to the most generalized isospondylous fishes, the Microcyprini bear more resemblance to the Salmopercae [=Percopsiformes] and Synentognathi [=Beloniiformes], especially the latter." Regan did not amplify these statements.

Eaton (1935) stressed the similarity in jaw musculature between the cyprinodontoid *Fundulus* and the mugiliform (percesocine) genus *Mugil* (also between *Ahpredoderus* and the gadids). Finally, Clark Hubbs and Drewey (1959) have called attention to the fact that hybrids between *Fundulus* and the atherinid *Menidia* have been raised through the hatching stage several times.

The primary material upon which the present investigation has been based consists of the stained specimens cited in the introduction to this paper. Unstained material in Berg's (1940:465) families Cyprinodontidae, Goodeidae, Jenynsiidae, Anablepidae, and Poeciliidae has also been examined, and it is these families that are here connoted by the term cyprinodontoid fishes. Kulkarni's (1940, 1948) accounts of the family Horaichthyidae leave little doubt that it, too, belongs in Berg's suborder Cyprinodontoidei. No specimens of the aberrant family Adrianichthyidae have been available. The phallostethid fishes, originally placed among the Cyprinodontiformes (Microcyprini), do not belong there but appear to be related to the mugiliform family Atherinidae, as Myers (1928) long ago suggested (see also Gosline, 1962).

Preliminary investigation showed that certain postulated cyprinodontoid relatives, e.g., the Esocoidei and Beloniiformes, could be dismissed from further consideration (see Hubbs, 1919). Indeed, it soon became apparent that in some features the cyprinodontoids resemble

the amblyopsoids, and thence the percopsiform fishes; in others, the mugiliform fishes, especially the atherinids; and in still others, that they stand quite alone. A description and discussion of these three categories of characters form the subject matter of the present section.

THE HEAD SKELETON AND ASSOCIATED STRUCTURES

A very extensive background knowledge regarding the head bones of cyprinodontoid fishes has been provided by Ramaswami (1945, 1946), Kulkarni (1948), Rosen (1960), Sethi (1960), and others. It seems clear from these works that there has been within the cyprinodontoids a tendency toward the simplification of the head skeleton through the loss or fusion of parts.

Before dealing with ossifications that have been lost within the cyprinodontoids, it seems advisable to discuss certain bones that are absent in all cyprinodontiform fishes. The invariable absence of the orbitosphenoid (and in the pectoral girdle the mesocoracoid) has probably been the situation since ancestral times, for the bone is also absent in both percopsiform and mugiliform fishes. The basisphenoid is also missing in the Cyprinodontiformes (despite Starks, 1904b:260), but warrants some discussion.

In *Atherinops* and *Sphyraena argentea* the usual median basisphenoid is present, with the median stem giving rise to a pair of lateral flanges above, each of which abuts against the posterolateral rim of a pleurosphenoid (alisphenoid). In *Mugil*, however, as in *Percopsis* and *Aphredoderus*, the basisphenoid is missing and the pleurosphenoids are supported below by the prootics, which in turn are suturely united to the lateral processes of the parasphenoid (Figs. 1, 2). In all of the fishes mentioned above the parasphenoids have only the one pair of lateral expansions just noted.

In *Chologaster* the vault of the skull is much broader and lower than in the other fishes cited so far. The prootic is attached to the lateral flanges of the parasphenoid as usual, but in addition the widely separated pleurosphenoids, instead of abutting against the prootics, run down anterior to and somewhat internal to the prootics, to end just above a second (anterior) pair of parasphenoid flanges (Fig. 3). (*Amblyopsis* appears to be essentially as in *Chologaster* in these respects, but the bones involved, especially the "pleurosphenoids," are too fragile for certainty in the matter.) In *Rivulus bondi* (Sethi, 1960, fig. 46) the two pairs of parasphenoid flanges, particularly the anterior, are better developed than in *Chologaster*, but have the same relationships. The maximum development of the anterior flanges, however, is

probably found in some species of *Fundulus* (cf., Sethi, 1960:94); in *Cyprinodon* (Sethi, 1960, fig. 8, A, DLP) they have degenerated to a pair of short tabs on the parasphenoid (which Starks, 1904*b*, undoubtedly and understandably mistook for a basisphenoid).

In addition to the bones just mentioned, an intercalar (opisthotic) and a separate ectopterygoid are absent in all cyprinodontoids. Only in the *Aplocheilus* group is there a separate metapterygoid; in most there is no parietal; in some no vomer; and in *Horaichthys*, even the maxillary is gone (Kulkarni, 1948).

Further discussion of the head skeleton is divided under functional systems.

