AMERICAN MUSEUM NOVITATES

Number 295

Published by The American Museum of Natural History New York City

Feb. 1, 1928

59.7,5 . . . P (59.3)

THE SYSTEMATIC POSITION OF THE PHALLOSTETHID FISHES, WITH DIAGNOSIS OF A NEW GENUS FROM SIAM

BY GEORGE S. MYERS¹

In 1913, C. T. Regan announced the discovery, in Johore on the Malay Peninsula, of one of the most remarkable fishes known up until that time. This minute species, *Phallostethus dunckeri*, he placed with the cyprinodonts, although it differed remarkably from all the members of that group, and, indeed, presented structures until then entirely unknown among fishes. Pelvic fins were reported as vestigial in the female and absent in the male, whilst below the head and throat of the latter was a most peculiar appendage containing the coiled vas deferens and the end of the intestine, together with a complicated skeletal system mostly of what appeared to be entirely new elements. This appendage, called by Regan the priapium, bore externally two long curved bones apparently used as clasping organs. These are the toxactinium and ctenactinium of his descriptions.

In 1916 Regan published a detailed account of the anatomy of this peculiar group of fishes, based primarily on studies of a new genus and species, *Neostethus lankesteri*, from the Muar River and Singapore, describing also another new form, *N. bicornis*, from Kuala Langat, and reviewing the morphology of *Phallostethus*. All three forms were from brackish water and this habitat and their appearance seemed to force the conclusion that they were killifishes, a family common in such situations throughout the tropics. Regan states that they "obviously belong to the large and varied family Cyprinodontidæ," in which he erected for them the subfamily Phallostethinæ.

Nothing more was heard of these fishes for a number of years, Weber and de Beaufort (1922, p. 381) merely raising Regan's subfamily to family rank. Jordan (1923) also accorded the group family standing, along with several other groups of cyprinodonts.

In 1925 a new genus of phallostethids, Gulaphallus, was described by A. W. T. C. Herre, from hill-streams in Luzon, Philippines. The habitat of the two species, G. eximius and G. mirabilis, is thus quite

¹Of Stanford University, California.

different from the brackish one of the two previously known genera. More remarkable, however, was Herre's report that both of his species possessed a spinous dorsal fin. This should have immediately suggested a new view of the family relationships, but Dr. Herre did not attempt a re-allocation. In fact, in a later paper (Herre, 1926), he has stated the group to be cyprinodonts.

Very recently Herre (1926) has announced another new genus and species, *Mirophallus bikolanus*, from Lake Bato and Lake Lanigay, South-eastern Luzon. This he describes as having no trace of a spinous dorsal.

Not long ago, in correspondence concerning some cyprinodonts, Dr. Hugh M. Smith of the Siamese Fisheries Department mentioned to me that he had found *Neostethus lankesteri* in streams about Bangkok. At my request he kindly sent me some specimens, telling me that the fish possessed a spinous dorsal, and that upon his request, Mr. J. R. Norman had examined Regan's types in the British Museum and found them likewise to possess this structure. Mr. Norman's letter, kindly forwarded by Dr. Smith, reads in part:

"I have carefully examined the types of *Neostethus lankesteri* and N. bicornis, and find that the structure mentioned in your letter is present in both species. This has the form of a single, rather short, flexible ray, situated a short distance in front of the dorsal fin. It appears to have been overlooked by Mr. Regan in his description."

Thus it will be seen that the first dorsal is present in *Neostethus*, but with one ray instead of the two of *Gulaphallus*. That it was overlooked by Regan in his detailed morphological study is surprising, but the ray is extremely inconspicuous in material that I have examined, sent by Dr. Smith. Whether or not *Phallostethus* has such a structure is not stated.

Recently Dr. Smith has published some interesting observations (Smith, 1927) on the species that he has observed at Bangkok. Most interesting of his statements is that the fish is oviparous, although he says he has not observed the spawning habits. This is the more remarkable since it has been supposed, on account of the peculiar priapial structures of the male, that the phallostethids are viviparous. Dr. Smith further states that they live in very turbid water, feeding on plankton. They swim in small schools, and, due to the translucency of the body, would not easily be seen "were it not for a triangular glistering yellow area on top of the head with its apex on the nape." Dr. Smith has suggested that the spinous dorsal precludes placing the group with the cyprinodonts, but no allocation is attempted.

