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On the Relationships of Phallostethid Fishes (Atherinomorpha), With Notes on the Anatomy of *Phallostethus dunckeri* Regan, 1913

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ABSTRACT

The Phallostethidae (including Neostethidae) is a family comprised of approximately 20 species of small, fresh, brackish, and occasionally saltwater atherinomorph fishes of Indo-Australia. Phallostethids have variously been suggested as closest relatives of the atherinoid or cyprinodontiform fishes among the atherinomorphs, or of the polynemids or gobioids among the percomorphs. Phallostethids uniquely share several derived characters of the jaws and the anal fin with a group of Indo-Australian and Pacific atherinoids. The western Pacific *Dentatherina* Patten and Ivantsoff is proposed as the sister group of the Phallostethidae.

The anatomy of *Phallostethus* Regan, the type genus, is poorly known because of the scarcity and unsatisfactory condition of available material. A report on the anatomy of *Phallostethus dunckeri* Regan, the sole species in the genus, based on examination of the syntypes and on unpublished notes and sketches is also included.

INTRODUCTION

The phallostethids (Atherinomorpha, Phallostethidae) are a little-known group of coastal fishes distributed throughout the Philippines, Borneo, Java, Malay Peninsula, and Southeast Asian mainland.[2] They are defined as monophyletic by a complex subcephalic copulatory organ in males, termed the priapium (Regan, 1913, 1916), and among others, a series of derived characters related to reproduction as, for example, the anterior placement of the urogenital opening and reduction and/or modification of the pelvic fins and fin girdles (see Roberts, 1971b).

The primary purpose of this report is to

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[2] Report of a collection of phallostethids from northwestern Sumatra (Aurich, 1937) is considered to be unconfirmed.

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present the hypothesis of close relationship among the phallostethids and several atherinoid genera of Indo-Australia and the Pacific. The definition and relationships of phallostethid species and genera are the subjects of an ongoing study (Parenti, in prep.). However, such a study could not be carried out without a detailed, well-corroborated hypothesis of the relationship of phallostethids to other fishes.

When phallostethids were first discovered, it was assumed that they were viviparous cyprinodontiforms (then Microcyprini) because the priapium superficially resembles intromittent organs found among some members of that group, for example, poeciliids (Regan, 1913, 1916). Smith (1927) reported that phallostethids which he observed in Thailand were oviparous. The priapium is apparently used by males for passing sperm bundles to females who subsequently lay fertilized eggs, although details of priapial function are unknown.

Both Herre (1925) and Myers (1928) pointed out that some phallostethids have a spinous first dorsal fin which is lacking in the cyprinodontiforms. On this basis, and because of the overall resemblance of phallostethids to atherinid fishes (the silversides or hardyheads), Myers transferred the phallostethids to the order Percesoces, which then contained the silversides, mullets, barracudas, and threadfins. Bailey (1936) proposed that phallostethids were close relatives of the threadfins (the polynemids) based on a superficially similar association of the pectoral and pelvic fins.

Hubbs (1944) concurred with Myers that the phallostethids were more closely related to the atherinids than to the cyprinodontiforms; however, whereas Myers considered the cyprinodontiforms and the atherinids to be closely related, Hubbs considered the percesocans (including the phallostethids and atherinids) to have a relatively more derived fin structure than that of the cyprinodontiforms. Thus, Hubbs supported an alignment of the percesocans closer to some of the perciform fishes.

Rosen (1964) placed the phallostethids, atherinids, cyprinodontiforms, along with the adrianichthyoids (the ricefishes), and the exocoetoids (flying fishes, halfbeaks, sauries, and needlefishes) into the newly named series Atherinomorpha, which he considered to be most closely related to the series Percomorpha. Rosen and Parenti (1981) formally defined the atherinomorph fishes, giving as several of their derived characters specializations of the egg, embryo, sperm formation, rostral cartilage and association of the premaxillary ascending processes, and dorsal gill arches. Phallostethids remained in the Atherinomorpha based on their possession of several of these derived characters. Rosen and Parenti (1981) concluded that the atherinoid fishes are not currently definable as monophyletic and simply listed the families of atherinoids in their Division I of the Atherinomorpha, abandoning the use of the term atherinoid in formal classification to emphasize uncertainty in our knowledge of relationships of these fishes (table 1).

The phallostethids have undergone elevations and reductions in taxonomic rank since their discovery; however, no formal statement concerning their relationship to another group of fishes has been made previously. Myers (1935) created a new suborder within the Percesoces, what he termed Phallostethoidea, which served to emphasize further the unique characters of these fishes. Rosen (1964) placed the phallostethids in the superfamily Phallostethoidea, suborder Atherinoidei, but suggested that they may be more closely related to the cyprinodontiforms. Roberts (1971b) speculated that phallostethids are closely related to the atherinid subfamily Taeniomembradinae of Schultz (1948, 1950). However, the Taeniomembradinae was not defined by Schultz as monophyletic. He stated only that these atherinids possess the primitive state of the swimbladder character used to define a relatively more derived subfamily. Even the idea that phallostethids are atherinomorph fishes has been questioned recently by V. G. Springer (personal commun.) who suggests that they may be closely related to the gobioid fishes.