NASAL STRUCTURE

Consideration of cyprinodontoid nasal structure may be divided into two rather distinct parts—the mechanism by which water is passed over the olfactory organ and the olfactory organ itself with its innervation.

To start with the mechanism by which water is passed over the nasal organ, all cyprinodontoids examined have on each side a single, deep excavation extending ventromedially from the posterior portion of the nasal sac (Fig. 8). This excavation, which probably expands when the mouth is open, thus acting as a suction pump, joins the nasal sac lateral to the olfactory nerve and posterior to the olfactory epithelium. It thus can hardly be the homologue of the ethmoidal sac as Burne (1909:606) very tentatively suggested. Rather, this excavation seems to

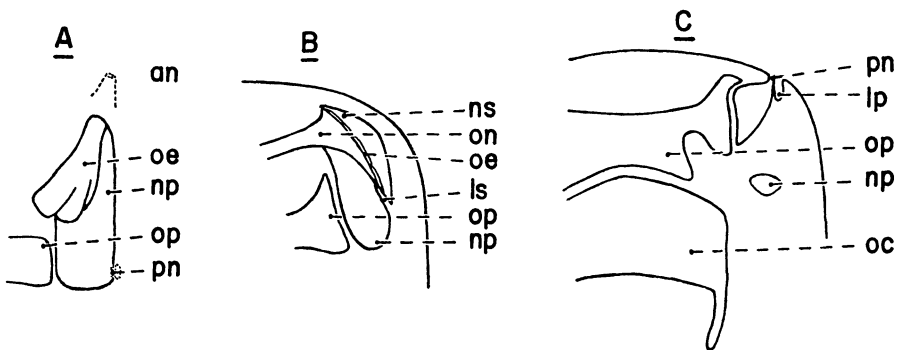


FIG. 8. Right nasal organ of *Profundulus guatemalensis*, semidiagrammatic: A, from above, with nasal bone removed; B, transverse section between anterior and posterior nostril; C, transverse section through posterior nostril; an, anterior nostril; lp, lateral pit; ls, lacrimal shelf; np, nasal pocket; ns, nasal sac; oc, oral cavity; oe, olfactory epithelium; on, olfactory nerve; op, supraoral cavity; pn, posterior nostril.

be most closely paralleled by the single (lacrimal?) accessory sac of the stickleback *Pungitius* (Liermann, 1933) and many atherinids. (It may be worth noting that *Mugil* has both ethmoidal and lacrimal sacs.)

All cyprinodontiform fishes have (like *Aphredoderus*) two well-separated nostrils, with the anterior at the end of a short tube. The nature of the posterior nostril varies. In *Chologaster* (as in *Aphredoderus*) it is an open hole, and in *Amblyopsis* and *Aplocheilus* it is a hole more or less covered by a flap extending back from its anterior rim. In all the cyprinodontoids examined except *Aplocheilus* each posterior nostril is bordered laterally by a deep pit. The wall between the pit and the nostril is a thin ridge of skin which doubtless closes against the medial nostril wall to act as a shut-off valve when water is being sucked into the nasal cavity.

Some, at least, of the atherinids have a lateral pit and valve construction alongside the posterior nostril rather similar to that of the (non-*Aplocheilus*) cyprinodontoids, and numerous fishes including the genus *Atherina* have a simple flap over that nostril such as occurs in *Aplocheilus*.

The olfactory organ of cyprinodontoids lies on a sort of shelf that extends across the anterior portion of the nasal sac, from the lacrimal bone (Fig. 8, B, ls) lateroventrally, to attach to the bottom of the nasal bone mediodorsally. In *Aplocheilus* and *Profundulus* the olfactory organ consists of a few broad, low, flat-topped, longitudinal lamellae (Fig. 8, B). In the remaining cyprinodontoids the olfactory epithelium takes the form of a plate in which the individual components are arranged in the form of radiating striae. (To call such a structure a "nasal rosette" as Burne, 1909:630, does in *Anableps* seems a highly dubious procedure.)

In the amblyosoid *Chologaster* there are four longitudinal lamellae somewhat higher than those of *Aplocheilus* and *Profundulus*; *Amblyopsis*, as previously noted, has a typical rosette. Apparently, the change from a typical rosette to a series of longitudinal folds has occurred repeatedly in fishes. A very brief investigation shows such folds to occur in *Umbra*, *Pungitius* and atherinids. The atherinid folds, however, differ from those of *Aplocheilus* in that they are high and thin rather than broad and low.