Dr. Smith has identified his fish with Neostethus lankesteri Regan, and in his paper he has mentioned the ctenactinium, a bone characteristic of that genus. It is thus remarkable that the specimens he sent to me, presumably the species mentioned in his article, either have no ctenactinium or have that bone so modified as to be extremely unlike that of Neostethus. They have a priapium more like that of Phallostethus, with a curved toxactinium at the anterior end, and they represent, in fact, a new generic type connecting Phallostethus with Neostethus and Gulaphallus.

In view of the evident systematic misplacement of the family, of the discovery of a new genus, and of the fact that Dr. Herre seems to have made certain errors in the interpretation of the priapial elements of his material, it seems desirable to review briefly the genera and species of Phallcstethidæ and give some notes on the probable position of the group.

No member of the order Cyprinodontes (Microcyprini) is known to have a spinous dorsal fin, the older classifications placing the group, as a single family (or two), in the Haplomi, next to the Esocidæ, far from the highly developed spiny rayed Acanthopterygii. Regan, in 1909 (p. 78), first showed that the cyprinodonts could not be placed with the Haplomi, and he erected a new order, Microcyprini (=Cyprinodontes), for them. Later (1911) he enlarged upon this view and presented a classification of the order. Again, Hubbs (1924, p. 3) has pointed out that in premaxillary form, position of the pectoral and pelvic fins, pelvic rays, number of vertebræ, and the character of the branchiostegals, the cyprinodonts approach much nearer to the acanthopterygian type than has generally been supposed.

Were it not for the spinous dorsal fin, the position of the Phallostethidæ among the cyprinodonts would scarcely be questioned. Yet that character assuredly prevents us placing them there, and casting about for possible relations, we are struck with the resemblance of the phallostethids to atherinoids. In fact, none of the characters of these fishes at present known, and not connected with the peculiarly modified priapial region, would offer any serious obstacle to placing the family in the order Percessoces close to the Atherinidæ.

In making this transfer, one comes to ask himself if there is really so great a difference between the cyprinodonts and the percesocians as has been assumed in the systems of classification now in vogue. The character of the cyprinodont ethmoid region, widely divergent from that of *Esox*, does not greatly depart from the atherinoid type. Further, the cyprinodonts seem to be uniformly physoclistous and the peculiarly

[No. 295

typical mouth of this group is closely approached by the Atherinidæ. The strongest point of difference is the small first (spinous) dorsal of the atherines, and in at least one form this may occasionally be absent. The idea that the two groups may not be very distantly related has been suggested to me recently by Mr. Carl L. Hubbs (*in litt.*). The possibility had occurred to me sometime previously, in fact before I had studied the phallostethids, but Mr. Hubbs's suggestion has somewhat strengthened my own notion. This view is not a new one, however, for as long ago as 1870, Cope (p. 455) suggested that the atherinids and cyprinodonts might be very close. Later, when describing *Protistius semotilus*, Cope (1874) remarked on the similarity of the fish to both the Mugilidæ, percesocian relatives of the Atherinidæ, and the cyprinodonts, and in later papers he referred to this really atherinoid genus as a cyprinodont. Cope's views on the matter have generally been overlooked or ignored by recent workers.

However close the Cyprinodontes may be to the Percesoces, I do not believe that the phallostethids are more closely related to the cyprinodonts than are any of the known Atherinidæ. They probably represent a specialized offshoot of the atherinoid stem. Neither do I believe that the occasional absence of a spinous dorsal in *Basilichthys* (*Protistius*) or its apparent constant absence in the phallostethid *Mirophallus* shows direct relationship to the cyprinodonts. Likewise the cyprinodont *Lamprichthys* of Lake Tanganyika, which has assumed the form and habits of an atherinid, cannot be held as showing relationship to that group. *Lamprichthys* appears to have independently evolved its characters from a high-pectoraled cyprinodont group such as the tribe Aplocheilichthyin now is.

It is unfortunate that we have as yet no detailed account of the phallostethid skull, Regan's paper dismissing most of the skeleton with the statement that it is "typically cyprinodont." Study of the skeleton of these excessively minute fishes is extremely difficult and I have not had sufficient material or proper equipment for an examination detailed enough to be of value.

Phallostethidæ

Percesocians at times lacking the external manifestation of a spinous dorsal fin, differing from the Atherinidæ in the reduction or absence of the pelvic fins and the presence, in the male, of a highly developed copulatory or clasping organ (the priapium) beneath the head, supported by a system of bones not (at present) capable of homologization with any bones of the other families of the order. Physoclistous. Premaxillaries protractile. Teeth conical, in rows. Pectoral fins high. Caudal emarginate or forked. Hæmal arches of caudal vertebræ not expanded.

