OSTEOLOGY OF THE MALAYSIAN PHALLOSTETHOID FISH *CERATOSTETHUS BICORNIS*, WITH A DISCUSSION OF THE EVOLUTION OF REMARKABLE STRUCTURAL NOVELTIES IN ITS JAWS AND EXTERNAL GENITALIA[1]

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ABSTRACT. The osteology of the phallostethoid *Ceratostethus bicornis* (Regan) is described and figured. Comparative observations on osteology of atherinoids, cyprinodontoids, and other phallostethoids are also given. Phallostethoids apparently originated from atherinids. The most closely related atherinids are Taeniomembrasinae. The osteological observations tend to support the idea that atherinoids and cyprinodontoids are related, as postulated by Rosen (1964) in proposing the order Atheriniformes. Atheriniforms exhibit a widespread tendency to develop teeth with two and three cusps, especially on the pharyngeal bones. The trend is pronounced in cyprinodontoids, exocoetoids, and scomberesocids, practically absent in atherinoids, and completely absent in phallostethoids and belonids.

The Phallostethoidea can be divided into two families, Phallostethidae and Neostethidae. Neostethidae comprises two subfamilies, Neostethinae and Gulaphallinae. These groups are distinguishable on the basis of morphological differences in the jaws and external genitalia. The highly protractile jaws of Neostethinae (as exemplified by *Ceratostethus* and *Neostethus*) are remarkable in having several pairs of bones without homologues in other fishes. These new bones, involved mainly in protrusion of the jaws, evolved in soft structures already present in the jaws of atherinids. The functional anatomy of the jaws of phallostethoids is briefly discussed. Phallostethidae and Gulaphallinae lack the neomorphic jaw bones found in Neostethinae. Two ctenactinia formed from pelvic fin spines or rays occur only in *Ceratostethus*. The so-called "second ctenactinium" of *Gulaphallus* is an externalized pelvic bone. Phallostethidae apparently arose from *Neostethus*. The toxactinium, the main externalized bony element in the priapium of Phallostethidae, is derived from the inner pulvinular bone, which is the anteriormost internal bony element in the priapium of Neostethidae. The inner pulvinular bone of *Neostethus* bears a small lateral projection, the pulvinular spine, which may be a rudimentary toxactinium. The structure of the papillary bone, intimately associated with the genital pore, is relatively simple in Gulaphallinae and Phallostethidae, but in Neostethinae it divides into numerous thin processes each bearing a hooklet at its tip. A comprehensive definition is given for the superfamily Phallostethoidea. All taxa used in this paper were proposed by previous authors.

Oviparous Atheriniformes with internal fertilization have external genitalia far more complicated than the gonopodium of any of the viviparous Atheriniformes. The explanation of this difference is sought in terms of selection pressures for and against the evolution of highly complicated external genitalia in forms with internal fertilization. Neotenic characters probably played an important role in the origin of phallostethoids from Atherinidae.

INTRODUCTION

Ichthyologists have marvelled at phallostethoids since they were first made known by C. T. Regan (1913; 1916). Males of these delicate little fishes from Southeast Asia can be distinguished in an instant by their strange subcephalic copulatory organ, or priapium, as Regan designated it. The 19 species now known have been divided
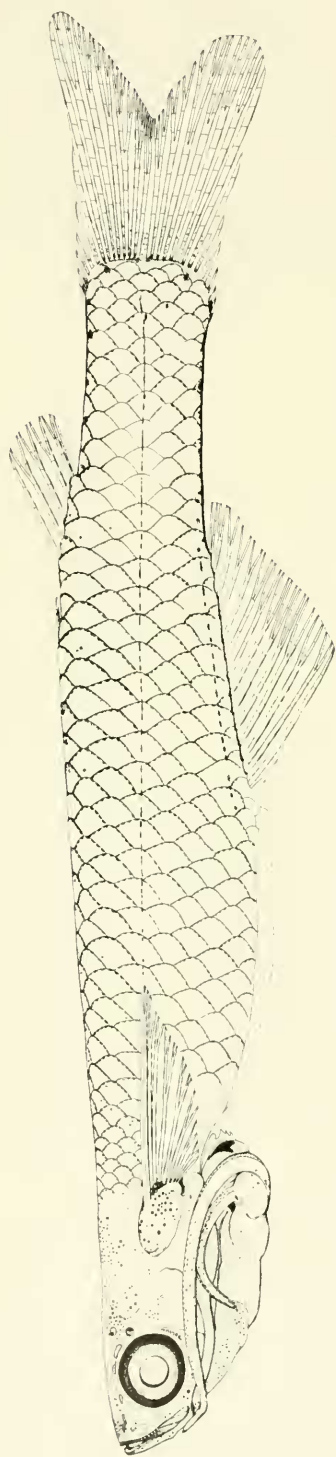
Figure 1. *Ceratostethus bicornis*, 25.3-mm sinistral male (MCZ 47305), from estuary of Chantaburi River, Chantaburi Province, Thailand.

into two families and ten genera, largely based on differences in the external armature of the priapium (see Herre, 1942). H. M. Smith (1927) made the surprising announcement that phallostethoids he observed in Thailand are oviparous. This discovery was confirmed in species from the Philippines by Villadolid and Manacop (1934) and Woltereck (1942a). Despite their outstanding interest, phallostethoids have remained virtually unknown to the general zoological public.

The present paper gives a relatively complete, illustrated account of the osteology of *Ceratostethus bicornis* (Regan) (Fig. 1), with special attention to the hitherto undescribed jaws and their functional anatomy. Previous osteological work on Phallostethoidea (with the exception of brief observations by Regan [1913; 1916], who lacked adequate skeletal preparations) has been almost totally restricted to the priapium (Bailey, 1936; Aurich, 1937; Woltereck, 1942a, b). The priapium is derived mainly from pelvic bones and fin rays, with contributions from the anteriormost ribs and pectoral girdle. The pelvic elements are so excessively modified that their homologies remain unresolved. This copulatory organ is perhaps even more specialized than the copulatory organs derived from the anal fin in the cyprinodontoids *Horaichthys* and *Tomeurus*. Interestingly enough, *Horaichthys* and *Tomeurus* are also oviparous, and they exhibit numerous morphological and ecological similarities to phallostethoids. The morphological similarities, however, do not extend to the jaws of *Ceratostethus*: although basically similar to the jaws of atherinoids, they are even more highly protractile and possess two major and two minor paired bones found so far in no other fishes except the closely related *Neostethus* (probably also present in *Solenophallus* and *Plectrostethus* and possibly *Phallostethus*, but absent in *Phenacostethus* and *Gulaphallus*). No observations have ever

been made on the feeding movements of *Ceratostethus* or any other phallostethoids; I have tried to determine the main features of their functional anatomy by manipulation of alizarin-stained specimens macerated in potassium hydroxide and cleared in 50 percent glycerine.

My initial objectives in studying the osteology of *Ceratostethus* were to provide information that might lead to a better understanding of 1) relationships of Phallostethoidea to other fish groups, and 2) relationships among phallostethoid genera. I chose *Ceratostethus* because, judging from priapial structure, it seemed to represent a relatively primitive phallostethoid, and I had an abundant supply of fresh material from Thailand. Regan (1913; 1916) regarded the phallostethoids as an aberrant subfamily of Cyprinodontidae, and noted that their osteology was "typically cyprinodontid." He did not indicate to which cyprinodontids they might be most closely related. Subsequent to the discovery by Herre (1925) that phallostethoids possess a spiny (albeit minute) first dorsal fin, most ichthyologists followed Myers (1928) in relating them to the Atherinidae. Myers intimated that Atherinidae and Cyprinodontidae might actually be fairly closely related, a suggestion generally viewed with disfavor (cf. Hubbs, 1944) until Rosen (1964) pointed out a large number of anatomical, morphological, and reproductive characters and trends common to atherinoids, cyprinodontoids, and allied forms (including Phallostethoidea) and united them in a new order, Atheriniformes. While placing the superfamily Phallostethoidea in the suborder Atherinoidei (*ibid.*: 261), he suggested that it might be more closely related to cyprinodontoids than to atherinoids after all (*ibid.*: 242). During the course of the present study numerous supplemental observations were made on cyprinodontoids and atherinoids. Phallostethoids apparently are more closely related to atherinoids than to cyprinodontoids.

The most closely related forms appear to be *Stenatherina* and its Indo-Pacific allies (placed by Schultz, 1948, in the atherinid subfamily Taeniomembrasinae).

If one considers only zoogeographic distribution and priapial morphology (which has been worked out in considerable detail for almost all of the genera by Bailey [1936] and especially by Aurich [1937]), a relatively simple picture of phyletic relationships within Phallostethoidea emerges. There are two families: Phallostethidae and Neostethidae. Phallostethidae, presumably most highly modified from the primitive or ancestral type of phallostethoid, comprise two genera, *Phallostethus* and *Phenacostethus*, confined to the Malay Peninsula and adjacent parts of the mainland of Southeast Asia. Neostethidae comprise six to eight genera (Herre, 1942, probably went too far in splitting genera) belonging to two subfamilies, Neostethinae and Gulaphallinae. Gulaphallinae are restricted to the Philippines. Neostethinae, which include *Ceratostethus, Solenophallus, Plectrostethus,* and *Neostethus,* are more widely distributed. *Neostethus* and *Ceratostethus* occur in the Philippines, Borneo, and both sides of the Malay Peninsula.[1] The priapium of Neostethinae, in which the only externalized elements are derived from pelvic spines and rays, is evidently more primitive than are the priapia of Phallostethidae and Gulaphallinae. In phallostethid priapia the main externalized element is homologous with the neostethid outer pulvinular (Bailey, 1936; Roberts, 1971), which is the anteriormost internal element in the priapium of Neostethidae. *Neostethus,* alone among Neostethidae, has a single spur near the base of its ctenactinium, resembling the series of spurs on the ctenactinium of *Phallostethus* (the ctenactinium of *Phenacostethus* is absent or

[1] There are two records of indeterminable phallostethoids: from Sabang, northwestern Sumatra (Aurich, 1937: 282–284) and from Zamboanga (Banjagan, 1966: 46).

greatly reduced). In addition, the outer pulvinular bone of *Neostethus* has a small but distinct lateral projection, immediately anterior to the pulvinulus (absent in other neostethids), which might be an incipient or rudimentary toxactinium. Regan (1916: 6, fig. 3) referred to this projection as the pulvinular spine. It would be of great interest to compare the osteology of *Neostethus* and *Phallostethus*. Unfortunately, *Phallostethus* is represented in collections by only four type specimens in poor condition. The priapial characteristics of *Phenacostethus* have been treated in detail elsewhere (Roberts, 1971). Both *Gulaphallus* and *Ceratostethus* have been described as having two ctenactinia. The second ctenactinium of *Ceratostethus*, however, is evidently a modified pelvic spine or ray, whereas that of *Gulaphallus* is an externalized pelvic bone. In addition, in Gulaphallinae (*Gulaphallus* and *Mirophallus*) the anterior end of the ctenactinium fits into a fleshy sheath in the anterior end of the priapium, whereas in Neostethinae it remains uncovered (see Aurich, 1937: 266, figs. 1 and 2).