This report was prompted by: (1) the recent discovery and diagnosis of a new genus and species of atherinid, *Dentatherina merceri* by Patten and Ivantsoff (1983), which I propose as the closest living relative of the phallostethid fishes; (2) the opportunity to examine Regan's syntypes of *Phallostethus dunckeri* at the British Museum (Natural History); and, (3) most important, by the gift of notes and sketches prepared by Dr. Ethelwynn Trewavas in the 1930s as part of her planned revision of phallostethid fishes. Both because of the scarcity of material and present poor condition, which precludes a formal redescription, Dr. Trewavas's notes and sketches of *P. dunckeri* contain some of the only data available on the anatomy of this unique species.

ACKNOWLEDGMENTS

Dr. Donn E. Rosen, American Museum of Natural History, New York, has frequently discussed aspects of atherinomorph anatomy and systematics with me. Dr. Tyson R. Roberts, California Academy of Sciences, San Francisco has, on numerous occasions, freely given information on the anatomy and distribution of phallostethids. Drs. Walter Ivantsoff, Macquarie University, Australia, and Brian White, Los Angeles County Museum of Natural History, Los Angeles, kindly shared information on atherinoids. The report on the anatomy of *Phallostethus dunckeri* Regan would not have been possible without the gift of notes and sketches made by Dr. Ethelwynn Trewavas, Curator Emerita, British Museum (Natural History) as well as her kind permission to use them here.

I thank Drs. P. Humphry Greenwood, British Museum (Natural History), London (BMNH), Gareth Nelson, American Museum of Natural History, New York (AMNH), and Richard P. Vari and Ms. Susan L. Jewett, National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM), for lending or allowing me to examine specimens in their care. Dr. Clyde Barbour, Wright State University, Dayton, and Dr. Roberts, kindly donated specimens to the American Museum of Natural History which were used in this study. This project was initiated during the tenure of a NATO Postdoctoral Fellowship at the British Museum and completed while I was a Research Associate at the American Museum of Natural History. Drs. Ivantsoff, John Patten, and Rosen read and commented on the manuscript.

TABLE 1
Classification of Atherinomorph Fishes
(From Rosen and Parenti, 1981)

- Series Atherinomorpha
  - Division I
    - Family Atherinidae
    - Family Bedotiidae
    - Family Isonidae
    - Family Melanotaeniidae
    - Family Phallostethidae
    - Family Telmatherinidae
  - Division II
    - Order Cyprinodontiformes
    - Order Beloniformes

Phallostethus dunckeri Regan

Phallostethid anatomy has been the focus of numerous studies published since Regan's (1913) description of *Phallostethus dunckeri* (e.g., Regan, 1916; Myers, 1928; Bailey, 1936; Aurich, 1937; TeWinkle, 1939; Herre, 1942; Woltereck, 1942a, 1942b; Hubbs, 1944). Roberts (1971a, 1971b) presented the most recent reviews of some problems in phallostethid anatomy and systematics. He stated that basic comparative data of *Phallostethus* are unknown because Regan (1913) did not report states of characters which we now consider to be useful in defining phallostethid relationships, and because *P. dunckeri* is known today only from syntypes (Roberts, 1971b). For example, Roberts stated that the number of branchiostegal rays, and whether or not *P. dunckeri* has a first dorsal fin, were unknown.

Regan (1913) based his description of *Phallostethus dunckeri* on seven specimens collected from Johore, on the Malay Peninsula. The description centered on the structure of the priapium and included other characters that are still considered to distinguish *P. dunckeri* from all other phallostethid species. One such character is a high number of anal fin rays, ranging from 26 to 28 as opposed to 14 to 15 in *Phenacostethus*, the presumed closest relative (Roberts, 1971a).