THE SENSORY CANALS AND RELATED BONES

The lateral line of the body is not developed in any cyprinodontoid fishes. There is not even any lateral line canal running along the back

of the head through (or over) the pterotic, tabular, and post-temporal. All signs of cross commissures are missing in both the interorbital and temporal regions. The tabular bones, which usually bear parts of the canals absent in cyprinodontoids, are also gone. The sensory canals on the anterior part of the head are modified and always more or less discontinuous (Gosline, 1949). Thus, the infraorbital canal of cyprinodontoids is always restricted to an anterior portion in the lacrimal and a posterior section in the uppermost circumorbital (dermosphenotic). Between these two portions neither the sensory canal nor the circumorbital bones are present.

The loss of the middle section of the circumorbital series has occurred many times, e.g., in the salmonoid *Galaxias*, the esocoids *Umbra* and *Dallia*, the Beloniformes, Syngnathiformes, Gasterosteiformes (except Aulorhynchidae), mugiliform fishes (Mugilidae and Atherinidae but not Sphyrænidae), Scorpaeniformes, etc.

Whether the abbreviation and interruption of the lateralis system of cyprinodontoids has been compensated by a specialization of the remaining parts cannot be determined from gross morphology. In any event the amount to which the remaining canals are covered by, or even form grooves in, the underlying head bones is less than in the amblyopsoids and percopsiform fishes. Among the majority of mugiliform fishes, by contrast, most of the sensory canals of the head are bone enclosed, and the tabular bones are retained.

THE JAW MECHANISM AND ASSOCIATED STRUCTURES

The great majority of cyprinodontoids have a very unusual way of opening the mouth. Apparently associated with this, at least functionally, are the accessory nasal excavation (previously mentioned) and peculiarities of the suspensorium.

One superficial character diagnostic for the whole Cyprinodontiformes, i.e., including the amblyopsoids, may be noted. At the corner of the mouth the lower lip folds over the upper, giving the impression that the upper jaw is enclosed in the lower. This curious reversal of the usual lip configuration does not appear to occur elsewhere among the prepercoid groups.

In most cyprinodontoids the premaxillary can be and is protruded when the mouth opens, but the maxillary remains behind as a very slightly movable part of the cheek. Only, apparently, in *Aplocheilus* (Sethi, 1960:191) does a fairly normal type of jaw protrusion occur, with the outer ends of the premaxillary and maxillary moving forward together. Since it is the maxillary that normally closes off the corner

of the open mouth in holostean and teleostean fishes, it would appear that the association of the maxillary with the cheek in most cyprinodontoids must be secondary. In short, it seems necessary to trace the development of cyprinodontoid upper jaw protrusion back through an upper jaw construction rather similar to that now found in *Aplocheilus*. The crucial question would seem to be: from what is the *Aplocheilus* type of upper jaw derived? There are several possible answers to this question, and I cannot find that any is particularly convincing. One point seems clear. *Aplocheilus* (Fig. 5, C) and *Rivulus* have well-developed ethmoid-maxillary ligaments with no attachment to the palatine heads. Consequently, the *Aplocheilus* jaw cannot be derived directly from that found in amblyopsoids and the percopsiform fishes (see above). There seems to be no reason why the *Aplocheilus* and amblyopsoid-percopsiform jaws should not both have been derived from a single ancestral type.

Among the amblyopsoids and percopsiform fishes, the upper jaw is non-protrusile or essentially so. By far the closest parallel to the cyprinodontoid jaw protrusion is that found among the mugiliform fishes. Thus *Mugil* and such atherinids as *Atherina hepsetus* essentially duplicate the condition found in *Aplocheilus* while other atherinids such as *Atherinops*, *Chirostoma*, and *Odontesthes* have developed what is essentially a *Fundulus* type of jaw protrusion (these three genera differ from *Fundulus*, however, in that the premaxillary pedicels have apparently disappeared and have been replaced by a movable median nodule).

The strange shape of the premaxillary in most cyprinodontoids is doubtless associated with the unusual method of upper jaw protrusion in these fishes. In any event there seems to be only a single premaxillary pedicel in cyprinodontoids (Fig. 5, C) as compared with the usual two in amblyopsoids (Fig. 5, B), percopsiform fishes (Fig. 5, A), etc. Furthermore, there is in the great majority of cyprinodontoids, but not *Aplocheilus*, a very peculiar and diagnostic forward projection from the lateral tip of the premaxillary.

PECTORAL GIRDLE

As previously noted, the postcleithrum of *Amblyopsis* is usually absent whereas that of *Chologaster* seems to be represented by a strut that lies free in the flesh. In cyprinodontoids there is no normal postcleithrum; however, what looks like a deeply embedded scale extends in below the supracleithrum and this may possibly be a postcleithrum (Sethi, 1960). In *Rivulus bondi* (Sethi, 1960, fig. 48, A)

the supracleithrum is bar-like and largely covered by the posttemporal. In *Aplocheilus* the supracleithrum and posttemporal have fused.