The discovery of neomorphic jaw bones in *Ceratostethus* and *Neostethus* adds a new dimension to the above sketch. Their presence in these genera and their absence in *Gulaphallus* indicate the distinctness of the subfamilies Neostethinae and Gulaphallinae and make direct derivation of Gulaphallinae from Neostethinae harder to conceive. Absence of the neomorphic elements is perhaps to be expected in the minute species of *Phenacostethus*; they may well be present in *Phallostethus*. Their absence in *Gulaphallus,* in which the jaws are distinctly less protractile than in *Neostethus, Ceratostethus,* and *Phenacostethus,* indicates that more diversity exists among Phallostethoidea than might otherwise have been thought.

The intergeneric relationships of Phallostethoidea, as currently understood, may be represented in a diagram as follows:

Phenacostethus

Phallostethus

Manacopus

Solenophallus   Plectrostethus   Gulaphallus

Neostethus   Mirophallus

Ceratostethus
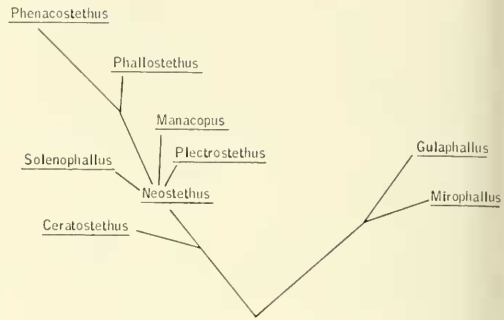
As previously indicated (Roberts, 1971), I am inclined to believe that the order Atheriniformes, as conceived by Rosen (1964), constitutes a natural assemblage. Thus far my researches have not uncovered any facts that cast serious doubt on this concept. Although Rosen (1964: 255) stated that the circumorbital series in Atheriniformes is represented only by lacrimal and dermosphenotic (lacrimal with separate ventral piece in a few cases), in some phallostethoids and atherinids there is a large, trough-shaped infraorbital bone immediately beneath the lacrimal, and in some atherinids (*Melanotaenia* and *Telmatherina*) there are two separate, troughlike or laminar infraorbitals below the lacrimal. Rosen (p. 288) found in melanotaeniids a small, spatulate element broadly and firmly joined to the ventral surface of the lacrimal, and noted that these two bones in melanotaeniids together resemble the single elongate lacrimal of *Xenopoecilus.* The second infraorbital bone (considering the lacrimal as the first infraorbital) in phallostethoids and atherinids observed by me is quite separate from the lacrimal. A first pharyngobranchial is present in *Ceratostethus, Melanotaenia,* and *Allanetta,* although Rosen (p. 237) stated that the first pharyngobranchial is lacking in Atheriniformes (*Melanotaenia* indicated as a possible exception). The Atheriniformes are diverse, and it is understandable that as additional representatives are studied more thoroughly, definitions will

have to be revised and expanded. It is undeniable that certain evolutionary trends, for instance those concerning reproduction, seem to be more readily understandable if the groups placed in Atheriniformes are indeed related. Thus some observations on the widespread occurrence of bi- and tricuspid teeth in Atheriniformes, which seem to confirm their relationship, are reported in this paper even though the dentition of phallostethoids is entirely conical. My own feeling, however, is that the concept of Atheriniformes should be verified by thorough osteological comparisons among the primitive or annectant representatives of the suborders assigned to it.

Villadolid and Manacop (1934) analyzed stomach contents throughout one year in wild-caught *Gulaphallus mirabilis*, and observed courtship, copulation, and egg-laying of this species in aquaria. These aspects of behavior have not been observed in any other phallostethoids. No new species of Neostethidae have been described since the genera and species were reviewed by Herre (1942). I reviewed the Phallostethidae, described a new species of *Phenacostethus* from the Indian Ocean coast of Thailand, and remarked upon the ecology of Phallostethidae and Neostethidae in Thailand. I also discussed the selective advantage of internal fertilization in Phallostethoidea as well as trends in the reproductive biology of atheriniforms that might be conducive to the evolution of internal fertilization (Roberts, 1971). The discussion section of the present paper deals with evolutionary topics such as the origin of the neomorphic jaw bones found in *Ceratostethus* and *Neostethus*, neotenic characters in phallostethoids, and the nature of selection pressures for and against the development of highly complicated external genitalia in atheriniforms.

ACKNOWLEDGMENTS

OSTEOLOGY OF *CERATOSTETHUS* (Figures 2–12)

The following osteological account is based on 14 specimens (ten males and four females) 17.0–26.8 mm in standard length, part of a large series collected in a roadside ditch shaded by nipa palm about two miles from Tha Chalap on the road to Chantaburi City, Chantaburi Province, Thailand (MCZ 47304). The only osteological differences detected between males and females involve genitalia, and the anteriormost ribs and the cleithrum (modified in males to form a suspensorium for the priapium). The figures are based on four specimens, 24.8–26.8 mm. A few observations are included on the osteology of *Phenacostethus*, *Neostethus*, and *Gulaphallus*. Comments and comparative observations on cyprinodontoids and atherinoids
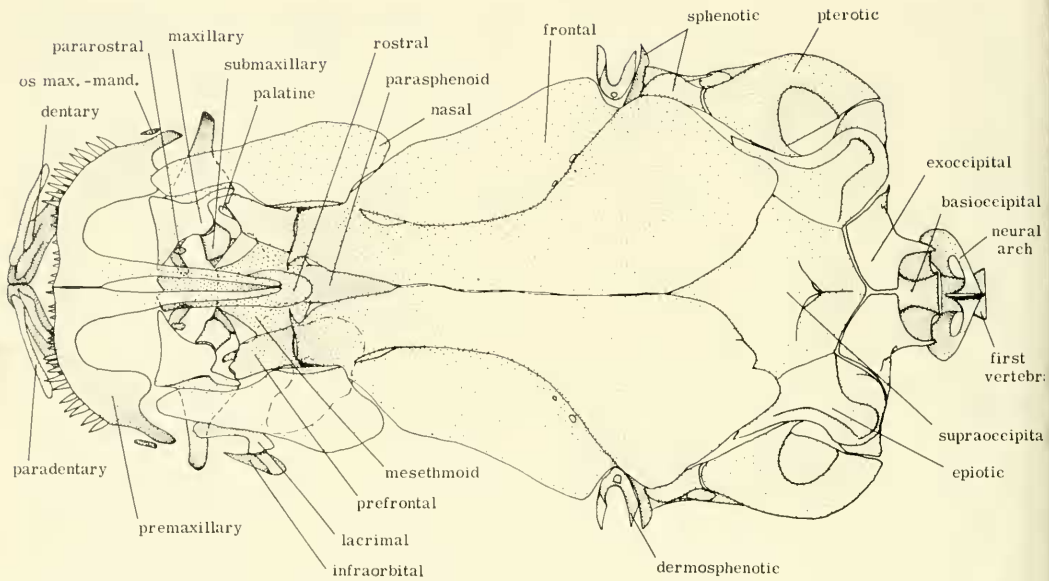
Figure 2. *Ceratostethus bicornis.* Dorsal view of skull and first vertebra; jaws slightly protruded.

are inserted in numerous places. I have examined alizarin preparations of a considerable variety of cyprinodonts (a number of them kindly provided by Neal Foster) and atherinoids (including alizari preparations in the Department of Ichthyol ogy of the American Museum of Natura History). The osteology of atherinids i

Figure 3. *Ceratostethus bicornis.* Ventral view of cranium and first vertebra; with portions of jaws, suspensorium, and shoulder girdle of right side.

Figure 4. Cerotostethus bicornis. Lateral view of skull, first vertebra, and part of pectoral girdle.

the subfamily Taeniomembrasinae shows much in common with that of *Cerato-stethus*. The parts of the skeleton are taken up in the following order: cranium, jaws, suspensorium, facial bones, hyoid and gill arches, pectoral girdle, median fins, vertebral column, and priapium.
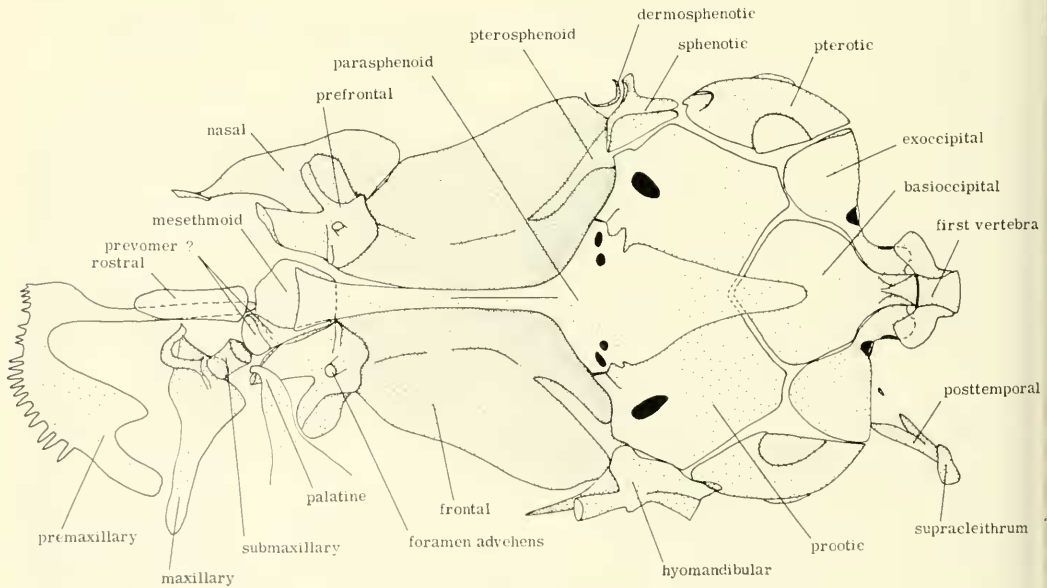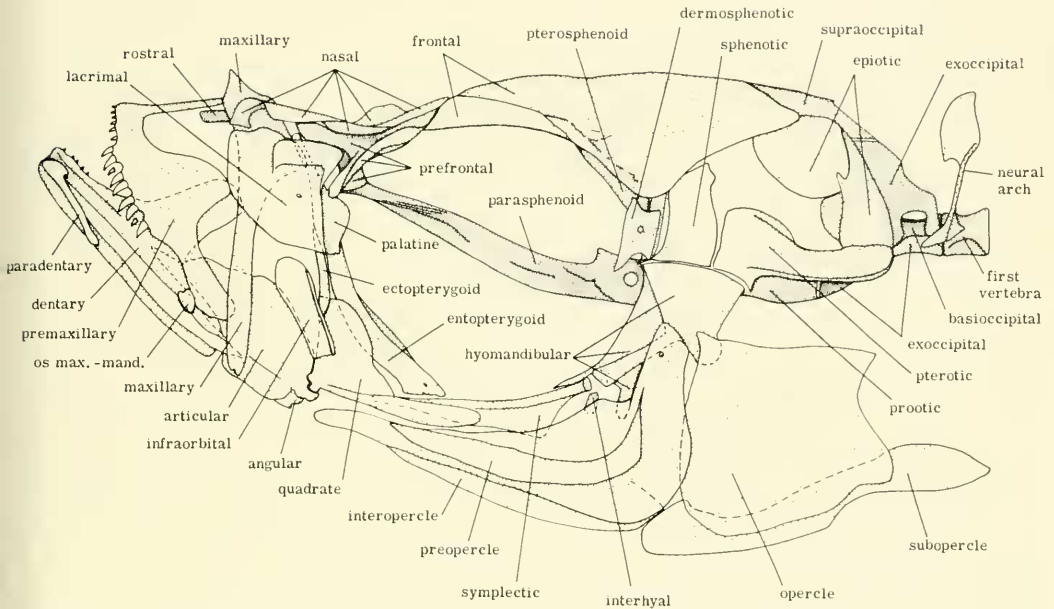
Cranium (Figs. 2–4). Bones in cranium: prevomer, mesethmoid, prefrontals, front-als, parasphenoid, pterosphenoid, sphenotic, prootic, pterotic, epiotic, supraoccipital, exoccipitals, and basioccipital. Basisphe-noid, parietals, and intercalar absent.