Regan (1913, pp. 548–555) stated that his

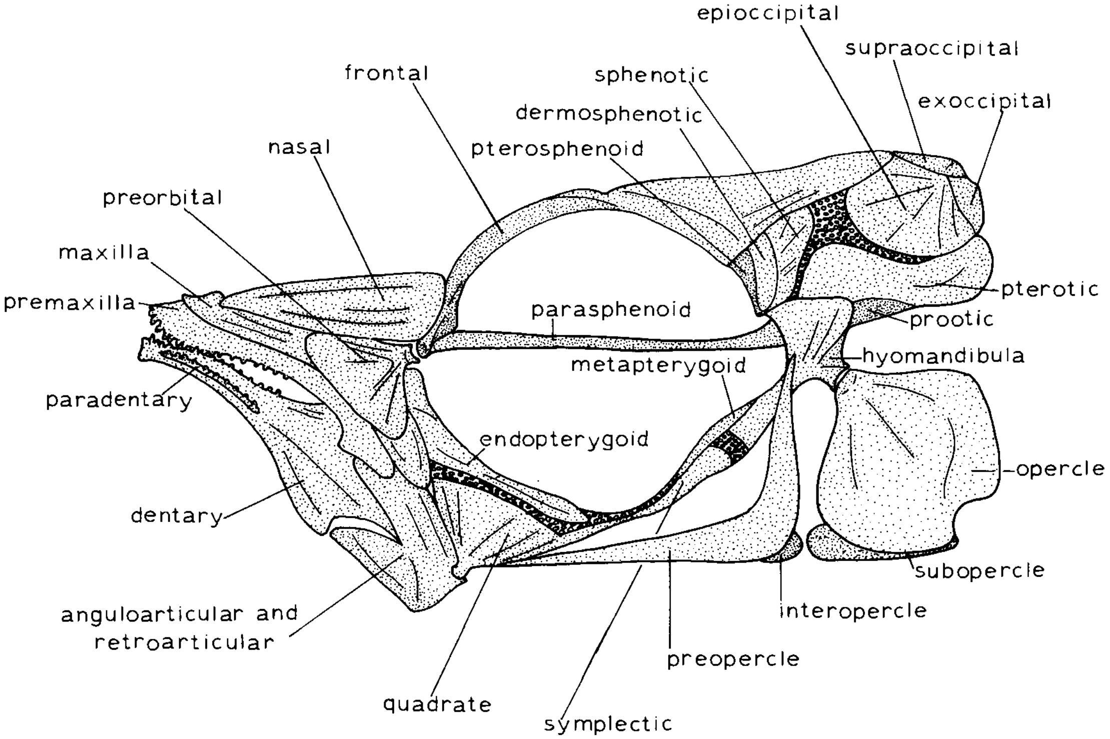

FIG. 1. Lateral view of neurocranium, jaws and jaw suspensorium, and opercular series, *Phallostethus dunckeri* Regan, Syntype, BMNH 1913.5.24:22. From a sketch prepared by Dr. Trewavas. Bone stippled; cartilage open circles.

description was based on seven specimens, two of which were sectioned for study of internal anatomy. Five specimens, four alcohol (BMNH 1913.5.24:18–20, BMNH 1913.5.24: 21) and one cleared and stained (BMNH 1913.5.24:22), are present in the Recent fish collection of the British Museum (Natural History) and hence, are treated as the remaining syntypes. The syntypes, augmented by notes and sketches of Trewavas, constitute the study material on which the following anatomical description is based.

NEUROCRANIUM (figs. 1, 2): Supraoccipital overlapped anteriorly by frontals. Frontals forming convex roof of orbits, a lateral limb posterior to nasal capsule, articulating with preorbital, and anterior limb reaching anterolateral surface of lateral ethmoid. Parietals absent. Temporal region concave. Ossified epioccipital and pterotic present. Intercalar absent. Pterosphenoid small, not meeting sphenotic and just meeting frontal. Basisphenoid absent. Exoccipital and basioccipital (not shown in fig. 1) with condyles well developed. Infraorbital series represented by a dermosphenotic and a preorbital bone. Mesethmoid an ossified triangular plate, the base anterior, with a notch for passage of olfactory nerve. Vomer, with small toothplate and patch of teeth, ventral to ethmoid cartilage.

JAWS AND JAW SUSPENSORIUM (figs. 1, 2): Upper jaw represented by premaxilla with ascending process long and narrow; maxilla with a process dorsal and a process ventral to premaxilla. Lower jaw represented by dentary, paradentary, articular and retroarticular bones, the last two bones not necessarily distinct. Premaxilla, dentary, and paradentary with small, unicuspid teeth. Submaxillary bone between maxilla and vomer. Rostral cartilage long and of moderate width. Hyomandibula with a large, single dorsal head articulating with sphenotic anteriorly and

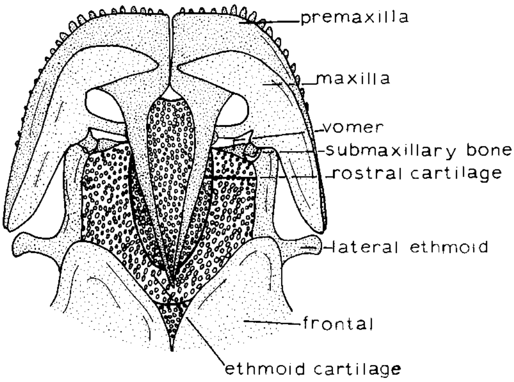

FIG. 2. Dorsal view of upper jaw, ethmoid region and anterior portion of neurocranium, *Phallostethus dunckeri* Regan, Syntype, BMNH 1913.5.24:22. From a sketch prepared by Dr. Trewavas. Bone stippled; cartilage open circles.

pterotic posteriorly. Symplectic a long, narrow bone. Metapterygoid present as a small bone at hyomandibular-symplectic junction. Quadrate with slender posterior ramus. Endopterygoid narrow and elongate; ectopterygoid minute. Autopalatine reaching maxilla anteriorly.

OPERCULAR SERIES (fig. 1): Opercle oval with posteroventral indentation, lacking serrations. Preopercle, subopercle and interopercle narrow.

HYOBRANCHIAL APPARATUS (fig. 3): Hyoid bar represented by a single hypohyal, and anterior and posterior ceratohyal. Four branchiostegal rays. Interhyal ossified. Ossified portion of basihyal narrow and elongate. Three ossified basibranchials.[3] Hypobranchials, if present, not ossified. First ceratobranchial with 12 slender gill rakers, second ceratobranchial without gill rakers, the third and fourth ceratobranchials each with a toothplate and patch of teeth, fifth ceratobranchial expanded medially and with a toothplate bearing a patch of curved, pointed teeth. Four epibranchial bones, the first with gill rakers. Two upper pharyngeal bones, the anterior (pharyngobranchial 2) articulating with the second epibranchial, the posterior (pharyngobrancial 3) with the third and fourth epibranchials.

