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HALFBEAKS, KILLIFISHES,  
SILVERSIDES, AND  
THEIR RELATIVES

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## INTRODUCTION

THE KILLIFISHES, OR CYPRINODONTIFORMS, are small fresh- and brackish-water fishes of worldwide distribution in tropical and temperate latitudes. The largest species attains a length of a little over 200 mm., but most are less than half of that size. With a few exceptions, they are soft-rayed fishes with cycloid scales, thoracic, subabdominal, or abdominal pelvics, pectorals high on the sides, an emarginate or rounded caudal, a lateral line reduced to a series of unconnected pits on the midlateral scale row, and a hyoid and branchiostegal apparatus of acanthopterygian type (Hubbs, 1919). In the earliest taxonomic treatment of the Cyprinodontiformes, they were regarded as a distinct group allied to or included with the Cyprinidae (see Garman, 1895). Gill, who was responsible for the term Cyprinodontes (1865), gathered together the cyprinodontiforms and the esocoid fishes (1874) in an alignment that became known as the Haplomi. It was from the Haplomi that Regan (1909) extracted the cyprinodontiforms and assigned them ordinal rank as the Microcyprini, although he still accepted their relationships to the esocoid fishes. Earlier, Boulenger (1904) had suggested an affinity between cyprinodontiforms and beloniforms (synentognaths). At this time it was not uncommon for the beloniforms and mugiliforms (Percesoces) to be either included in a single taxon or at most narrowly separated, and out of this relation grew the idea that the cyprinodontiforms and mugiliforms also are related. Jordan and Evermann (1896), for example, had remarked that the Synentognathi are "... allied to the *Haplomi* on the one hand and to the *Percesoces* on the other, and like those groups, [they mark] the transition from the soft-rayed to the spiny-rayed fishes. In their anatomical characters the *Synentognathi* most resemble the latter." At various other times the cyprinodontiforms were compared with the gasterosteiforms (including the syngnathiforms), the Channiformes, and the Anabantoidae.

The composition of the order Cyprinodontiformes has been somewhat less fluid. Originally established to include only the cyprinodontoid or typical killifishes, the

order was enlarged by Regan (1911a) to contain the very different North American cavefishes, later treated by Myers (1931) as a suborder, the Amblyopsoidei. In 1913 Regan described the first known phallostethid and assigned it to the cyprinodontoid section of the Cyprinodontiformes, but the phallostethids were stated by Myers (1928) to be a specialized offshoot of an ancient atherinid stock (order Mugiliformes). Also in 1913 Weber described *Adrianichthys kruxi* and assigned it to its own family in the Beloniformes because it possesses the chief ordinal character of that group. But an allied genus, *Xenopoecilus*, had previously been erected by Regan (1911b) and included in the killifish family Cyprinodontidae. Recognizing the familial relationship of *Adrianichthys* with *Xenopoecilus*, Weber and de Beaufort (1922) transferred the enlarged Adrianichthyidae to the Cyprinodontiformes, where it has since remained almost forgotten in the Cyprinodontoidae.

Until 1962 the composition of the order Cyprinodontiformes was unchanged. At the time the Cyprinodontoidae consisted of seven families (Cyprinodontidae, Goodeidae, Jenynsiidae, Anablepidae, Poeciliidae, Horaichthyidae, and Adrianichthyidae), and the Amblyopsoidei of a single family (Amblyopsidae). In that year Rosen presented evidence which indicates a relationship of the Amblyopsidae with the percopsiform genera and, more distantly, with the Gadiformes. He isolated the cavefishes as an order, the Amblyopsiformes, and recommended its alignment near the Percopsiformes and Gadiformes in a phyletic sequence. Gosline (1963), however, thought that the Amblyopsidae should be retained as a suborder of the Cyprinodontiformes and that the order should be further enlarged to include also the percopsiform genera, but no firm recommendations were made. Gosline believed that the cyprinodontoid killifishes could conceivably have been derived from an amblyopsid-like ancestor, but much of the osteological and myological evidence at variance with this view was not considered.

The idea for the investigation reported

herein was conceived following an initial osteological analysis of the adrianichthyid fishes. The Adrianichthyidae were found to have a mixture of beloniform, cyprinodontiform, and mugiliform features, and the initial investigation was therefore broadened to include representatives of all these groups as well as a species of phallostethid. The specific objectives of this report are to present a number of new considerations on the relationships and taxonomic position of the Beloniformes, Cyprinodontiformes, and Mugiliformes, and secondarily to define further the phylogenetic separation of the cyprinodontoid killifishes from the assemblage that includes the Amblyopsiformes and Percopsiformes.

In any study that involves taxonomic rearrangements, inevitably there arises the question of what to call various groups during the presentation of new evidence, especially when new group names are proposed and when groups of long standing are dismembered and the components are redistributed. In order to minimize herein possible confusion from these sources, various equivalences are established.

The terms "Beloniformes," "Cyprinodontiformes," and "Mugiliformes" are not used except in historical contexts.

Substituting for the term "Beloniformes" are the vernacular names "exocoetoid" (=Exocoetoidei, and including the Hemiramphidae and Exocoetidae), and "scomberesocoid" (=Scomberesocoidei, and including the Belonidae and the Scomberesocidae).

Substituting for the term "Cyprinodontiformes" are the vernacular names "adrianichthyoid" (including the Oryziatidae, a new family group name for the genus *Oryzias*, see below, the Adrianichthyidae, and questionably the Horaichthyidae) and "cyprinodontoid" (including the Cyprinodontidae, Goodidae, Jenynsiidae, Anablepidae, and Poeciliidae).

Substituting for the term "Mugiliformes" are the vernacular names "atherinoid" (including the Atherinidae, Melanotaeniidae, and the Isonidae, a new family group name for the genera *Iso* and *Notocheirus*, see below), "phallostethoid" (=Phallostethiformes or Phallostethoidei, and including the Neostethidae and Phallostethidae), "mugiloid"

(including the Mugilidae), "sphyraenoid" (=Sphyraenoidei, and including the Sphyraenidae), and "polynemoid" (=Polynemiiformes or Polynemoidei, and including the Polynemidae).

Various other teleost groups are discussed in customary taxonomic phraseology.

The specimens examined in this study are given in the Appendix.

#### ABBREVIATIONS USED IN ILLUSTRATIONS

A, adductor mandibulae muscle  
 AAP, adductor arcus palatini muscle  
 ACT, actinost or radial  
 ANG, angular  
 ART, articular  
 BB, basibranchial  
 BOC, basioccipital  
 CB, ceratobranchial  
 CH, ceratohyal  
 CL, cleithrum  
 CO, coracoid  
 DN, dentary  
 DO, dilatator operculi muscle  
 DSPH, dermosphenotic  
 EB, epibranchial  
 ECT, ectopterygoid  
 EH, epihyal  
 ENT, entopterygoid (mesopterygoid)  
 EOC, exoccipital  
 EP, epiotic  
 ETH, ethmoideum  
 FR, frontal  
 GH, glossohyal  
 HB, hypobranchial  
 HH, hypohyal  
 HYO, hyomandibular  
 IF, inferior pharyngeal tooth plate  
 IH, interhyal  
 IOP, interoperculum  
 LAC, lachrymal  
 LAP, levator arcus palatini muscle  
 LAT, lateral ethmoid  
 MET, metapterygoid  
 MX, maxilla  
 NA, nasal  
 OP, operculum  
 PA, parietal  
 PAL, palatine (autopalatine with or without dermopalatine)  
 PAS, parasphenoid  
 PASA, arm of parasphenoid  
 PB, pharyngobranchial tooth plate  
 PCL, postcleithrum  
 PFR, prefrontal  
 PGQU, pterygoquadrate cartilage  
 PLS, pleurospenoid

PMX, premaxilla  
 POP, preoperculum  
 PRO, pro-otic  
 PT, pterotic  
 PTT, posttemporal  
 PV, prevomer  
 QU, quadrate  
 SB, sesamoid bone  
 SC, scapula  
 SCL, supracleithrum  
 SOC, supraoccipital  
 SOP, suboperculum  
 SPAL, sesamoid bone capping autopalatine  
 SPH, sphenotic  
 SYM, symplectic  
 UTE, underlying triangle of endochondral bone

#### ACKNOWLEDGMENTS

The present work was begun in 1959 following a suggestion by Dr. George S. Myers that the adrianichthyid fishes might be of exceptional interest taxonomically. Soon thereafter Dr. Myers presented to me one of the two specimens of *Xenopoecilus poptae* then in the Stanford University Ichthyological Collection. From that time almost to the moment when this report went to press Dr. Myers' prophetic suggestions and the numerous loans and gifts of material continued to spur and guide the work. It is therefore with the utmost pleasure that I extend to Prof. Myers my sincerest thanks and deepest appreciation for providing materials, enthusi-

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For their many comments and recommendations on special aspects of the work I thank Drs. James W. Atz, Reeve M. Bailey, James Böhlke, Charles M. Breder, Jr., Donald P. de Sylva, Mr. Neal Foster, Drs. Warren C. Freihoffer, P. H. Greenwood, Carl L. Hubbs, Clark Hubbs, Colin Patterson, C. Richard Robins, Bobb Schaeffer, C. Lavett Smith, and William N. Tavolga. Drs. Breder and Smith kindly read and criticized the typescript. Dr. Klaus D. Kallman and Mr. R. Elwood Logan provided photographic aid; Miss Mary Grace Dromi, technical assistance; and Dr. Reeve M. Bailey, Mrs. Lillian Dempster, Mr. William I. Follett, and Drs. J. J. Hoedeman and Earnest E. Lachner lent specimens in their care. Materials were generously supplied by the California Academy of Sciences, the Florida State Museum, the Museum of Zoology of the University of Michigan, Stanford University, the United States National Museum of the Smithsonian Institution, the Zoological Museum of Amsterdam, and the University of British Columbia Institute of Fisheries.

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## HISTORICAL AND COMPARATIVE ANATOMICAL NOTES ON THE ADRIANICHTHYIDAE

THE ADRIANICHTHYIDAE are fishes of small size, apparently confined to the fresh-water lakes of Celebes. The first one was discovered in 1902 and described by Popta (1905) as *Haplochilus sarasinorum*. Later Regan (1911b) erected the genus *Xenopocilus* for Popta's species, pointing to some superficial differences between it and *Haplochilus* (= *Aplocheilus*). In 1913, Weber described a new family, genus, and species from Celebes, *Adrianichthys kruyti* (Adrianichthyidae), but it was not until 1922 that Weber and de Beaufort, in describing a new species of *Xenopocilus*, *X. poptae*, showed that *Xenopocilus* and *Adrianichthys* are intimately related. Weber and de Beaufort placed the Adrianichthyidae in the Microcyprini (= Cyprinodontiformes) and set it apart from all other cyprinodontiforms on the basis of differences in mouth structure. In their diagnosis of the Adrianichthyidae were included the following statements: "Mouth large, horse-shoe shaped. Intermaxillaries (=premaxillae) not protractile, firmly united even coalesced with maxillaries. Maxillaries articulating with a prominent knob at the anterior extremity of the palatines." Myers (1931) followed Starks (1904) in subdividing the cyprinodonts as the Amblyopsoidea (North American cavefishes) and Poecilioidea (all others), into the latter of which he provisionally included the

Adrianichthyidae with the remark that they "... differ considerably from other families." In this provisional status they have since remained.

Most cyprinodontoid killifishes possess many distinctive osteological features, not the least of which concerns the structure of the jaws and the palatoquadrate arch. Eaton (1935) has called attention to the remarkable nature of the protractile mechanism of the upper lip. Its principal element is the bent and twisted maxilla that has at its upper end a deep internal hook reaching into a socket on the under side of the premaxillary process. The large lower trapezoidal part of the premaxilla is sandwiched between the bases of the maxilla and mandible where it is held by elastic ligaments. Closing of the jaws is greatly facilitated by a coronoid expansion of the articular bone dorsally providing additional surface for insertion of the adductor muscle. In the ethmoid region of the skull a mesethmoid bone is developed as a thin, circular, scale-like plate that is bent down to form a seat for the ascending premaxillary processes. The autopalatine, which is joined firmly to the lateral ethmoid posteriorly, holds the twisted maxilla close to the ethmopalatine connection on its anterior or maxillary process. Most of this mechanism is covered over dorsally by well-developed nasal

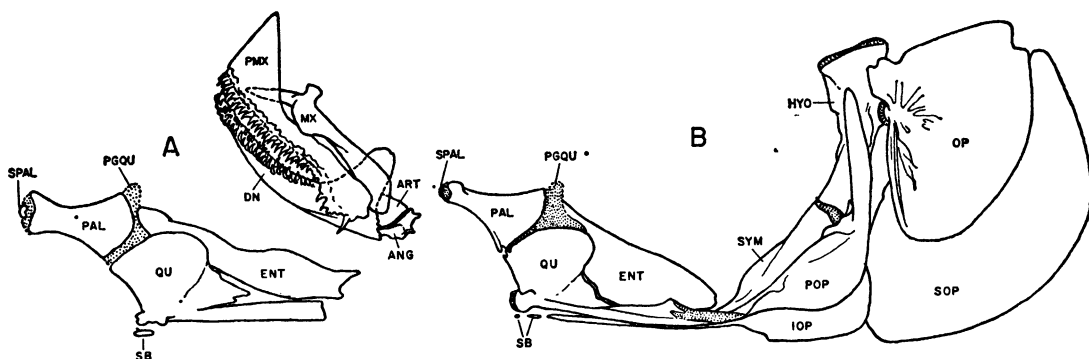


FIG. 1. Jaws and jaw suspension in adrianichthyoid killifishes. A. Jaws and palatopterygoid arch in *Oryzias latipes* (Temminck and Schlegel). B. Jaw suspension and opercular apparatus in *Xenopocilus sarasinorum* (Popta). Note sesamoid bone below quadrate and bony cap over tip of palatine in A and B. Note in A that lower arm of premaxilla lies over maxilla, large coronoid process on dentary, and absence of similar coronoid elevation on articular (and compare with fig. 2).



bones and the anterior portion of the extensive frontals.

*Xenopoecilus* is distinctive among killifishes in the development of an extensive chondrocranium; in possessing an enormous ethmoideum (30% to 40% of intact skull length) that includes (in *X. poptae*) a median dermal ethmoid; a single, median supraoccipital process formed by fusion of embryologically paired elements; a cup-like excavation on the distal tip of the autopala-

tine that is capped by a large ball of cartilage and a discoidal sesamoid bone; a dorsal enlargement of the pterygoquadrate cartilage that serves as a point of contact of the palatopterygoid arch with the prefrontal (fig. 1); a maxilla that is carried on the upper edge rather than on the outer face of the posterior end of the premaxilla; a premaxilla that lacks a hooked or pointed posteroventral process; a tremendously reduced articular bone without a coronoid process that is almost wholly

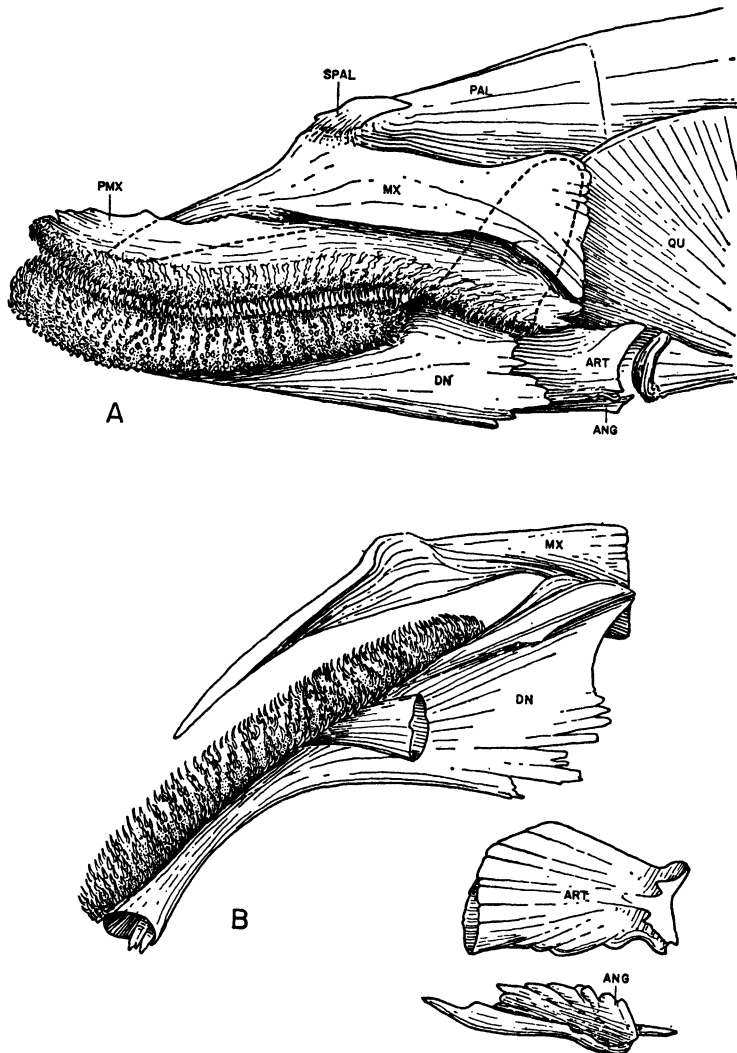


FIG. 2. Jaws and part of jaw suspension of *Xenopoecilus poptae* Weber and de Beaufort. A. Upper and lower jaws and anterior part of jaw suspension. B. Medial view of right maxilla and lower jaw elements. Note bony cap on palatine in A, and compare with figure 6.

contained within the posterior part of the dentary (fig. 2); the articulation of the first pleural rib on the third rather than on the second vertebra; pelvic girdles that are not in contact medially and that have a long lateral spur extending upward between the ribs; a dorsoventrally asymmetrical caudal skeleton with one or two very slender, rod-like epurals, and a caudal fin that is divided into indistinct upper and lower lobes by having a large gap

between the rays that articulate with the upper and lower hypural plates on the terminal half-centrum.

Except for the enlarged jaws and relatively large ethmoideum and the presence of a median supraoccipital process, all the above features can be identified in *Oryzias* (fig. 1) but in no other killifishes so far as known. It is therefore apparent, as already suggested by Myers (1960), that adrianichthyids and

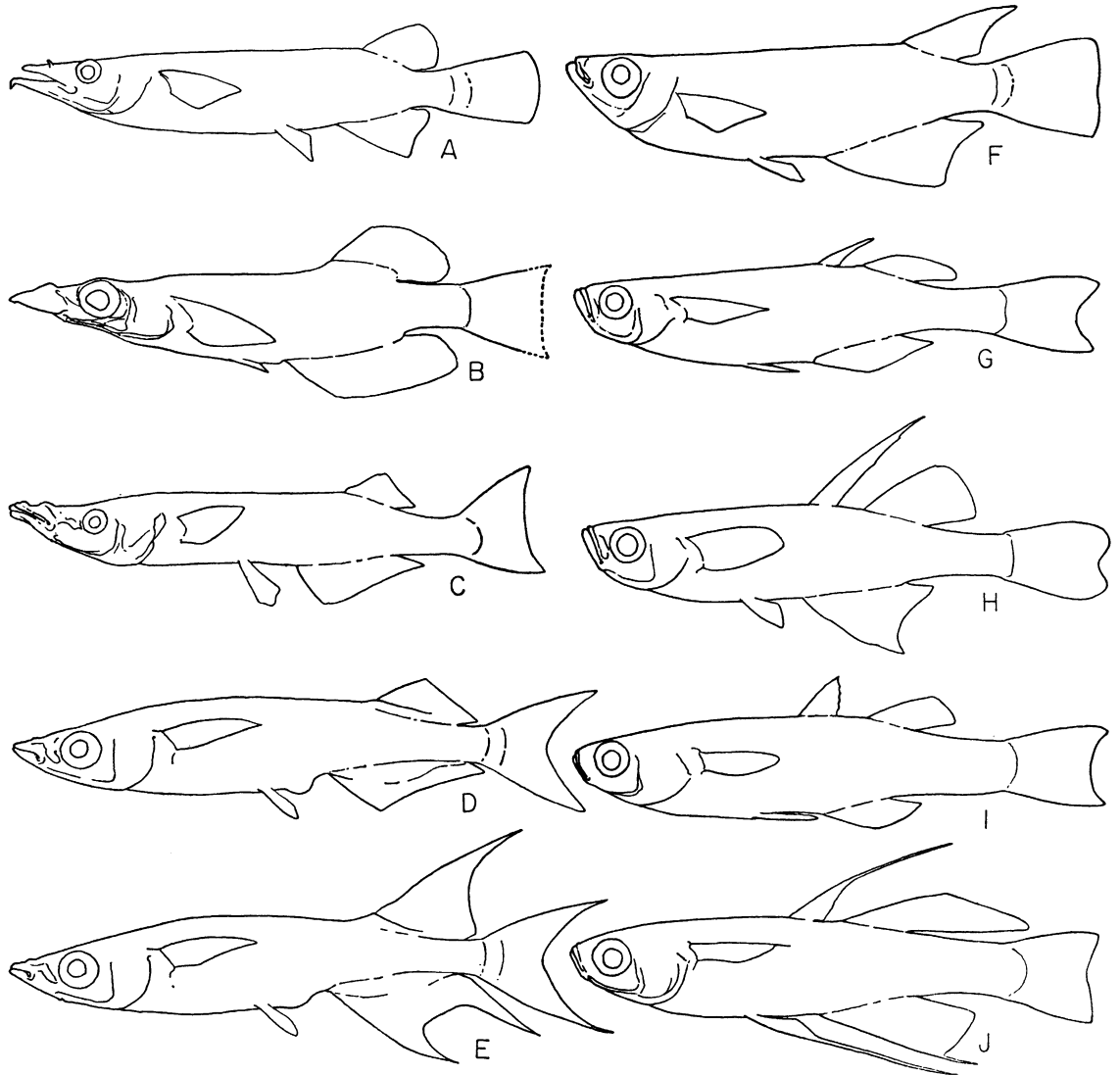


FIG. 3. Body form and fin shape in species of killifishes, silversides, and a halfbeak that inhabit the fresh waters of Indo-Australia. A. *Nomorhamphus celebensis* Weber and de Beaufort. B. *Adrianichthys kruyti* Weber. C. *Xenopoecilus poptae* Weber and de Beaufort. D, E. *Xenopoecilus sarasinorum* (Popta). D. Female. E. Male. F. *Oryzias celebensis* (Weber). G, H. *Pseudomugil novaeguineae* Weber. G. Female. H. Male. I, J. *Pseudomugil gertrudae* Weber. I. Female. J. Male.