Anterior end of each side of prevomer enlarged and rounded to form a joint sur-face with submaxillary bone. In some specimens the prevomer is a single ossifi-cation. In others (including the ones in Figs. 2–4) it is ossified in two separate parts, one on each side of the mesethmoid. Mesethmoid a laminar bone of irregular hexagonal form. In some atherinids the mesethmoid is a thin lamina. (In cyprin-odontoids mesethmoid either cartilaginous or a bilaminar ossification.)

Roof of skull convex, with a deep V-shaped trough between main body of frontal and supraorbital lamina; frontal bones depressed anteriorly where they meet prefrontals to form posterior floor of rostral fossa. In these features the roof of the skull resembles that of various atherinids; cyprinodontoids usually (always ?) have a uniformly flattened or only very slightly convex roof, without a trough between main body of frontal and supraorbital lamina. Skull roof smooth, without bony canals for cephalic laterosensory system; wings or crests absent excepting poorly developed (vestigial ?) supraoccipital crest. Supraoccipital spine undivided. Supra-occipital spine usually (invariably ?) un-divided in atherinoids, bifid in cyprin-odontoids (personal communication from D. E. Rosen). Dorsal border of foramen mag-num formed exclusively by exoccipitals.

Jaws (Figs. 5–7). Although bearing strong morphological and functional re-semblance to the highly protractile jaws of certain atherinids, the jaws of *Cerato-*
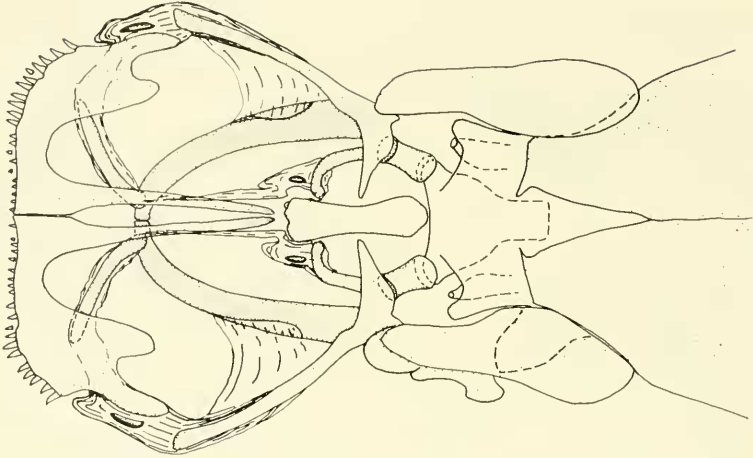
Figure 5. *Ceratostethus bicornis.* Dorsal view of anterior part of skull with jaws greatly protracted. Compare Fig. 6C.

stethus are perhaps even more specialized, for they include a number of hitherto unreported ossified elements, some of which are without known osseous homologues in atherinoids or cyprinodontoids or even analogues in other teleosts. These evidently neomorphic structures, apparently present only in phallostethoids, are functionally involved in the extreme protrusibility of the jaws (evidently including closure of the jaws in protruded position). The new bones, discussed below, are paired elements, named as follows (in order of occurrence anteroposteriorly): paradentary, maxillomandibular, pararostral, and submaxillary bones.

Bones in upper jaw: paired premaxillaries, maxillomandibularies, maxillaries, pararostrals, and submaxillaries; in lower jaw: dentaries, paradentaries, articulars, angulars, and coronomeckelians. Premaxillaries and dentaries with a single row of conical teeth; other jaw bones and palate toothless. Proximal third of premaxillary with eight to ten relatively small teeth, middle third with about ten enlarged teeth, distal third toothless. Dentaries with three to five very small (vestigial ?) teeth near symphysis; otherwise toothless. Ascending premaxillary processes slender, elongate (their length almost equal to a third of cranial length).

Posteriorly directed, broad-based, rounded processes ("articular processes") arising at midlength of premaxillaries; such processes (either rounded or pointed) characteristic of many atherinoids, are usually (invariably ?) absent in cyprinodontoids. Several atherinoids have slender elongate ascending processes as in *Ceratostethus;* ascending processes in cyprinodontoids usually (invariably ?) relatively short, broad-based, and wide. Maxillary with well-developed, strongly curved internal hooks. As in atherinoids (but not in cyprinodontoids) the maxillary has a laminar projection dorsal to the internal hook, part of which projects dorsally to the ascending premaxillary processes (when mouth is abducted). Lower (distal) limb of maxillary uniformly slender. A swelling (cranial condyle) at junction of internal hook with the main body of maxillary provides articular surface for submaxillary bone. Maxillary without ligamentous attachment to palatine. In atherinoids and in some (all ?) cyprinodontoids maxillary articulates directly to prevomer or to the ethmoid by a submaxillary meniscus. In atherinoids and cyprinodontoids there is usually (always ?) a direct ligamentou

connection between palatine and maxillary at or near cranial condyle. Head of maxillary bound in place, probably by ligamentous connections with nasal, lacrimal, and perhaps mesethmoid which, however, permit swinging and screwing movements. Lower (free) limb of maxillary uniformly slender. Internal hooks attached by dense connective tissue extending ventrally to rostral bone. Rostral connective tissue (ethmopremaxillary ligaments ?) with a pair of very small pararostral bones dorsolateral to anterior part of rostral bone. Near tip of lower limb of premaxillary, in the maxillomandibulary ligament lies the small, rounded, dorsoventrally compressed maxillomandibulary bone. The maxillomandibulary ligament connects the ends of the lower or free limbs of the premaxillary and maxillary to the dentary. The mouth is opened when movement originated by depressing the lower jaw is transferred by this ligament to the upper jaw. The attachment of the ligament to the dentary extends from middle of dentary to symphysis of lower jaws. Near symphysis main body of ligament very tough and round in cross section. In shape and extent of attachment the ligament resembles strongly that in certain atherinoids, particularly members of the subfamily Taeniomembrasinae (for definition and discussion of this taxon see Schultz, 1948). In other atherinids and in cyprinodontoids the attachment of the ligament does not extend much anterior to the middle of the dentary, and is spread out or sheetlike. The anterior part of the ligament in *Ceratostethus* differs strikingly from that in Taeniomembrasinae in that lying entirely within it is a very conspicuous and functionally significant ossification, the paradentary bone. Distal end of paradentary lies free in the ligament; its proximal end forms the ball of a ball and socket joint with the dentary at anteriormost point of attachment of ligament, i.e., near symphysis of lower jaw. Dentary with a high coronoid process, as in many atherinids; coronoid processes usually absent in cyprinodontoids.

In the following account I attempt to give an idea of functional (mechanical) relations of the jaw bones even though their movement was studied only in macerated specimens. I have assumed that in live specimens the mouth is opened mainly by depression of the lower jaw; that return of the jaws to normal "resting" position involves two distinct, consecutive stages, namely 1) closing of the mouth while it is still protracted, accomplished by retraction on the lower limb of the maxillary, drawing free ends and premaxillaries back (while position of lower jaw is unaffected), and 2) moving the entire assemblage back into the nearly vertical position it occupied before, probably accomplished by retraction on the coronoid process of the dentary and on the "articular process" of the premaxillary. From the work of Alexander (1966, 1967a, b) it seems likely that in many fishes with protractile jaws, the mouth is closed while the jaws are protracted. It is unclear whether the mouth can be closed when it is protracted in atherinoids, but it can be in some cyprinodontoids, as well as in cyprinoids, and acanthopterygians (Alexander, 1967a, b).

When mouth is in resting position, ascending premaxillary processes fit snugly into rostral concavity, their distal (free) ends lying between depressed anteriormost portion of frontal bones. When jaws are maximally protracted (as estimated by manipulation of KOH-macerated specimens) premaxillaries have moved forward about 125 percent of their length, or about 35 percent of the headlength.

Maxillaries of typically atherinoid form, excluded from gape and with well-developed internal hooks. With mouth completely closed, straight, slender ventral (distal) limb of maxillaries lies at an angle of about 10 degrees posterior to a vertical; with mouth fully protracted, ventral limb of maxillary at an angle of about 45 degrees anterior to a vertical (see Fig. 6.A–C).

Screw movement is slight or nonexistent

cyprinodontids examined by me failed to exhibit this movement. The screw movement evidently also causes dilation of the lower limbs of the premaxillary, causing the lateral series of enlarged premaxillary teeth (which are directed sideways when the mouth is in resting position) to point straight ahead.

As stated by Alexander (1967b: 241) protrusion of the jaws must be accompanied by screw movement of the maxillary, so that the internal hooks and consequently rostral bone are moved anteriorly. In *Ceratostethus*, however, at least some protrusion occurs before the screw movement begins. Furthermore, it is possible to cause considerably more protrusion (about 25 percent more) after the rostral has ceased to move forward by simply continuing to depress the lower jaw. If this is done, the premaxillary tilts upwards posteriorly so that the mouth opening is slightly downwards instead of vertical. While it is doubtful that the jaws are normally protruded so far, this observation indicates that depression of the jaws can act unaccompanied by screw movements of the maxillary to bring the premaxillaries forward.