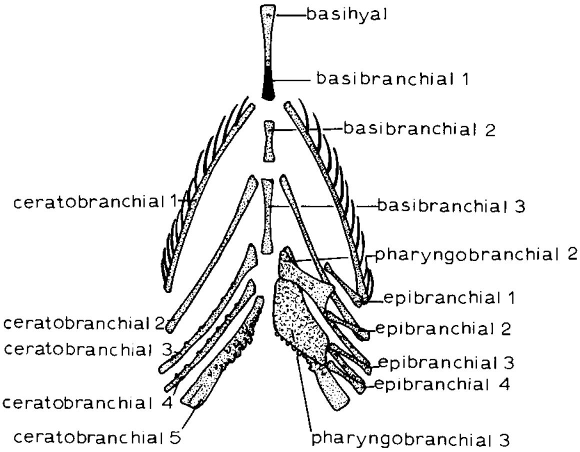

FIG. 3. Dorsal view of gill arches, with left dorsal portion removed, *Phallostethus dunckeri* Regan, Syntype, BMNH 1913.5.24:22. From a sketch prepared by Dr. Trewavas. See text for discussion on identification of structures.

VERTEBRAL COLUMN: Forty vertebrae, 13 abdominal, 27 caudal. First pleural rib on fourth vertebra. No epineurals or epipleurals.

CAUDAL SKELETON (fig. 4): Last vertebra consisting of a half-centrum (PU_2) with which are united a dorsal and a ventral hypural plate. Parhypural autogenous. Two epurals.

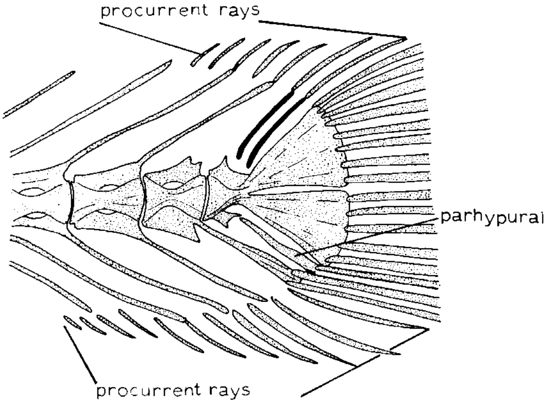

FIG. 4. Lateral view of caudal skeleton, *Phallostethus dunckeri* Regan, Syntype, BMNH 1913.5.24:22. From a sketch prepared by Dr. Trewavas. Epurals are blackened.

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[3] In her notes, Dr. Trewavas indicated that *Phallostethus dunckeri* has three ossified basibranchials. In her original sketch, there are just two ossified basibranchials posterior to an elongate ossified basihyal, however. I interpret the elongate basihyal as a basihyal and the first basibranchial.

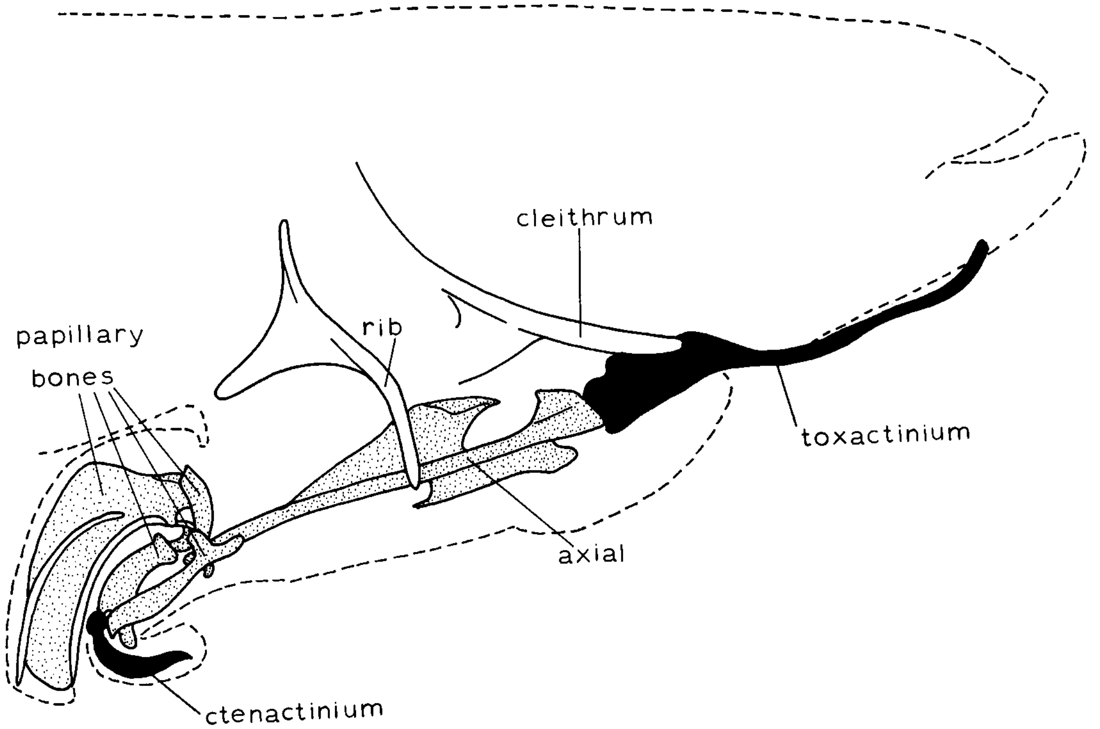

FIG. 5. Schematic diagram of internal priapial structure of *Phenacostethus smithi* Myers, BMNH 1927.12.29:1–10. From a sketch prepared by Dr. Trewavas.