The priapium has been very fully described and its structure investigated in the genera *Phallostethus* and *Neostethus* by Regan (1916). Internally it has a complex skeleton, the principal external manifestations of which are some long curved bones apparently used as claspers. One or two may project from one (the aproctal) side at the posterior end of the priapium; these are the ctenactinia. Another, the toxactinium, may project from the anterior end. The end of the intestine runs forward and down from the abdomen into the priapium, and opens at the proctal side of that organ. The vas-deferent similarly runs down into the priapium, where it enlarges and coils, its opening being somewhere at or near the posterior end of that structure.¹

The proctal side may be indifferently either the right or left of the fish; in other words, the males are either "rights" or "lefts." So far as observed all the females are symmetrical.

In the females there may be a groove in which the anus, oviduct, and ureter terminate, or the groove may be absent, the openings merely being in line on the abdomen. A pair of papillæ, possibly representing the pelvic fins, may or may not be present in differing positions on the abdomen.

In both sexes, beginning behind the priapial attachment or the ureter opening, there is a rayless fringe extending along the midline of the abdomen, terminating just before the anal fin origin. The fringe is not figured or described in Herre's account of *Mirophallus*.

SYNOPSIS OF THE GENERA

- A. Toxactinium present, a shield-like pulvinulus covering its base.
 - B. Anal fin very long, of 26 to 28 rays; jaws equal or the lower slightly included; spinous dorsal (?); abdomen of female with a groove.

Phallostethus Regan.

BB. Anal fin moderate, 14 or 15; lower jaw strongly prognathous; spinous dorsal of one spine; abdomen of female without groove.

Phenacostethus Myers.

- AA. Toxactinium absent, pulvinulus if present small and not shield- or disc-shaped.
 C. Spinous dorsal present.
 - D. One spine in spinous dorsal fin; nape and opercles naked (?); one or two ctenactinia.....Neostethus Regan.

DD. Two spines in spinous dorsal; nape and opercles naked;

two ctenactinia.....Gulaphallus Herre.

CC. Spinous dorsal absent; nape and opercles scaly.

Mirophallus Herre.

¹Herre, 1926, p. 538, has erroneously stated that the INTESTINE coils within the priapium.

Phallostethus Regan

REGAN, 1913, p. 548.

GENOTYPE.—P. dunckeri Regan.

This genus, the first known of the family, differs from all the others in the very long anal. A single, short, comb-shaped ctenactinium is present at the posterior part of the priapium. A long, curved toxactinium projects forward from the anterior end of the priapium, and at its base is a flat, oval, plate-like structure, the pulvinulus. The bones of the pectoral arch are expanded and largely free below and protect the base of the priapium. In the female the anus, oviduct, and ureter, as well as the abdominal fringe, lie in a groove. Jaws equal or the lower slightly included when mouth is closed. It is not known whether or not a spinous dorsal is present in this genus.

Phallostethus dunckeri Regan

REGAN, 1913, p. 549, Figs. 1-4; 1916, pp. 16-19, Figs. 12-15, Pl. 1, fig. A.

• Anal 26 to 28. Dorsal 8 to 10. Scales 40. Length (total) 29 mm. The known specimens come from Johore, Malay Peninsula, and are in the British Museum and the Hamburg Museum.

This fish bears a remarkable resemblance to the South American pœciliid cyprinodont *Tomeurus gracilis* Eigenmann, probably having similar habits and habitat. Named for Dr. Georg Duncker, who first mentioned these fishes (Duncker, 1904), though without giving them a name.

Phenacostethus, new genus

GENOTYPE.-P. smithi Myers.

Anal fin moderate in length. A spinous dorsal fin of one short, rather soft spine situated above the posterior half of the anal fin. Priapium low and elongate, lacking a ctenactinium unless the irregular structure beside the opening of the vas-deferens be this bone. A hooked toxactinium projecting forward from the anterior part of the priapium, its base emerging from a large, flat, oval pulvinulus. Pectoral girdle expanded, skin-covered, and largely free from the body below. In the female, the abdominal fringe, anus, the oviduct and ureter-opening not in a groove. Head, nape, and opercles unscaled.

Allied to *Phallostethus* in the presence of a shield-like pulvinulus and a toxactinium, and to *Neostethus* and *Gulaphallus* in the short anal and character of the female abdomen.