In cyprinodontoids the screw movement of the maxillary causes not only anterior movement of the internal hooks, but also lateral movement (Alexander, 1967b: 239 fig. 5). I have observed this in many cyprinodontoids. In *Fundulus* the rostral cartilage is Y-shaped, with the internal hooks attached firmly to the ends of the arms of the Y; as the internal hooks move laterally, the arms of the Y spread apart. In addition, in many (but not all) cyprinodontoids, the internal hooks are so firmly bound to the ascending premaxillary that when the hooks move laterally, the ascending processes diverge posteriorly (see Alexander, 1967b, fig. 6e of *Fundulus*). In *Ceratostethus* there is either no lateral movement or very slight lateral movement of the internal hooks; the ascending pro-

Figure 6. *Ceratostethus bicornis*. Lateral view of jaws in varying stages of protrusion (for explanation see text).

until after more than half of the swinging movement is completed and the premaxillaries are considerably protracted. Up to this point movement of the premaxillaries is equal to that of the rostral; from this point on, however, the premaxillaries move relatively further forward than do the rostrals. Thus not only does the rostral slide forward relative to the cranium, but the premaxillary processes slide forward relative to the rostral; Alexander (1967b) found a similar movement present in *Atherina* but absent in the cyprinodontids *Aplocheilus* and *Fundulus*. Alizarin preparations of various

maxillary processes never diverge from each other.

Submaxillary process of maxillary articulated to prevomer by submaxillary bone (developed in place of the usual submaxillary meniscus). Submaxillary bone forms a meniscus with submaxillary process of maxillary and with anterior end of prevomer. When mouth is closed, submaxillary bone lies with its upper end at an angle of about 15 or 20 degrees anterior to a vertical; when mouth is protracted, rotation of maxillary depresses upper end of submaxillary, which finally lies at an angle of about 45 degrees from vertical with mouth fully protracted. The curved, ventrally directed internal hooks of the maxillaries are ligamentously attached to a median ossified element or rostral bone lying ventrally to ascending processes of premaxillaries. (This element evidently is represented by a rostral cartilage in atherinoids; it is similar in position, but not in movement, to the cyprinoid kinethmoid.) With mouth closed, anterior tip of rostral is horizontal with the anterior tips of the nasal bones and anterior margins of maxillaries; when mouth is fully protracted, it moves forward approximately 50 percent of its length. Above the rostral, in thickened connective tissue attaching it to ascending premaxillary processes and internal hooks of maxillary, lies a pair of small bones or pararostrals. These are evidently equivalent to accessory rostral cartilages of some atherinoids. Movement of pararostrals equal to movement of rostral.

Lower jaws similar in form to those in atherinoids: dentaries with very large coronary process, and with ventrally opened flange forming a trough for mandibular segment of cephalic laterosensory system. Maxillomandibular ligament, linking tips of the ventral limb of maxillary and premaxillary to dentary, is similar to that in atherinoids (but not to that in cyprinodontoids) in that its connection to dentary extends anteriorly to ramus of lower jaws. In the maxillomandibular ligaments of

Figure 7. *Ceratostethus bicornis*. Hypothetic closure of protracted jaws (for explanation see text).

Ceratostethus are two paired bones: the small maxillomandibular bones, lying free in that part of the ligament connecting premaxillary and maxillary, and the elongate paradentaries, which are attached by a sort of ball and socket joint to the dentaries near ramus of lower jaw. Movement of the maxillomandibular bones is dependent on movement of the premaxillary; their position with respect to lower limb of premaxillary remains unchanged. Maxillomandibular bone forming conspicuous rounded prominence in angle of rictus of jaws when mouth fully opened (Fig. 6c). Paradentaries, with longitudinal axis parallel to that of dentary, lie snugly against dentaries in grooves; base of groove formed by dorsal surface of bony canal for mandibular segment of cephalic laterosensory system. With mouth about half open, paradentaries remain snugly against dentary; as mouth opens further, their distal (free) end swings sideways and upwards until, with mouth fully protracted, they are at right angles to dentary (Fig. 6c). When mouth closes in protracted position (closing accomplished in macerated specimens by pushing back on lower limb of maxillary), the paradentaries return to lie flush with side of dentaries, while only the lower limb of the premaxillary is retracted; the ascending premaxillary processes remaining as far or almost as far forward as they are when mouth is fully

opened (Fig. 7). Thus closure is accomplished almost entirely by movement of the upper jaw. The lower jaw remains depressed, the lower jaw bones, excepting the paradentary, undergoing little or no movement.

The paradentaries evidently are involved in increased protrusibility of the upper jaw. In specimens in which the maxillomandibulary ligaments have been cut immediately posterior to the distal end of the paradentaries, depression of the lower jaw still causes premaxillary protraction, but the premaxillaries do not project as far anteriorly and they project upwards (with leading margin considerably elevated) instead of straight forward. The paradentaries also help spread the gape sidewards as the mouth is opened.

Comments. Two objections that might be raised to this description of jaw function are 1) whether it is normal for the jaws to be so greatly protracted, and 2) whether closure actually occurs in the manner suggested. There are some fishes (including *Monocirrhus* among Nandidae [Liem, 1970], *Epibulus* among Labridae, several atherinoids) with protractile upper jaws and elongate ascending premaxillary processes in which the ascending premaxillary processes are advanced no more than a fraction (a half in *Epibulus*; about a third or less in *Monocirrhus* and the atherinoids) of their length when the jaws are fully protracted. In *Monocirrhus* and *Epibulus* (in which the lower jaws as well as the upper are protractile) the ascending premaxillary processes are exceedingly elongate—as long or longer than the total cranial length. The ascending premaxillary processes of *Ceratostethus* are relatively short compared to those of *Monocirrhus* and *Epibulus*: their length is about one-third of cranial length. Three facts indicate that the upper jaw is protracted as far or nearly as far forward as shown in Figure 5. First, protraction of the upper jaws this far is achieved by only moderate depression of the lower jaw. In various atherinoids and

in the neostethid *Gulaphallus* in which the upper jaws do not protract very far, the mandible must be depressed further before the upper jaw moves forward at all than when the upper jaw is fully protracted in *Ceratostethus*. Second, the paradentaries do not rotate outward until the upper jaw is considerably protracted, and only slightly more forward movement of the upper jaw is involved for the paradentaries to rotate as far outward as in Figure 5. It seems to me highly likely that the paradentaries do in fact rotate this much. Third, when one depresses the lower jaw of a macerated specimen, the entire jaw assemblage moves readily and smoothly as far forward as in Figure 5. In particular, the motion of the maxillary is unencumbered. This contrasts with *Gulaphallus* and with various atherinoids in which movement of the maxillary is relatively restricted.

Whether closure of the jaws occurs in the manner indicated is much less sure. It seems likely that the jaws are closed in protracted position. Granted this happens perhaps stages 1 and 2 envisioned in returning the jaws to resting position act in concert rather than consecutively. It may be that the mouth never closes with the upper jaw fully protracted (the position indicated in Fig. 7). It should be noted however, that the jaws of macerated specimens are readily manipulated into this position, and that from this position they can be readily manipulated back to resting position, i.e., closed and completely retracted.

Liem (1970: 106), considering fishes with protractile jaws, stated that the salient features of feeding (and respiratory) movements are 1) opening and closing of the jaws, 2) protrusion of the jaws, 3) volume and pressure variations in the buccopharyngeal cavity, 4) abduction and adduction of the opercular apparatus, and 5) complex movements of the gill arches. He pointed out that these functions are mutually interdependent and should be considered in conjunction. Assessment of

the movements of the opercular apparatus and gill arches and their relationships in *Ceratostethus* has not been attempted, since "natural" movements of these parts are less readily achieved (or achieved with less confidence) by manipulation of macerated specimens. The main, or at least a major, advantage of protractile jaws may lie in increasing the buccal component of the buccopharyngeal pumping mechanism; one of the advantages in closing the mouth with the premaxillaries protracted probably lies in increasing the volume of water that can be sucked into the mouth without being forced back out as the mouth closes (see more detailed discussion in Alexander, 1967a: 59–62). It seems likely that these factors operate in *Ceratostethus*.

Suspensorium (Fig. 4). Bones in suspensorium: palatine, ectopterygoid, entopterygoid, quadrate, symplectic, and hyomandibular. Anterodorsal part of palatine slender, tubular, apparently connected by ligaments to prefrontal, but free of attachment to nasal, lacrimal, and maxillary. Movement of jaws fails to induce movement in palatine. Anterior margin of suspensorium (formed by palatine, ectopterygoid and quadrate) almost vertically inclined. Ventral portion of hyomandibular with processes contacting symplectic and preopercle. Symplectic with a ventrally directed laminar portion.

Facial bones (Figs. 2–4). Nasal well developed, almost as long as orbit, a dorsally projecting flange on its medial margin immediately lateral to depressed anteriormost portion of frontal, and a ventrally directed flange at its anterior tip that is intimately associated with anterodorsal corner of lacrimal bone. Circumorbital series comprised of lacrimal, a single infraorbital directly beneath it, and dermosphenotic. Lacrimal a large lamellar plate with a flange in its dorsoposterior corner forming a gutter for a segment of cephalic laterosensory canal. Ventral to lacrimal a single, concave infraorbital, forming a bony trough for a segment of cephalic
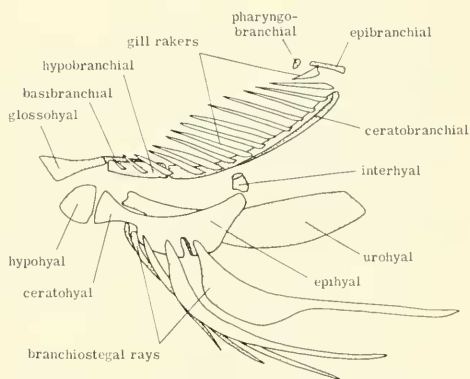

Figure 8. *Ceratostethus bicornis*. Lateral view of hyoid arch, urohyal, and first branchial arch. Hyoid and branchial arches slightly separated.

laterosensory canal. Dermosphenotic similarly troughlike, its attachment anterior to sphenotic (attachment of dermosphenotic posterior to sphenotic in *Horaichthys* and *Oryzias*). Preopercle with a ventrally open flange forming a trough for a segment of cephalic laterosensory canal. Opercle without spiny projections, its posterior margin concave as in some atherinids; in many (all ?) cyprinodontoids posterior margin of opercle broadly rounded. Posterior margin of gill cover formed by opercle, not by subopercle. Anterodorsal corner of opercle where it attaches to hyomandibular relatively unmodified, without a strongly reinforced socket to receive hyomandibular process. Interopercle and subopercle weakly ossified. Anterodorsal projection of subopercle weakly developed; posteriorly subopercle projects considerably beyond ventral margin of opercle.