FINS: No spinous first dorsal fin; second soft-rayed dorsal fin with eight to 10 rays. Caudal fin truncate, seven procurrent rays dorsally, 16 branched caudal rays, and 11 procurrent caudal rays ventrally. Minute pelvic fins and fin girdles in females; males with pelvic fins and fin girdles modified into priapium (see below).

PRIAPIUM: The present report does not require a comprehensive review of priapial anatomy, which will be considered in detail in a revision of the Phallostethidae *sensu lato* (Parenti, in prep.). However, certain details are pertinent to this discussion.

The priapium primitively has two conspicuous externalized bones, the ctenactinium and pulvinulus, both of which are derived from pelvic fin structures (Regan, 1913, 1916). *Phallostethus* Regan and *Phenacostethus* Regan are distinguished from other phallostethids by the type of externalized priapial bones; they have a ctenactinium and a toxactinium, rather than one or two ctenactinia and a pulvinulus. The currently accepted homologies of priapial parts requires that the toxactinium of *Phallostethus* and *Phenacostethus* be viewed as a modified pulvinulus (Roberts, 1971b). The ctenactinium of *Phenacostethus* (fig. 5) is rudimentary and not as well developed as that of *Phallostethus* in which it is serrated (see also Regan, 1913; Bailey, 1936; Roberts, 1971a).

RELATIONSHIPS OF THE PHALLOSTETHIDS

Characters in addition to the priapium and associated reproductive traits have been proposed as unique to phallostethids: a submaxillary bone (fig. 2), and a paradentary bone (fig. 1) (Roberts, 1971b). Rosen and Parenti (1981) treated the two families (Phallostethidae and Neostethidae) of phallostethoids *sensu* Myers as one, the Phallostethidae. The division of phallostethids into two families was based on differences in priapial morphology, and by the identification of submaxillary and paradentary bones in genera that had been assigned to the Neostethidae (Roberts, 1971b), such as *Ceratostethus* Myers and *Neostethus* Regan. Roberts (1971b) called these bones "neomorphs."

The recent discovery and diagnosis by Patten and Ivantsoff (1983) of *Dentatherina,* a western Pacific marine atherinid, allows for a reinterpretation of these as well as other characters used to hypothesize the relationships of phallostethids and other Indo-Australian and Pacific atherinoids.

SUBMAXILLARY BONES:[4] Submaxillary bones are prominent endochondral bones that lie between the medial ramus of the maxilla and the anterolateral portion of the vomer (figs. 2, 6). Bony elements in this position are found in *Dentatherina* (Patten and Ivantsoff, 1983, figs. 4, 5) and phallostethids in both the Phallostethidae and Neostethidae *sensu stricto, contra* Roberts (1971b), who stated they occur only in the latter. He did not know the condition in *Phallostethus.* In some phallostethids (e.g., *Gulaphallus mirabilis,* BMNH 1933.3.11:179–186) and taeniomembradine atherinids (e.g., *Craterocephalus cuneiceps,* AMNH 43184SW, fig. 7C) a submaxillary element is present as a large cartilage rather than a bone. Roberts (1971b) postulated that the submaxillary bones of neostethids *sensu stricto* contributed toward the extremely protractile mouths of these fishes.

It is not my purpose here to present a hypothesis of the relationships of all atherinid fishes, or even atherinid fishes of the subfamily Taeniomembradinae (comprising the genera *Taeniomembras, Craterocephalus, Stenatherina, Alepidomus, Hypoatherina, Atherinomorus,* and tentatively *Quirichthys*). Therefore, I have not surveyed all the genera of any such group to determine whether or not each has a submaxillary bone or cartilage. However, from the limited survey of Indo-Pacific atherinoids and the subfamily Taeniomembradinae, I have determined that most, but not all, members of these groups have submaxillary cartilages or bones. For example, the Western Australian isonid, *Iso rhothophilus* (AMNH 55027SW), as well as the New World taeniomembradine *Atherinomorus stipes* (AMNH 52025SW), have no such cartilages or bones. The maxilla and vomer are separated by a small connective tissue meniscus, which is a primitive character for acanthopterygian fishes.

Furthermore, other atherinoids, such as *Quirichthys stramineus* (AMNH 20571SW), *Telmatherina ladigesi* (AMNH 35378SW), and *Pseudomugil tenellus* (AMNH 36598SW) have prominent submaxillary cartilages. Each of these genera was placed in a different family of atherinoid fishes by Allen (1980). Accessory cartilages and bones in the ethmoid region are not uncommon among euteleosts, nor are elements in the position of the submaxillary bones. I judge these to be derived at one level within the atherinoid fishes, discussed below.

PARADENTARY BONES: A separate, slender bone, termed the paradentary, lies lateral to the dentary in both *Dentatherina* and the phallostethids. Patten and Ivantsoff (1983) noted what they called "calcified nodules" in the lower jaw ligaments, preferring not to consider them homologues of the paradentary bones of phallostethids. However, for two reasons I take the view that the structures are homologous.

First, the suggestion that they are fortuitous ossifications of jaw ligaments is contradicted by the presence of a paradentary bone with a single row of small, unicuspid teeth in *Phallostethus dunckeri* (fig. 1). As far as known, these bones are unique to *Dentatherina* and phallostethids. In some closely related taeniomembradine atherinids, such as *Craterocephalus cuneiceps* (AMNH 43184SW), there is a mass of connective tissue in the position of the paradentary.