The pectoral fin and primary pectoral girdle of cyprinodontoids are quite different from those of atherinids and mugilids. In the two mugiliform families (which have well-developed postcleithra) the pectorals are high on the body, falcate, and with very oblique bases; these characters are reflected in the primary girdle (Starks, 1930:193, 194). In the cyprinodontoids, as in the amblyopsoids and percopsiform fishes, the pectoral fin is, except in certain African forms, placed about on the middle of the side, and has a rounded outline and an approximately vertical base.

PELVIC FINS AND GIRDLE

The pelvic fins and girdle of cyprinodontoids are rather nondescript. The number of soft rays in the fin ranges from 0 to 9 (Carl Hubbs, 1944:75). There is no spine and a projection of the dorsal wing of the outermost ray base in such fishes as *Rivulus* may or may not represent the splint of *Aphredoderus* and *Percopsis*. The pelvic girdle lies free in the flesh of the abdomen and has no ligamentous attachment to other portions of the skeleton. Generally each half of the pelvic girdle has a median prong that overlaps its fellow from the other side, but in some poeciliids, especially in males, there is a sutural ankylosis between the two halves (personal communication from Howard Huddle).

CAUDAL FIN AND CAUDAL SKELETON

The caudal fin of the cyprinodonts is always rounded and, as so often happens in round-tailed groups, the number of branched rays is quite variable. Thus, for one specimen each in the following species, branched ray counts are: *Amblyopsis spelaea*, 12; *Chologaster agassizi*, *Aplocheilus panchax*, and *Floridichthys carpio*, 14; *Fundulus majalis* and *Belonesox belizanus*, 17; *Profundulus guatemalensis*, 18; and *Rivulus bondi*, 22.

The caudal skeleton of cyprinodontiform fishes has been treated in some detail by Hollister (1940) and more briefly by Sethi (1960) and Gosline (1961a). That of cyprinodontoids differs from the amblyopsoid type in the fusion of the hypurals to the terminal centrum and to one another to form a plate-like hypural fan.

To hypothesize a derivation of the cyprinodontoid caudal skeleton from that of the amblyopsoids requires the postulate of considerable fusion. Nevertheless, to hypothesize a derivation from the mugiliform