Hyoid and gill arches (Figs. 8 and 9). Hyoid arch of typical atheriniform structure, with a single hypohyal; five branchiostegal rays on each side, first four branchiostegal rays attached to ceratohyal, last one to epihyal; dorsal half of joint between ceratohyal and epihyal strongly ossified; ceratohyal with a concave anteroventral margin. Gill arches with three median basibranchials, four pairs of hypo-
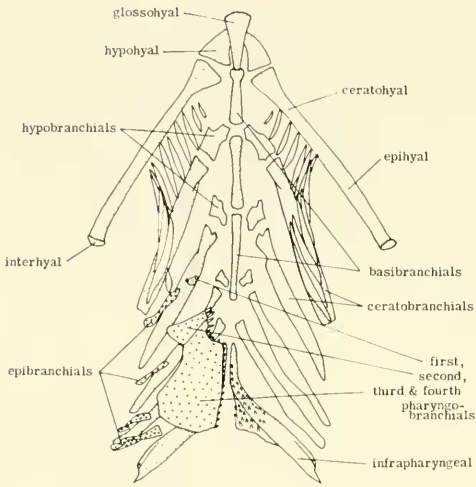
Figure 9. *Ceratostethus bicornis.* Dorsal view of hyoid arch (minus branchiostegal rays) and branchial arches. Uppermost branchial elements of right side removed.

Figure 10. *Ceratostethus bicornis.* Lateral view of pectoral girdle.

branchials, ceratobranchials, epibranchials, and pharyngobranchials, and a pair of infrapharyngeals. Third epibranchial T-shaped when viewed from side (figured only in dorsal view). Second, third, and fourth pharyngobranchials and anterior half of infrapharyngeals covered with moderately sized, irregularly arranged, conical teeth. Infrapharyngeals separate. Gill rakers only present on leading margin of first gill arch, 12 or 13 rakers on each side. First epibranchial bearing a single smaller raker, i.e., all rakers except this one are borne on lower half of gill arch. Anteriormost eight gill rakers on lower limb with distal ends directed laterally and posteriormost four or five rakers with distal ends directed increasingly medially, arrangement of these uppermost rakers thus simulating normal arrangement of rakers on upper limb of arch found in many fishes.

Pectoral fin (Fig. 10). Posttemporal forked; upper fork tightly bound to epiotic, lower fork short and not reaching base of cranium. Supracleithrum (as in other atheriniforms) a small scalelike element completely interposed between posttemporal and cleithrum. Cleithrum slender, only
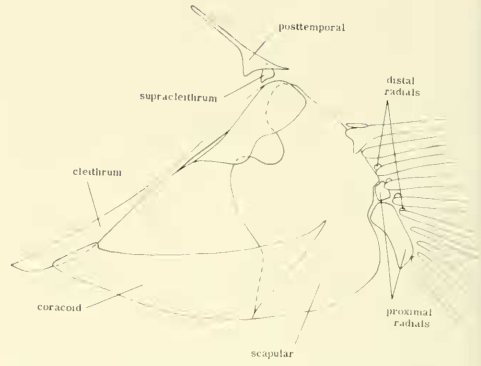
moderately expanded where it meet scapular to form scapular foramen, without an expanded portion extending poste riorly to scapular. In mature males anterio limb of cleithrum elongated anteriorly, t almost double relative length of cleithrum in immatures and females, approximating pulvinular bone of priapium. Cleithrum o one side elongated slightly more than tha of other side and ligamentously attached t pulvinular; at point of attachment slightl expanded to form a concave lamella fitting snugly over a convexity or bump in dorsa surface of pulvinular; anterior tip of op posite cleithrum ending in a fine point Relative development of anterior prolon gation of cleithra variable. In some speci mens tip of cleithrum unattached t pulvinular falls far short of it, in other speci mens equal in length cleithrum attached t pulvinular. Laterality of cleithrum attache to pulvinular independent of laterality c priapium itself. Apart from this differenc in development of the cleithrum, the pec toral girdle is similar in males and female Anterior end of coracoid not prolonged i males. Posterior end of coracoid fused wit ventrally expanded portion of scapular, an not associated with radials of pectoral fir Postcleithra absent. Proximal radials two i number, lowermost considerably enlarged their proximal ends fitting snugly into concavity in posterior border of scapula
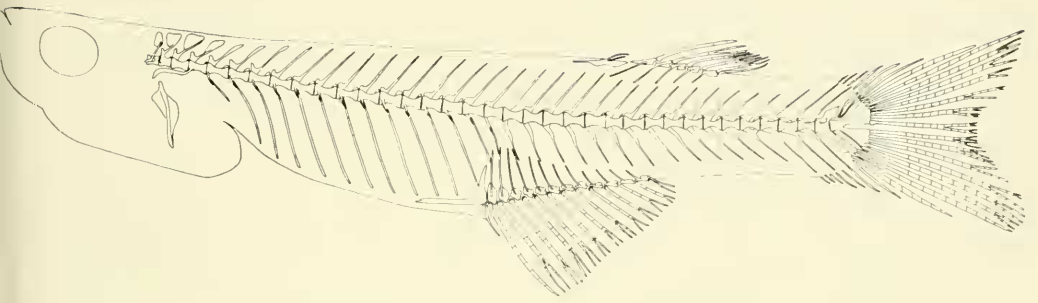
Figure 11.   *Ceratostethus bicornis.*   Axial skeleton.

A series of about four small distal radials. An unpaired splint attached to proximal dorsal surface of uppermost pectoral ray. Pectoral rays 10 or 11.

Median fins (Fig. 11). First dorsal fin with two very short, slender, refractile spines; second spine even shorter and slenderer than first, attached to a pterygium consisting of a single element. Second dorsal with five segmented rays. First ray unbranched; last ray divided to its base, anterior division branched, posterior division simple. Second dorsal fin pterygials each consisting of a single element, with slender proximal and expanded distal portions. Anal fin with 14 or 15 elements, first element simple, short, and unsegmented, second long and segmented; third through penultimate elements branched, segmented rays; last element divided to base, both divisions simple. Form of anal fin pterygials as in second dorsal fin, except for enlarged anteriormost pterygial, which is prolonged anteriorly in ventral midline for a distance equal to eye diameter in front of anal fin origin. Caudal skeleton (Fig. 11) with two hypurals, both fused to hypural centrum. No epineural or urostyle. Two slender epurals. Penultimate vertebra with well-developed haemal spine but neural spine reduced to expanded basal portion only. Neural and haemal spines of vertebrae preceding penultimate vertebra equally slender and elongate. No accessory haemal spine or separate slender element

interposed between haemal spines of antepenultimate and penultimate vertebrae (such an element present in *Dermogenys, Oryzias,* and *Xenopoecilus;* see Rosen, 1964, fig. 21). Caudal fin with 7 upper and 7 or 8 lower procurrent rays, and 7 upper and 7 lower principal rays, the outermost principal ray in each lobe unbranched. Posterior margins of hypurals straight and vertically aligned.

Vertebral column (Fig. 11). Vertebrae 35 or 36 excluding hypural; precaudal plus caudal either 18 + 17, 17 + 18 or 18 + 18. Distal ends of all except a few of the anteriormost and posteriormost ribs (which are associated with anteriormost pterygial elements of anal fin) meet opposite members in ventral midline of body. In females, anteriormost ribs are borne on third vertebra: first pair short and slender, without modified parapophyses; first three or four pairs of ribs gradually increasing in length. In males, first ribs borne on fourth vertebra. These ribs greatly expanded, their distal ends entering priapium just anterior to pulvinulus; parapophyses of fourth vertebra greatly enlarged, projecting anteriorly beneath vertebral column to a point below first and second vertebrae (Fig. 11). First three vertebrae without parapophyses. Ribs of fifth vertebra short and slender, their parapophyses unenlarged and posteriorly directed. Ribs of sixth vertebra of full length, reaching ventral midline of abdomen. Haemal arches not expanded (swim-
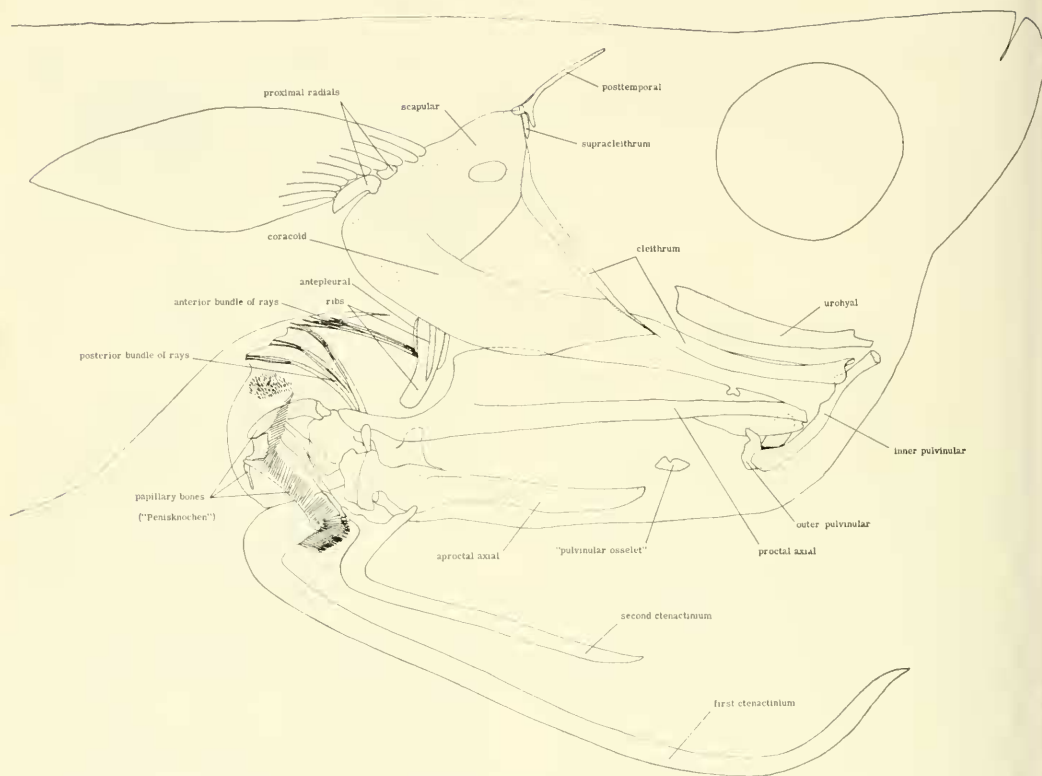
Figure 12. *Ceratostethus bicornis.* Lateral view of shoulder girdle, urohyal, and priapial skeleton of dextral male; ctenac tinia abducted.

bladder fitting snugly against posterior wall of abdominal cavity, without posterior projection into haemal arches). Intermuscular bones absent. First four vertebrae with distal ends of neural spines longitudinally expanded. Supraneurals absent.