Second, the homology of paradentary bones in *Dentatherina* and phallostethids is supported by parsimony. Reasons for their inclusion in yet a larger group of atherinoids, is discussed below. The same ontogenetic sequences of paradentary formation in both groups would support this homology, however, no such data are available. Histological

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[4] This element should not be confused with one between the maxilla and autopalatine, called a subautopalatine cartilage by Parenti (1981, p. 406, fig. 35A). Such an element, found in some cyprinodontiforms, is apparently primitive for acanthopterygian fishes.

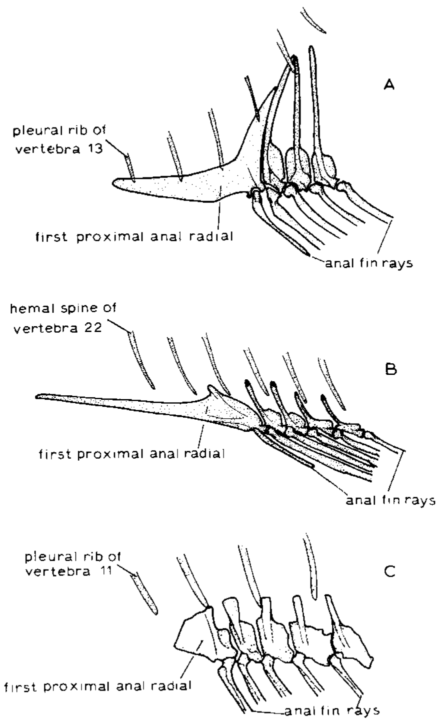

FIG. 6. Internal view of anal fin, anterior to left, of A. *Gulaphallus mirabilis*, BMNH 1933.3.11:179–186; B. *Dentatherina merceri*, USNM 230374; C. *Pseudomugil tenellus*, AMNH 36598SW. Bone stippled; cartilage open circles.

study is also needed to determine whether these are dermal or endochondral bones.

PREMAXILLA AND ROSTRAL CARTILAGE: In phallostethids (fig. 2), *Dentatherina* and some taeniomembradine atherinids, such as *Craterocephalus cuneiceps* (fig. 7C), the ascending processes of the premaxillae, as well as the rostral cartilage, are thin and elongate, as opposed to being short in many other atherinids. There are exceptions among New World menidiine atherinids such as *Melanorhinus microps* (AMNH 25878SW) in which there are elongate premaxillary ascending processes; however, I view these as independently derived in *Melanorhinus* because other characters indicate that it is distantly related to the phallostethids.

ANAL FIN: In phallostethids, *Dentatherina*, taeniomembradine atherinids (of the genera *Craterocephalus*, *Atherinomorus* and *Quirichthys*), telmatherinids (the genus *Telmatherina*) and *Pseudomugil*, the first proximal anal radial is expanded anteriorly. In phallostethids (fig. 6A) and *Dentatherina* (fig. 6B) the first proximal anal radial is a long, bladelike element. The main shaft of the radial is oriented dorsally. That is, the radial is expanded anteriorly, rather than being recumbent.

In the other taxa listed above, the first proximal anal radial is expanded anteriorly and may be bladelike, as in *Atherinomorus stipes* (AMNH 52025SW), or may be expanded just slightly, as in *Pseudomugil tenellus* (fig. 6C). In each case, the main shaft of the radial is evident. In other atherinoids (e.g., *Bedotia geayi*, AMNH 28132SW) the first proximal anal radial has no anterior expansion; it is represented solely by the main, dorsally directed shaft.

ADDITIONAL CHARACTERS: Two other derived characters, the absence of parietal bones from the skull, and the absence of a dorsal or first postcleithral bone from the pectoral skeleton support a close relationship between *Dentatherina* and phallostethids.

RELATIONSHIPS OF ATHERINOMORPH FISHES

It is hypothesized that the Phallostethidae and *Dentatherina* are sister groups, and that they in turn are members of a group of Indo-Australian and Pacific, and some New World, atherinoids that include the taeniomembradines as far as I have examined them. Thus, Roberts's (1971b) speculation that phallostethids and taeniomembradines are closely related is corroborated. Patten and Ivantsoff (1983) named a new subfamily, the Dentatherininae, for their new genus, because they could not place it in any other known subfamily of the Atherinidae. The definitions and relationships of the six families of Division I, the atherinoids, of the Atherinomorpha (table 1), are poorly known. As stated above, genera that I believe to be closely related to phallostethids and *Dentatherina* have been placed in several different families by recent workers. One such genus, *Quirichthys*, endemic to three river systems in northern Australia, has been placed most recently in the Atherinidae by Allen (1980, p. 483); however, previously it has been considered a close relative of the Telmatherinidae, which now contains a single genus, *Telmatherina.* Allen (1980) also placed *Pseudomugil* in the Melanotaeniidae. The Isonidae (or Notocheiridae) has been considered by Patten (1978, in Patten and Ivantsoff, 1983) to constitute a subfamily of the Atherinidae. These changes, or suggested changes, in classification serve to point out where additional work is needed. For example, Allen (1980, p. 465) claimed that melanotaeniids, as he defined them, are distinguished from atherinids in having males with elongate dorsal, anal, and pelvic fin rays, and more brightly colored than females. However, not only does *Pseudomugil* share this characteristic, it is found also in other atherinids such as, for example, *Telmatherina.* No definition of the Atherinidae in terms of unambiguous, derived characters has ever been proposed. It is inherent in the present argument concerning the relationship of the phallostethids, that one does not exist. That is, the Atherinidae is not monophyletic.