*Oryzias* are intimately related and that they constitute a distinct subgroup of the killifishes, the adrianichthyoids, containing the families Adrianichthyidae (*Adrianichthys* and *Xenopoecilus*)<sup>1</sup> and Oryziatidae (see below), in contrast to the remainder of the families which may be grouped together as cyprinodontoids. Whether the Horaichthyidae, which have been suggested as a derivative of *Oryzias*, should also be included with the adrianichthyoids is a question requiring

<sup>1</sup> The fossil species *Lithopoecilus brouweri* de Beaufort, from a presumably fresh-water deposit in the Gimpoe basin, central Celebes, must also be included provisionally in the Adrianichthyidae. De Beaufort (1934) believed *Lithopoecilus* to be more or less intermediate between adrianichthyids and *Aplocheilus* (of which he regarded *Oryzias* a synonym), but somewhat closer to the former in the shape of the mouth and in body size. The age of the fossil-bearing deposit is unknown.

additional study.

For a number of reasons the Oryziatidae are regarded as the most generalized living killifishes. This conclusion is based partly on the relatively unreduced condition of the caudal skeleton and the rather simple structure of the mouth parts as compared with those of the adrianichthyids and with those of the still more functionally specialized cyprinodontoids. Partly it is based on the fact that oryziatids alone, of all killifishes, show a remarkable anatomical congruence with the fresh-water hemirhamphids and atherinids that live together with them in the same region of Australasia (fig. 3). One of the fresh-water Indo-Australian genera of the Atherinidae, *Pseudomugil*, has likewise been regarded as among the most primitive members of its group by Jordan and Hubbs (1919; see below).

## NEW FAMILY GROUP NAMES FOR SPECIES OF KILLIFISHES AND SILVERSIDES

### ORYZIATIDAE, NEW FAMILY

TYPE GENUS: *Oryzias* Jordan and Snyder, 1906.

DIAGNOSIS: The Oryziatidae differ from their closest relatives, the adrianichthyids, in lacking the tremendously enlarged jaws and ethmoideum, in having paired supraoccipital processes (rather than a single median

process), and in having the inferior pharyngeal bones distinctly separated (rather than united), and from all cyprinodontoids as follows: autopalatine usually capped by sesamoid bone; pterygoquadrate cartilage forming dorsal process; lower end of premaxilla not hooked or trapezoidal, situated below maxilla rather than between maxilla and dentary;

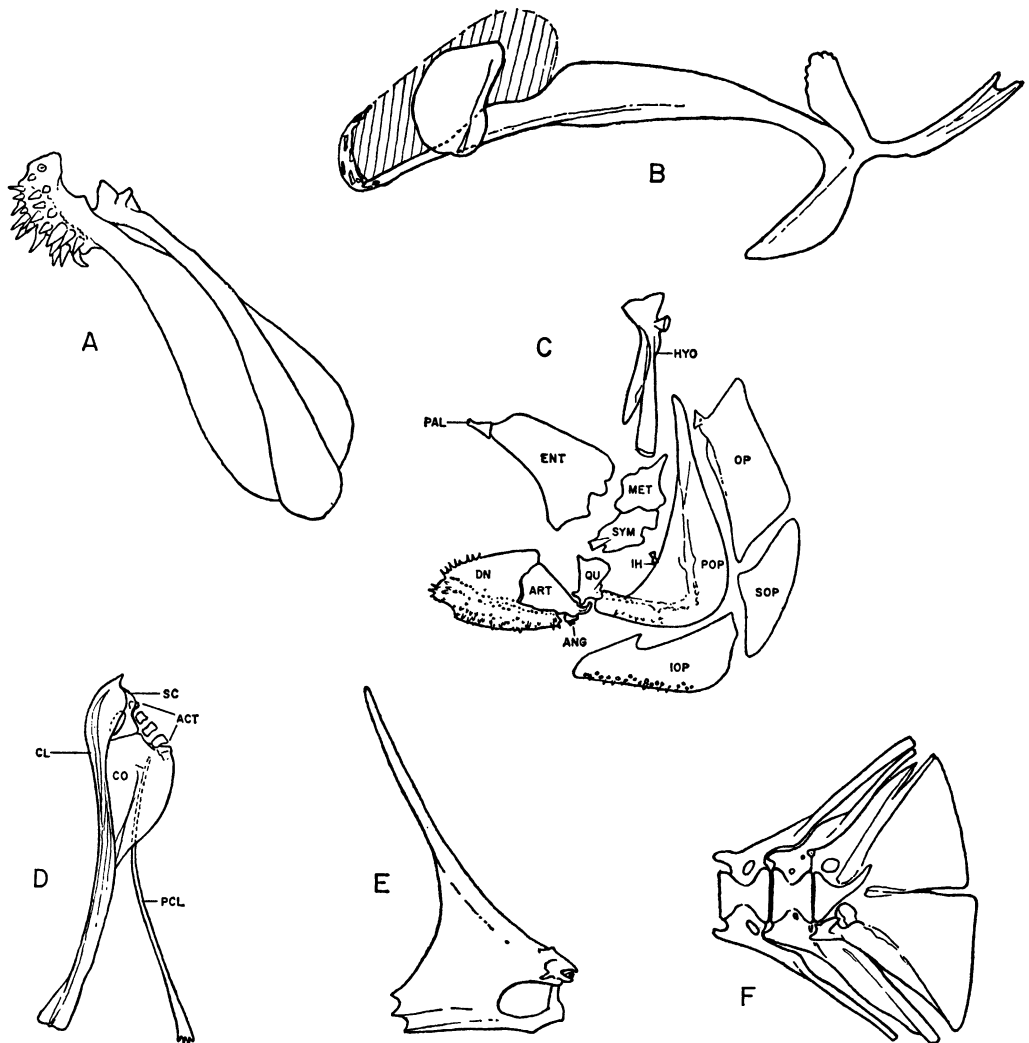


FIG. 4. Osteological features of *Notocheirus hubbsi* Clark. A. Left maxilla and premaxilla. B. Parasphenoid with associated ethmoid block and prefrontal. C. Jaw suspension and opercular apparatus, exploded view. D. Shoulder girdle. E. Left pelvic girdle. F. Caudal skeleton. A, B, and E to same scale; C, D, and F drawn to half of scale of A, B, and E.

first pleural rib on third vertebra; supra-cleithrum wanting; pelvic bones with upright lateral spurs and not joined midventrally; hypochordal musculature present on caudal fin skeleton; caudal fin forming incipient lobes.

COMPOSITION: A single genus, *Oryzias*, with seven species, *O. latipes* (Temminck and Schlegel), *O. melastigma* (McClelland), *O. celebensis* (Weber), *O. timorensis* (Weber and de Beaufort), *O. javanicus* (Bleeker), *O. curvinotus* (Nichols and Pope), and *O. minutillus* Smith, in fresh and brackish water.

#### ISONIDAE, NEW FAMILY

TYPE GENUS: *Iso* Jordan and Starks, 1901.

DIAGNOSIS: The Isonidae differ from all other groups of atherinoid fishes in the following respects (fig. 4A-F): premaxilla with swollen symphyseal part to which clustered upper jaw teeth are confined; autopalatine minute, triangular, supported entirely by

rostral edge of extensive mesopterygoid; prevomer lacking; parasphenoid with median blade-like process arising ventrally; scapula and coracoid entirely above midlateral line; cleithrum a long strut extending from above scapula to midventral line where it joins fellow; postcleithrum almost as long as cleithrum, its ventral tip expanded and dentate where it joins fellow at midventral line somewhat posterior to cleithral symphysis; pelvic bone with lateral spur extending upward between pleural ribs nearly to vertebral column; last few caudal vertebrae, neural and hemal spines bunched together; caudal skeleton without epurals, the last neural spine fused to uroneural.

COMPOSITION: The genus *Notocheirus* Clark (1937), with a single species, *N. hubbsi* Clark, and the genus *Iso*, with five species, *I. flosmaris* Jordan and Starks, *I. flosindicus* Herre, *I. hawaiiensis* Gosline, *I. rhothophilus* (Ogilby), and *I. natalensis* Regan, all marine.

## ANATOMICAL EVIDENCE FOR RELATIONSHIPS

### BRAINCASE

IN THE STRUCTURE of the neurocranium (fig. 5) hemiramphids, cyprinodontoids, phallostethoids, and atherinoids have in common a usually toothless prevomer overlain by a double, rarely single, laminar, disc-like, mesethmoid (supraethmoid) ossification, the upper ethmoidal disc representing the dermal component. The nasals are broad, triangular bones closely joined to the frontals. The frontals are in most species rectangular, truncate or indented rostrally, with prominent orbital and temporal divisions. The epiotic is with or without crests. The pro-otic has a ventrally opening trigeminofascialis recess and a separate foramen for the orbital artery medially. The intercalar is of moderate size or is minute when rarely present. The supraoccipital is of constant form, shaped like the head of a battle-ax and underlain anteriorly by an acute equilateral triangle of endochondral bone. The parietal when present has the long axis extending ob-

liquely forward from the supraoccipital. The infraorbital bones are represented by the first (lachrymal) and last (dermosphenotic) elements only, except in melanotaeniids in which a small, spatulate, additional element is broadly and firmly joined to the ventral surface of the lachrymal.<sup>1</sup> Parin (1961) has illustrated most of the above features in the Exocoetidae.

Notable exceptions to this general pattern occur in the scomberesocoids, in which the entire skull is drawn out in connection with the development of mandibular and premaxillary prolongations. In these fishes much consolidation and enlargement of separate ossifications are evident in the rostral region. In the largest species of adrianichthyid (*Xenopoeilus poptae*) the mouth is unusually large, and the dermal ethmoid is correspondingly reënforced (figs. 6, 7), as it is also in some of

<sup>1</sup> These two bones of melanotaeniids together resemble the single elongate first suborbital or lachrymal of *Xenopoeilus*.

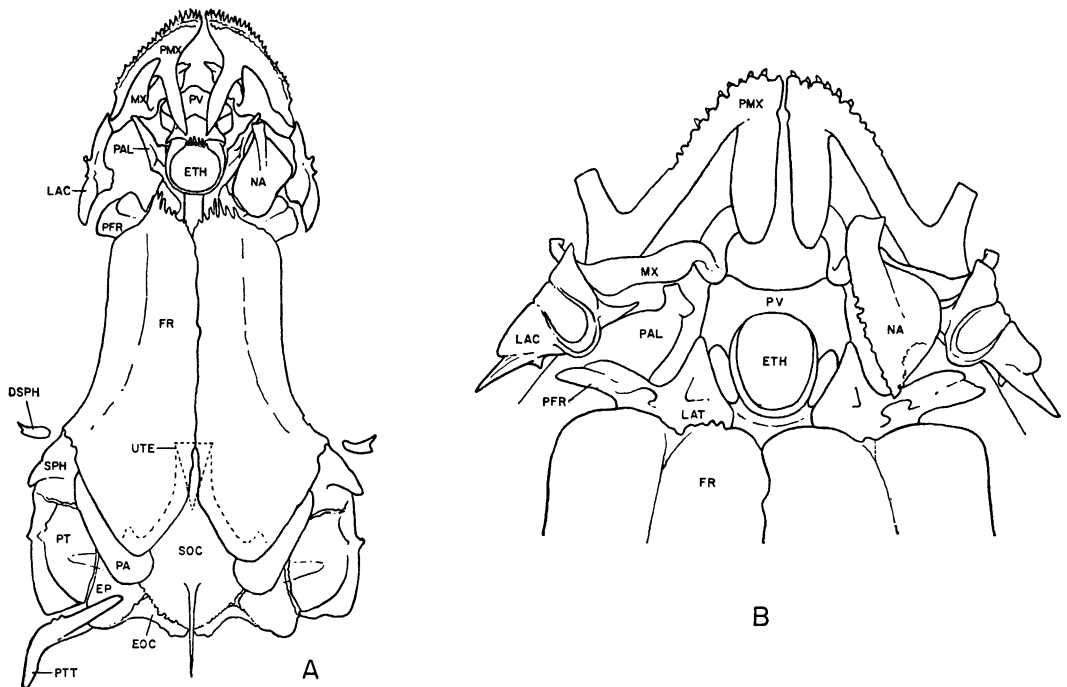


FIG. 5. Jaws and crania. A. Upper jaw and cranium in *Menidia beryllina* (Cope). B. Upper jaw mechanism and anterior part of cranium in *Fundulus confluentis* Goode and Bean.

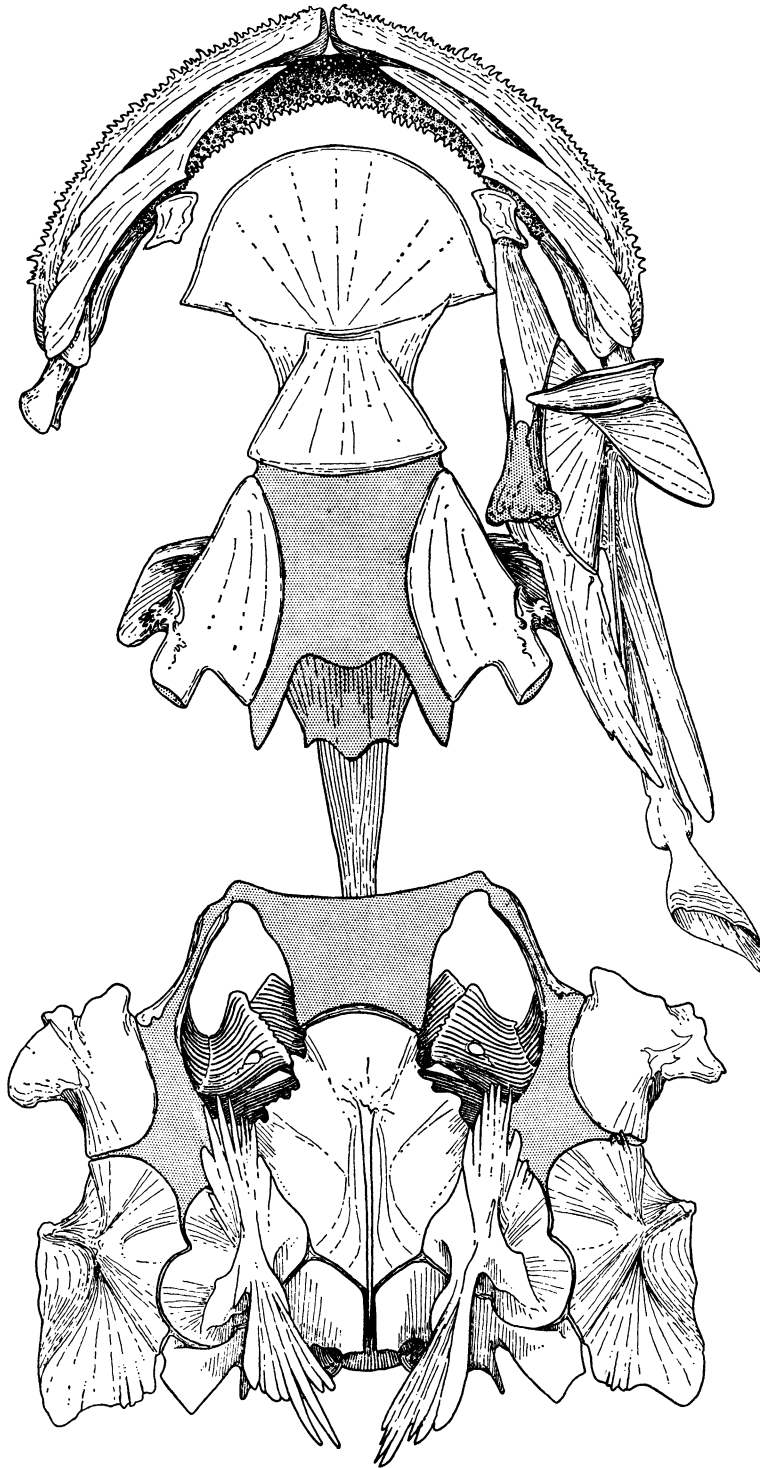


FIG. 6. Dorsal view of skull in *Xenopoecilus poptae* Weber and de Beaufort, frontal and nasal bones removed, showing underlying parts of chondrocranium (stippled), jaws, and right palatopterygoid arch.

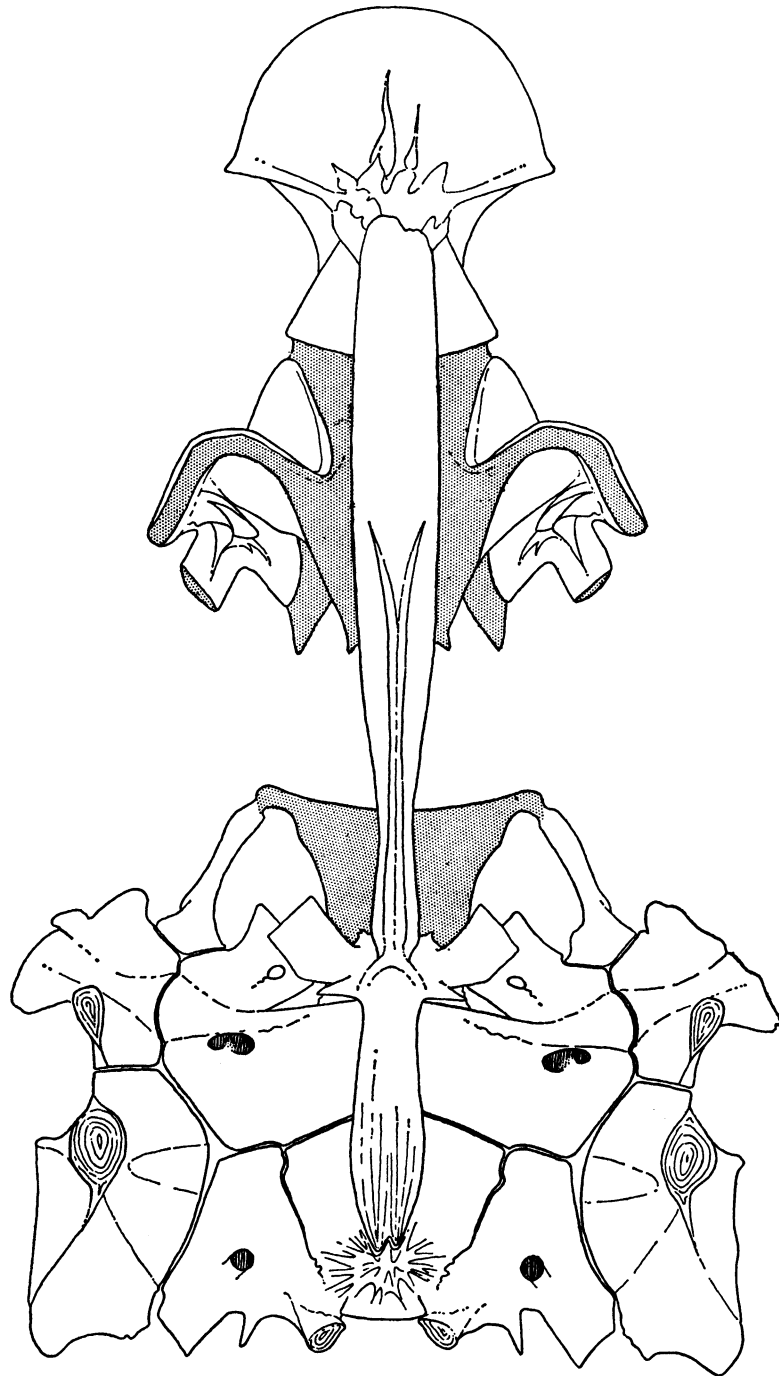


FIG. 7. Basicranium of *Xenopoecilus poptae* Weber and de Beaufort.



the melanotaeniids with similar jaw structure e.g., *Rhombattractus*. In the smaller species, *Xenopoecilus sarasinorum*, the mesethmoid structure, although large, is clearly double-laminar and dislike (fig. 8).

The structure of the supraoccipital crests is similar in exocoetoids, cyprinodontoids, and the Oryziatidae (paired) and in adrianichthyids and atherinoids (single). Adrianichthyids show striking resemblances to many of the larger species of atherinoids, mugiloids, and sphyraenoids in the decided branching of the epiotic crests (see also Starks, 1899). In over-all skull architecture, however, mugiloids, sphyraenoids, and polynemoids are unlike all the other groups herein considered. In these the prevomer is usually toothed (edentulous in mugilines); the mesethmoid ossification is never laminar and dislike and is always represented by a complex dermal ethmoid (fig. 9); the nasals are slender and arcuate, flare outward rostrally, and in most cases lie free of the frontal; the supraoccipital and parietal bones are of variable form; and a complete series of infraorbital bones is pres-

ent. Perhaps most significant is the fact that agonostomine mugilids, *Sphyraena barracuda*, and polynemids possess a subocular shelf. In the mugilid genus *Cestraeus* and in polynemids it is large and well developed. It is smaller in the mugilid *Agonostomus*, and in *Sphyraena barracuda* it is present but rudimentary. Of this structure Smith and Bailey (1962) wrote: "There is indication that changes in the form of the shelf take place slowly and that the shelf may serve as an indicator of phyletic history." They point out that in the course of fish evolution there have been two prominent trends in the skull bones. The dermal bones have migrated inward so that they no longer present sculptured external surfaces, and there has been a reduction in size and increased mobility of the skull bones. The circumorbital bones have in general conformed to these trends except when environmental stresses have imposed additional demands that have been met by the stiffening of the circumorbital ring. They show that in beryciforms and perciforms this stiffening has been accomplished through the

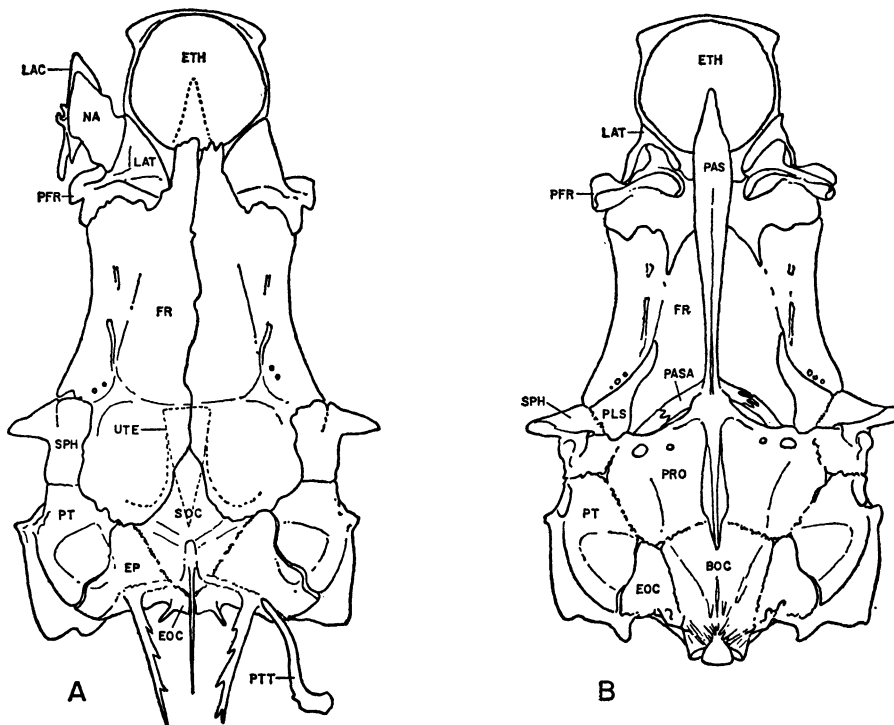


FIG. 8. Neurocranium in *Xenopoecilus sarasinorum* (Popta). A. Dorsal view. B. Ventral view.