Phenacostethus smithi, new species

HOLOTYPE.—No. 9247 A. M. N. H., left adult male, 13.5 mm. standard length (16.5 mm. total). Bangkok, Siam, freshwater stream. H. M. Smith, collector. December, 1926.

SPECIFIC CHARACTERS.—Body well compressed. First dorsal I. Second dorsal 6½. Anal 14 or 15. Scales about 30 to 33, mostly lost on the types, the number and position apparently agreeing with the very conspicuous myotomes; scales transparent

1928]

and inconspicuous. Dorsal fins placed far back, the first above the posterior half of the anal, the second originating above the end of the anal base. Depth 5 to $5\frac{1}{2}$. Head about $4\frac{1}{2}$. Eye large, about 2.66 in head, without lower jaw. Mouth fairly large, extending to beneath the anterior part of the eye. Lower jaw projecting. I have not been able to determine whether or not there is more than one row of teeth.



Fig. 1. Phenacostethus smithi, new species. Left σ^2 adult, aproctal side. 13.5 mm. standard length.

Snout a little over half eye. Pulvinulus much larger than eye, its face inclined to the side toward which the hook of the toxactinium turns, this being termed the aproctal side. This may be either right or left. Priapium much elongate, projecting downward but little. Vas-deferens coiled within and opening at the tip of a curved ending (Fig. 2, no. 5). Next to this is a peculiar, irregular, curved, hard projection (Fig. 2, No. 7) which may be the homologue of the ctenactinium. The largely free, skin-covered pectoral girdle extends downward on each side of the base of the priapium.



Fig. 2. Underside of head of *Phenacostethus smithi*, left σ^3 adult. 1. Toxactinium. 2. Pulvinulus. 3. Opercle. 4. Pectoral process. 5. Vas-deferens. 6. Abdominal fringe. 7. Ctenactinium? A. Proctal side. B. Aproctal side.

On the aproctal side it covers what appears to be the "glandular groove," while a shallower groove is on the proctal side. The specimens being small and not very well preserved, some of the minute characters, such as the position of the anus and ureter opening of the male, cannot be made out, even under high magnification of the binocular.

The female is in general similar to the male, excepting of course, in the priapial region. There is no groove on the abdomen of the female. What appear to be the homologues of the post-anal papillæ are present, if my observations are correct, BEHIND THE OPENING OF THE URETER, and they appear very like small pelvic fins.

Their position is rather different from that of the papillæ of Regan's three forms.

Colorless; dorsum with a slight dark shade; occiput darker. Myotomes very evident.

Nineteen paratypes, 11 males and 8 females, are deposited in The American Museum of Natural History, the United States National Museum, and my own collection.

This little fish is, next to *Mistichthys luzonensis*, a Philippine goby described by Dr. Smith, the smallest of vertebrate animals, the largest adult in the type series being but 14 mm. standard length and only 17 mm. total.¹ One 11.5 mm. (standard) male paratype is somewhat immature and though the priapium in general seems to have attained adult form, the toxactinium is only half grown, the bone soft and scarcely hooked. The exterior priapial bones seem to be the last parts of the organ to mature.

Named for Dr. Hugh M. Smith, Fisheries Commissioner to the Siamese Government.

There is a possibility that this species is not the one mentioned by Smith (1927). If it is not, two phallostethids must occur at Bangkok.

Neostethus Regan

REGAN, 1916, p. 2.

GENOTYPE.—N. lankesteri Regan.

Anal fin moderate. One spine in first dorsal fin. One or two unserrated cetenactinia projecting from the posterior part of the priapium. In the female, anus, oviduct, ureter, and abdominal fringe not in a groove. A pair of papillæ covering the oviduct and ureter openings. Lower jaw somewhat projecting. Head and nape presumably naked, but this not stated in description.

Neostethus lankesteri Regan

REGAN, 1916, pp. 2–14, Figs. 1–10, 12, Pls. 1–1V. WEBER AND DE BEAUFORT, 1922, p. 382, Fig. 103.

Anal 15 or 16. First dorsal I. Second dorsal 5 or 6. Scales 34 to 36. A single long ctenactinium. Posterior end of priapium with comb-like projections. Total length about 30 mm. The known specimens come from the Muar River, Malay Peninsula, and from Singapore, in brackish water. Named for Sir E. Ray Lankester, British morphologist.

Since the above was in type Dr. Herre has described *Pandaka pygmæa*, a Philippine goby still smaller than *Mistichthys*.