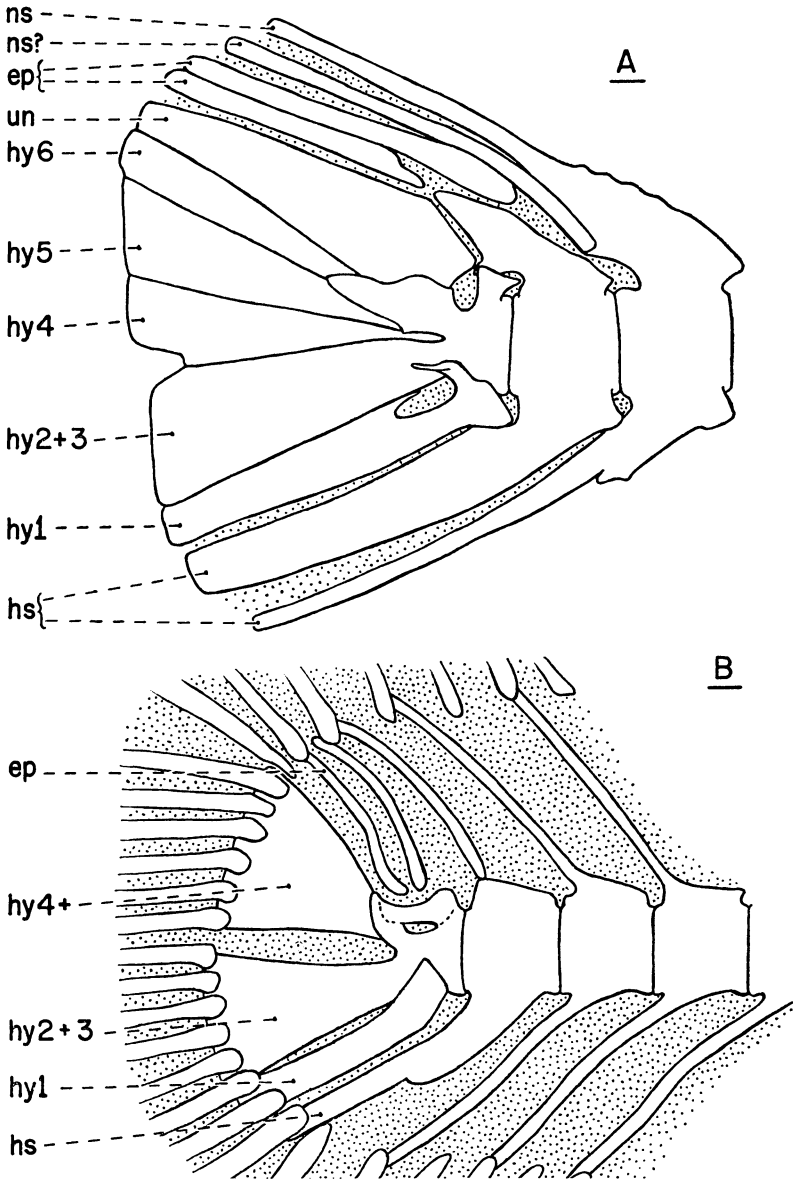


FIG. 9. Caudal skeletons: *A*, *Atherinops affinis*; *B*, *Phenacostethus smithi*; *ep*, epural; *hs*, hemal spine; *hy*, hypural; *ns*, neural spine; *un*, uroneural.

caudal structure involves even more drastic changes. These may be treated in some detail.

Among the mugiliform fishes (see Hollister, 1937), the terminal centrum of the adults may fuse with the upper hypurals (Sphyraenidae, Mugilidae) or it may fuse with the lower hypurals (Atherinidae, Phallostethidae, Fig. 9), but apparently not with both. So far as fusion is concerned, the ultimate point reached appears to be that of the phallostethid *Phenacostethus* (Fig. 9, B). However, the caudal skeleton of *Phenacostethus* differs from that of cyprinodontoids in several respects. First, probably associated with the forked caudal fin of *Phenacostethus*, the upper and lower hypural plates are well separated from one another. Second, only the lower plate is fused to the terminal centrum. Finally, the two usual epurals of the atherinids are retained.

VERTEBRAL COLUMN AND RIBS

According to Starks (1904*b*) and Woods and Inger (1957, fig. 7, c,d), Baudelot's ligament in the amblyopsoids runs from the pectoral girdle to the base of the first vertebra; in the cyprinodontoids, however, it attaches to the basioccipital.

In the amblyopsoids and percopsiform fishes, the anterior vertebrae all have epipleurals, but the first pleural rib comes off the third vertebra as in the percoids and a host of other fishes. The cyprinodontoids, however, seem to be unique among the pre-perciform fishes in having the anteriormost pleural rib on the second vertebra.

From the position of Baudelot's ligament, but more particularly

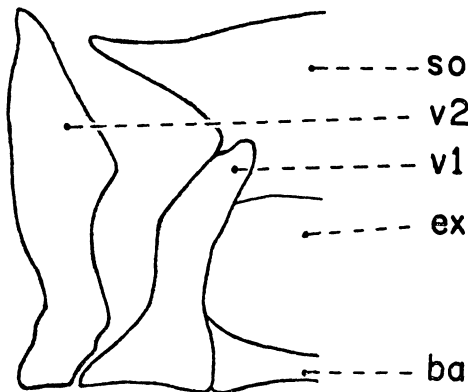


FIG. 10. Anterior vertebrae and rear of skull of *Floridichthys carpio*: ba, basioccipital; ex, exoccipital; so, supraoccipital; v, vertebra.

from that of the first pleural rib in cyprinodontoids, it would appear very much as if the first vertebra of ancestral fishes had been absorbed in the cyprinodontoid skull. How such fusion might have taken place is easily envisioned from *Floridichthys*, which appears to be in the process of losing a second vertebra to the skull (Fig. 10). The loss of vertebrae in this way has, of course, occurred many times in fishes (see, for example, de Beer, 1937).

DISCUSSION AND CONCLUSIONS

Of the various postulated cyprinodontiform relatives, the esocoid and beloniform fishes have been dismissed without discussion. Indeed, so far as the cyprinodontoids are concerned, only two possible relationships seemed to warrant serious consideration, namely, that with the amblyopsoids and that with the atherinid-mugilid groups of mugiliform fishes. As a basis for discussing these two possibilities, the characters in which the cyprinodontoids resemble the atherinids, the amblyopsoids, and those in which they resemble neither group are listed below in synoptic form.

A. Characters in which the cyprinodontoids resemble the atherinids rather than the amblyopsoids.

1. Head mostly scaled.
2. Head without rows of sensory papillae (other than pit organs).
3. Anus normal in position.
4. Premaxillaries usually protrusile, extending laterally to the tips of the maxillaries.
5. A deep excavation extending down from the rear of the nasal sac, posterior to the olfactory epithelium and lateral to the olfactory nerve.
6. Circumorbital series of bones incomplete.
7. Baudelot's ligament attached to the basioccipital.