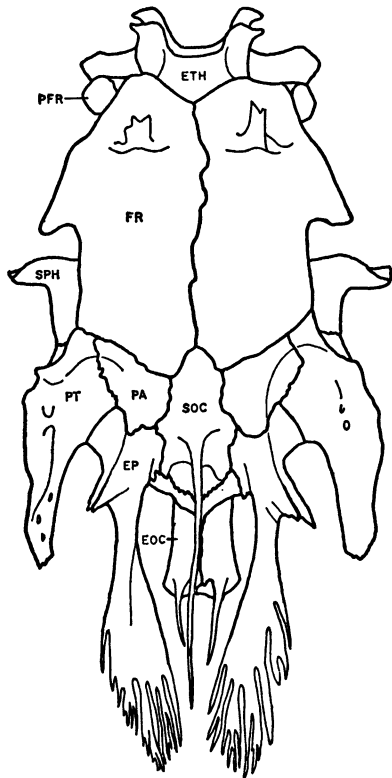


FIG. 9. Dorsicranium of *Mugil cephalus* Linnaeus, after Starks (1899). Note complex ethmoidium and compare with figures 5 to 8.

development of a subocular shelf along the infraorbital series. In contrast, clupeiforms and cypriniforms possess modifications that "... serve to make the suborbital series more flexible. The bones are reduced in size, the connections between them are ligamentous, and the diarthrosis between the lachrymal and the prefrontal is developed to allow movement in any plane. The lachrymal has been specialized to protect the anterior end of the maxilla. At the same time the trend in the supraorbitals is toward reduction, loss, or fusion so that the dorsal rim of the orbit is rigid. No malacopterygian is known to have a subocular shelf." Hence, one may wonder whether the loss of the infraorbital bones in exocoetoids (and also scomberesocoids), adrianiichthyoids, cyprinodontoids, phallostethoids, and atherinoids, and their persistence together with a subocular shelf in mugiloids, sphyraenoids, and polynemoids do not actually represent distinctly different trends

of phylogenetic significance. The loss of the infraorbital bones may be a secondary feature of halfbeaks, killifishes, and silversides, however, related to the development in all of a relatively very large orbit. It seems not unlikely that an unusually large eye under certain circumstances may be an adaptation which competes for space with the infraorbitals, ultimately crowding them out.

#### JAW SUSPENSION AND FEEDING MECHANISM

The jaw suspension of exocoetoids, adrianiichthyoids, cyprinodontoids, phallostethoids, and atherinoids includes an autopalatine (i.e., the dermal tooth-bearing component is absent) with which maxillary contact is established entirely by diffuse ligamentous tissue instead of by a ball-and-socket or other similar joint. The ectopterygoid is small and distinct, or fused with the autopalatine (fig. 10), or very much reduced, or absent. The mesopterygoid ossification (entopterygoid) is extensive in exocoetoids and in atherinoids, in which it forms the floor of the orbit (nearly touching the parasphenoid). In cyprinodontoids, adrianiichthyoids, and phallostethoids the mesopterygoid does not extend appreciably into the orbit. The difference in extent of the mesopterygoid apparently is related inversely to the extent of the adductor arcus palatini muscle, as de-

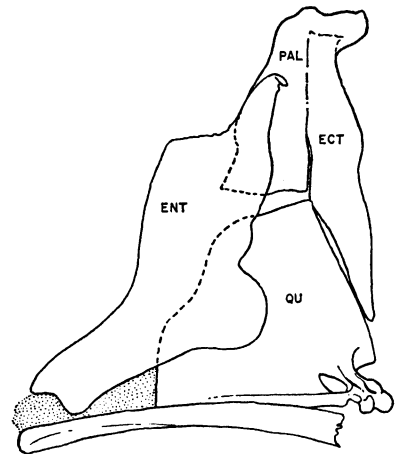


FIG. 10. Palatopterygoid arch in *Xiphophorus helleri* Heckel, illustrating the structures typical of cyprinodontoid killifishes. Medial view; anterior to right. Compare with figure 1.

scribed below. In general, the jaw suspensions in exocoetoids and atherinoids are very much alike. The adrianichthyoids, cyprinodontoids, and phallostethoids show varying amounts of reduction from the exocoetoid-atherinoid condition.

The length of the symplectic, and consequently the angle of the palatine, are related to the degree of protusability of the jaws. In exocoetoids, cyprinodontoids, atherinoids, and phallostethoids with protrusile mouth parts the symplectic is long and the autopalatine is nearly vertical; in the members of these groups with non-protrusile premaxillae the symplectic is relatively short and the autopalatine is inclined sharply forward. The latter fishes tend to have longer gapes and mandibles and more pointed upper jaws.

In all the above groups (horaichthyids aside) the maxilla has a very distinctive form and relation to adjacent bones.<sup>1</sup> Basically it is a flattened strip of bone that is bent and twisted along its length. At its posteroventral tip it lies over the premaxillary arm. At its midpoint it bends inward toward the midline over the upper edge of the premaxillary arm and then twists slightly forward so that the anterodorsal tip slips under the premaxillary head. At the point where the forward twist is most evident, there arises on the posterior edge of the maxilla a flange of bone that extends slightly dorsal and then abruptly forward, in extreme cases forming a large shelf that lies over the premaxillary head. The concave form of the maxilla dorsally is most evident in species with protrusile premaxillae, e.g., in some exocoetids and in various cyprinodontoids and atherinoids. In species with essentially non-protrusile jaws the dorsal shelf is poorly developed on the maxilla, as in hemirhamphids, scomberesocoids, adrianichthyoids, and melanotaeniids.

The premaxilla is a very broad bone that has a distinct upper and lower expansion. In exocoetoids and adrianichthyoids the distinction is not marked, although the head of the premaxilla is in most cases in the form of a large triangular plate. In many exocoetids, cyprinodontoids, and atherinoids the tri-

angular plate may be drawn posteriorly into distinct ascending processes, the tips of which rest on the disclike mesethmoideum when the mouth is closed. In melanotaeniids the premaxillary head is either in the form of a triangular plate or is much reduced, thus approaching the condition in the Adrianichthyidae. Also in adrianichthyids and in some melanotaeniids (*Rhombatractus* species), and apparently uniquely among the fishes being considered here, the forward edge of the premaxilla folds under and backward, and a distinct dentigerous layer of many fine teeth is cemented along the folded outer surface of this bone (the teeth on the dentary are of this same peculiar type and the dentary itself is tubular in cross section).

In marked contrast to all the above features of the jaws and their suspension, mugiloids (particularly those of the subfamily Agonostominae), sphyraenoids, and polynemoids have the following: the prevomer and palatine possess large toothed dermal components and the head of the palatine has a ball-and-socket joint with the maxilla; the palatine head, in the shape of a ballpeen hammer, has a distinct maxillary and ethmoidal processes; the maxilla is always larger posteroventrally than the premaxilla and always carries the latter bone; and the association between the maxillary and premaxillary heads is determined by the presence of a distinctive articular process on the premaxilla that is held firmly by a large, lobed, maxillary structure. Moreover, in sphyraenoids and polynemoids the lower end of the maxilla is equipped with one or two accessory bones, the supramaxillae, which are characteristic of many percoids.

Functionally, the protrusile mechanism of the jaws of many exocoetoids, cyprinodontoids, atherinoids, and phallostethoids is very different from that of mugiloids, sphyraenoids, and polynemoids.<sup>2</sup> In members of the

<sup>1</sup> The maxilla is lacking in the Horaichthyidae. In this family the autopalatine, which is of approximately normal development, articulates directly with a posterolateral notch in the premaxilla.

<sup>2</sup> Gosline (1963), in his discussion of jaw mechanisms, reported observations suggesting that in cyprinodontoids the lower lip folds out over the upper laterally, whereas atherinids show the reverse condition. In the present material, however, there is no evidence of such a distinction, the lower lip forming the outermost fold in cyprinodontoids, the inner or outermost fold in exocoetoids, and the outermost fold in all the atherinids examined except *Basilichthys australis* which fails to develop either a distinct upper or lower fold.

former groups with protrusile mouths, the maxilla rotates on its long axis during the excursion forward of the premaxilla, allowing the upper portion of the maxilla which extends under the premaxillary head to follow the premaxilla forward. When the premaxilla is drawn back, the head of the maxilla returns with it, and the premaxilla becomes once again seated in the maxillary concavity. Both upper jaw bones are held together by a bed of spongy connective tissue and by a dorsal, straplike, ligamentous covering. In mugiloids, sphyraenoids, and polynemoids the protracted premaxilla loses contact with the head of the maxilla, and the movement forward of the premaxillae is controlled, not by contact with the maxilla, but by a system of crossed ligaments that provides multidirectional strength (see, for example, Burne, 1909, fig. 204). Such crossed rostral ligaments are absent in exocoetoids, scomberesocoids, adrianichthyoids, cyprinodontoids, atherinoids, and phallostethoids. The mugiloid-sphyraenoid-polynemoid system of crossed ligaments is typically percoid (see Schaeffer and Rosen, 1961, fig. 5).

The presence or absence of the system of crossed rostral ligaments appears to be specifically related not only to the type of maxilla and premaxilla that develops, but equally to the maxillary-palatine connections and the detailed form of the mesethmoideum. In mugiloids, for example, the complex mesethmoideum has paired lateral outgrowths that serve as points of attachment for the ethmomaxillary ligaments, and the palatine head possesses a large posterior extension for the palatopremaxillary ligament. In striking contrast, exocoetoids, cyprinodontoids, and atherinoids lack crossed rostral ligaments, possess a simple disc-shaped mesethmoideum, and have no posterior enlargement of the palatine head. It is therefore evident that the differences between these two systems of jaw protrusion are not differences of individual anatomical details but rather of a syndrome of features that encompass the entire rostral part of the syn-cranium. Hence the dissimilarities between atherinoids and mugiloids assume a significance not hitherto recognized, as do the similarities among exocoetoids, cyprinodontoids, and atherinoids. It cannot be gainsaid that

such a complex assemblage of functionally interrelated structures could have arisen independently in unrelated groups, but to make this assumption at the present time is surely to open a Pandora's box that will ever raise our doubts about even the most palpable examples of similarities that reflect a common lineage. This general view may be still further emphasized by pointing out that even the apparently most primitive atherinoids (e.g., *Bedotia*) and mugiloids (e.g., *Agonostomus*) exhibit the full spectrum of the above fundamental differences in jaw structure and function.

#### JAW MUSCULATURE

In general in teleosts two or three sheets of cheek, or adductor mandibulae, muscles insert on the jaws, and these are usually arranged as superficial ( $A_1$ ), middle ( $A_2$ ), and internal ( $A_3$ ) layers, or a combined  $A_2$  and  $A_3$ . Partly above and partly internal to the cheek muscles are two or more muscles that insert on the jaw suspension (adductor and levator arcus palatini) and on the opercular apparatus (dilator operculi). An additional cluster of muscles, usually smaller, arises between the adductor mandibulae and the adductor arcus palatini. This muscle cluster was assigned to the levator maxillae superioris series by Rosen (1962).

The form of the cheek muscles and their tendons and associated ligaments that regulate jaw movements provides a contrast between mugiloids, sphyraenoids, and polynemoids on the one hand, and exocoetoids, scomberesocoids, adrianichthyoids, cyprinodontoids, atherinoids, and phallostethoids on the other. In mugiloids, sphyraenoids, and polynemoids the tendon from the superficial division of the adductor mandibulae series (i.e.,  $t \cdot a_1 \cdot mx$  from  $A_1$ ) attaches fairly high on the maxilla, usually just ventral to its palatine hinge, whereas in exocoetoids, scomberesocoids, adrianichthyoids, cyprinodontoids, atherinoids, and phallostethoids,  $t \cdot a_1 \cdot mx$  attaches to the posteroventral section of the maxillary arm at a point far removed from the maxillary-palatine hinge. Moreover, in the latter fishes there is almost always present a small, internal tubular section of the adductor mandibulae ( $A_3$ ) which is overlain by the two much larger, straplike, superficial divi-

sions of this muscle ( $A_1$  and  $A_2$ ). The muscle  $A_3$  inserts in the Meckelian fossa,  $A_2$  inserts on the coronoid process of the mandible, and often on the lower premaxillary arm, and  $A_1$  inserts on a long tendon,  $t \cdot a_1 \cdot mx$ , to the lower maxillary arm (fig. 11; pl. 14). In mugiloids, sphyraenoids, and polynemoids  $A_2$  and  $A_3$  are either consolidated or  $A_3$  is lost, and the remaining muscle inserts on the inner mandibular surface and on the coronoid process;  $A_1$ , as already noted, inserts on a long tendon to the middle or upper maxillary arm.

The anterior levator maxillae superioris muscle of teleosts is usually divided. It originates on a flat tendon on the metapterygoid from which point it passes obliquely forward along the palatopterygoid arch to in-

sert high up on the posterior edge of the maxilla. It occurs in amblyopsiforms, percopsiforms, gadiforms, and perhaps in other groups as well, but is wanting in cyprinodontoids, as shown by Rosen (1962). That it is not a displaced  $A_1$  or part thereof is suggested by the occurrence of a distinct though small  $A_1$ , together with a well-developed levator maxillae muscle in some amblyopsiforms, percopsiforms, and gadiforms.

In exocoetoids, cyprinodontoids, adrianichthyoids, atherinoids, and phallostethoids  $A_1$ ,  $A_2$ , and  $A_3$  are always present and  $A_2$  and  $A_3$  are usually distinct (although  $A_3$  is small in exocoetoids and atherinoids), but the levator maxillae series is in all cases absent. In mugiloids, sphyraenoids, and polynemoids  $A_1$  also is present and well developed. The

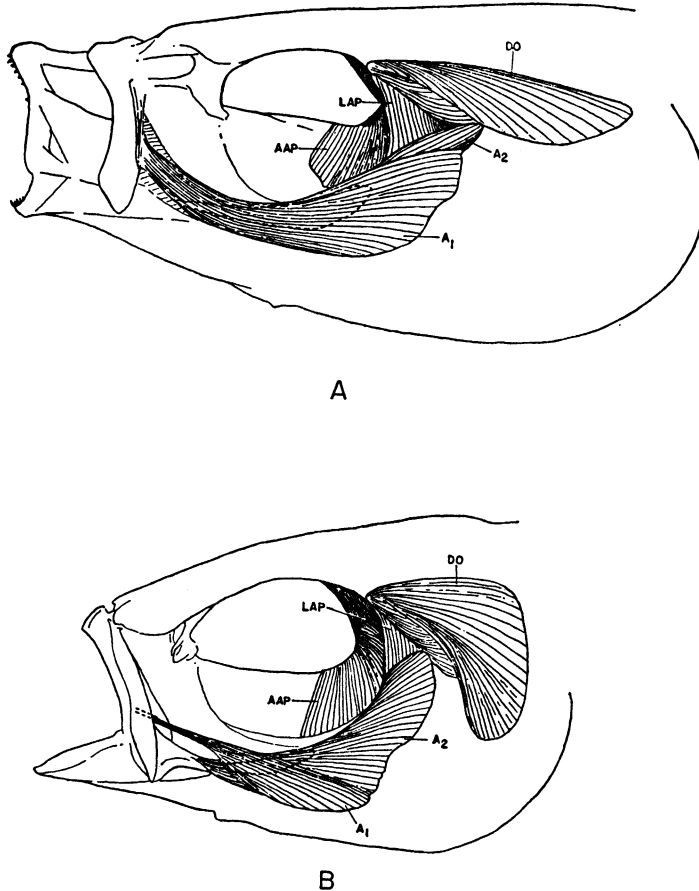


FIG. 11. Jaw muscles of silversides, semidiagrammatic. A. *Austromeniidia regia* (Humboldt). B. *Eurystole eriarcha* (Jordan and Gilbert). The pattern in A is essentially like that in *Kirilandia pachylepis* (Günther). The tubular  $A_3$  is shown by the dashed line.

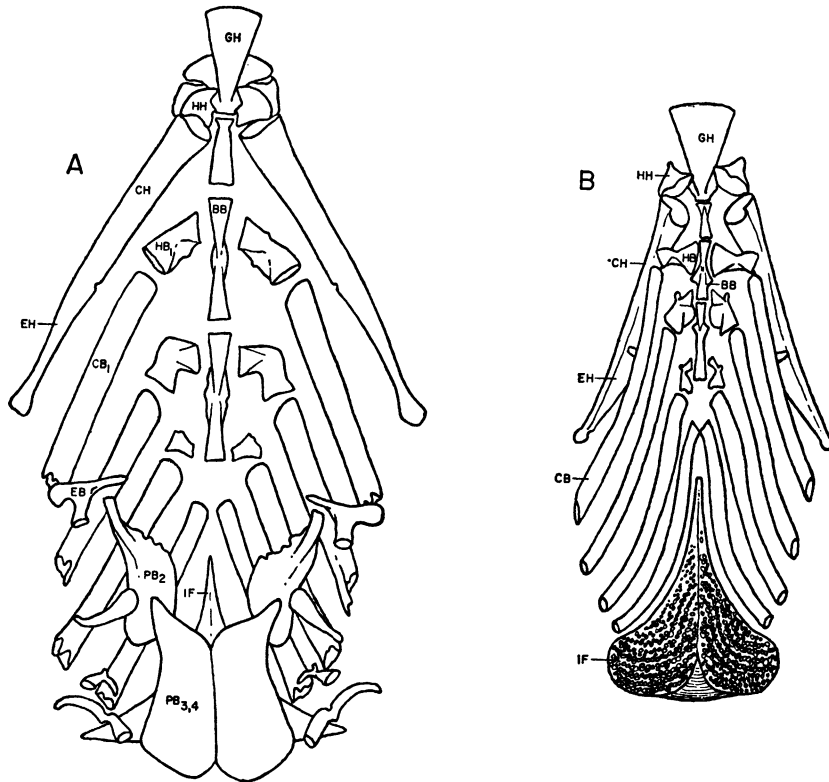
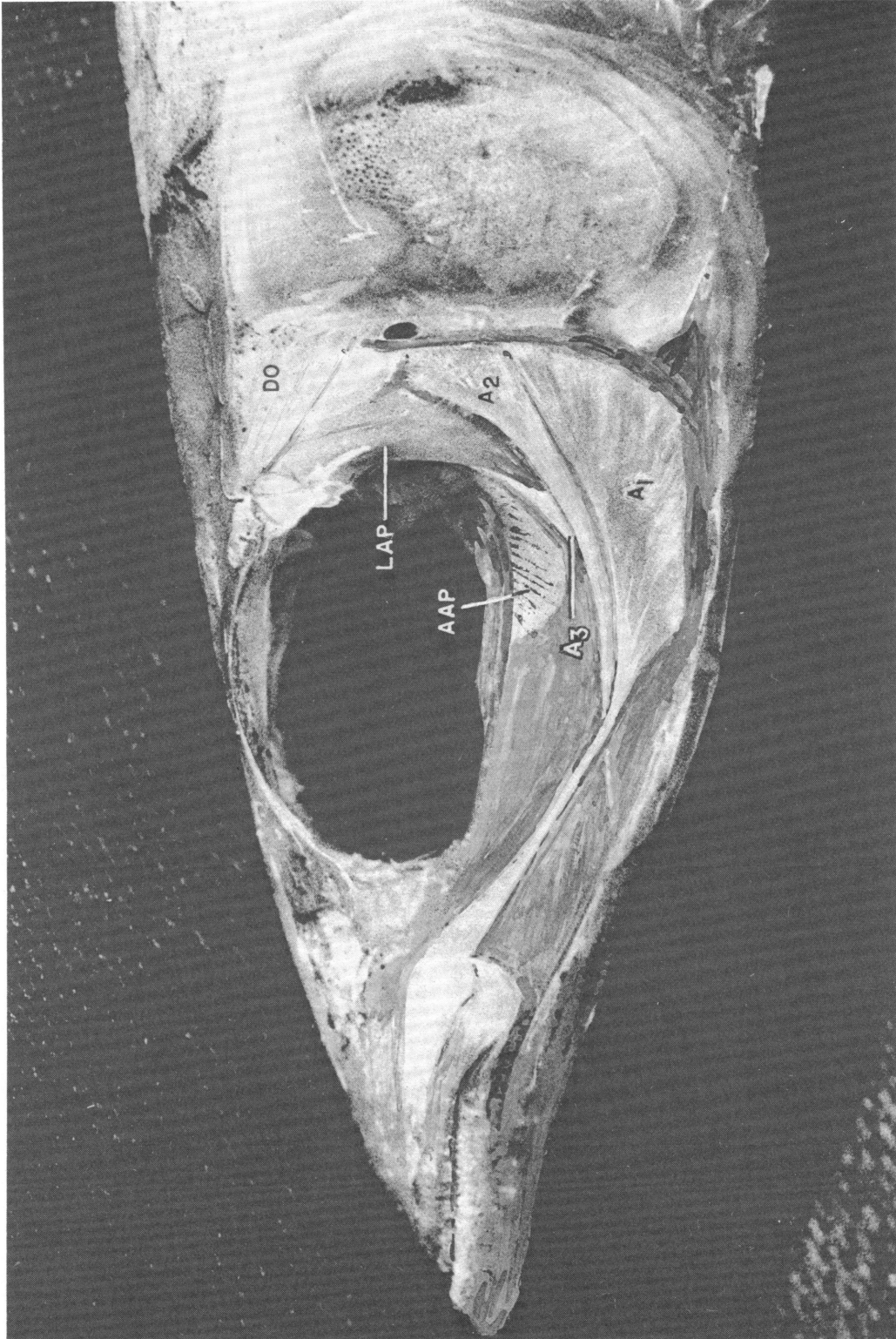


FIG. 12. Pharyngobranchial apparatus. A. *Dermogenys sumatranus* (Bleeker). B. *Xenopoecilus sarasinorum* (Popta), with the epibranchials and superior pharyngeals removed to show the united inferior pharyngeal bones.