More important, I believe that there is additional evidence to support Rosen and Parenti's (1981) claim that the atherinoids cannot be defined as monophyletic. Two of the characters for the monophyly of the atherinomorph fishes as a group, of the 10 listed by Rosen and Parenti (1981, pp. 20–21) are the derived ethmoid region (their character 9), and the decoupling of the rostral cartilage from the ascending processes of the premaxillae (their character 7). With these characters, Rosen and Parenti (1981) supported the monophyly of the Atherinomorpha, but they could not make a firm statement concerning its relationship to other acanthopterygians. They stated only that it was the sister group of the Percomorpha, a group that is itself not definable as monophyletic. To hypothesize the polarity of particular characters within the Atherinomorpha, therefore, particular groups of percomorphs may be chosen for outgroup comparison. The holocentrid beryciforms, which in some characters are primitive and in others derived relative to atherinomorphs, comprise such a group chosen to hypothesize polarity of characters of the upper jaw and ethmoid region.

Primitively for acanthopterygian fishes, as in the holocentrid *Holocentrus rufus* (fig. 7A), the ethmoid region consists of a well-developed mesethmoid bone. This is not the case in atherinomorphs (with the exception of the apomorphic *Iso*) in which the mesethmoid is represented by a small wedge or disc of bone (fig. 7B–C) or may be cartilaginous as in some aplocheilichthyine and orestiine killifishes (Parenti, 1981).

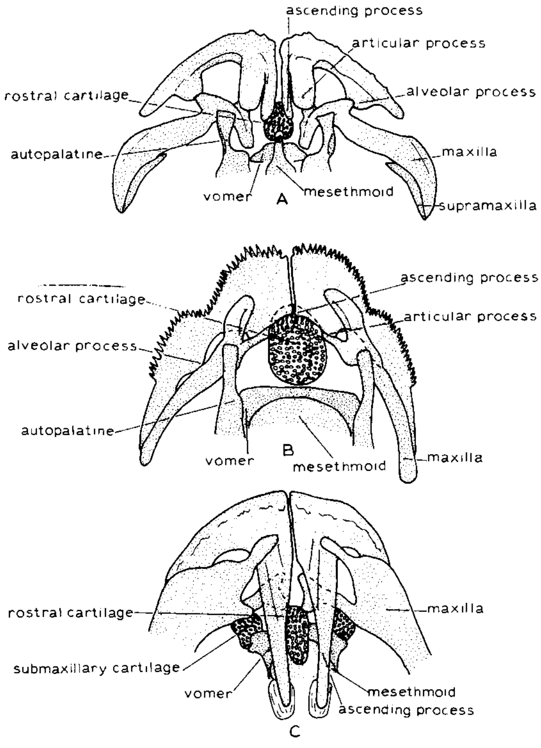

FIG. 7. Dorsal view of upper jaw and ethmoid region of A. *Holocentrus rufus,* AMNH 27118SW; B. *Bedotia geayi* AMNH 28132SW; C. *Craterocephalus cuneiceps,* AMNH 43184SW. Bone stippled; cartilage open circles.

Furthermore, acanthopterygian fishes primitively have distinct ascending and articular processes of the premaxillae, with the ascending processes intimately in contact with the rostral cartilage, and often wrapped around the cartilage so that the processes and the cartilage move together as one unit upon opening and closing of the mouth (fig. 7A) (see Alexander, 1967).

Primitively for atherinomorphs, as in the bedotiid *Bedotia geayi* (fig. 7B), the rostral cartilage is not as firmly attached to the ascending processes of the premaxillae, and yet there is what I identify here as a distinct articular process that comes in contact with the maxilla.

Generally, the ascending is identified as that process of the premaxilla in contact with the rostral cartilage or connected to it via ligaments, and the articular as that process in contact with the maxilla, either directly or via a connective tissue meniscus. Greenwood et al. (1966) claimed that atherinomorphs do not have true ascending processes of the premaxillae. Alternatively, Alexander (1967) claimed that atherinomorphs have no articular processes of the premaxillae, only ascending processes. Rosen and Parenti (1981) called the processes in atherinomorphs ascending. I claim that there is a distinct articular as well as ascending process in some primitive atherinomorphs and that the articular process is reduced or lost in relatively more derived members. In most atherinomorphs of table 1, *minus* the Bedotiidae and the Melanotaeniidae *sensu stricto,* there is no distinct articular process of the premaxilla, only a distinct ascending process, as in *Craterocephalus cuneiceps* (fig. 7C). Furthermore, there is less contact between the rostral cartilage and the ascending processes, and the two often move rather independently during jaw movement (Alexander, 1967).

DISCUSSION

Rosen and Parenti (1981, p. 14) suggested that the Bedotiidae and Melanotaeniidae *sensu stricto,* may be primitive relative to all other atherinomorphs (that is, the atherinids, telmatherinids, pseudomugilids *sensu stricto,* phallostethids, cyprinodontiforms, and beloniforms). Characters suggested to support this alignment, although just briefly explained, were conditions of the state of the dorsal fins, pelvics, extent of spine development, and number of vertebrae.