B. Characters in which the cyprinodontoids resemble the amblyopsoids rather than the atherinids.

1. Lower lip folding out over the upper laterally.
2. Parasphenoid with two pairs of expansions or flanges.
3. Fourth ceratobranchials with pharyngeal-like teeth.
4. Lateral line canals of head not enclosed in bone (except for a short section at the back of the frontals).

5. Olfactory lamellae, when present, broader than high.
 6. Pectoral fins usually originating on middle of sides, rounded in outline, and with an approximately vertical base.
 7. Postcleithra apparently absent (possibly represented by a scale-like bone).
 8. Pelvic fins without a spine and with 0-9 rays.
 9. Dorsal fin single.
 10. Caudal fin rounded.
 11. A single epural in the caudal skeleton.
- C. Characters in which the cyprinodontoids resemble neither the atherinids nor the amblyopsoids.
1. Dermethmoid ossification, if present, separated from the frontals by cartilage.
 2. Premaxillary with a single pedicel (a single pedicel, but of different type, is sometimes present in atherinids).
 3. Ectopterygoid absent.
 4. Intercalar absent.
 5. First pleural rib on the 2nd vertebra.
 6. Hypurals fused to one another to form a hypural fan.

Now, either the cyprinodontoids, amblyopsoids, and atherinids are all interrelated or they are not; if not, then the cyprinodontoids may be related to the amblyopsoids or to the mugiliform fishes, but not to both.

If the three groups are interrelated, then a percopsiform-amblyopsoid-mugiliform-perciform relationship of some sort would seem to be a necessary corollary. Because of the nature of the caudal skeleton, pelvic spine, predorsal spines, bone-enclosed sensory canals of the head, and subocular shelf, it seems to me most improbable that the mugiliform-perciform groups have any but a remote relationship to the percopsiform fishes.

The remaining possibility is that the cyprinodontoid fishes are related to the amblyopsoids or to the atherinids but not to both. In my opinion the amblyopsoid-cyprinodontoid resemblances listed in the synopsis have mostly a primary phylogenetic basis whereas those between the cyprinodontoids and the atherinids are mostly the result of secondary convergence. The alternative—that the cyprinodontoids are in many respects simplified mugiliform fishes—does not appeal to

me. For one thing, the atherinids apparently did give rise to a group of minute fishes, namely the phallostethids, but these bear little beyond a superficial resemblance to cyprinodontoids.

With regards to the cyprinodontoid-atherinid resemblances, I would set up the hypothesis that these have been brought about, as also presumably were the galaxiid-umbrid, gadid-brotulid, and carangid-scombrid similarities, as a result of adaptations to the same mode of life. The hypothesis suggested here is that a basic attribute of both atherinids and cyprinodontoids is that of feeding at or near the surface of the water. Though any mode-of-life hypothesis seems rather like a sheet of thin ice upon which one should venture with care, that of cyprinodontoid (and atherinid) near-surface feeding could furnish an explanation for a great many cyprinodontoid peculiarities as well as cyprinodontoid-atherinid resemblances—flat-headedness, forward premaxillary protrusion, the invasion of peripheral and evanescent habitats with associated small size which in turn gives rise to a simplification of the skeleton except for those structures related to internal fertilization, etc. These matters could be amplified at wondrous length, but it seems doubtful that such amplification would stand up under its own weight; the question will not be tested here.

However, certain items of evidence favorable to the view that the atherinids and cyprinodontoids evolved their similarities by paths of convergent evolution will be pointed out. The first has to do with the peculiar premaxillary protrusion, which in the more specialized members of both the atherinids and of the cyprinodontoids extends forward without the maxillary. However, the more generalized members of the same two groups, e.g., *Atherina* and *Aplocheilus*, have the lateral ends of the maxillaries and premaxillaries moving forward and back together in quite normal fashion. Thus, it looks very much as if the more remarkable resemblances of jaw protrusion have been developed independently in the two groups. Again, the advanced members of atherinids and cyprinodontoids have developed a peculiar pit and valve system associated with the posterior nostril, but the more generalized *Atherina* and *Aplocheilus* have no such specialization. As a final example, in the caudal skeleton of the atherinid offshoots, the phallostethiform fishes, and in the cyprinodontoids the hypurals have gone most or all of the way toward fusing into a hypural fan, but judging from the epurals, this fusion has taken place over different routes from different sources in the two groups.

The cyprinodontoid-amblyopsoid resemblances listed in the synopsis include various presumably unrelated aspects of fish structure.

The largest single group of similarities, however, deals with fin structure, and this is the only group that seems to merit further discussion.