Neostethus bicornis Regan

REGAN, 1916, pp. 14-15, Fig. 11.

Anal 13 to 15. First dorsal I. Second dorsal? Scales 35 to 37. Two ctenactinia. Posterior end of priapium without comb-like structure. The largest of the three known specimens, which were taken in brackish water at Kuala Langat, Malay Peninsula, is 25 mm. long and not wholly adult. It is thus impossible to tell the structure of the adult ctenactinia.

Gulaphallus Herre

HERRE, 1925, p. 508.

GENOTYPE.¹—G. eximius Herre.

This genus appears to differ from *Neostethus* only in having two spines instead of one in the first dorsal fin. On this basis alone I should not hold the genus as distinct from *Neostethus*, but there may be other differing characters not apparent from the descriptions, and *Gulaphallus* should not be synonymized without actual comparison with material of the other genus.

Dr. Herre described *Gulaphallus* as new while unaware that Regan's material possessed the spinous dorsal. In his descriptions Dr. Herre has mentioned both the toxactinium and ctenactinium as present in Gula*phallus.* In looking over his figures and my material of this genus, it is very evident that the bone Herre calls the toxactinium is not the homologue of the toxactinium of Phenacostethus and Phallostethus. The toxactinium in these two genera projects from the anterior end of the priapium and its base is covered by the pulvinulus. There seems little doubt that Herre's "toxactinium," which projects from the posterior part of the priapium, is exactly homologous with the ctenactinium of *Neostethus*. The bone called by Herre the ctenactinium may very well be the homologue of the second (shorter) ctenactinium of Neostethus bicornis. If this last be true, it would argue either for the transfer of *bicornis* to *Gulaphallus*. or the abolishment of the latter genus, unless, of course the adult bicornis be found to have characters warranting a special genus for that species. Then too the very similar, irregular, curved organ at the posterior end of the priapium of *Phenacostethus* might well be a ctenactinium, but I hesitate to so designate it without more detailed anatomical examination than has been possible.

Gulaphallus eximius Herre

HERRE, 1925, p. 509, Pl. 1, figs. 1-5, Pl. 11, figs. 1-2.

Anal 15 to 17. First dorsal II. Second dorsal 7. Scales 56 to 58. Length (total ?) 35 mm. Mountain creeks at Santa Fé, Nueva Vizcaya Province, Luzon, Philippines.

¹Here designated for the first time.

This form is remarkable for the small scales. With the next species, it is the largest of the Phallostethidæ.

Gulaphallus mirabilis Herre

HERRE, 1925, p. 511, Pl. 11, figs. 3-5.

Anal 17 or 18. First dorsal II. Second dorsal 7. Scales 36 to 38. These data are from Herre's description. The types, up to 33 mm. (total?) length, were from the mouth of the Ibo, a small mountain creek flowing into the Angat River, Bulacan Province, about 60 km. northeast of Manila, Luzon, Philippines.

Dr. Herre has very kindly sent me some hitherto unrecorded material of this species, consisting of 14 males and 15 females, the largest (a female) 27.5 mm. standard length (35 mm. total), from Molawin Creek, Los Baños, Luzon. In this material the scale number varies from 31 to 35, but aside from this there seem to be no differences of note. Herre did not mention that the scales are smaller and much more irregular anteriorly. Some difficulty is encountered in correctly ascertaining the number in the perhaps slightly enlarged row along the side-stripe, for the scales of the rows above and below frequently meet between those of the mid-side series. The scales are especially small and crowded in the predorsal region. There are two small tuft-like pseudobranchiæ present, similar to those seen in the cyprinodonts allied to *Rivulus* and *Panchax*.

The colors, entirely unmentioned by Herre, are as follows: Myotomes not evident. A fine, median, dark line down the sides to the caudal base, rather obsolete forward. Scales above this line dark-edged, this more accentuated toward the mid-dorsal line, and absent or rapidly fading below the lateral stripe. Occiput black. A collection of large melanophores, forming a conspicuous black blotch, at the lower edge of the abdomen, at the mid-length of the abdominal fringe but not extending on it. This spot in most cases is over or a little posterior to a dark visceral patch (in formalin specimens). A fine dark line just above anal base, as in *G. eximius*. The colors are the same in both sexes.

Mirophallus Herre

HERRE, 1926, p. 539.

GENOTYPE.—M. bikolanus Herre.