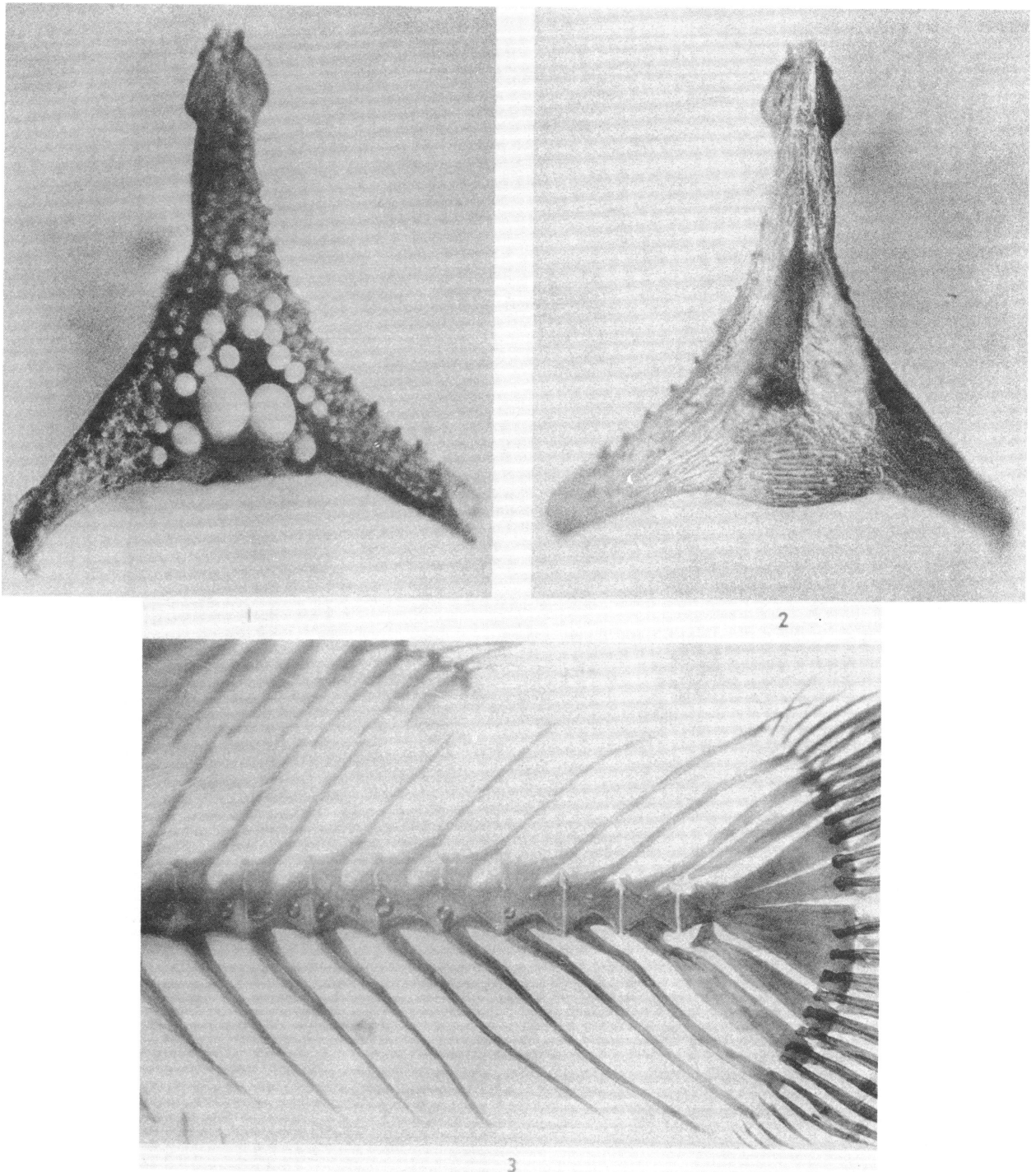
levator maxillae series is similarly absent, but in its place a long ligament runs upward from the pterygoquadrate to the maxillary head just below its palatine articulation. A ligament or tendon was described in this approximate position in *Scomber* by Allis (1903) who labeled it as a tendon,  $t \cdot a_3 \cdot mx$ , from  $A_3$ . The inner mandibular adductor  $A_3$ , however, typically inserts in the Mekelian fossa, and Rosen (1962) suggested that this tendinous element may instead represent the connective tissue remains of the anterior levator maxillae superioris muscles which characteristically follow this course. If this interpretation is correct, then prepercoids seem to have followed two alternative myological developments, one emphasizing the levator maxillae and reducing the external mandibular adductor,  $A_1$  (Amblyopsiformes, Percopsiformes, Gadiformes), and the other reducing the levator maxillae series to a ligament and strengthening the external ad-

ductor (perciforms generally). Neither levator maxillae muscles nor their ligamentous remains have been found in exocoetoids, scomberesocoids, adrianichthyoids, cyprinodontoids, atherinoids, or phallostethoids, so that the origin of their particular pattern of jaw muscles remains obscure.

A favorable myological comparison between cyprinodontoids, adrianichthyoids, and amblyopsiforms may be made on the basis of the great development in all of the adductor arcus palatini muscle (see Rosen, 1962, figs. 3, 6A), which in exocoetoids and atherinoids is rather small and confined to the posterior wall of the orbit. But phallostethoids also have the adductor arcus palatini filling the entire floor of the orbit, and such a comparison therefore appears to be of little significance. The extent of this muscle, as stated above, is inversely proportional to the size of the mesopterygoid ossification. In general it seems that the same myological evidence



Retouched photograph of the head of *Arrhamphus brevis* (Seale). The left cheek muscles, the upper jaw bones, and the connecting tendon have been exposed, and the eye has been removed to reveal the extent of the adductor arcus palatini muscle



1, 2. Photomicrographs of inferior pharyngeal bones in *Fundulus similis* (Baird and Girard). 1. Dorsal. 2. Ventral  
3. Photomicrograph of the caudal skeleton in *Aplocheilichthys panchax* (Hamilton-Buchanan)



which suggests a relationship of cyprinodontoids and adrianichthyoids with exocoetoids, atherinoids, and phallostethoids, reinforces the hypothesis of their phyletic separation from the amblyopsiforms.

#### PHARYNGOBRANCHIAL APPARATUS

In exocoetoids, scomberesocoids, cyprinodontoids, adrianichthyoids, atherinoids, and phallostethoids, pharyngobranchial 1 is lacking (a minute ossification is present in some examples of *Melanotaenia*, but not in the other melanotaeniids examined), pharyngobranchial 2 is tooth-bearing, of small or moderate size, and closely applied to or fused with the anteroventral margin of pharyngobranchial 3, and pharyngobranchials 3 and 4 are toothed, much enlarged, and nearly or completely fused together into a single large bone (figs. 12, 13). In *Bedotia*, pharyngobranchials 3 and 4 are joined together by a straight suture, which is perhaps additional evidence that this genus, and the related *Rheocles*, contain some of the most primitive atherinoids (see also Jordan and Hubbs, 1919,

pp. 9, 10, 20). In exocoetoids (fig. 12A), scomberesocoids, adrianichthyids (fig. 12B), and some cyprinodontoids (various species of *Fundulus*) the lower pharyngeals are fused together into a single, tooth-bearing, triangular plate. A delicate straight suture is visible between the two halves in adrianichthyids, although the two bones cannot be separated. In *Fundulus* an evident interlocking suture is present in many cases (pl. 15, figs. 1, 2). The lower pharyngeals in all the above groups, whether fused or not, possess a large bony wing ventrally for insertion of fibers from the sternohyoid muscles.<sup>1</sup>

Pharyngobranchials 3 and 4 are separate in sphyraenoids and polynemoids and are sutured united in mugiloids. The separation of elements 3 and 4 appears to be rather widespread in teleosts, occurring in esocoid clupeiforms and in the percoid *Centropristes*, as well as in amblyopsiforms and percopsiforms, as pointed out by Rosen (1962).

<sup>1</sup> In contrast to the fused lower pharyngeals of the Cichlidae which lack ventral processes.

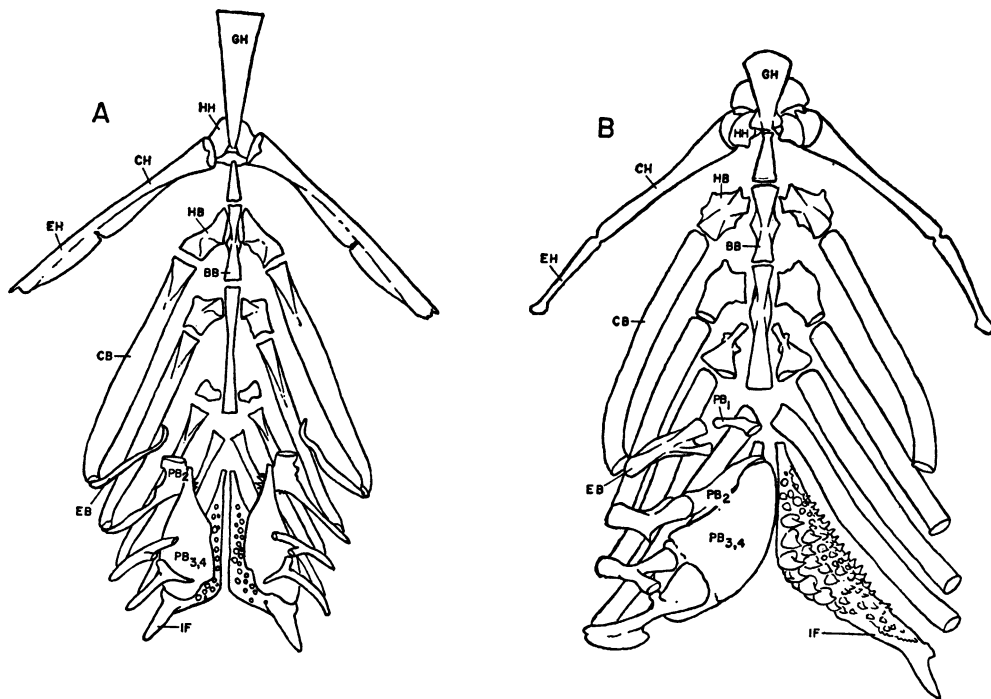


FIG. 13. Pharyngobranchial apparatus in silversides. A. *Menidia beryllina* (Cope). B. *Melanotaenia nigrans* (Richardson), with the right epibranchials and superior pharyngeals removed to show underlying inferior pharyngeal element.

Hence it may represent a rather primitive teleost condition that has been largely retained except in certain groups.

#### HYOID APPARATUS

In exocoetoids, adrianichthyoids, cyprinodontoids, atherinoids, phallostethoids, mugil-

loids, sphyraenoids, and polynemoids, the proximal half of the ceratohyal (near its hypohyal articulation) is slender, and typically the distal half (near its epihyal articulation) is abruptly elevated. The ceratohyal and epihyal are rigidly joined together dorsally by a reinforcing bridge of bone. The

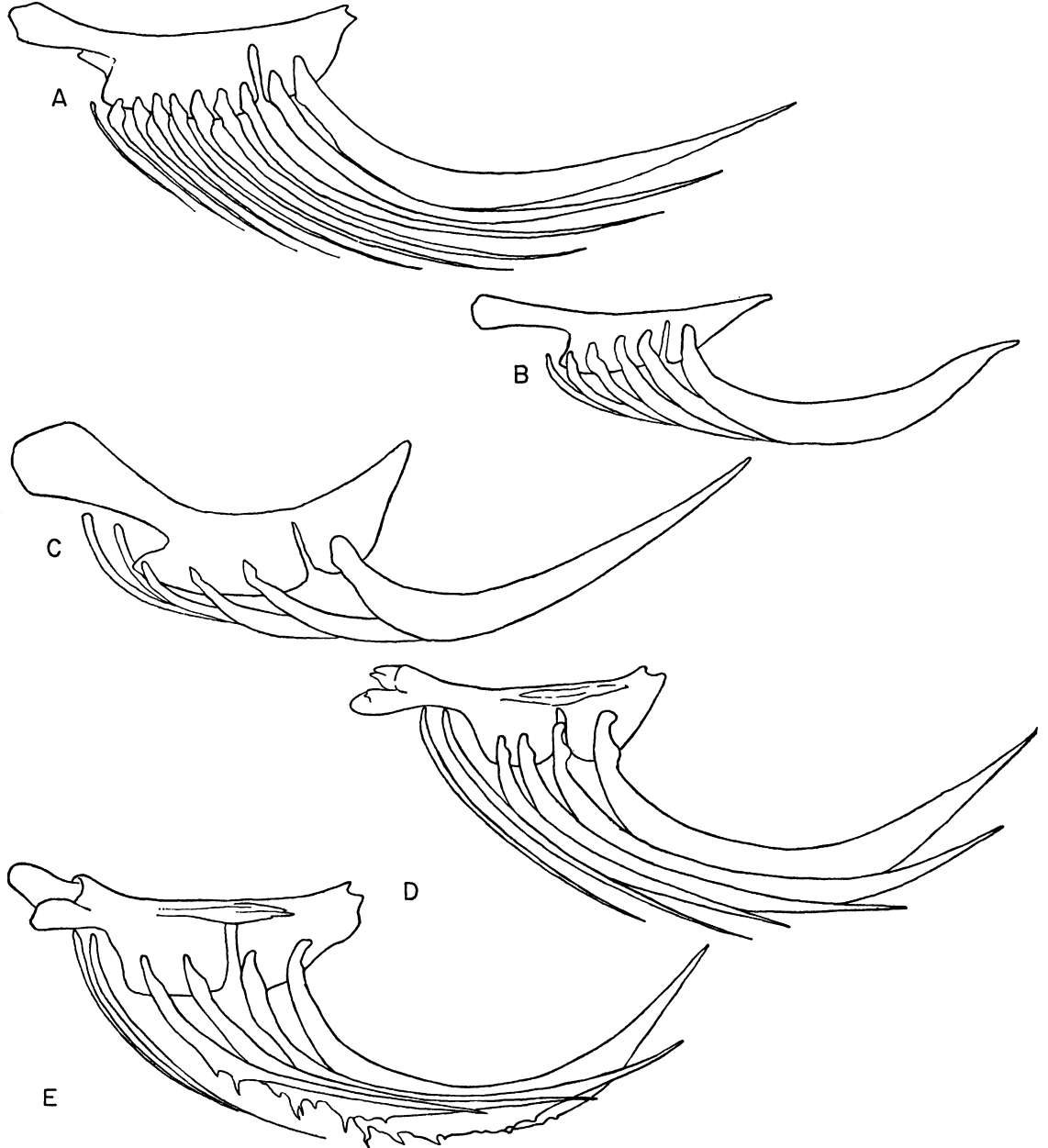


FIG. 14. Hyoid bar and branchiostegal rays. A. *Dermogenys sumatranus* (Bleeker). B. *Xenopocilus sarasinorum* (Popta). C. *Gulaphallus mirabilis* Herre. D. *Pachypanchax playfairi* (Günther). E. *Pseudomugil novaeguineae* Weber.

number of branchiostegal rays ranges from nine to 15 in exocoetoids and four or five to seven in the other groups. In some species of Hemiramphidae there may be as many as nine branchiostegal rays on the elevated part of the ceratohyal and on the epihyal (fig. 14A). In adrianichthyoids there are five rays on the elevated part of the hyoid bar (fig. 14B). In phallostethoids (fig. 14C), cyprinodontoids (fig. 14D), and atherinoids (fig. 14E) there are never more than four. The anterior, hair-like branchiostegal rays are attached to the depressed part of the ceratohyal in a variety of ways. In exocoetoids, the hypohyal is larger than that in the other groups, often filling the space under the depressed part of the ceratohyal (as is true also of some percoids, e.g. *Pogonias*). When this occurs, the hair-like rays make a loose contact with the under side of the hypohyal. In adrianichthyoids, the anterior rays when present occupy the same position as those of exocoetoids, except that the hypohyal is not enlarged and the rays are merely seated in connective tissues some distance from the depressed anterior part of the ceratohyal. In cyprinodontoids, the hair-like branchiostegals attach directly or through the intervention of connective tissues to the depressed section of the bar. When attachment is direct in cyprinodontoids the proximal tips of the rays make point contact with the under surface of the bar, or the rays are bent sharply inward proximally and contact is established between the bent proximal piece and the bar. The two latter methods of contact (i.e., point and bent proximal piece) are characteristic of atherinoids, with point contact being typical in *Pseudomugil* and allied forms. From the above, it appears that adrianichthyoids bridge the gap between exocoetoids and cyprinodontoids-atherinoids in branchiostegal pattern.

It has been claimed that the exocoetoid-scomberesocoid branchiostegal plan follows an isospondylous pattern (Hubbs, 1919; Gosline, 1963). In a representative isospondyl, such as the salmonid, the hyoid bar does not have a separate elevated distal segment, nor are the ceratohyal and epihyal joined by a dorsal bridge of bone. The two main segments of the truly isospondylous structure are joined by flexible cartilage, and the numerous branchiostegal rays, which increase

gradually in size anteroposteriorly, are evenly distributed along the length of the bar. The exocoetoid structure is, therefore, hardly isospondylous in a complete sense. It is, in fact, clearly percoid in the form of the bar itself, and a loss of but two branchiostegals in some exocoetoids would bring the group within the range of percoids in ray number.

Scomberesocoids, however, present a somewhat different picture. The branchiostegal ray number is generally high, about 11 to 15. Moreover, no section of the hyoid bar is distinctly elevated, although the ceratohyal and epihyal are joined dorsally by a long lamella. The bar itself is greatly attenuated, apparently in response to the lengthening of the branchial apparatus and the jaw suspension that is associated with the much enlarged upper and lower jaws. Among the Perciformes, high branchiostegal ray number again is encountered in species with similar modifications of the jaws, for example, in the istiophorid *Tetrapturus* in which there are eight instead of the more usual six or seven, although a similarly high number is to be found among some blennioids, and an even higher number among echeneids. The important feature of *Tetrapturus*, however, is that in association with the long jaws, jaw suspension, branchial apparatus, and high branchiostegal number is an unusually long hyoid bar in which the characteristic percoid elevation of the ceratohyal has been suppressed. These observations naturally lead to the question of whether secondary elongation of the jaw suspension and associated structures could, at the pre-perciform level, have resulted in a secondary though slight increase in branchiostegal number. Has the exocoetoid number, for example, resulted from a slight secondary increase and that of scomberesocoids from a further expression of such a trend to keep pace with an increased lengthening of the jaws?

There is another view of the matter that does not require the assumption of great or small structural transformations to account for the differences among exocoetoids, cyprinodontoids, and atherinoids in hyoid and branchiostegal anatomy. First, however, it must be recognized that this apparatus in exocoetoids is closer to the percoid form in some species (fig. 14A) than in others, and in almost all instances more so than in scom-

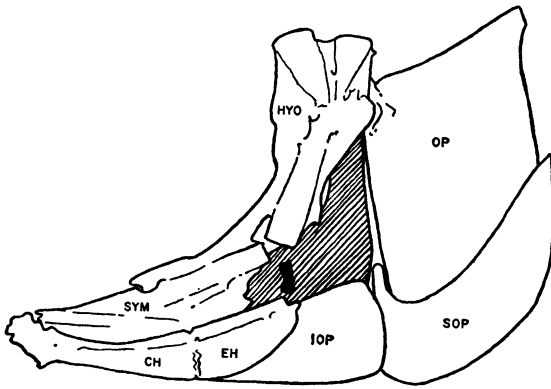


FIG. 15. Hyosymplectic and opercular apparatus in *Menidia beryllina* (Cope), showing the absence of a distinct expansion of the hyoid bar and the absence of armature on the opercular bones. Preoperculum obliquely lined; interhyal solid. Compare with figure 16.

beresocoids. Likewise, hyoid and branchiostegal structures of cyprinodontoids approach the percoid type more closely than do those of adrianichthyoids, and some atherinoids possess a hyoid apparatus that lacks the typically percoid expansion of the ceratohyal, for example, *Menidia* (fig. 15). Now, we may with every reason look upon these structures in the above fishes as being close to, if not in many cases identical with, those of percoids but showing, nevertheless, a range in form that suggests a structural complex in transition. Variability in the hyoid and branchiostegal apparatus far greater than that seen here can be found in numerous phylogenetically valid groups of malacopterygians (e.g., the osteoglossoids; Ridewood, 1905, and Greenwood, 1963), so that the differences being discussed herein are not in themselves of great magnitude. Moreover, the differences dwindle further in significance if exocoetoids, adrianichthyoids, atherinoids, and their allies represent a phylogenetically natural series that stands somewhere near the ancestry of the percoid fishes. In forming such a group, they have in fact exactly the combination of broad transition, secondary specialization, and close approach to the new evolutionary grade that would be expected of the descendants of a group of ancestral acanthopterygians.

#### OPERCULAR APPARATUS

In exocoetoids, scomberesocoids, adrianichthyoids, cyprinodontoids, atherinoids (fig. 15), and phallostethoids the operculum is evenly rounded posteriorly and ventrally and is without spines. The preoperculum is without serrations.

In mugiloids, sphyraenoids, and polynemoids the operculum has one or two spines posterodorsally. In mugiloids and sphyraenoids the preopercular margin is entire; in polynemoids, serrate. The sphyraenoid-polynemoid opercular pattern is of a generalized percoid type (fig. 16).