Carl Hubbs (1944) emphasized the value of fin structure in "taxonomic and phylogenetic research." His paper deals specifically with the phallostethid fishes and Hubbs demonstrated in detail their similarity in fin structure to that of the mugiliform fishes. In the present paper the similarity in fin structure between the amblyopsoids and cyprinodontoids has been emphasized. As to the cyprinodontiform and the mugiliform fishes, Hubbs (1944:74, 75) pointed out that, in detail, the two groups differ significantly in every fin. At the end of his comparison Hubbs stated (1944:75): "It now seems clear that the points of special resemblance between the Cyprinodontes and the Atherinidae, which once impressed me forcibly and which Myers (1928:3-4) considered with a degree of favor, may be ascribed plausibly to convergent evolution." Nothing that the present author has been able to find leads him to disagree in any way with this statement of 19 years ago.

SECTION III. TAXONOMIC ALLOCATION

In the two previous sections I have presented data which, in my opinion, indicate a phylogenetic relationship among the gadiform, percopsiform, amblyopsoid and cyprinodontoid fishes.

Of the four groups, the gadiform fishes have at various times received taxonomic allocations so various as to defy brief summary. Recent workers, however, seem fairly well agreed on placing them among the acanthopteran (in the sense of Carl Hubbs, 1919), perciform groups. The suggestion of a relationship between the Gadiiformes and Percopsiformes seems first to have been made by Eaton (1935).

Osteologically, the closest similarity between any two of the four groups under consideration is that between the Percopsiformes and the Amblyopsoidei. Suggestions of a relationship between these groups can be traced back from the present paper through Rosen (1962), Gosline (1961*a*) and Eaton (1935) at least to Regan (1911*a*).

With the postulate of an amblyopsoid-cyprinodontoid relationship only Eaton (1935) and Rosen (1962) among modern authors would disagree. Rosen (1962:24, 28) summarizes: "Osteological and functional differences between amblyopsids and cyprinodontoids appear to warrant the idea here advocated that the Amblyopsidae must be removed from the Cyprinodontiformes and placed elsewhere in the

teleost assemblage." Later (p. 32): "It is recommended that the Amblyopsidae be relegated provisionally to an order, the Amblyopsiformes, adjoining the Percopsiformes in current classification." Where the Cyprinodontiformes should go, Rosen does not say.

That the amblyopsoids and cyprinodontoids are very different fishes is generally agreed, and I would be the first to admit that cyprinodontoids are highly specialized and widely differentiated from all other fishes. If, however, it is granted that the cyprinodontoids do have relationships and that a major function of classification is to express affinities, then the basic question with regard to the cyprinodontoids would seem to be the determination of to what they are related. It is this question that I have attempted to investigate, and the results are summarized in Section II. The unoriginal conclusion, as noted there, is that the cyprinodontoids appear to represent a specialized offshoot of an amblyopsoid stock.

With regard to taxonomic treatment, Rosen (1962) would recognize an additional order, Amblyopsiformes. My original inclination was to go in the opposite direction of including the Percopsiformes (along with the amblyopsoids) in the order Cyprinodontiformes. The philosophy behind such action would have been that (1) the high number of presently recognized teleostean orders is out of line with the ordinal categories in other animal groups and (2) that groups with one or a few species should be accorded ordinal rank only under exceptional circumstances. However, subsequent work has indicated the possibility that both the Syngnathiformes and Gasterosteiformes might have been derived from a percopsiform-like fish. At least until this possibility can be disproved it seems best to retain the Percopsiformes as a separate order.

The rather unimpressive characters that are held by the Syngnathiformes and Gasterosteiformes in common with the Gadiformes, Percopsiformes, and Cyprinodontiformes are as follows:

Branchiostegal rays 8 or fewer. No supramaxilla. No orbitosphenoid or basisphenoid. Postcleithrum single or absent. Pelvic fins, if present, frequently with more than five soft rays, either abdominal or without a spine. Caudal skeleton either with an intervertebral-like articulation between upper hypural bases and the terminal centrum or the hypurals all fused into a fan; epurals 2, 1, or 0. Dorsal frequently with, or preceded by one or more spines.

Whether or not the above resemblances indicate relationships remains to be seen. If these five orders are considered related, however, the major basis for such consideration would seem to be the absence

of an orbitosphenoid and basisphenoid. These losses have occurred repeatedly among lower teleosts with relatively depressed, broad skulls, e.g., *Umbra*, *Galaxias*. If the same losses are the result of genetic relationship in the series Percopsiformes through Gasterosteiformes, then the Lampridiformes must be immediately excluded from the group for it contains high-skulled forms retaining an orbitosphenoid.