Priapium (Fig. 12). The priapial skeleton of *Ceratostethus* is very similar to that of *Solenophallus* (Aurich, 1937) and *Neostethus*. The first and second ctenactinia of *Ceratostethus* evidently are homologous, respectively, with the ctenactinium and short, hooklike "Priapklaue" of *Solenophallus*. The anterior bundle of three segmented branched rays and posterior bundle of three segmented branched rays also are present. These rays lie in the wall of a sac that becomes filled with spermatophores. The branched ray tips protrude slightly

from this sac, providing its posterior mar gin with a "fringe" or "comb."

As in *Solenophallus*, the main element in the axial skeleton of the priapium are the two pelvic bones. The proctal pelvic bone (i.e., the one opposite the ctenactina) is considerably enlarged and acts as the suspensorium of the entire priapium. It is suspended anteriorly by the outer pulvin ular and inner pulvinular ("Pulvinulus träger" of Aurich), which are in turn suspended by the attachment of the pulvin ulus to the cleithrum and perhaps also the urohyal. The inner pulvinular is absent in *Gulaphallus* and *Mirophallus* (cf. Bailey, 1936; Aurich, 1937). Posteriorly it is sus pended from the vertebral column by its ligamentous attachment to the antepleural cartilage and anteriormost modified rib.

(see Aurich, 1937, fig. 3 of *Solenophallus*). The proximal ends of rays in posterior ray bundle firmly articulated to side of posteriormost part of proctal pelvic bone. Aproctal pelvic bone movably articulated to proctal pelvic bone by a series of complicated bones, the morphology of which is difficult to make out in intact priapia (see also Aurich, 1937). Two ctenactinia movably articulated to aproctal pelvic bone. Lying between anterior end of aproctal pelvic bone and accessory pulvinular is a small bone, the pulvinular osselet, evidently homologous with the pulvinular cartilage in *Solenophallus*. At the posterior end of the priapium, in the axis of the ctenactinia, is a series of excessively modified bones surrounding or partly surrounding the genital pore. These elements represent the "dorsal," "middle," and "ventral penisbones" of Aurich. In *Ceratostethus* and *Neostethus* the "ventral penisbone" gives rise to a large number of straight, thin bony projections, constituting a sort of flap over the genital pore. Many, if not all, of these projections are doubled back at the tip, and end as a hooklet. In *Neostethus* the projections, about 80 in number, are parallel to one another. In *Ceratostethus* the projections are much more numerous, some are considerably enlarged, and at each end of the genital pore a large number of the projections are oriented away from the main body of projections. The "ventral penisbone" of *Solenophallus ctenophorus* is similarly modified. It evidently is homologous with the greatly enlarged "ventraler Penisknochen" of *Gulaphallus* (called papillary by Bailey, 1936), with the slender "ventraler Penisknochen" of *Mirophallus,* and perhaps with the enlarged papillary bone in the base of the penis in *Phenacostethus*. In *Gulaphallus, Mirophallus,* and *Phenacostethus,* however, the parallel projections and hooklets are absent.

Plectrostethus Myers (1935) is said to be closely related to *Neostethus*, "from which it differs trenchantly in the presence of the spine-bearing process of the priapium and in the wing-like margin of the ctenactinium." The ctenactinium has a broad membranous margin along the lower side of its proximal half. At the base of the ctenactinium is a flat fleshy process armed on its upper and posterior border with a row of nine or ten short sharp recurved spines and on its anterior border by two longer spines directed forward (Myers, 1935: 5–6). The flat fleshy process is presumably homologous with the "ventral Penisbone" (= papillary bone ?) of *Ceratostethus* and *Neostethus*. The only known specimens of *Plectrostethus* are 12 type specimens of *P. palawanensis* Myers (U. S. National Museum nos. 93421–93423).

CHARACTERIZATION OF THE SUPERFAMILY PHALLOSTETHOIDEA

This characterization of Phallostethoidea is based on a survey of the literature and my own observations on *Phenacostethus* (both species), *Ceratostethus bicornis, Neostethus siamensis* (probably equals *N. lankesteri*) and *Gulaphallus mirabilis*. My observations have been relatively complete only for *Ceratostethus*. Many, if not most, of the characters cited below can be found scattered in the literature; virtually all of these characters have been verified by me, and erroneous statements in the literature rectified (e.g., concerning the pectoral girdle and first pleural ribs). The characters are presented in the following order: 1. general body features, size, habitat; 2. reproduction; 3. sensory organs; 4. squamation; 5. fins; 6. skull and visceral arches; 7. dentition; 8. pectoral girdle; 9. vertebral column (including ribs and intramuscular bones).

1. Largely translucent, bilaterally compressed and moderately elongate, tiny or very small, atheriniform fishes, adults from 14 (*Phenacostethus smithi*) to 37 mm (*Gulaphallus eximus*) in standard length (females usually slightly larger than males). Inhabiting fresh to brackish, usu-

ally turbid, coastal streams of mainland and insular Southeast Asia, usually within range of the tides.

2. Oviparous; gonad single; fertilization internal, males with a clasping and intro-mittant organ, the priapium, derived mainly from the pelvic fins; pelvics evanes-cent, vestigial or absent in females. In males anus opens on side of priapium op-posite genital pore, in females anal and genital openings close together on throat. Eggs demersal, chorionated, with adhesive filament (not verified in Phallostethidae); sperm transferred in large masses held to-gether by a mucoid substance (sper-mozeugma), at least in Neostethidae. Newly hatched young are miniatures of adults, probably immediately capable of active feeding and swimming.

3. Eyes large, laterally directed, free from orbital rim. Nostrils, if present, minute (a single opening which may be a nostril lies on the side of the snout near the upper jaw in *Neostethus* but is apparently absent in *Ceratostethus;* olfactory lamellae are not evident beneath the skin of the snout). A large pore midway between tip of snout and anterior margin of eye in Neostethidae is evidently a pore opening into supra-orbital canal of cephalic laterosensory system. Cephalic laterosensory system well developed, supraorbital, preorbital, post-orbital, preopercular, and mandibular canals with large pores in Neostethidae. In Phallostethidae laterosensory organs on top of head housed in a membranous dome, evidently without pores (see Roberts, 1971). Lateral line canal absent on body. Otoliths absent (dissolved by formalin ?). Contact organs absent.

4. Scales cycloid; body except "neck" completely scaled; scales in lateral series 31–58. Head scaleless or sparsely scaled, scales on head confined to posterior border of skull roof and preopercle.

5. Pectoral fin set high on sides of body, its shape slightly falcate, with ten or eleven rays. First dorsal fin usually present (ab-sent in *Mirophallus, Solenophallus thessa*

and perhaps absent in *Phallostethus*), con-sisting of one or two tiny, weak (nonerectile ?) spines movably articulated to an elon-gate pterygium. The second spine, when present, usually even thinner and shorter than the first. First dorsal completely separated from second dorsal, but much closer to it than in atherinids, its origin posterior to a vertical through anal fin origin. Second dorsal with one or two simple, unbranched, segmented rays (no spines), and three to nine branched rays. Origin of second dorsal well behind anal fin origin, or even posterior to anal fin. Anal fin with a short flexible spine, fol-lowed by an unbranched, segmented ray and ten to 28 branched rays. Initial pteryg-iophore of anal fin an enlarged backwards L-shaped bone (Fig. 11). A translucent median, abdominal, membranous keel in-variably present. Caudal fin forked; in at least some species the upper lobe is slightly longer than the lower lobe and is pointed, while the lower lobe is rounded (Fig. 1; Roberts, 1971, figs. 2 and 3 of *Phenaco-stethus*); principal caudal rays from $5 + 7$ or $6 + 7$ to $7 + 8$ or $8 + 8$.

6. Upper jaw usually highly protractile. Mesethmoid a single, irregularly hexagonal lamina; intercalar absent; parietals absent; infraorbital series represented by lacrimal, second infraorbital and dermosphenotic; dermopalatine absent. Lower arm of maxilla separated from mandible by ex-panded lower arm of premaxilla; maxillo-mandibulary ligament round in cross sec-tion where it attaches to dentary, the attachment near symphysis of lower jaws. Hind border of opercle concave; opercle and preopercle without spines or serrations; interoperculum not extending posterior to vertical from preopercle or overlapping subopercle. Distal half of ceratohyal abruptly expanded, a dorsal bridge of bone joining it to epihyal; branchiostegal rays four or five; gill rakers present only on leading edge of first gill arch, other arches rakerless.

7. Teeth strictly conical, confined to

premaxillary, dentary, second through fourth pharyngobranchials, and infrapharyngeals. Teeth on premaxillary and dentary in a single row (*Ceratostethus, Neostethus, Phenacostethus*) or in two to four rows (*Gulaphallus*). Dentition of lower jaw well developed in *Gulaphallus*, poorly developed (vestigial ?) in *Ceratostethus* and *Neostethus*.

8. Supracleithrum a small bone sandwiched between posttemporal and dorsal tip of cleithrum; cleithrum without wing-like dorsal expansion; scapula and coracoid fused together; only two proximal pectoral radials or actinosts, the lowermost enlarged; cleithra extended anteriorly in males, one or both of them attached to pulvinular bone of priapium.

9. Vertebrae 34 to 38. In Neostethidae the numbers of precaudal and caudal vertebrae are about equal. In Phallostethidae caudal vertebrae more numerous than precaudal: *Phenacostethus* with 14 to 16 precaudal and 19 or 20 caudal, *Phallostethus* with about 10 precaudal and 28 caudal vertebrae. First pair of ribs borne on third vertebra in females and on fourth vertebra in males of *Ceratostethus, Neostethus,* and *Phenacostethus.* In *Gulaphallus mirabilis* (MCZ 33904) a 23.1-mm immature male and a 22.0-mm specimen that appears to be an immature female both have the first ribs on the fourth vertebra. First pair of ribs in males greatly enlarged and attached to axial support of priapium; parapophyses of aproctal priapial rib enlarged and directed anteriorly so that its distal end, to which the rib is attached, lies beneath second vertebra. Intramuscular bones absent.