Anal moderate. Spinous dorsal fin entirely absent. Posterior end of priapium of a peculiar bulbous form. Toxactinium apparently absent and two ctenactinia present. The remarks under *Gulaphallus* concerning Herre's description of the priapial bones should be consulted. Nape and opercles scaly.

This is the only phallostethid so far known in which we can be reasonably sure that the external manifestation of a spinous dorsal is absent.¹ Further, it appears to be unique in the scaled nape and opercles, but Regan did not describe these characters in his specimens.

Mirophallus bikolanus Herre

HERRE, 1926, p. 540, Pl. III, figs. 1-6.

Anal 15. Dorsal 7. Scales 32. Length 27 mm. (total ?). Lake Bato, Camarines Sur Province, and Lake Lanigay, Albay Province, Luzon, Philippines. There is no mention of the abdominal fringe in this species, and it is not figured in the plate.

DISCUSSION

Five genera and seven species of Phallostethidæ are now known, three forms from brackish water in the Southern Malay Peninsula and Singapore, and four from freshwater streams in Siam and the Philippines. My friend, Dr. Deogracias V. Villadolid, of the College of Agriculture, Los Baños, Philippines, who was studying at Stanford when I began the present work, has written that he has recently collected phallostethids in brackish water in Manila Bay. We shall await with interest his report on them, particularly if life-history and ecological notes accompany it.

No doubt a number of new species and new generic types of these most remarkable little fishes remain to be discovered. They doubtless occur throughout the Malayan region and we may go so far as to predict that they will certainly be found in Borneo and Sum tra, probably in Java, and very possibly as far as Celebes, Timor, and Burma.

The greatest interest attaches to the observation of living phallostethids, particularly in regard to the use of the priapial structures. Dr. Smith has stated one species to be oviparous although he has not actually seen the breeding, but it would seem that the complicated structures present indicated viviparity.

Doubtless the larger phallostethids devour mosquito larvæ, but if they are as delicate in captivity as are their relatives the atherines, we can scarcely expect them to stand transport and to be of use as larvicide.

PAPERS CITED

COPE, E. D. 1870. 'A partial synopsis of the fishes of the fresh waters of North Carolina.' Proc. Amer. Philos. Soc., pp. 448-495.

1874. 'Description of some new species of reptiles obtained by Dr. John F. Bransford, Assistant Surgeon, United States Navy, while attached to the Nicaraguan Surveying expedition in 1873.' Proc. Acad. Nat. Sci. Philadelphia, XXVI, p. 64–72.

¹See under *Phallostethus*.

(Description of Protistius semotilus, pp. 66-67.)

- DUNCKER, G. 1904. 'Die Fische der malayischen Halbinsel.' Mitt. Naturhist. Mus. Hamburg, XXI, pp. 133–207, Pls. 1, 11. (Phallostethids first mentioned, p. 171.)
- HERRE, A. W. T. C. 1925. 'Two strange new fishes from Luzon.' Philippine Journ. Sci., XXVII, pp. 507-513, Pls. I, II.
 - 1926. 'Four new Philippine Fishes.' Philippine Journ. Sci., XXXI, pp. 533– 543, Pls. 1–111.
- HUBBS, C. L. 1924. 'Studies of the fishes of the order Cyprinodontes.' Mise. Publ. Mus. Zool., Univ. Michigan, No. 13, pp. 1-31.
- JORDAN, D. S. 1923. 'A classification of fishes, including families and genera so far known.' Stanford University. (Phallostethidæ, p. 160.)
- REGAN, C. T. 1909. 'The classification of teleostean fishes.' Ann. Mag. Nat. Hist., (8) III, pp. 75-86.
 - 1911. 'The osteology and classification of the teleostean fishes of the order Microcyprini.' Ann. Mag. Nat. Hist., (8) VII, pp. 320-327, Pl. VIII.
 - 1913. 'Phallostethus dunckeri, a remarkable new cyprinodont fish from Johore.' Ann. Mag. Nat. Hist., (8) XII, pp. 548-555, Figs. 1-4.
 - 1916. 'The morphology of the cyprinodont fishes of the subfamily Phallostethinæ, with descriptions of a new genus and two new species.' Proc. Zoöl. Soc. London, pp. 1–26, Pls. 1–1V.
- Sмітн, H. M. 1927. 'The fish Neostethus in Siam.' Science, N. S., LXV, pp. 353-355.
- WEBER, M. AND DE BEAUFORT, L. F. 1922. 'The fishes of the Indo-Australian Archipelago.' IV. Leiden. (Phallostethidæ, pp. 381-383.)