#### SHOULDER GIRDLE

In exocoetoids, scomberesocoids, adrianichthyoids, cyprinodontoids, atherinoids, and

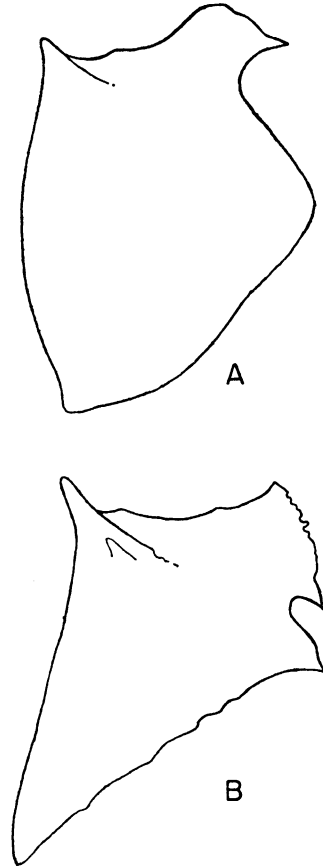


FIG. 16. Operculae. A. *Agonostomus monticola* (Bancroft). B. *Sphyraena barracuda* (Walbaum).

phallostethoids the scapula and the coracoid share in the formation of a recess (fig. 17) for the four cuboidal actinosts (a single specimen of *Xenopoecilus sarasinorum* has five actinosts on the left side). The supracleithrum is a small disc or triangle of bone that is confined within the dorsal limits of the cleithrum or is wanting (in adrianichthyoids); the posterior, flattened articular surface of the posttemporal lies directly over this.

Mugiloids, sphyraenoids, and polynemoids possess a shoulder girdle of more generalized form in which the four cuboidal or dumbbell-shaped actinosts are more marginal in position and in which the supracleithrum is formed as a long flat strut that is half, or more than half, of the length of the cleithrum (see Rosen, 1962, fig. 15).

In all the above groups, however, the

shoulder girdle is attached by a ligament (Baudelot's ligament) to the basicranium. In *Umbra*, amblyopsiforms, and percopsiforms, the shoulder girdle is attached by a ligament to the first vertebra.

#### PELVIC GIRDLE

In exocoetoids, scomberesocoids, adrianichthyoids, and many atherinoids the pelvic bones are more or less separate and possess a posterolateral styler or flattened process that extends upward in the body wall near the tips of or between the pleural ribs (figs. 4E, 18). In cyprinodontoids and in most Atherinidae the posterolateral process is reduced or absent, and the pelvic bones are joined together medially by a variety of processes. In most cyprinodontoids and in numerous New World atherinids (e.g., *Menidia*) the two bones are

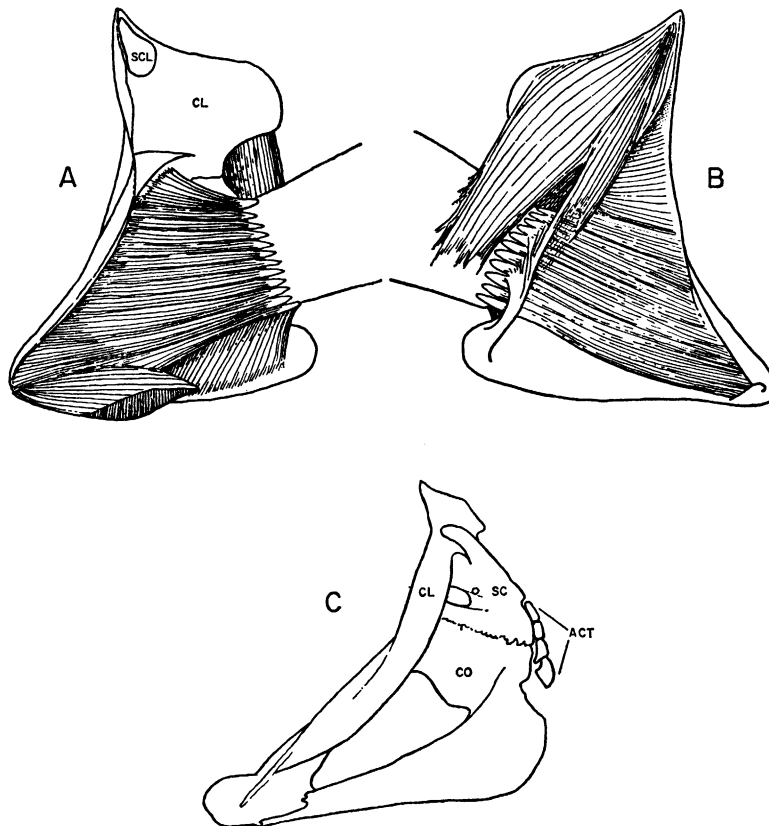


FIG. 17. Shoulder girdle in killifishes. A, B. *Xiphophorus helleri* Heckel, showing musculature and extent of supracleithrum. Compare with Grenholm (1923, figs. 48-50, 57-59) and Rosen (1962, fig. 15). A. Lateral. B. Medial. C. *Xenopoecilus sarasinorum* (Pošta).

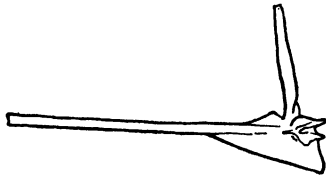


FIG. 18. Left pelvic girdle of *Oryzias latipes* (Temminck and Schlegel), lateral view. Anterior to left. Note upright lateral spur.

joined by overlapping finger-like outgrowths (fig. 19). In *Mugil*, *Melanotaenia*, and some cyprinodontoid species they are joined by the sutural contact of a spatulate process with its opposite member; such processes commonly have a posterior extension near the midventral line as is true also of some exocoetoids (e.g., *Oxyporhamphus*). This type of sutural contact via platelike medial outgrowths of the pelvic bones occurs also in the iniomous genera *Myctophum* and *Synodus*.

In sphyraenoids, polynemoids, and some mugiloids neither posterolateral nor postero-medial processes are present. The pelvic bones are joined together by a broad bony contact along more than half of their length. A similar condition is found in the beryciform genus *Holocentrus*. In mugiloids, sphyraenoids, and polynemoids the pelvic bones are

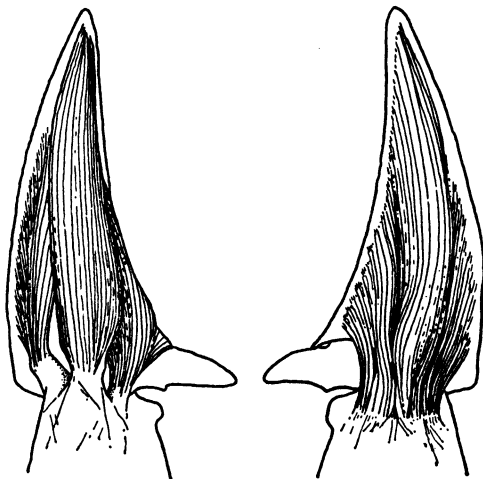


FIG. 19. Left pelvic girdle and pelvic musculature in *Xiphophorus helleri* Heckel. Anterior up. Ventral view to left; dorsal view to right. A girdle of this type occurs also in *Menidia*. Note finger-like medial process and the absence of a lateral spur.

in contact with the postcleithrum and inclined obliquely upward toward the cleithral symphysis. Among cyprinodontoids and atherinoids the pelvic bones are more superficial and are in contact with the postcleithrum in several cases (in some Cyprinodontidae, Poeciliidae, Atherinidae, and in all Melanotaeniidae). In some Exocoetidae the pelvic bones have shifted forward but fail to touch the postcleithrum.

#### PLEURAL RIBS AND VERTEBRAL NUMBER

In exocoetoids, scomberesocoids, adrianichthyoids, and atherinoids the first pleural rib originates on the third vertebra. In cyprinodontoids and phallostethoids (i.e., *Gulaphallus*) it originates on the second vertebra. Gosline (1963) suggested that this character may be of importance in the defining of the relationships of the cyprinodontoid killifishes. If so, *Gulaphallus* appears to be closer to cyprinodontoids than to atherinoids, and adrianichthyoids apparently are close to all the above groups except the cyprinodontoids and phallostethoids. Moreover, *Horaichthys* (Horaichthyidae) appears to be related to *Oryzias* (Kulkarni, 1948), yet its first pleural rib stems from the second vertebra. The utility of this feature of the axial skeleton in aiding phylogenetic analysis will thus remain in doubt until the developmental mechanism underlying the difference in origin of the first pleural rib is understood.

Vertebral number is equally difficult to interpret, although it is somewhat more suggestive. Exocoetoids have approximately 45 to 73 vertebrae, of which as many as 18 to 27 may be precaudal. The range in vertebral number of cyprinodontoids is 26 to 53; precaudal vertebral number ranges from 10 to 25, 15 being the modal number for representatives of 20 genera in five families. In atherinoids the total count extends from 31 to 60, the usual precaudal count being 22 or 23. Variation in the total atherinoid count is accomplished through increase or reduction of the caudal vertebrae, those forms with the fewest vertebrae still retaining a precaudal count of approximately 22 (e.g., melanotaeniids). Phallostethoids have a range of 34 to 38 vertebrae, and hence fall more or less in line with cyprinodontoids.

In contrast to the high total and precaudal

counts in the above groups, mugiloids have 24 to 26 vertebrae (11 precaudal), and sphyraenoids uniformly 24 vertebrae (12 precaudal), as do the great majority of perciform fishes.

#### CAUDAL SKELETON

The condition of the caudal skeleton of exocoetoids, in which the caudal fin is forked and the lower lobe enlarged (presumably for skittering at the surface or other similar locomotor behavior), is as follows (fig. 20): the last two hemal spines enlarged and blade-like; a single, blade-like, usually free hypural with a distinct retrorse hook proximally

(partially fused to terminal half centrum in *Oxyporhamphus*); terminal half centrum bearing two large, triangular, hypural plates of equal size and opposite symmetry; uroneural either free or partially or completely fused to upper hypural plate; neural arches of terminal half centrum and several preceding centra with massive bony neural plates; three epural elements of variable size, shape, and position usually situated above terminal half centrum.

In the hemiramphids with rounded or truncate caudal fins (fig. 21A) only the hemal spine on the last complete centrum is blade-like, and plates of bone do not develop from

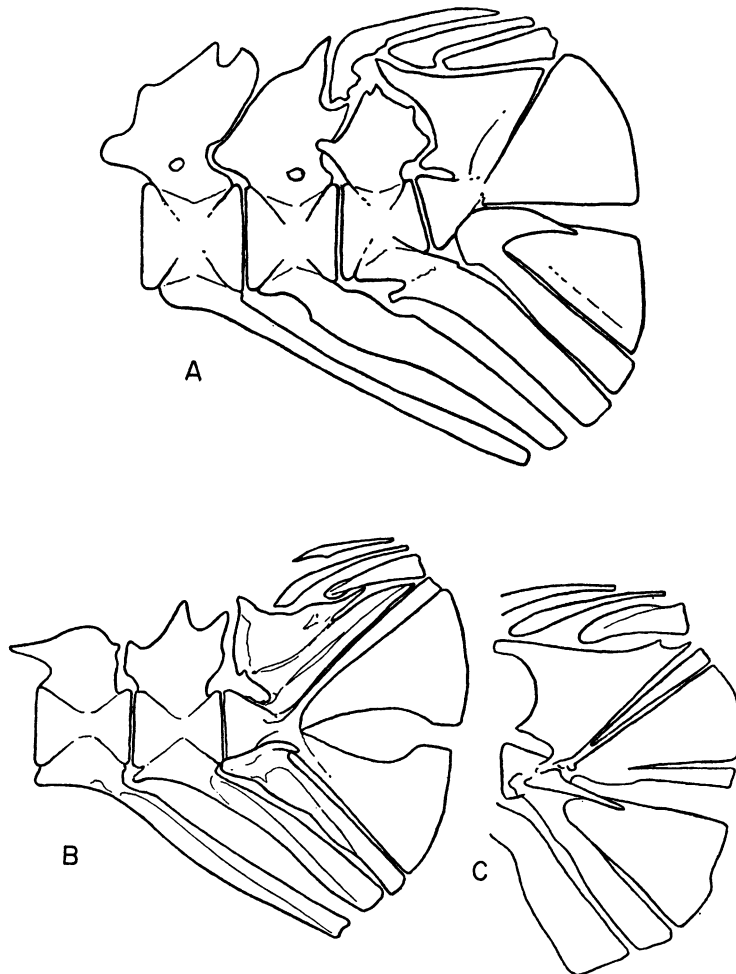


FIG. 20. Caudal skeletons in marine halfbeaks and in a flyingfish. A. *Parexocoetus brachypterus* (Richardson). B. *Chriodorus atherinoides* Goode and Bean. C. *Oxyporhamphus micropterus* (Valenciennes).

the last several neural arches. In *Dermogenys* the hypural that carries the proximal retrorse hook is joined to the lower of the two hypural plates, and the uroneural is partially fused with the upper plate. The three epurals are long and slender and extend downward toward the vertebrae, rather than mostly backward, as in fork-tailed hemiramphids. The structural relations of the epurals in *Dermogenys* suggest strongly that the anteriormost epural is little more than a detached neural spine from the neural arch of the last complete centrum. If so, and if the simpler, less-modified condition of the *Dermogenys* caudal skeleton indicates the primitive con-

dition for exocoetoids, there are but two epurals ancestrally in this group of fishes.

Between the caudal skeleton of *Dermogenys* and that of adrianichthyoids (fig. 21B-D), that of atherinoids (fig. 22B, C), and that of phallostethoids (fig. 22D), there are no fundamental differences. Adrianichthyoids differ mainly in having the lowermost hypural free as in most exocoetoids and in having the neural spine on the last complete centrum continuous with the neural arch. *Xenopoecilus poptae* has two epurals; *X. sarasinorum*, only one. In both, the uroneural has completely merged with the upper hypural plate or is reduced to a small ossification near the base of

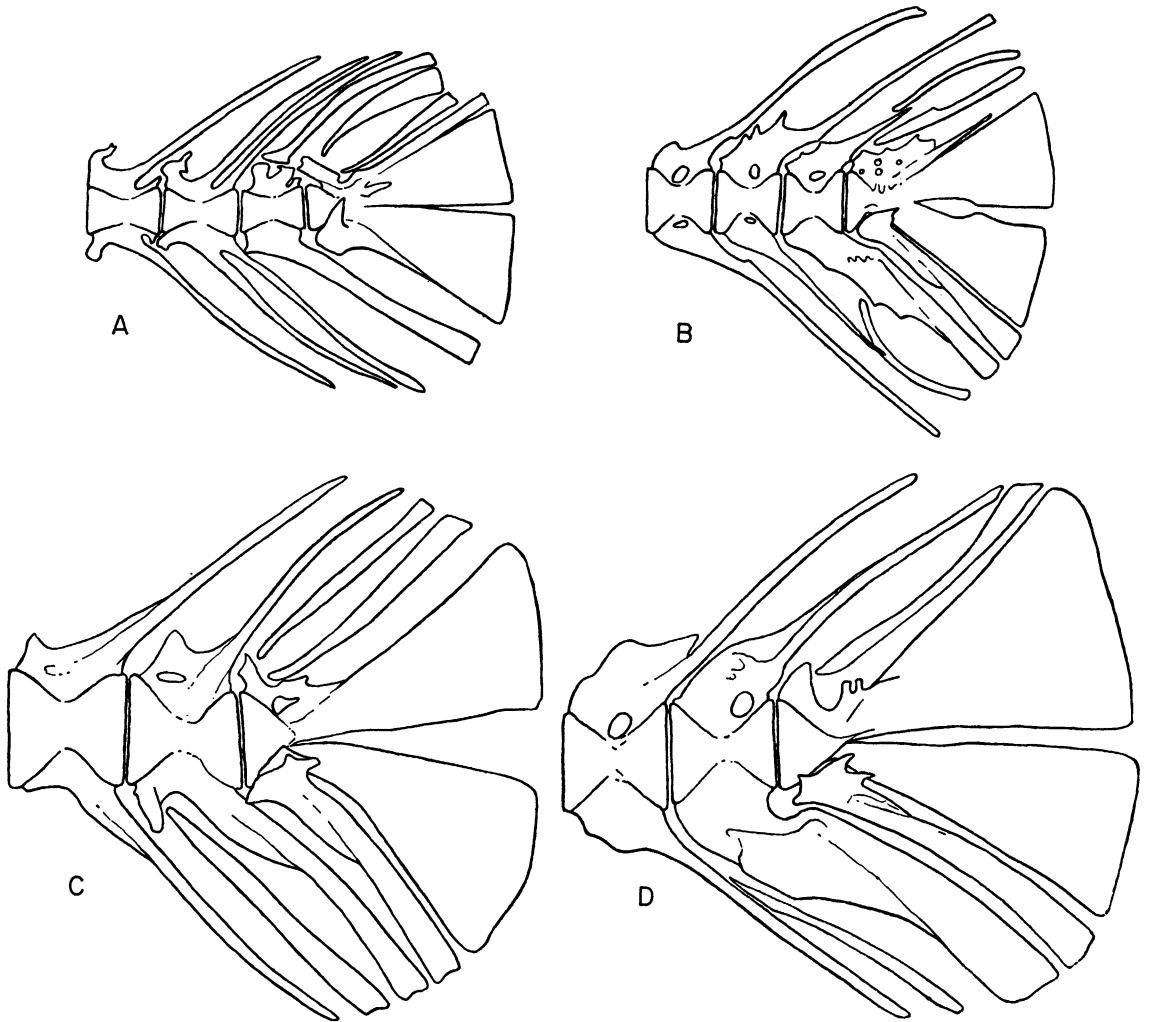


FIG. 21. Caudal skeletons. A. *Dermogenys sumatranus* (Bleeker). B. *Oryzias latipes* (Temminck and Schlegel). C. *Xenopoecilus poptae* Weber and de Beaufort. D. *Xenopoecilus sarasinorum* (Popta).



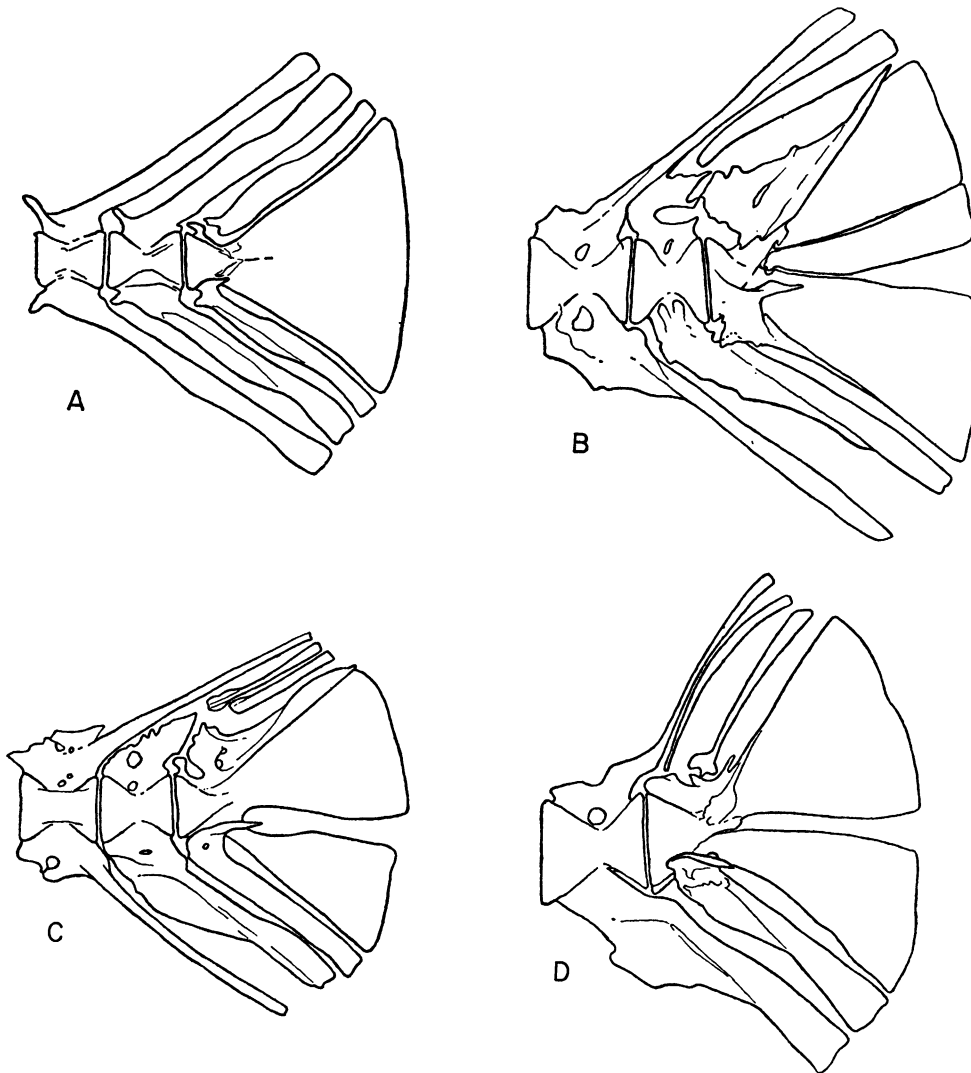


FIG. 22. Caudal skeletons. A. *Fundulus cingulatus* Valenciennes B. *Melanotaenia nigrans* (Richardson). C. *Menidia beryllina* (Cope). D. *Gulaphallus mirabilis* Herre.

the plate, as in the exocoetoid *Parexocoetus*. In *Melanotaenia* the lowermost hypural is fused with the lower hypural plate as in *Dermogenys*, as is the uroneural fused with the upper. The dorsal hypural plate is often composed of two incompletely fused pieces, and there is but a single epural. In atherinids the lowermost hypural bone is free, and the uroneural is fused with the upper hypural plate. There are constantly two epurals, and in this family as well as in melanotaeniids the neural arch of the last complete centrum does not carry a neural spine, although one of the two

epurals may represent the remains of this ossification. In the phallostethoid *Gulaphallus* the adrianichthyid pattern (of *X. poptae*) is readily seen; it differs from the atherinid pattern in the smallness of the uroneural.

The caudal skeleton of cyprinodontoids (fig. 22A) shows greater over-all symmetry than does that of the above groups in that the upper and lower hypural plates are in many species completely fused together, and in that the single epural is bladelike and forms a symmetrical dorsal counterpart of the free lowermost hypural element. In certain spe-

cies and in the young of many, in which the enlargement of free bones and interhypural fusion has progressed less far, the differences between the caudal skeleton of cyprinodontoids and that of round-tailed hemiramphids, adrianichthyoids, atherinoids, and phallostethoids are much less obvious. For example, in *Aplocheilus panchax* (pl. 15, fig. 3) even the upper hypural plate is divided ventrally as is that of some atherinids and melanotaeniids. In view of the over-all similarities noted among all the above groups, Gosline's (1961a, 1963) attempt to derive the cyprinodontoid caudal skeleton from the amblyopsiform-percopsiform-gadiform type appears to be unsound.