Comments. The Phallostethoidea constitute a distinctive and well-defined taxon. Almost all of their characters are in reasonable agreement with Rosen's concept of the Atheriniformes, with the (probably minor) exception of number of pectoral radials and relationship of the scapula and coracoid. Within the Atheriniformes it appears to be most closely allied to the atherinoids, and within atherinoids, to the subfamily Taeniomembrasinae. The suggestion by Rosen (1964: 242) that phallostethoids might be more closely related to cyprinodontoids than to atherinoids was based solely on the erroneous idea that the first pair of pleural ribs in phallostethoids originated on the second vertebra. In phallostethoids, as in many (all ?) atherinoids, the first pair of ribs is borne on either the third or the fourth vertebra, whereas in cyprinodonts the first pair of ribs is usually (invariably ?) borne on the second vertebra. It is noteworthy that the lowest vertebral count in atherinoids is 31, only three less than the lowest count in phallostethoids, whereas a number of cyprinodontoids have as few as 26. Cyprinodontoids usually (invariably ?) have intramuscular bones, while at least some (but not all) atherinids agree with phallostethoids in lacking them. Various other points in which phallostethoids agree with atherinoids more than with cyprinodontoids have been pointed out in my osteological description of *Ceratostethus.* Among the most important of these are the basically similar morphology of the jaws and attachment of the maxillomandibulary ligament to the dentary.

While phallostethoids are the only Atheriniformes known to me in which the first pair of ribs is ligamentously attached to the pelvic girdle, a ligamentous connection between the pelvic girdle and the distal ends of a pair of ribs evidently is a primitive atheriniform character. Which pair of ribs is attached depends mainly on the position of the pelvic girdle. Thus the ribs attached to the pelvic girdle are the third pair in *Melanotaenia,* the fourth in *Telmatherina,* the fifth in *Fluviphylax,* the sixth in *Menidia,* etc.

According to Bailey (1936: 464), in *Gulaphallus mirabilis* the distal ends of the first pair of ribs are "embedded in a heavy triangular mass of fibrocartilage, the antepleural cartilage, which is attached by fibers to the posterior crest of the axial

bone." In *Phenacostethus* (*ibid.*: 472) the tips of the priapial ribs are embedded in the antepleural cartilage, "which is ossified throughout most of its length and forms a distinct rod-like antepleural bone." An ossified antepleural is present in *Cerato- stethus* and *Neostethus*. In atherinoids and cyprinodontoids a "secondary postclei- thrum" is intimately associated with the distal end of each of the first pair of ribs. There is no trace of this element in female phallostethoids, and none in males either, unless it corresponds with the antepleural. The antepleural cartilage or bone of phallo- stethoids is perhaps neomorphic. The inner pulvinular bone of *Ceratostethus* and *Neo- stethus*, which apparently gave rise to the phallostethid toxactinium, probably is neo- morphic. It apparently has no homologue in atherinoids. For a discussion of the homologies of the priapial elements see Woltereck (1942b: 343–347).

The haemal spines of the anteriormost caudal vertebrae are expanded to permit extension of the swimbladder posterior to the abdominal cavity in various exocoetoids (only in the family Exocoetidae ?), cyprin- odontoids, and atherinoids. In phallo- stethoids the swimbladder extends to, but not beyond, the posterior wall of the ab- dominal cavity (as in taeniomembrasines), and the haemal spines are unexpanded.

The single gonad of Phallostethoidea (observed in *Phallostethus* and *Neostethus* by Regan [1916], in *Phenacostethus* and *Gulaphallus* by TeWinkel [1939]) is prob- ably a primitive character widespread in atheriniforms. The gonads are usually (in- variably ?) single in cyprinodonts, includ- ing *Oryzias, Rivulus, Fundulus*, and others.

The teeth of phallostethoids, both on the jaws and in the pharynx, are evidently invariably simple conical teeth, as one would expect in fishes of their tiny size. Hence, they fail to exhibit one of the most persistent trends of the atheriniforms, namely possession of tricuspid teeth.

Widespread occurrence of tricuspid teeth in atheriniforms. While most atherini-

forms have conical jaw teeth, bi- and tri- cuspid teeth occur in the jaws of diverse representatives; this is especially true in cyprinodontoids but is not confined to them. Miller (1956: 8–9) hypothesized that tricuspid teeth evolved independently at least three times in New World cyprin- odontids, and suggested that the Old World cyprinodontid genera with tricuspid teeth also originated independently. Tricuspid jaw teeth occur in some genera of Poe- ciliidae; the outer row of jaw teeth of Jenynsiidae has tricuspid teeth. Bicuspid jaw teeth characterize the atherinid genus *Atherinops*, and tricuspid jaw teeth occur in some genera of Exocoetidae and Hemiramphidae. The significance of these facts has not been fully appreciated, be- cause the remarkably widespread occur- rence of bi- and tricuspid pharyngeal teeth in atheriniforms has passed virtually un- noticed. Garman (1895, pls. I–V) showed that practically all cyprinodontoid groups exhibit a considerable variety of tooth forms in the jaws and pharyngeals; in a number of instances the pharyngeal teeth exhibit considerably more variation in form than the jaw teeth. *Anableps*, for example has conical jaw teeth, but the pharyngeal teeth exhibit a wide variety of forms in cluding tricuspid. Many cyprinodonts with conical teeth in the jaws nevertheless have some pharyngeal teeth of bi- or tricuspid form. *Pantanodon podoxys*, with no trace of jaw teeth, has tricuspid teeth on the pharyngeals, even in specimens only 17 mm in standard length (Whitehead, 1962, fig 8). As one might expect, however, the smallest cyprinodontids and poeciliids usu ally have simple conical teeth in both jaws and pharynx. This does not seriously de tract from the generalization that most, i not all, groups of cyprinodontoids have the tendency to develop bi- and tricuspid teeth and that this is seldom completely sup pressed. This generalization can be ex tended to include most groups of atherini forms. Thus tricuspid teeth occur on the pharyngeals in exocoetids and hemiram

hids (some of which also have tricuspid jaw teeth) and in scomberesocoids (jaw teeth usually or invariably conical; verified in *Scomberesox saurus*). Belonidae examined by me have conical pharyngeal teeth; the conical pharyngeal teeth of several belonids are figured by Collette 1966, figs. 2 and 3). The pharyngeal teeth of adrianichthyoids are conical (verified in *Xenopoecilus poptae* and *X. sarasinorum*). Throughout the atheriniforms, the smallest forms are likely to have simple conical teeth (e.g., phallostethoids, *Oryzias*); again, this does not seriously detract from the generalization that atheriniforms have a remarkable predisposition to develop bi- nd tricuspid teeth.

DISCUSSION

The protractile jaws of phallostethoids. The diversity of jaw mechanisms in teleosts s becoming ever more apparent. Probably more neomorphic joints and bones have arisen in the jaws than in any other of the major teleostean functional anatomical units (as defined by Liem, 1967). A great many of these structural innovations are associated with mobility of the upper jaw. t has been estimated that the jaws are protractile in about half of the living teleosts. While the majority of forms with protractile upper jaws are acanthopterygians, paracanthopterygians, or cyprinoids, protractile upper jaws also occur in Atheriniformes, in the gonorhynchoid *Phractolaemus,* and the characoid *Bivi-branchia*. The functional mechanism of protractility is completely different in acanthopterygians, cyprinoids, *Phracto-laemus* and *Bivibranchia* (for acanthopte- rygians, see Alexander, 1967a; Liem, 1970; Osse, 1969; Schaeffer and Rosen, 1961; for cyprinoids, Matthes, 1963; Alexander, 1966; or *Phractolaemus* and *Bivibranchia*, Géry, 1963). The functional mechanisms in atheriniforms are relatively similar to those n acanthopterygians. Although both per- nit protraction of the upper jaws, the

attachments and movements of the acanthopterygian rostral and cyprinoid rostral or kinethmoid are radically different. As fishes with protractile jaws are studied more closely, additional evolutionary novelties are bound to be discovered. For example, in *Epibulus insidiator* (family Labridae) the lower jaw is just as protractile as the upper jaw. As might be expected, this extraordinary adaptation involved major changes in the suspensorium. The outstanding jaw mechanisms of many teleosts remain equally uninvestigated. Some of the most peculiar jaws occur in tropical inshore fishes for which no observations on feeding have been recorded, and suggestions as to how the jaws are used would necessarily be fairly speculative.

To my knowledge, no other fishes have bony structures comparable to the paradentaries and submaxillaries of Neostethidae. The rostral bone of neostethids is probably homologous to the rostral cartilage of acanthopterygians, and cartilaginous elements similar to or homologous with the pararostrals occur in atherinoids (accessory rostral cartilages). Analogous rostral cartilages or bones and accessory rostral cartilages occur in cyprinoids. Bones analogous to the submaxillaries occur in Cobitidae. The maxillomandibular bones are small bones, and similar elements in other fishes, if they occur, are likely to have been overlooked. A small bone similar to the maxillomandibular bone, but lying dorsal to the lower limb of the maxillary instead of ventral to it, occurs in the characoid *Chilodus*. Such "supramaxillary" bones probably have evolved independently in numerous lines. The presence of such an element in *Chilodus* cannot be construed as a primitive character.

The paradentaries and submaxillaries are large elements, obviously of considerable functional significance. They are evidently involved in increasing the extent to which the jaws can be protracted. The paradentaries probably are also important in keep-

ing the mouth wide open when it is fully protracted and perhaps in permitting the upper jaw to close down over the lower jaw while the lower jaw remains fully depressed. The paradentaries are joined by a ball and socket joint to the dentaries near the symphysis of the lower jaw, and are capable of rotating outward 90 degrees and upward 45 degrees from their resting position in a trough on the side of the dentary. The submaxillaries are tubular bones with a meniscus at either end: the anterior meniscus with the maxillary bone, the posterior meniscus with the prevomer.

Although novel as bony elements, the paradentaries and submaxillaries arise in structures that are characteristic of atheriniforms, and particularly of atherinoids, the group to which they seem most closely related. Furthermore, the paradentary bones and submaxillary bones can be seen as the ultimate consequences of clearly defined evolutionary trends exhibited in atherinoids. Thus the anteriormost part of the maxillomandibulary ligament in some atherinoids (notably in the Taeniomembrasinae) has the peculiarities of the anterior part of the maxillomandibulary ligament in phallostethoids except that no paradentary bone develops in it. That is, in these atherinids the attachment of the ligament to the dentary is extremely far forward, near the symphysis; the body of this portion of the ligament is tough and round in cross section, and when the mouth is closed it lies in a trough on the side of the dentary identical with the trough in which the paradentary bone lies in neostethids. Concerning the submaxillary bone, it evidently serves much the same function as the submaxillary meniscus in atherinids. Alexander (1967b: 234) found the submaxillary meniscus much thicker in *Atherina* than in *Melanotaenia*; in *Atherina* "the submaxillary meniscus can swing anteriorly and somewhat medially about its articulation with the cranium, carrying the cranial condyle of the maxilla anteriorly and ventrally" (*ibid.*: 236). Movement of

the submaxillary bone and maxillary in neostethids is similar but of greater magnitude

The condition of the prevomer should be noted. In almost all fishes this dermal bone is a single, median element. In *Ceratostethus,* however, it sometimes ossifies in two pieces that remain separate, each with its anterior end greatly expanded where i is joined by a meniscus to the submaxillary bone. While dermal bones usually maintain their integrity, it is not impossible for them to give rise to separately ossifying elements Frazzetta (1970) described and discusses the subdivision of the maxillary bone to form two maxillary bones united by a intramaxillary joint in bolyerine snakes.