Eliminating the Lampridiformes on the one hand and the Syngnathiformes and Gasterosteiformes on the other from consideration, the remaining groups dealt with here may be differentiated as follows:

- 1a. Foramen for the exit of the glossopharyngeal nerve contained in the intercalar (Svetovidov, 1948, etc.); upper jaw with crossed premaxillary-palatine and ethmoid-maxillary ligaments; no pharyngeal teeth on the fourth ceratobranchials; scapular foramen usually between the scapula and the coracoid; pelvic girdle attached to the cleithra either by special ligaments or directly; epipleurals from the third vertebra; dorsal fin or fins long. Order Gadiformes
- 1b. Foramen for the exit of the glossopharyngeal nerve not contained in the intercalar; upper jaw either with the ethmoid-maxillary ligament in part attached to the palatine or with the premaxillary-palatine ligament absent; pharyngeal-like teeth on the fourth ceratobranchials; scapular foramen enclosed in the scapula; pelvic girdle abutting against the tip of the postcleithrum (*Aphredoderus*) or lying free in the flesh; epipleurals from the first vertebra. 2
- 2a. Ethmoid-maxillary ligament with a palatine attachment; premaxillary not extending as far laterally as the maxillary, little or not protrusile; nasal sac without an accessory vesicle; circumorbital series of bones complete; ectopterygoid and intercalar present; Baudelot's ligament attaching to the base of the first vertebra; first pleural rib on the third vertebra; base of one or more of the upper hypurals with an intervertebral-like articulation between it and the terminal vertebra. 3
- 3a. Parasphenoid with a single pair of lateral flanges; pleurosphenoid meeting the prootic below; postcleithrum well developed and attached to the cleithrum above; a bony splint bordering the outside of each pelvic fin; dorsal fin with spines anteriorly, relatively far forward on the body, its first pterygiophore extending down ahead of the fifth neural spine; caudal skeleton with two epurals; scales ctenoid; lateral line present.
 Order Percopsiformes
- 3b. Parasphenoid with two pairs of flanges, the posterior meeting the prootic and the anterior extending to the pleurosphenoids, which do not touch the prootics; postcleithrum either absent or a thin splint lying free in the flesh; no bony splint at the outside of the pelvic fin; dorsal fin relatively far back, without spines, its first pterygiophore behind the tenth neural spine; caudal skeleton with one epural; scales cycloid; lateral line absent.
 Order Cyprinodontiformes, Suborder Amblyopsoidei
- 2b. Ethmoid-maxillary ligament, if present, without a palatine attachment; premaxillary extending as far laterally as the maxillary, usually protrusile;

nasal sac with a deep excavation posteriorly; ectopterygoid and intercalar absent; circumorbital bones in an incomplete series; Baudelot's ligament attaching to the basioccipital; first pleural rib on the second vertebra; upper and lower hypurals fused together to form a hypural fan.....
 Order Cyprinodontoidei, Suborder Cyprinodontoidei

For purposes of general orientation, the way in which the fish groups mentioned in the foregoing paper might fit into the scheme of modern teleostean fishes is suggested in Fig. 11.

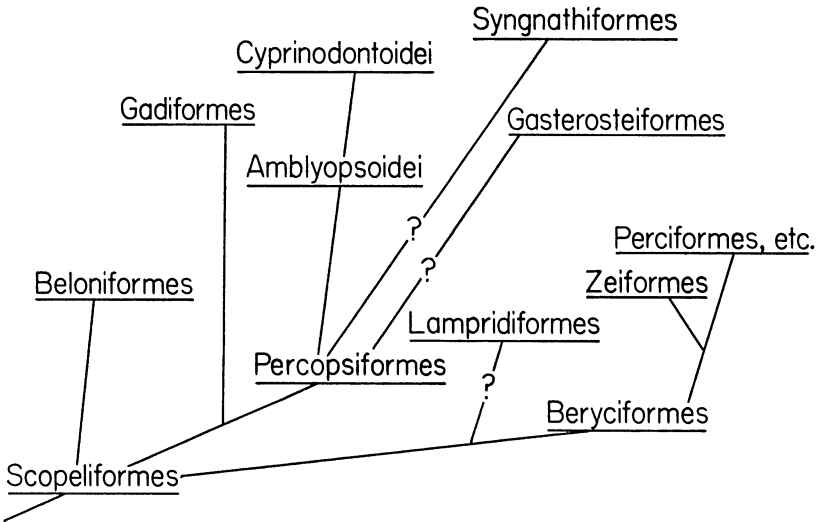


FIG. 11. Diagram of possible relationships of certain fish orders.

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