Superficially the mugiloid-sphyraenoid caudal skeleton resembles that of atherinoids, but Hollister (1937) pointed to an important developmental difference between them. In *Atherina* the lowermost hypural plate develops as a single entity. In *Mugil* (fig. 23A) and *Sphyraena* this plate forms from two distinct elements, the dorsal one being narrow and strutlike and the lower one broad and triangular. This division persists in adult *Sphyraena* and in some species of *Mugil*, although all the hypural elements tend to become locked together by intervening bone. *Sphyraena* further differs from atherinoids in having two uroneurals instead of one, and *Mugil* differs in having the very large uroneural and the uppermost hypural free from the terminal half centrum except in the largest individuals. Although the caudal skeleton of *Sphyraena* clearly resembles that of percoids more than it does this structure in atherinoids, in *Mugil* the resemblances are more difficult to define. Developmentally, *Mugil*, as Hollister has shown, is more like *Sphyraena* in having the lower hypural plate formed from two separate elements, some species even retaining a vestige of this early subdivision. It is not now possible to say whether the early developmental differences between the caudal skeletons of mugiloids and those of atherinoids are more important phylogenetically than their final adult similarities, but it seems probable that both are important. The developmental differences may mean, as advocated here, that atherinoids and mugiloids are members of different lineages. The similarities may mean that those lineages are intimately related. This interpretation leads

again to the view expressed above that the halfbeaks, killifishes, and silversides are the descendants of a transitional group that stood in the ancestry of the perch-like fishes.

The caudal skeleton of polynemoids (fig. 23B) shows a relative complexity and lack of fusion between elements. In *Polydactylus*, for example, seven distinct hypural bones combine to form two fan-shaped hypural complexes. Fusion of elements within each complex would result in the formation of two triangular hypural plates, but the lower plate must necessarily include the lowermost hypural with the proximal retrorse process in order to achieve symmetry with the upper plate. Moreover, there are a completely separate uroneural and four epurals (although one is generally minute), and the three ventral hypural bones are not fused to the terminal half centrum in smaller (not juvenile) specimens. No distinctions whatever could be found between the caudal skeleton of *Polydactylus* and that of *Roccus* illustrated by Gregory (1957), and no major distinctions could be found to separate it from the caudal skeleton of *Kuhlia* illustrated by Gosline (1961b).

The definition of what constitutes a percoid type of caudal skeleton is confused by the discovery of a similar, if not identical, structure in the genus *Myctophum* (fig. 23C). Here, as in polynemoids, the terminal half centrum supports the entire hypural complex. The lower half of the complex consists of three hypurals bound together by intervening bone. The lowermost hypural has the typical proximal hook for the origin of the hypochordal musculature. It is followed by a broad, triangular hypural and by another which is strutlike. The upper complex consists of three hypurals, also joined together, and a single free element just under the tip of the uroneural. A similar condition occurs in *Beryx*. Gosline (1961a) illustrated the caudal skeleton of another myctophiform, *Chlorophthalmus*, in which the hypural elements are supported on two centra and which hence appears to be somewhat more generalized. A system not unlike that of *Chlorophthalmus*, however, is to be found in the beryciform genus *Holocentrus* (fig. 23D). Although in *Holocentrus* the hypurals are distributed on two vertebral centra (i.e., the upper complex on a terminal half centrum, and the lower

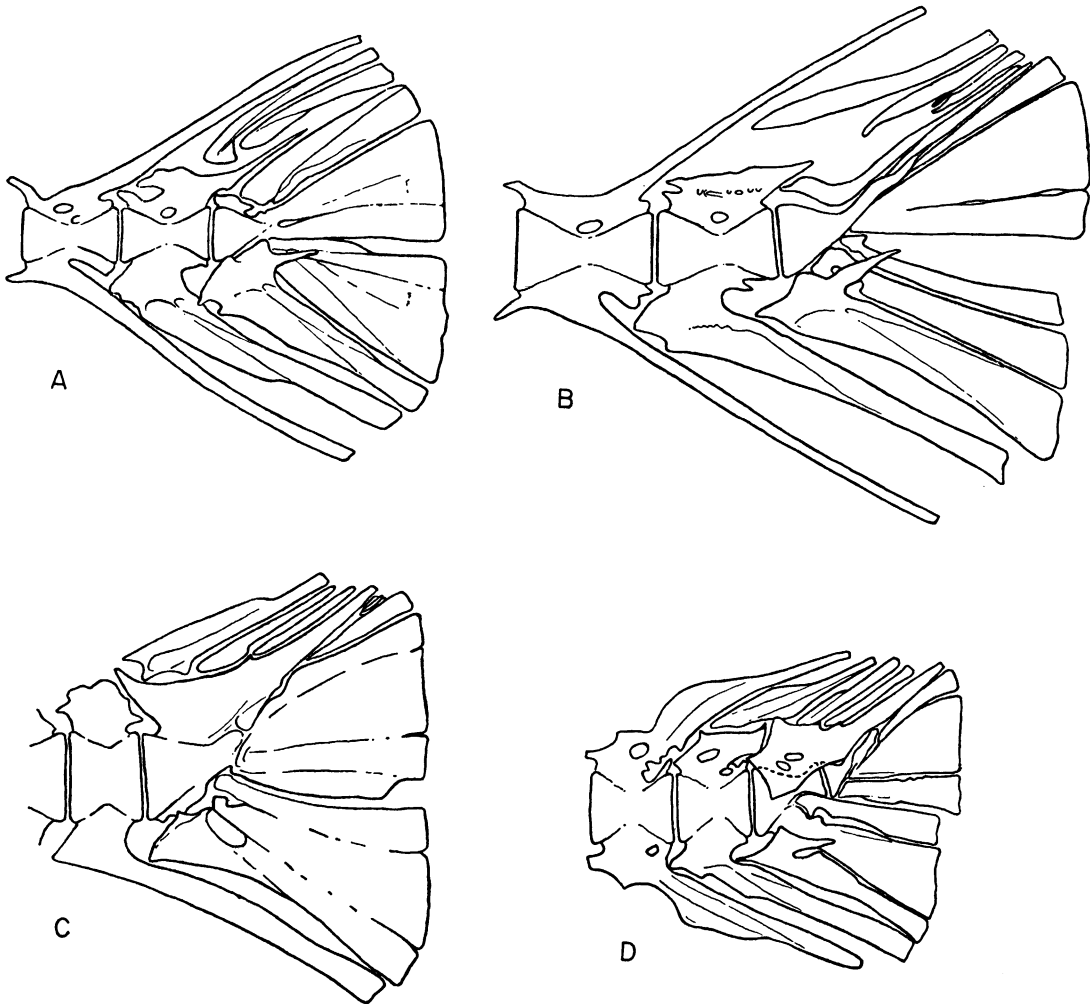


FIG. 23. Caudal skeletons. A. *Mugil cephalus* Linnaeus. B. *Polydactylus octonemus* (Girard). C. *Myctophum affine* (Lütken). D. *Holocentrus ascensionis* (Osbeck).

complex on the last complete centrum), the form of the individual hypural elements is precisely as illustrated by Hollister (1937) for *Sphyaena* and is typical of percoids generally.

Because the basic percoid caudal skeleton can be traced back through a beryciform type to that of the iniomous fishes, and because at least one myctophiform group (Myctophidae) and one beryciform group (Berycidae) show the transition to the percoid level (all hypurals emanating from the terminal half centrum), it seems evident that the type of caudal skeleton in question may have originated more than once in phyletic lines that go back to an ancestral or archetypal inioime. By extension, it must be judged possible that

the developmental and structural differences between the atherinoid and the mugiloid-sphyraenoid caudal skeletons reflect separate ancestries. If one accepts this argument, it is also evident that the double-centrum caudal skeletons of amblyopsiforms, of percopsiforms, and of gadiforms could also have had their origins at different levels. The cranial characteristics of these groups, however, argue in favor of a single origin, or at least of separate but closely approximated origins, somewhere near the beryciform level of organization (see Rosen, 1962, figs. 4, 10, 16, and 24).

Another view of the matter may be had in a consideration of the number and position of the principal caudal fin rays. As a preamble,

it should be noted that the articulation of the principal caudal rays, almost without exception, is restricted to the hypural elements, whereas the procurrent rays articulate with the hemal spines, uroneurals, epurals, and neural spines. In the iniomous genus *Myctophum* there are 19 principal rays. Of these 19, nine branched rays join the upper hypural complex, and eight branched rays articulate with the lower complex. A simple ray borders the branched rays above and below. This caudal fin-ray formula, I, 9, 8, I, occurs also in the Percopsiformes and Beryciformes. [Freihofer (MS) pointed to another similarity among these fishes, viz., that the ramus canalis system of nerves innervating the superficial cephalic sense organs of myctophids is fundamentally like that of the Percopsiformes and a beryciform, *Melamphaes* (as well as that of Apogonidae and *Gadus*, although this pattern in the latter seems to be in a reduced state)]. In all the other groups that are considered here there is a reduction in the total principal rays associated with the hypural bones. In percoids, for example, and in the mugiloids and sphyraenoids as well, the formula is reduced to I, 8, 7, I. A similar formula is found in atherinoids, although it is still further reduced in some forms (species of *Pseudomugil*) to I, 6, 5, I. In scomberesocoids and exocoetoids the formula is I, 6, 7, I, except in such genera as *Dermogenys* in which it drops to I, 5, 6, I or I, 6, 6, I. In adrianichthyoids the formula is typically I, 5, 6, I or I, 5, 5, II. Surprisingly, the formulas for cyprinodontoids are higher, modally I, 6, 7, I. They are also more variable, ranging from I, 4, 4, II to I, 8, 7, I, in cases in which the branched rays are restricted to the hypural bones. The phallostethid *Gulaphallus* is represented by I, 6, 6, I. Many, if not most, cyprinodontoids, however, possess accessory branched rays on the hemal and neural spines and on the single epural bone, so that the conventional system for expressing caudal fin ray number is inapplicable. For example, various species of *Fundulus* have 14 branched rays on the hypurals and four additional branched rays distributed above and below these. *Pachypanchax* has 19 branched rays of which 13 are on the hypurals.

Two questions are raised: (1) Are not cy-

prinodontoids more primitive than adrianichthyoids in having a higher branched caudal fin-ray count? (2) Are cyprinodontoids possibly unrelated to adrianichthyoids in embracing species in which the branched ray counts exceed even the count of certain iniomous fishes?

An answer to the first question is most readily found in a comparison of caudal skeletal structure and caudal musculature in the two groups. Adrianichthyoids possess a full complement of caudal muscles as do exocoetoids, scomberesocoids, atherinoids, and percoids (see Grenholm, 1923). This muscle pattern includes the hypochordals, dorso-laterals, proximals, two dorsal and two ventral flexors, and interradians. Cyprinodontoids, on the other hand, possess only the proximals, dorsal and ventral flexors, and interradians. It is clearly a reduced condition and can hardly be expected to have given rise to the more complex adrianichthyoid system which in turn is similar to that of numerous other groups of fishes.

In asking the second question of whether or not the cyprinodontoids are unrelated to the adrianichthyoids, we may refer to the unusual degree of hypural fusion and dorso-ventral symmetry that has developed in their caudal skeleton. Nevertheless, through forms such as *Aplocheilus* and *Hypsopanchax* the path that these changes have followed from an adrianichthyoid type can be traced. The attainment of a high degree of symmetry has a number of correlatives. First, it appears to be associated with the development of a rounded or truncate fin and the consequent loss of distinct lobes. Second, additional hemal and neural spines have been mobilized for fin-ray support, the distal ends of these spines becoming bladelike and extending backward to the caudal origin. Third, the musculature has been simplified, the muscles that are normally associated with moving upper and lower caudal fin lobes being absent. Fourth, the total number of fin rays, and particularly branched rays, is high. Probably the high branched ray count is directly related operationally to the assumption by additional neural and hemal spines of the role of hypurals. Hence, the exceptional structure of the caudal fin and its supports in cyprinodontoids in no way suggests that

these fishes are unrelated to adrianchthyoids, but it does strongly urge the hypothesis that the high principal ray count of many species represents a secondary increase that is associated with the origin of a rounded caudal fin and the assumption of hypural function by neural and hemal spines. To assume, as Gosline (1963) has done, that the rounded caudal of cyprinodontoids and amblyopsiforms constitutes prima-facie evidence of their relationship would make it manifestly impossible to understand the origin of adrianchthyoid caudal structure, unless one supposes that adrianchthyoids and cyprinodontoids are not related!

#### STRUCTURE AND POSITION OF PAIRED AND UNPAIRED FINS

The most obvious difference in fin structure among the exocoetoids, scomberesocoids, cyprinodontoids, adrianchthyoids, atherinoids, and phallostethoids is the presence or absence of an anterior spinous dorsal. Before the significance of this structure is considered, certain aspects of fin position and size are discussed.

In the more generalized representatives of all groups, the anal fin and the dorsal fin, whether or not the latter is associated with and anterior spinous dorsal, are placed far back in the body on the posterior half of the caudal peduncle. The caudal fin may be rounded, truncate, emarginate, lobed, or forked. The differences between species or genera in number of principal caudal rays is discussed above.

The pectoral fin tends to be moderately or very high on the side. The differences in height of the fin on the side is mostly related to the angle of insertion of the pectoral rays, or their number, or differential growth (i.e., whether middle or upper rays are emphasized). The position of the actinosts may shift up or down slightly, but the structure of the primary shoulder girdle itself is virtually the same in all, including the flying fishes. Gosline (1963) stated that the sharply acuminate pectorals of atherinids differ from those of cyprinodontoids which are broad and rounded. The pectoral in various atherinids, as well as in the probably primitive atherinid genus *Pseudomugil*, is, however, distinctly rounded.

In scomberesocoids and hemiramphids, the pelvic fins are abdominal in virtually all cases; they are subabdominal in a few exocoetoids. The pelvics are apparently six-rayed in all. In cyprinodontoids the pelvics are abdominal, subabdominal, or thoracic, and typically have six rays. A few species lack pelvics, and still others have as few as three or four rays. In adrianchthyoids these fins are abdominal in position and six- or seven-rayed. In atherinoids the pelvics are abdominal, subabdominal, or thoracic, but they are six-rayed in all cases. In phallostethoids the pelvic fin and girdle as such are lacking, and in mugiloids, sphyraenoids, and polynemoids the fin is thoracic and six-rayed in all cases.

The absence of free pelvic actinosts and the presence of a single actinost fused with the base of one-half of the last pelvic ray have been suggested as characters of possible phylogenetic importance (Gosline, 1961a). This condition, with a single minor exception, has been identified in all exocoetoids, cyprinodontoids, and atherinoids that have been examined. The exception occurs in some hemiramphids, which retain a single, free, relict actinost near the base of the third or fourth pelvic ray (e.g., in *Oxyporhamphus*). In contrast, free actinosts have been found in all specimens of the myctophiform, *Mycetophum*, and the beryciform, *Holocentrus*, at hand.

Fin spines are known to occur in all groups except adrianchthyoids. In a few species of exocoetoids [e.g., species of *Arrhamphus* (Hemiramphidae) and *Exocoetus* (Exocoetidae), and perhaps others] the pelvic fin is made up of a short spine and five branched rays. In *Arrhamphus* the spine may or may not be segmented near its tip, and in *Exocoetus* it commonly has no segments. No anterior line of fusion is visible in some of these spines which thus appear to be formed as median elements rather than from consolidation of the symmetrical halves of a soft ray. Among cyprinodontoids, a pelvic spine is known to occur only in the males of *Pantodon* (Whitehead, 1962); in *Pachypanchax* the first pelvic ray is median and unpaired, although normally segmented; *Jordanella* has a large anterior spine (without a segmented tip) in the dorsal fin of both sexes. Most atherinids possess a pelvic, anal, and dorsal

spine in addition to the spines that compose the first dorsal. Some Indo-Australian freshwater atherinids and the species of the marine genera *Notocheirus* and *Iso* (Isonidae), however, lack some or all fin spines. Other Australasian silversides possess an anal and dorsal spine, but none in the pelvic, or a pelvic spine, but no anal spine. Weber and de Beaufort (1922), in their diagnosis of the family Atherinidae, stated: "First dorsal with 4-8 weak spines or 4-5 undivided rays or 1 spine and 3-6 undivided rays, only in one genus 5 strong spines." Hubbs (1944) objected to the use of the term "undivided rays" for these elements in atherinids, but there is no doubt that these often weak and poorly formed fin supports and the associated internal elements in atherinoids are not at all like the generally robust and well-formed spinous dorsals of other acanthopterygians. Moreover, the present study by the author of developing *Leuresthes tenuis* shows that unquestionably in this species the exoskeletal elements of the first dorsal begin as double structures instead of as the single median structure that ultimately gives rise to the dorsal spines of cichlids (see François, 1958). Mugilids, sphyraenoids, and polynemoids, however, possess a full complement of spines. In phallostethoids, one or two minute spines occur in the first dorsal only, when this fin is present.

Except for the frequency with which spines occur, the chief difference in fin structure between exocoetoids, scomberesocoids, adrianchthyoids, and cyprinodontoids, on the one hand, and that of atherinoids, phallostethoids, mugiloids, sphyraenids, and polynemoids on the other appears to be the occurrence of the anterior spinous dorsal in the latter five groups. If, as is suggested by the above osteological and myological evidence, mugiloids, sphyraenoids, and polynemoids are unrelated to the atherinoids, the occurrence of the spinous dorsal assumes much less significance. Moreover, the spinous dorsal apparently is unstable in atherinoids. It is lacking or reduced in *Notocheirus hubbsi* and *Basilichthys semotilus*, and various fin spines of atherinoids are known to occur in the segmented form, both in juvenile and adult individuals. Regarding *Basilichthys semotilus* [the type of Cope's (1874) genus *Protistiis*] Jordan and Hubbs (1919) quoted a letter

from Eigenmann describing specimens of this species from two localities at 12,000 feet in elevation in the Peruvian Andes: "Of these, two have no dorsal spines whatever, nine have two, one hundred have three, eighty-one have four, and six have five." Penczak (1963) has found evidence that the genetic difference between races of *Gasterosteus aculeatus* having three or four spines may be one of simple Mendelian dominance.

Hubbs (1944) contested the association of the phallostethoids with cyprinodontoids on the grounds that the former group shows all the fin characteristics of atherinids but none of those typical of cyprinodontoids. He cited as evidence the occurrence in phallostethoids of a first dorsal of one or two spines, the extension to the tip of the fins of the first ray of the second dorsal, the invariable modification of the first anal ray as a spine and the development of a second unbranched ray, the occurrence of two to three times as many anal as soft-dorsal rays, and the development of a lobed caudal with fewer than 17 principal rays and of an acuminate pectoral with the first ray well developed and unbranched. Of this evidence Gosline (1963) stated that nothing he had been able to find led him to disagree in any way with Hubbs's findings. With the exception of the evidence provided by the first dorsal which does not occur in killifishes, the following objections may nonetheless be raised: (1) The first ray of the second dorsal in various atherinids (e.g., *Basilichthys australis*) does not extend to the tip of the fin. (2) The first anal ray is normally segmented and not spinous in *Pseudomugil* and certain other Indo-Australian atherinids and is double to its tip in *Gulaphallus*. (3) The second anal ray is unbranched in more than half of the species of cyprinodontoids. (4) The anal fin of the adrianchthyoid killifishes *Oryzias* and *Xenopoecilus* has at least twice as many rays as the dorsal. (5) The caudal fin of adrianchthyoids is made up of an indistinct upper and lower lobe and fewer than 17 principal rays. (6) The pectoral of various Indo-Pacific atherinids is rounded (e.g., *Pseudomugil* and *Rhombattractus*, and see Jordan and Hubbs, 1919) and acuminate in adrianchthyoids. (7) The first pectoral ray of adrianchthyoids is well developed, extending to the tip of the fin, and is unbranched.

How a first dorsal may have arisen in atherinoids as distinct from the typical soft dorsal is a question that cannot now be answered. Did it arise by fragmentation of what was a once continuous dorsal? The occurrence of internal radial elements between the two dorsals of atherinoids certainly suggests this mode of origin. Jordan and Hubbs (1919) discussed a fossil from the Miocene of California that they assigned to the Atherinidae (*Zanteclites hubbsi* Jordan and Gilbert), in which the two dorsal fins are not separated but are distinct from each other in size, the first one being larger. Jordan and Hubbs stated: "Among living genera *Zanteclites* bears the closest resemblance to *Rheocles* of Madagascar and *Pseudomugil* of Australia and New Guinea, types which we regard as relatively primitive among the Atherinidae."

On the other hand, did the first dorsal arise more or less spontaneously as the result of fin-ray formation in a separate and more anterior portion of the embryonic fin fold? Supernumerary dorsals have been reported in this position in trout (Gemmill, 1912) and in *Esox* (Crossman, 1961). In the latter case, the author radiographed the pike and found that the first, or supernumerary, dorsal had well-developed, although not well-formed, interneural and radial supports for the fin rays which themselves were quite normal in appearance. It might be queried whether the first dorsal of phallostethoids, which together with its internal supports is always poorly formed and poorly developed when it is present at all, may not be a dorsal fin of this kind in the making, instead of a degraded structure that has come down from the better-developed first dorsal of an atherinid ancestor.

With cause, it may be asked whether a divided or supernumerary dorsal is so distinctive among teleosts that great significance should be attached to it? The occurrence of more than one dorsal, whether with spines or without, is certainly not in any sense uncommon. The order Gadiformes includes species with one, two, or three dorsals, the first of which in only some cases has a spine, and the perciform family Uranoscopidae includes species with a spinous first dorsal as well as species without a first dorsal of any kind. The vagaries of fin and spine formation are per-

haps best illustrated by the Paleocene zeoid *Palaeocentrotus*, in which the anteriormost of three continuous dorsals is soft, the second spinous, and the last soft again, and by some blennioids in which the posterior dorsal rays, rather than the anterior ones, develop as spines. More specifically, is the occurrence of a first dorsal of such overriding biological significance that one should overlook in its favor the impressive array of similarities among exocoetoids, adrianichthyoids, atherinoids, and phallostethoids in general fin and body form (fig. 3), dimorphic fin shapes and color patterns, osteological and myological characters, and reproductive structures and behavior?