Neotenic characters of phallostethoids In teleosts it is extremely unusual for th anus and urogenital openings to be placed anterior to the pelvic fins. In most teleost in which these openings lie at the throa the pelvics are either absent or are even farther forward than the openings. In thi respect phallostethoids are exceptional. I males and in females in which the pelvic are vestigial or evanescent, anal and urogenital openings are morphologically anterior to pelvic fins. In adult atherin oids the position of the openings i variable, but they always lie posterior t the pelvic origin. It may be immediatel in front of the anal fin, distinctly in front c it, or even between the pelvic fins. Wolte reck (1942a: 256) made the importan discovery that the openings lie anterior t the pelvic fins in larval *Atherina*. This sug gests that the condition in phallostethoid may be neotenic.

It may well be that the anterior positio of the pelvic fins, and perhaps even thei attachment to the shoulder girdle, ar neotenic, at least in part. In atherinoid thought to be primitive, *Rheocles* an *Bedotia,* the pelvics are relatively far for ward. The ancestors of atherinoids ma have had the acanthopterygian character istic of thoracic pelvic fins connected wit the shoulder girdle.

The subcephalic position of the priapiu

cannot, however, be ascribed entirely to neoteny. No atherinoids or atheriniforms of any kind have the pelvics anywhere near as far forward as they are in phallostethoids. The anteriad prolongation of the cleithrum and of the parapophyses of the fourth vertebra in male phallostethoids indicates that the priapium has "migrated forward" (in an evolutionary sense). The selective advantage of an anteriorly located, i.e., subcephalic, priapium may lie in greater visual coordination during mating.

The phallostethoid "neck" may also be considered a neotenic character, for it appears to result in large part from absorption of the yolk. In larval phallostethoids the compact yolk sac lies immediately posterior to the head; it occupies considerable space where the neck eventually forms.

Almost certainly neotenic is the phallostethoid abdominal keel, derived from the median embryonic fin fold. In larval phallostethoids the fin fold extends continuously from its origin at a point on the dorsum about midway between snout and caudal base (where the first dorsal fin arises), round the caudal lobe and then on the ventrum uninterruptedly until it ends at the posterior margin of the yolk sac (see Villadolid and Manacop, 1934, pl. 2, fig. 2, pl. 3, figs. 1 and 2 of larval *Gulaphallus mirabilis*). In adult phallostethoids the abdominal keel consists of actinotrichia (the fibrous rays characteristic of embryonic fins).

The abdominal keel presumably plays the most important of the hydrodynamic roles formerly played by the pelvic fins. If, as may have been, acquisition of the abdominal keel permitted phallostethoids to utilize the pelvic fins for an entirely new function, it was a key step in their evolution.

Evolution of complicated external genitalia. Internal fertilization is a regular feature in the reproductive biology of many groups of atheriniforms (excepting Phallostethoidea, these groups belong to the Cyprinodontoidea). In three groups—

Poeciliidae, Goodeidae, and Jenynsiidae-Anablepidae—it has led to viviparity. Gonopodial morphology in these viviparous forms ranges from relatively simple in Goodeidae and in the poeciliid tribe Poeciliini to remarkably complex in the poeciliid tribe Cnesterodontini (see Rosen and Bailey, 1963, for figures of the poeciliid gonopodia). It is a striking fact that in the three groups that evolved internal fertilization and are oviparous—Tomeuridae, Horaichthyidae, and Phallostethoidea—the primary copulatory organ is far more complex than in any of the viviparous forms.[1] The gonopodium of *Tomeurus* can be compared directly with that in Poeciliidae, since *Tomeurus* is evidently related to the poeciliids and its gonopodium is derived mainly from the same rays in the anal fin as the poeciliid gonopodium. Perhaps the most complicated gonopodium in any poeciliid is that of the cnesterodontin *Phallotorynus,* which bears an enlarged scooplike element at its tip (*ibid.,* fig. 31a, b). The gonopodium of *Tomeurus* is much more complex: its tip bears a pair of greatly enlarged antlerlike processes, a far more complicated scooplike arrangement, and the distal end of the fifth anal ray, which is modified in a manner recalling the even more greatly modified papillary bone of neostethids (*ibid.,* figs. 7, 13–16). The gonopodium of *Horaichthys* (Kulkarni, 1940), which evolved independently of the gonopodium of Poeciliidae and Tomeuridae, is as complicated as that of *Tomeurus.* The neostethid priapium is morphologically as complex as or even more complex than the gonopodia of *Tomeurus* or *Horaichthys,* and far more complicated than the gonopodium of any of the viviparous forms. The question may now be raised, why are these structures in oviparous forms more complex? Conversely, why have viviparous

[1] The situation is admittedly complicated by the development in viviparous forms of modified pelvic or pectoral fin structures that function as accessory copulatory structures, but this does not seriously alter the main theme under consideration.

forms failed to evolve gonopodia as complicated as those in oviparous forms? The puzzle increases when we recall that the gonopodium of *Horaichthys* is not an intromittant organ but serves only to convey spermatophores with dartlike attachments that are implanted externally near the female's vent.

It would seem that perfection of the organs of fertilization would be just as important to viviparous forms as to oviparous ones; and yet nature has favored the more complicated structures in oviparous forms, and selected against their development in the viviparous forms.

The explanation of this seemingly contradictory state of affairs perhaps lies in two considerations: first, effects on mating behavior of differences in the habitats occupied by oviparous and viviparous atheriniforms, and second, deleterious effects of excessively complicated external genitalia. Evidence concerning these factors was gathered during my fieldwork on phallostethoids in Thailand.

In Thailand neostethids and phallostethids occur only a short distance inland, in waters strongly influenced by tides. Usually the current is strong and the water muddy. They are swift swimmers, generally stay in midwater and can maintain themselves in the current. During flood waters they are likely to be widely dispersed. Thus several hours of collecting at Khlong Langu in Satul Province during high tides combined with heavy rain yielded only a half-dozen immature *Neostethus*, all taken singly. Whenever either *Ceratostethus* or *Neostethus* were found during low water, they were usually aggregated and sometimes exceedingly numerous (as in the estuary of Chantaburi River, where *Neostethus* and *Ceratostethus* were found together in large numbers). When the tide is out, *Ceratostethus* are likely to be confined to well-defined creeks and channels; when the tide is in, they are probably dispersed over a wide area of partially submerged mangroves and nipa palm. *Horaichthys* and *Tomeurus* apparently occur in comparable habitats, *Horaichthys* along the Bombay-Kerala coast of India, *Tomeurus* along the northeastern coast of South America, including the mouth of the Amazon. The selective advantage of internal fertilization in these fishes may lie in permitting temporal separation of mating and egg-laying corresponding, respectively, with periods of low water and high water (Roberts 1971). It seems likely that mating in such habitats is difficult, because of current and low visibility. The waters in which these fishes live are probably especially turbid during the rainy season, when mating probably reaches its peak. In this connection it is noteworthy that copulation in *Gulaphallus mirabilis* is prolonged, the male clasping the female for one to two minutes (Villadolid and Manacop, 1934: 200).

In contrast to phallostethoids, poeciliids tend to occur in habitats in which mating can occur much of the time and under relatively favorable conditions. Poeciliid gonopodial thrusts are relatively short in duration, some almost instantaneous; they may be repeated several times without sperm transfer and often strike wide of the mark perhaps even more in some forms with less specialized gonopodia. Yet such males are undoubtedly quite efficient at fertilizing females; the number of females in populations of poeciliids is generally greatly in excess of that of males.

In all my collections of neostethids, males outnumbered females. In places where they were particularly abundant, it was sometimes possible to catch 25 or 50 at once, and in these instances the ratio of males to females was sometimes about equal. From some places where individuals were relatively scarce or collecting was particularly difficult, collections of half-a-dozen or dozen specimens of *Ceratostethus* are entirely males. During fieldwork it appeared that 1) males of neostethids are at least as abundant, if not more abundant, than females, and 2) males are more readily caught because the priapium prevents them

from swimming away as quickly as females. This suggests that males are more susceptible to predation than females. It seems probable that the exceptionally large gonopodia of *Horaichthys* and *Tomeurus* would encumber their swimming.

Another disadvantage of highly complicated genitalia may lie in an increased proportion of developmental anomalies. Developmental anomalies in the priapium of phallostethoids are probably relatively frequent. Woltereck (1942a) mentioned, but did not describe, developmental anomalies in the priapia of neostethids from the Philippines. I find a number of anomalies in my material, including a *Neostethus* with a peculiarly bowed ctenactinium (which could not be properly swung into resting position beneath the head) and additional externalized elements or "supernumerary ctenactinia" and a *Ceratostethus* in which the priapium is equally developed (but not fully formed) on both sides.

Finally, the development of a large external genitalium requires a considerable diversion of energy and materials, and such "expenditures" will always be selected against unless they confer a selective advantage. The highly complicated copulatory organs presumably ensure successful sperm transfer with each copulatory episode. In fishes in which copulatory episodes are rare this will have great selective advantage.

Provided environmental conditions are such that internal fertilization has a selective advantage, there is little to prevent its development in fishes. There are numerous records of internal fertilization occurring in fishes, such as trout, which normally have external fertilization; sperm simply enter the oviduct and fertilize eggs within the female. Such occurrences do not lead to the evolution of internal fertilization, but are selected against, when the life history strategy of the fishes involved overwhelmingly favors external fertilization. Oviparous atheriniform fishes, on the other hand, which tend to have relatively small numbers of eggs that are expelled in small batches or even singly, and in which embryonic development or hatching can be deferred, may be preadapted to the evolution of internal fertilization (Roberts, 1971). If internal fertilization is favored, then every modification of pelvic or anal fins (no matter how slight) that increases the probability of sperm entering the oviduct will confer a selective advantage. Thus the stage is set for intensification of function (Mayr, 1960), which eventually can lead to structures as complicated as the priapium and papillary bone of *Ceratostethus bicornis*.

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