The two characters proposed here, reduction of the articular process on the premaxilla and the further decoupling of the rostral cartilage from the ascending processes of the premaxillae, support the hypothesis that all other atherinomorphs are derived relative to the bedotiids and melanotaeniids (minus *Pseudomugil*).

The two characters proposed here are in conflict with two proposed by White, Lavenberg, and McGowen (in press) who claim the atherinoid fishes can be defined as monophyletic by a short preanal length at flexure, and a unique dorsal pigmentation pattern. They propose using the ordinal term Atheriniformes for the atherinoids, the fishes of Division I (table 1). Parsimony does not allow us to choose between the hypothesis of White, Lavenberg, and McGowen and that proposed here. However, I feel it is perhaps premature to treat the fishes of Division I as monophyletic. Much comparative anatomical work needs to be done, particularly with regard to fin spine development, to hypothesize the polarity of characters that exhibit different states among the atherinoids. It has been stated repeatedly (e.g., Myers, 1928; Rosen, 1964; Rosen and Parenti, 1981) that atherinomorph fishes are acanthopterygians in which the spinous first dorsal fin is reduced phylogenetically, from the strongly developed spinous dorsal of the bedotiids, to the reduction or loss in phallostethids and numerous atherinids, and to its eventual loss (absence) in cyprinodontiforms and beloniforms. Yet, the ontogenetic sequence of this reduction and loss, as well as other characters with which it may be correlated, have never been stated clearly.

Therefore, I propose the following classification of atherinomorphs to reflect some of the findings of this paper:

- Series Atherinomorpha
  - Division I
      - Family Atherinidae
      - Family Bedotiidae
      - Family Isonidae
      - Family Melanotaeniidae
      - Family Telmatherinidae
    - Superfamily Phallostethoidea
      - Family Phallostethidae (including Neostethidae)
      - Family Dentatherinidae
  - Division II
    - Order Cyprinodontiformes
    - Order Beloniformes

Patten and Ivantsoff (1983) placed their new genus in its own subfamily, the Dentatherininae; I raise the rank to family. The order of the taxa is arbitrary, as in the classification of Rosen and Parenti (1981). Any classification of atherinomorphs must, in my opinion, reflect the sister group relationship of the phallostethids and *Dentatherina.* I have chosen not to place the Dentatherininae in the Phallostethidae solely for reasons of tradition. However, it is critical to recognize the phallostethids and *Dentatherina* as belonging to a group distinct from other members of Division I. To list all the families without this indication would represent a loss of information in the printed classification. Should we wish to include some of the taeniomembradine atherinids in the group including phallostethids and *Dentatherina,* they may be included in the Phallostethidae, Dentatherinidae, or a third family to be placed in the superfamily Phallostethoidea.

On the other hand, I cannot support the monophyly of the fishes of Division I, and do not use the ordinal term Atheriniformes for them.

I tentatively accept the definition of the Melanotaeniidae of Allen (1980) to include *Pseudomugil* and its presumed close relative *Popondetta* Allen; however, the evidence herein suggests that *Pseudomugil* (and perhaps *Popondetta*) is not closely related to other melanotaeniids, but is rather more closely related to a group that includes phallostethids, *Dentatherina,* some taeniomembradines and *Telmatherina.*

The primary goal of the present paper is the clear definition of the relationship of phallostethids to other atherinomorphs for the purpose of carrying out a taxonomic revision of the included species. The definitions and relationships of the families not treated in detail here are currently under study by other workers.

SUMMARY

1. The Indo-Australian fresh, brackish, and occasionally saltwater fishes of the family Phallostethidae and the western Pacific marine atherinid *Dentatherina* are hypothesized to be sister groups that share three derived characters: a paradentary bone, absence of parietals, and absence of a dorsal (first) postcleithrum from the pectoral skeleton.

2. A submaxillary bone or cartilage between the maxilla and vomer is present in phallostethids, *Dentatherina,* the Australian taeniomembradine atherinids *Craterocephalus* and *Quirichthys,* the Australian melanotaeniid or pseudomugilid *Pseudomugil,* and *Telmatherina,* endemic to Sulawesi. Other taeniomembradines examined, for example the New World *Atherinomorus,* have the primitive state of a connective tissue meniscus.

3. An enlarged first proximal of the anal radial fin is present in phallostethids, *Dentatherina, Craterocephalus, Quirichthys, Pseudomugil, Telmatherina,* and *Atherinomorus,* the taxa listed in 2, above. It has not been found in bedotiids, melanotaeniids, and in other nontaeniomembradine atherinids examined.

4. The atherinoid fishes, those of Division I of Rosen and Parenti (1981), are not currently definable as monophyletic.

5. The classification of atherinomorph fishes proposed above represents the finding of this paper that phallostethids are most closely related to the western Pacific atherinoid *Dentatherina.* Other families listed in the classification, such as the Atherinidae, cannot currently be defined as monophyletic. They are currently under revision by other workers.

6. At least some of the taeniomembradine atherinids appear to be most closely related to the phallostethids and *Dentatherina.* In particular, the western Australian *Craterocephalus* shares the derived character of elongate premaxillary ascending processes and rostral cartilage with these two groups. Other taeniomembradines most likely share this as well as other characters with the phallostethids and *Dentatherina.* A clearer statement of the relationship of all taeniomembradines awaits a revision of the subfamily, as well as the rest of the Atherinidae.

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