The taxonomic significance of fin spines has been given an excellent general review by Marshall (1962) who pointed out that in notocanth fishes all stages in the transition from typical, segmented, and branched soft rays to fin spines can be traced. He suggested the use of the term "pseudacanth" for the segmented spines in this group. Marshall concluded that "... if spinous rays have always had soft-rayed precursors [ontogenetically and phylogenetically], this transmutation, which involves the suppression of the twin structure, jointing and branching of the lepidotrichia, has occurred several times in the evolution of the teleost fishes." He cited François' work, however, in concluding that some spines arise directly as spines, that is, from a median and unpaired blastematous mesenchyme in the fin fold, and hence never pass through a pseudacanth stage. In the present context it is clear that the pseudacanth is characteristic of some exocoetoids and cyprinodontoids (in the pelvic fin) and atherinoids (in the pelvic, anal, and first and second dorsal fins). Furthermore, all stages in the transition from pseudacanth to fin spine occur in these groups. Phylogenetically this situation may represent a difference in emphasis on the developmental transition from ray to spine in the different lineages, rather than a qualitative difference of distinctive biological origin between any two groups. If the difference between such groups is merely a matter of the degree of expression of a ray-spine transition, then the possession of spines cannot be considered taxonomically more important than many other distinctive

features of the anatomy and behavior. Structural transitions of many other kinds also are to be found among and within scomberesocoids, exocoetoids, cyprinodontoids, adrianchthyoids, atherinoids, and phallostethoids, for example, in the position of the pelvic fins, height of the pectoral fin on the side, degree of premaxillary protrusibility, number of branchiostegal rays, degree of consolidation of elements in the caudal skeleton, and the expression of an anterior dorsal fin.

In a detailed study of the mechanisms of joint and bone formation in the skeletal rays of fish fins, Haas (1962) found that segmented and non-segmented (i.e., spinous) bony rays grow in a different manner. The segments in a typical soft ray are preformed by strips of closely packed mesenchymal cells. These cell strips ossify in a proximodistal direction while increasing in length and thickness by the aggregation of more mesenchymal cells. Growth in length of the segmented skeleton keeps ahead of ossification as long as the fin is growing. In non-segmented bony rays (spines) growth and ossification are synchronized. After a few cells have aggregated at the distal part of the already formed bone, they ossify immediately. This process is continuous, and cellular stages at the distal part of spines do not exist. Haas also found that cell divisions in the blastema of soft rays occur in periodically alternating high and low rates, but no evidence for this periodic behavior was found in growing spines. From Haas's work it thus seems evident that Marshall's term "pseudacanth" may refer in many cases to a segmented ray in which growth and ossification are becoming synchronized, and that the difference between soft rays and spines phylogenetically may be not more significant than is the developmental transition from an allochronic to a synchronic state.

Certain striking similarities in fin development between exocoetoids and atherinids may be noted. In postlarval *Oxyporhamphus* (Hemiramphidae) of 4.8 to 5.6 mm. (Chrapkova-Kovalevskaya, 1963) and *Cheilopogon* (Exocoetidae) of 4.9 mm. (Gorbunova and Parin, 1963) body and fin form are much like those of the young cyprinodontoid, that is, a rather high-set, rounded pectoral fin is developed, the caudal fin is rather long and

rounded, and the pelvics, dorsal, and anal are well formed and rayed but not elongate. In both genera, the caudal eventually becomes lobed and the pectoral prolonged, and in *Cheilopogon* the pelvics also elongate. In various atherinids, for example, in *Kirtlandia* of 11 mm. (Kuntz, 1916), in *Menidia* of 13 mm. (Kuntz and Radcliffe, 1917), in *Leuresthes* of 15 mm. (studied by the writer), and in *Odontesthes* of 19 mm. (Fischer, 1963) the postlarval fin and body configurations are much the same except for the slightly more anterior position of the pelvic fins and abdominal cavity—in this respect more like those of some cyprinodontoids. In none of these four postlarval atherinids is the spinous dorsal present. In *Menidia* there is no trace of it or of the blastema in which it will ultimately arise. In *Kirtlandia* there is present at the stage illustrated a delicate membrane somewhat in advance of the soft dorsal, but no rays are present in this tissue. In *Menidia*, *Leuresthes*, and *Odontesthes* the soft dorsal is fully formed in the adult configuration (size, shape, and ray number), although not even the precursor of the spinous dorsal has yet appeared. It would seem, then, that the broader aspects, at least, of larval and early postlarval development are very similar in exocoetoids, cyprinodontoids, and atherinids, and that the spinous dorsal is a secondary feature added in subsequent development of atherinids. Is the addition of this single highly distinctive feature during an intermediate stage of development really indicative of wide phyletic separation from fishes that lack this detail?

One final speculation on the origin of the spinous dorsal concerns the occurrence of what Gosline (1962) terms supraneurals together with interneural elements (pterygiophores). Supraneurals are usually upright bones that lie in the muscle between or above the neural spines and that do not bear soft rays or spines. The interneural elements are usually more strongly developed and spine-ray-bearing. In the fishes with a separate first dorsal, the two dorsal fins may be connected internally via a series of supraneurals. There may also be a series of supraneurals, usually smaller, anterior to the first dorsal. Supraneurals need not occur together with interneurals, however, and in fact probably arose before a spinous dorsal was developed.



They occur well developed in the myctophiforms *Myctophum* and *Synodus*. In *Myctophum* the supraneurals are columnar bones, in some cases with a small anterior and posterior flange. In *Synodus*, however, the supraneurals are platelike, with an anterior and a posterior point, and a prominent, acutely pointed, ventral prong that extends downward between the neural spines. These supraneurals are similar in form to the anterior supraneurals in *Sphyræna*, to the supraneurals and interneurals in many atherinoids, and to the interneurals of phallostethoids. Associated with the development of supraneurals in *Synodus* are many long, rod-like ossifications that lie under the dermis lateral to the supraneurals. Since these rods occur in *Synodus* in conjunction with a series of specialized supraneurals, the question may be raised whether both structures develop from the same ectomesenchyme that is responsible for the fin fold and fin rays more posteriorly. If so, then some myctophiforms appear to possess the basic structural materials for the production of an anterior dorsal, and such capabilities may even have existed in their pre-iniomous ancestors. An anterior spinous dorsal may thus have been elaborated more than once among teleosts, an interpretation that is consistent with the occurrence of dorsal spines in notacanthids, which apparently form a primitive group allied to the elopoid and anguilloid fishes (Marshall, 1962). This interpretation, if confirmed, may also mean that the spinous dorsals of atherinoids and phallostethoids were acquired independently or at least developed to different degrees (not at all in some phallostethoids) from a common ancestral population, with the tendency for the formation of a spinous dorsal incipiently developed. It could also mean that the spinous dorsal of atherinoids and that of mugiloids-sphyrænoids had either separate origins or a common origin very long ago, both interpretations being sufficient to account for the existing large structural and functional differences between these two groups of fishes.

#### REPRODUCTIVE CHARACTERISTICS

Prominent secondary sexual characters occur in exocoetoids, adrianichthyoids, cyprinodontoids, atherinoids, and phallostethoids. These include sexually dimorphic modifica-

tions of the body and fins, the presence of contact organs, sensory "hairs," dimorphic mouth parts and coloration, and a wide variety of fleshy genital papillae and bony external male genitalia. The presence in these fishes of brilliant color patterns and special modifications of the external male genitalia is frequently associated with complex courtship behaviors. In place of high egg production, nest building and guarding, or other care of the young, numerous exocoetoids and cyprinodontoids have developed viviparity and the elimination or completion in the egg of the larval phase of development. The new-born or newly hatched young of many of these species are miniatures of the adults which are immediately capable of active feeding and swimming.

A large, spherical, demersal, chorionated egg with adhesive filaments occurs in all the above groups.

A gelatinous, unencapsulated spermatoaphore, or spermatozeugma, occurs in poeciliid cyprinodontoids and in phallostethoids (Regan, 1916), and an encapsulated spermatoaphore develops in *Horaichthys*. No other teleost is known to possess such sperm aggregates.

Internal fertilization, aided by claspers or gonopodia developed from the anal, pelvic, and pectoral fins, occur in hemiramphids (anal fin), the killifishes (Poeciliidae: anal, pelvic, and pectoral; Horaichthyidae, Anablepidae, and Jenynsiidae: anal fin), and phallostethoids (Phallostethidae and Neostethidae: pelvic and pectoral). In the cyprinodontoid family Goodeidae internal fertilization is accomplished by a fleshy organ that is employed in some manner in conjunction with the shortened first few anal rays in the male. Internal fertilization also occurs exceptionally in *Oryzias* and *Fundulus*, and apparently normally in *Xenopoecilus poptae*, but the sperm transfer mechanisms are unknown.

Similarities in mating and courtship patterns might be anticipated from the similar sexually dimorphic color patterns and fin shapes in the fresh-water viviparous forms of the Hemiramphidae, in cyprinodontoids, Old World fresh-water atherinids, melano-taeniids, and phallostethids. N. R. Foster (personal communication) noted similarities in courtship patterns between various Amer-

ican cyprinodontids and an Australian melanotaeniid. All forms with external male genitalia would, of course, be expected to have roughly comparable courtship behaviors.

C. Hubbs and Drewry (1959) cited Pinney's (1928) report of hatched hybrid young from reciprocal crosses of *Fundulus heteroclitus* (Cyprinodontidae) and *Menidia notata* (Atherinidae), and they commented as follows: "These results are not fortuitous as Moenkhaus (1910) and Newman (1915) also had success with these hybrids and Clark and Moulton (1949) had both reciprocals of the related *F. heteroclitus* by *Menidia beryllina* (Cope) hybrid reach late embryonic stages. *Fundulus* and *Menidia* belong to the families Cyprinodontidae and Atherinidae and these families are assigned to different orders, Cyprinodontiformes and Mugiliformes, respectively, by Berg (1947 [1940]). As cyprinodonts are soft-rayed fishes and atherines have spines in their fins, early classifiers considered the two groups distantly related. Other workers, notably Regan (1911 [a]), Hubbs (1920 [1919]; 1924; 1955; 1950), Gregory (1953 [1933]), Boldyreff (1935), and Lagler (1947) have suggested that cyprinodonts are closely related to the spiny-rayed fishes and perhaps are descendants of primitive spiny-rayed fishes. Cope (1870) and Myers (1928) mentioned the similarity between the atherines and cyprinodonts and questioned the difference between them implied in systems of classification then (as now) in vogue. Moreover, the phallostethid fishes have been placed with the cyprinodonts by Regan (1913b [1913]; 1916), Weber and de Beaufort (1922), Jordan (1923), Hubbs (1924), and Herre (1926), while Herre (1939; 1942), Myers (1928, 1935; 1937), Bailey (1936), Aurich (1937), Te Winkel (1939), and Hubbs (1944) allied them with the atherines, and Berg (1947 [1940]) placed the phallostethids in a separate order close to the cyprinodonts. Similarly, *Basilichthys semotilus* (Cope) has been placed in the Mugilidae (Cope, 1874), Cyprinodontidae (Cope, 1875), and Atherinidae (Jordan, 1923). These changes in the taxonomic allocation of the phallostethids and *B. semotilus* suggests [*sic*] a closer relationship of those fishes than that implied by current classifications. This is

supported by the data derived from hybridization experiments. Thus, the *Fundulus* and *Menidia* hybrids actually may not be interordinal."

Blair and C. Hubbs (1961) reported additional *Menidia-Fundulus* hybrids, and C. Hubbs (personal communication) described various atherinid-cyprinodontid crosses (involving the genera *Leuresthes*, *Atherinops*, *Fundulus*, and *Crenichthys*) in which hybrid embryos developed to the hatching stage. When atherinid and cyprinodontid gametes were combined with those of various representatives of the Clupeiformes, Syngnathiiformes, and Perciformes, no embryo developed much beyond the gastrula stage. C. Hubbs also pointed out that certain characteristic features of the vascular apparatus (especially the first major yolk vessel) of the early embryo in *Leuresthes*, *Atherinops*, *Fundulus*, *Crenichthys*, and *Empetrichthys* contrast strongly with the condition found in several cottoids, a blennoid, gobioid, and probably also a salmonoid.

Orton (1955a) had previously compared the embryos of *Exocoetus* with those of allotriognaths, two groups that typically have large eggs. Although superficially much alike in having a large yolk sac, no oil globule, and in general proportions, these two kinds of embryos differ greatly in later development. [In contrast, the embryos of mullet (Anderson, 1957) and barracuda (Orton, 1955b) are small and contain a large oil globule.] In the allotriognath embryo the heart is in the typical chordate position, under the neck, and it remains in that position throughout embryonic development. In the embryo of *Exocoetus* the heart is displaced forward onto the front of the yolk sac. A forward-displaced heart is also characteristic of *Oryzias* (Rugh, 1948) and *Menidia* (Clark and Moulton, 1949) but not of *Sphyræna* (Orton, 1955b; Shojima, Fujita, and Uchida, 1957) and probably not of *Mugil*. Tavalga (1949) described the condition in the embryo of the cyprinodontoid *Xiphophorus maculatus*, and the reorientation of the heart during absorption of the yolk, as follows: "With this reduction in yolk volume, the locus of the sinus venosus describes an arc extending caudad and dorsad until the heart eventually takes up its final position in the intra-embryonic

pericardium with no intervening yolk sac portal circulation between the ducts of Cuvier and the sinus venosus." Tavolga (personal communication) pointed out that the condition of exocoetoid, adrianichthyoid, and atherinoid embryos is exceptional in having as a consequence of the inverted position of the heart the complete separation of the afferent from the efferent circulation in the pericardial serosa, whereas the embryos of fishes with a more usual position of the heart have the afferent and efferent circulations superimposed.

#### SUMMARY OF ANATOMICAL EVIDENCE

The exocoetoids, scomberesocoids, adrianichthyoids, cyprinodontoids, atherinoids, and phallostethoids have in common the following major features:

Mesethmoid a double-laminar, dislike ossification in almost all cases; pro-otic with a ventrally opening trigeminofascialis chamber and a separate interosseous passage for the orbital artery; intercalar of moderate size, a minute ossicle, or absent; supraoccipital in form of a battle-ax with anterior section underlain by acute equilateral triangle of endochondral bone; infraorbital series of bones represented only by lachrymal and dermosphenotic (lachrymal with separate ventral piece in few cases); supracleithrum, when present, confined within dorsal tip of cleithrum; dermopalatine absent in all but one case; lower arm of maxilla separated from mandible by expanded lower arm of premaxilla; opercular and preopercular margin entire, without spines or serrations; suboperculum broadly comma-shaped, excavated above and convex below; interoperculum not extending posterior to vertical from preoperculum or overlapping suboperculum; distal half of ceratohyal abruptly expanded in almost all cases and joined to epihyal dorsally by bridge of bone; pharyngobranchial 1 absent (a minute edentulous ossicle present in some melanotaeniids); pharyngobranchial 2 a small, tooth-bearing bone applied to or fused with the anteroventral edge of pharyngobranchial 3; pharyngobranchials 3 and 4 fused or sutured together into a large, subrectangular or oval, tooth-bearing bone; three hypobranchials joined to copula on two basibranchial ossifications (first two hypobranchials

slightly advanced in phallostethoids); ligamentous support of shoulder girdle (Baudelet's ligament) to basicranium; cleithrum with wing-like expansion dorsally; scapula and coracoid recessed to receive four actinosts; pectoral fin actinosts cuboidal, in no case hourglass-shaped; caudal skeleton with two large, triangular, hypural plates of opposite symmetry on terminal half centrum, in no case with more than one lower hypural and three epurals, with uroneural reduced, partially or completely fused with upper hypural plate, in no case large and separate; external division of adductor mandibulae muscle well developed in all cases and with a distinct tendon to posterior end of maxilla; without a levator maxillae superioris muscle on palatopterygoid arch; upper jaw lacking crossed ethmomaxillary and palatopremaxillary ligaments.

Cyprinodontoids further resemble exocoetoids in the structure of the supraoccipital crests which in both groups are paired, and in including some species in which the lower pharyngeal bones are fused together into a triangular plate. Adrianichthyids also recall the exocoetoids and scomberesocoids in the possession by the three known species of fused lower pharyngeals, and, in the two species of *Xenopocilus*, in the rather long abdominal cavity and posteriorly inserted pelvics. Adrianichthyids also show striking similarities to the larger atherinids in the form of the occipital crests, to some melanotaeniids in the peculiarly modified mouth parts, and to the Old World fresh-water hemiramphids, to the atherinoids, and to the phallostethoids in the structure of the caudal skeleton. A further resemblance among adrianichthyoids, exocoetoids, and atherinoids is the possession of a lateral spur on the pelvic girdle. In the number of branchiostegal rays on the expanded part of the hyoid bar adrianichthyids are intermediate between hemiramphids and the cyprinodontoids, atherinoids, and phallostethoids, but at least one species (*Xenopocilus poptae*) approaches the cyprinodontoids in having the number of epurals in the caudal skeleton reduced to a single element.

Cyprinodontoids, horaichthyids, and phallostethoids (as represented only by *Gulaphallus*) have the first pleural rib attached to the

parapophysis of the second vertebra; exocoetoids, scomberesocoids, adrianichthyoids, and atherinoids have this rib attached to the third vertebra.

Spines occur in the fins of all groups except adrianichthyoids, but they are present in only a few cases in exocoetoids and cyprinodontoids and are present in virtually all cases in atherinoids. Phallostethoids have one or two spines in an anterior dorsal fin when this fin is present. Atherinoids possess an anterior or first dorsal fin in all but two species. Some Old World fresh-water atherinids have the dorsal, the anal, or the pelvic spines, or some combination of these, segmented. In general, it appears that, in all groups, fin spines have now or have had in the past jointed rays as precursors. The spinous or first dorsal itself arises relatively late in ontogeny in atherinids, only after the soft dorsal (and other fins) have formed fully. It has apparently been lost by two species of atherinoids, and in phallostethoids has either largely disappeared in the group or has never become more than poorly established in some species. Evidence that an anterior dorsal with a complement of internal supports can appear spontaneously in other fishes (trout and pike) is discussed and is suggested as one possible mode of origin for the atherinoid and phallostethoid spinous dorsal.

Similar reproductive modifications are widespread in all groups. All have numerous representatives with large, spherical, demersal eggs with adhesive threads, and with a notable sexual dimorphism in fin size or color, or both. Phallostethoids and some cyprinodontoids develop unencapsulated sper-

matophores of apparently identical structure.

In the neurocranium, jaws, jaw suspension, opercular apparatus, pharyngobranchial apparatus, shoulder girdle, and caudal skeleton, sphyraenoids and polynemoids strongly resemble percoids. Mugiloids differ from the basic patterns of sphyraenoids only in having the third and fourth upper pharyngeal bones largely fused together. Freihofer (1963) pointed out, however, that *Mugil*, *Polynemus*, and *Polydactylus* have a *Serranus* pattern for the recurrent facial nerve, whereas it is reduced in *Sphyraena*. A reduced pattern occurs also in *Menidia* of the Atherinidae, i.e., there are no branches to the pectoral fin as there are in *Mugil* and *Serranus*, but, and perhaps more significantly, the same pattern of the recurrent facial occurs in the Atherinidae, Hemiramphidae, and Exocoetidae. The recurrent facial has also recently been provisionally identified by the writer in *Oryzias* (to be reported in detail in a subsequent paper), although Freihofer was unable to detect it in *Fundulus*.

Lastly, Engström (1963) has found significant differences between cyprinodontoids on the one hand and amblyopsiforms and gadiforms on the other in the cone arrangements in their retinas, a discovery that is consistent with the taxonomic separation of these groups proposed by Rosen (1962). Engström associates the arrangement found in cyprinodontoids with that characteristic of the acanthopterygian types. Comparable data were not available for exocoetoids and atherinoids. The pattern found in amblyopsiforms and gadiforms apparently is characteristic of a large number of malacopterygian fishes.

## DISCUSSION OF RELATIONSHIPS AND TAXONOMIC CONCLUSIONS

THE POSTULATED RELATIONSHIPS of the Beloniformes with cyprinodontoids were believed by various authors to be unsound, largely on the evidence of branchiostegal structure. Although the beloniform branchiostegal apparatus was likened to that of the isospondylous fishes, it is shown above that the exocoetoid hyoid structure is not dissimilar to that of some percoids, that, in number of branchiostegals on the elevated part of the hyoid bar and in the placement of the anterior hairlike elements, adrianchthyoids are more or less intermediate between exocoetoids and cyprinodontoids, and that a relatively high branchiostegal count could represent a secondary increase related to a lengthening of the jaws and the orobranchial chamber.

Holstvoogd (1960) attributed taxonomic significance to the development of the retractores arcuum branchialium muscles which, in teleosts, extend from the upper pharyngeal bones to the fifth or sixth vertebra. He believed that these muscles were characteristic mainly of the "higher" groups. These retractor muscles were stated to be present in *Dermogenys* (Hemiramphidae), *Fundulus* (Cyprinodontidae), and *Rhombatractus* (Melanoetaeniidae), as well as in selected representatives of the Myctophiformes, Gadiformes, Gasterosteiformes, Syngnathiformes, Perciformes, Pleuronectiformes, Tetraodontiformes, and Gobiesociformes. They were not found in the clupeiforms, mormyriiforms, cypriniforms, and anguilliforms examined.

It has also been contended that the primary shoulder girdle of beloniforms is quite distinct from that of other fishes treated herein, but osteological study of numerous species failed to reveal more than small differences in structure as is also evident from the work of Grenholm (1923) and Starks (1930).

Of the single narial opening of exocoetoids (the openings of cyprinodontoids and atherinoids are paired), Burne (1909) commented, ". . . the single opening of the olfactory pit is not primitive, but a secondary modification, the original openings having spread to include within the pit what at one time was the external surface of the face."

The unlikelihood of a relationship between the cyprinodontoids and the mugiloids (=atherinoids and mugiloids of the present study) has been argued. Gosline (1961a) wrote: "[There are] superficial resemblances between *Mugil* and *Fundulus*, but I believe these to be secondary. The peculiarities of the mugilid jaw structure can be traced, via the atherinids and sphyraenids, directly back to the percoid type. The protrusile upper jaw of cyprinodonts operates on a rather different system." This same view, again without elaboration, was expressed by Gosline (1962) in a study of the mugiliform fishes. In 1963, however, Gosline more specifically dealt with the question of a postulated cyprinodontoid-atherinid relationship. In this paper he withdrew somewhat from the above position when he stated: "By far the clearest 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." At the same time, however, he expressed the view that the similar condition of the jaws in the two groups of fishes was arrived at through convergent evolution. In support of this contention, Gosline pointed out that the more generalized members of these groups possess a simpler (and similar) protrusion mechanism than the "advanced members," which suggests that the more specialized mechanism was independently derived in each group. This point has merit, but it in no way establishes the fact that convergent evolution led to the similarity in jaw structure of the cyprinodontoid and mugiloid lines. If one reasonably assumes that the great similarity of the more generalized members of each group is a measure of their common heritage, then the existing similar specializations in each line are really parallel modifications of the same basic raw materials. Actually, however, Gosline's arguments may be spurious if atherinids and mugilids are members of different even

though perhaps related lineages, as suggested above. The mugilid jaw, although functionally similar to that of atherinids or cyprinodontoids, operates on a system of crossed upper jaw ligaments and associated maxillary and palatine modifications that are common to percoids but not silversides and killifishes. Undoubtedly we have here two equally effective solutions to the problem of upper jaw protrusion, and it is scarcely surprising that the members of two lineages which are at approximately the same level of organization should evolve similar structures serving the same or similar functions. Regarding the problem of multiple solutions in evolution, Schaeffer<sup>1</sup> pointed out that, although related lineages evolving more or less in parallel will approach or enter a new major level in varying degrees, the amount of evolutionary experimentation is limited by ancestry. Hence, the modification of a character complex toward a particular adaptive mode will be accomplished only as the preëxisting functional and structural specificity will permit. Gosline is almost certainly correct in thinking that the "advanced" protrusion mechanisms of cyprinodontoids and atherinids were derived independently from simpler systems, but not even the simplest members of these groups possess the maxillary-palatine connections and upper jaw ligaments that the mugilids have in common with sphyraenoids and percoids.

We may examine the question of the cyprinodontoid relationships from yet another position. If, as suggested by Gosline, the distinctive premaxilla of the cyprinodontoids reflects no common ancestry with atherinids, and if the cyprinodontoids were derived from an amblyopsiform ancestor, then it is probable that adrianichthyoids and cyprinodontoids are not related! Either an *Oryzias*-like form was ancestral to the cyprinodontoids, or it was not. If an amblyopsiform ancestor gave rise to cyprinodontoids directly, then the adrianichthyoids are a derived group or they are unrelated to the cyprinodontoid complex. If an amblyopsiform ancestor gave rise to the cyprinodontoids indirectly through an intermediate adrianichthyoid series, then the very similar exocoetoids, atherinoids, and phallostethoids may also have had an ambly-

opsiform archetype. Adrianichthyoids, however, probably represent a primitive cyprinodontiform type, as argued here, so that they quite evidently are neither derived from nor unrelated to cyprinodontoids. On the other hand, it is improbable to the highest degree that amblyopsiforms are ancestral to the hemiramphids or atherinids, with which they have virtually nothing in common save a few general features of body and fin shape.

That cyprinodontoids were derived from an *Oryzias*-like ancestor, which in turn had sprung from a still older amblyopsiform group, is regarded as unlikely for additional reasons, for this interpretation would necessitate the assumption of a truly remarkable series of evolutionary convergences between adrianichthyoids, exocoetoids, and atherinoids. Moreover, the proposal that hemiramphids, adrianichthyoids, and atherinids form a natural group quite unrelated to the assemblage that includes amblyopsiforms, percopsiforms, and gadiforms requires the assumption of convergence in only a single character: the first dorsal fin of the Atherinidae and derivatives with that of perciforms. The "law of parsimony" certainly favors the latter hypothesis. Zoogeographically amblyopsiforms and percopsiforms are New World north temperate groups and the gadiforms are north temperate and arctic. Exocoetoids, adrianichthyoids, atherinoids, and phallostethoids, on the other hand, show a heavy concentration in the Old World tropics. Furthermore, we may wonder just how atherinids would be classified if the spinous dorsal were not present. Is the remaining assemblage of atherinid characters sufficient to set them off adequately from cyprinodontoids?

A partial answer to the above question is supplied by the history of the phallostethoids which had been consistently regarded as a peculiar group of small killifishes until a minute spinous dorsal was discovered to be present in some species. Were the spinous dorsal to be consistently absent in phallostethoids, their placement among the cyprinodontoids would be assured, for, unlike atherinoids but in common with cyprinodontoids, an unencapsulated spermatophore is developed in some species, the first pleural rib originates on the second vertebra, the adductor arcus palatini muscle fills the floor of the orbit, and

<sup>1</sup> An address given by Bobb Schaeffer before the XVIth International Congress of Zoology (1963) entitled "Experimentation in Evolution."

the caudal fin (including the number of branched rays) and caudal skeleton are typical of some adrianchthyoids. Let those persons who would disparage the original question be reminded that even some of the strongest opponents of an atherinoid-cyprinodontoid relationship would place the latter near two groups, the gasterosteiforms and syngnathiforms, in which fin spines are well developed in some species and in which a distinct first dorsal may be present (e.g., in *Solenostomus*).

Myers (1928) commented on the significance of the phallostethoid spinous dorsal thus: "Were it not for the spinous dorsal fin, the position of the Phallostethidae among the cyprinodonts would scarcely be questioned. Yet that character assuredly prevents us placing them there, and casting about for possible relations, we are struck with the resemblance of the phallostethids to atherinoids. In fact, none of the characters of these fishes at present known, and not connected with the peculiarly modified priapial region, would offer any serious obstacle to placing the family in the order Percesoces close to the Atherinidae.

"In making this transfer, one comes to ask himself if there is really so great a difference between the cyprinodonts and the percesocians as has been assumed in the system of classification now in vogue. The character of the cyprinodont ethmoid region, widely divergent from that of *Esox*, does not greatly depart from the atherinoid type. Further, the cyprinodonts seem to be uniformly physoclistous and the peculiarly typical mouth of this group is closely approached by the Atherinidae. The strongest point of difference is the small first (spinous) dorsal of the atherines, and in at least one form this may occasionally be absent. The idea that the two groups may not be very distantly related has been suggested to me recently by Mr. Carl L. Hubbs (*in litt.*). The possibility had occurred to me sometime previously, in fact before I had studied the phallostethids, but Mr. Hubbs's suggestion has somewhat strengthened my own notion. This view is not a new one, however, for as long ago as 1870, Cope (p. 455) suggested that the atherinids and cyprinodonts might be very close. Later, when describing *Protistius semotilus*, Cope (1874) remarked on the similarity of the fish

to both the Mugilidae, percesocian relatives of the Atherinidae, and the cyprinodonts, and in later papers he referred to this really atherinoid genus as a cyprinodont. Cope's views on the matter have generally been overlooked or ignored by recent workers."

Except for the question of mugilid relationships, the writer finds no argument with the views of Myers or Hubbs cited above.

In comparisons of exocoetoids, adrianchthyoids, cyprinodontoids, atherinoids, and phallostethoids, frequent and principal reference is made to those representatives of each group that are characteristic only of the fresh and brackish waters of the tropical Indo-Pacific region. Such comparisons are not fortuitous, for it is only through analysis of these Old World representatives that notable similarities between the larger groups can be fully delineated. Consequently, the hypothesis is advanced that these fishes had a common ancestry in the fresh and brackish waters of Australasia, and that from this region they subsequently spread around the world into virtually all of the tropical and temperate marine and fresh-water environments.

That the Atherinidae may have originated in this part of the Old World is suggested by the present distribution of the living genera (based on Jordan and Hubbs, 1919). Twelve genera are known from Australasia, 11 of which contain species that are confined to fresh or brackish waters; two genera are represented in the fresh waters of Madagascar; the south and western Pacific contains seven marine genera; western North and South America have 10 genera, three of which are in fresh water; eastern North and South America contain 11 genera, five with species that enter or live in fresh waters; and western Europe includes a single marine genus.

Of the killifishes, Rosen and Bailey (1963), in their discussion of the origin of New World types with a short-based anal fin, speculated that "... the evolution of the primary groups with short-based anal fins from those with long-based anal fins and their subsequent radiation took place in the Old World and that these then migrated from some central position west to Europe, western Asia, and the Near East (*Aphanius*, *Anatolichthys*, *Tellia*, *Valencia*, and others) and east to the Americas where they underwent an explosive secondary radiation."

A similar case can be made for the Hemiramphidae, for seven of the 11 recognized genera occur in Australasia and the tropical Pacific, three of which contain species confined to fresh or brackish water. The fossil genus *Cobitopsis* from the Upper Cretaceous of western Asia has been questionably assigned to the Hemiramphidae (see Romer, 1945). Darlington (1957) amassed considerable evidence which suggests that at least some fresh-water fishes radiated from the Old World tropics, with the north temperate zone acting as a filter bridge for those that remained more or less confined to fresh waters in their passage to the New World.

Most important, however, is the fact that all the members of these groups that most resemble one another occur in the fresh and brackish waters of Australasia and nowhere else. The fact that such forms are entirely restricted to this region provides the basis for the suggestion that these groups had a common genesis in the fresh waters of the Old World tropics.

The history of these fishes, their evolutionary divergence, and subsequent distribution can be envisioned by our postulating a probable ancestral type which surely must have possessed all the numerous features of the skull, fin girdles, and caudal skeleton that are shared by the atherinids, fresh-water hemiramphids, and adrianichthyoids. In short, the precursor of these groups may have been of a basically hemiramphid form with a truncate or slightly emarginate tail, a normal mouth without beaks or prolongations, separate lower pharyngeal bones, upper and lower fins with an incipient tendency to develop spinous rays, no spinous or anterior dorsal fin, a lateral line situated near the horizontal septum, and nine or more branchiostegal rays. From such a hypothetical ancestor, hemiramphids could have arisen by complete fusion of the lower pharyngeals into a single bone, the prolongation of the dentary bone, and the lowering of the lateral-line canal to a position along the lower sides.<sup>1</sup> Adrianichthyoids could be derived more sim-

<sup>1</sup> Although the lateral-line canals are low on the sides in exocoetoids and scomberesocoids, the lateral-line nerve remains in the midlateral position. The development of the lateral-line nerve is indistinguishable in the exocoetoids, adrianichthyoids, cyprinodontoids, and atherinoids examined in this study.

ply by a reduction of the lateral-line canal to a pit line and the loss of as few as two branchiostegal rays (or, alternatively, exocoetoids and scomberesocoids may show a secondary increase in branchiostegal number from an adrianichthyoid form with about seven rays, as discussed above). Derivation of the atherinids would similarly have required the loss of two branchiostegals (unless the alternative applies) as well as the development of a first dorsal fin. None of the above changes appear to be of great magnitude, nor do they seem to be of a sort that one normally associates with divergence at the ordinal level. The lower pharyngeal bones have become united in many unrelated groups of fishes; the lateral line has altered its course or been reduced repeatedly; special modifications of the jaws are everywhere evident; branchiostegal number has been reduced over and over even as far back in actinopterygian history as in the paleoniscoids and has apparently been increased in istiophorids; and, finally, a first dorsal is present or absent within many related groups, for example, among halosaurs and notacanth, morids, syngnathiforms, agonids, cyclopterids, notothenioids, uranoscopids, and among the atherinids and phallostethoids of the fishes treated here. Moreover, the first dorsal of atherinids first appears late in development and has exoskeletal supports that are initially double structures which later fuse to form median spines.

The information gathered thus far points to the following three major conclusions:

1. The exocoetoids, scomberesocoids, adrianichthyoids, cyprinodontoids, atherinoids, and phallostethoids form a phylogenetically natural group.

2. The mugiloids, sphyraenoids, and polyemoids are not separable from the Perciformes.

3. The fishes included under 1 above arose from a group that stood somewhere in the ancestry of the order Perciformes.

As a sequence to these conclusions, the exocoetoids, scomberesocoids, adrianichthyoids, cyprinodontoids, atherinoids, and phallostethoids are united in a single order as follows:

Order Atheriniformes, new order  
 Suborder Exocoetoidei  
 Superfamily Exocoetoidea



- Family Hemiramphidae
- Family Exocoetidae
- Superfamily Scomberesocidea
  - Family Belonidae
  - Family Scomberesocidae
- Suborder Cyprinodontoidei
  - Superfamily Adrianichthyoidea
    - Family Oryziatidae, new family
    - Family Adrianichthyidae
    - Family Horaichthyidae
  - Superfamily Cyprinodontoidea
    - Family Cyprinodontidae
    - Family Goodeidae
    - Family Jenynsiidae
    - Family Anablepidae
    - Family Poeciliidae
- Suborder Atherinoidei
  - Superfamily Atherinoidea
    - Family Melanotaeniidae
    - Family Atherinidae
    - Family Isonidae, new family
  - Superfamily Phallostethoidea
    - Family Neostethidae
    - Family Phallostethidae

The distinctive features of the atheriniform suborders and superfamilies are presented in the accompanying provisional key:

- a. Lateral line running low on sides; lower pharyngeal bones united without visible suture into triangular plate; parietals absent; branchiostegal rays nine to 15; no first dorsal fin; anal fin not preceded by spine; narial opening single . . . . . EXOCOETOIDEI
- b. Lower jaw prolonged or not; paired fins enlarged in many cases; rostral bones separate; no dermal ethmoid . . . . . Exocoetoidea
- bb. Lower and upper jaw prolonged; paired fins not enlarged; rostral bones joined by sutures; dermal ethmoid present. Scomberesocidea
- aa. Lateral line wanting or represented by a series of pits at midside; lower pharyngeal bones usually separate, or, when united into triangular plate, with visible suture; parietals present or absent; branchiostegal rays four to seven; no first dorsal fin; anal fin not preceded by spine; narial opening paired . . . . . CYPRINODONTOIDEI
- c. Prevomer absent; supracleithrum wanting; except when having bony

- male genitalium and barbed, encapsulated spermatophore (*Horaichthys*), the following: autopalatine usually capped by sesamoid bone; pterygoquadrate cartilage forming dorsal process; lower end of premaxilla not hooked or trapezoidal, situated below maxilla; first pleural rib on third vertebra; pelvic bones with upright lateral spurs, not joined at midline; hypochordal musculature present on caudal skeleton; hypural plates in no case joined together; caudal fin forming incipient lobes . Adrianichthyoidea
- cc. Prevomer present in almost all cases; supracleithrum present; autopalatine not capped; pterygoquadrate cartilage not projecting dorsally; lower end of premaxilla trapezoidal, in many instances hooked forward, situated between dentary and maxilla; first pleural rib on second vertebra; pelvic bones without upright lateral spur, joined at midline by overlapping or sutured medial processes; hypochordal musculature absent on caudal skeleton; hypural plates forming single large hypural in most species; caudal fin rounded or truncate, without incipient lobes. . . . . Cyprinodontoidea
- aaa. Lateral line wanting or represented by series of pits or scale canals at midside; lower pharyngeal bones separate; parietals present; branchiostegal rays five to seven; usually with a first dorsal fin of flexible spines above or in advance of anal origin; anal fin usually preceded by spine; narial opening paired . . . . . ATHERINOIDEI
- d. Pelvic fins present and abdominal, subabdominal, or thoracic in position, not modified into clasp organ; first pleural rib on third vertebra; adductor arcus palatini muscle restricted to posterior part of orbit . . . . . Atherinoidea
- dd. Pelvic fins modified as complex thoracic clasp organ (priapium) in male, wanting in female; first pleural rib on second vertebra; adductor arcus palatini muscle filling floor of orbit . . . . . Phallostethoidea

## APPENDIX

### ABBREVIATIONS OF INSTITUTIONS

- A.M.N.H., the American Museum of Natural History  
 C.A.S., the California Academy of Sciences, San Francisco  
 S.U., Stanford University, Division of Systematic Biology, Stanford, California  
 U.B.C., the University of British Columbia, Institute of Fisheries, Vancouver, Canada  
 U.F., the Florida State Museum of the University of Florida, Gainesville  
 U.M.M.Z., the Museum of Zoology of the University of Michigan, Ann Arbor  
 U.S.N.M., United States National Museum, Smithsonian Institution, Washington, D. C.

Skeletons, dissections, or radiographs were prepared from the following comparative materials:

#### Atheriniformes

##### Exocoetoidei

##### Exocoetoidea

- Arrhamphus brevis* (Seale), S.U. No. 33946, U.M.M.Z. No. 100333  
*Chriodorus atherinoides* Goode and Bean, A.M.N.H. No. 8063, U.F. No. 7069  
*Cypselurus furcatus* (Mitchill), U.F. No. 7240  
*Dermogenys orientalis* (Weber), A.M.N.H. No. 9585  
*Dermogenys pusilis* van Hasselt, A.M.N.H. No. 9582  
*Dermogenys sumatranus* (Bleeker), A.M.-N.H. No. 9584  
*Dermogenys weberi* (Boulenger), A.M.N.H. No. 9578  
*Hirundichthys affinis* (Günther), U.F. No. 3777  
*Hyporhamphus unifasciatus* (Ranzani), U.B.C. No. 5462  
*Oxyporhamphus micropterus* (Valenciennes), U.F. No. 7236  
*Parexocoetus brachypterus* (Richardson), U.F. No. 7242  
*Zenarchopterus novaeguineae* (Weber), A.M.N.H. Nos. 12637, 13908

##### Scomberesocoidea

- Strongylura marina* (Walbaum), U. F. No. 904  
*Strongylura notata* (Poey), U.F. No. 4683  
*Strongylura timucu* (Walbaum), U.F. No. 2755

##### Cyprinodontoidei

##### Adrianichthyoidea

- Horaichthys setnai* Kulkarni, A.M.N.H. No. 20479

*Oryzias javanicus* (Bleeker), A.M.N.H. No. 20518

*Oryzias latipes* (Temminck and Schlegel), A.M.N.H. No. 20478

*Xenopoecilus poptae* Weber and de Beaufort, A.M.N.H. No. 20480

*Xenopoecilus sarasinorum* (Popta), A.M.-N.H. No. 20481

##### Cyprinodontoidea

*Aplocheilus panchax* (Hamilton-Buchanan), A.M.N.H. No. 5159

*Cyprinodon variegatus* Lacépède, A.M.N.H. No. 20474

*Fundulus cingulatus* Valenciennes, A.M.-N.H. No. 16127

*Fundulus confluentus* Goode and Bean, A.M.N.H. No. 20475

*Fundulus similis* (Baird and Girard), U.F. No. 3140

*Hypsopanchax platysternus* (Nichols and Griscom), A.M.N.H. No. 6078

*Jordanella floridae* Goode and Bean, A.M.N.H. No. 20477

*Lamprichthys tanganicanus* (Boulenger), A.M.N.H. Nos. 11728, 11732

*Pachypanchax playfairi* (Günther), A.M.-N.H. No. 20476

##### Atherinoidae

##### Atherinoidea

*Atherinomorus stipes* (Müller and Troschel), U.F. No. 5012

*Austromeniidia regia* (Humboldt), U.B.C. No. 56-235

*Basilichthys australis* Eigenmann, U.S.-N.M. No. 84326

*Basilichthys semotilus* (Cope), U.S.N.M. No. 83646

*Bedotia geayi* Pellegrin, A.M.N.H. Nos. 11693, 11701

*Craterocephalus randi* Nichols and Raven, A.M.N.H. No. 12477

*Eurystole eriarcha* (Jordan and Gilbert), U.B.C. No. 54-75

*Iso flosindicus* Herre, U.S.N.M. No. 123651

*Iso flosmaris* Jordan and Starks, U.S.N.M. No. 49817

*Iso hawaiiensis* Gosline, U.S.N.M. No. 152759

*Kirtlandia pachylepis* (Günther), U.B.C. No. 59-674

*Labidesthes sicculus* (Cope), U.F. No. 6902

*Melanorhinus cyanellus* (Meek and Hildebrand), A.M.N.H. No. 12651

*Melanoaenia maculata* Weber, A.M.N.H. No. 12526

*Melanotaenia nigrans* (Richardson),  
A.M.N.H. No. 9240

*Menidia beryllina* (Cope), U.F. No. 4827

*Nectarges nepenthe* Myers and Wade,  
A.M.N.H. No. 20473

*Notocheirus hubbsi* Clark, C.A.S. No. 5526

*Pseudomugil novaeguineae* Weber, A.M.-  
N.H. Nos. 9583, 20345

*Rheocloides pellegrini* Nichols and La-  
Monte, A.M.N.H. No. 11699

*Rhombatractus archboldi* Nichols and  
Raven, A.M.N.H. Nos. 12475, 12522,  
12523

*Rhombatractus goldiei* (Macleay), A.M.-  
N.H. Nos. 12524, 13280

#### Phallostethoidea

*Gulaphallus mirabilis* Herre, S.U. No.  
38903

#### Beryciformes

*Beryx splendens* Lowe, A.M.N.H. No.  
3555

*Holocentrus ascensionis* (Osbeck), U.F. No.  
3848

*Poromitra* (= *Melamphaes*) *cristiceps* (Gil-  
bert), A.M.N.H. No. 12816

#### Myctophiformes

*Myctophum affine* (Lütken), U.F. No. 3816

*Synodus foetens* (Linnaeus), U.F. No. 7100

#### Perciformes

##### Mugiloidei

*Agonostomus monticola* (Bancroft), U.F.  
No. 6930

*Cestraeus goldiei* (Macleay), A.M.N.H. No.  
12638

*Mugil cephalus* Linnaeus, U.F. No. 4617

*Mugil curema* Valenciennes, U.F. No. 6919

*Mugil trichodon* Poey, A.M.N.H. No. 2482

*Neomyxus chapalii* (Eyedoux and Sou-  
leyet), A.M.N.H. No. 18625

*Rhinomugil* sp., A.M.N.H. No. 17883

##### Polynemoidei

*Polydactylus octonemus* (Girard), U.F. No.  
3770

##### Sphyraenoidei

*Sphyraena barracuda* (Walbaum), A.M.-  
N.H. No. 20482

*Sphyraena borealis* De Kay, A.M.N.H. No.  
4339

Also examined were living materials of *Procatopus similis* Ahl, *Melanotenia nigrans* (Richardson), *Oryzias latipes* (Temminck and Schlegel), *Aplocheilus lineatus* (Valenciennes), and *Leuresthes tenuis* (Ayres). The last-mentioned species was reared from eggs, and the young stages were used to study the development of the first or spinous dorsal fin.

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