

A new species of *Neostethus* (Teleostei; Atherinomorpha; Phallostethidae) from Brunei Darussalam, with comments on northwestern Borneo as an area of endemism

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Abstract. Extensive collections of freshwater and coastal fishes from throughout northwestern Borneo reveal a distinct phallostethid biota. Seven of the 23 species in the phallostethid subfamily Phallostethinae, known commonly as priapiumfishes, live in northwestern Borneo and of those, three are endemics, including the new species described herein. *Neostethus geminus*, new species, is most closely related to *N. bicornis* Regan, 1916 with which it shares two, elongate curved ctenactinia (vs. one elongate and one short ctenactinium as in other *Neostethus*) in mature males, a brown blotch on the pelvic-fin rays of the proctal side of immature males, and a fleshy, hoodlike fold in females that includes the anus and genital and urinary pores. *Neostethus geminus* differs from *N. bicornis* in being smaller (adults reach no more than 25.7 mm SL vs. 31 mm SL), and in having males with a relatively compact priapium with a foreshortened, broad aproctal axial bone that meets but does not overlap the pulvinular appendage (vs. a relatively elongate priapium with a long and narrow aproctal axial bone that overlaps the pulvinular appendage medially) and thin, nearly translucent, broad papillary bone expanded distally into a tab (vs. having a short papillary bone). Females have a thickened fleshy, hoodlike fold that includes the anus, genital pore and urinary pore (vs. a relatively thin fold) and a thickened ridge just posterior to the fold (vs. lacking such a ridge). *Neostethus geminus* is described from coastal localities in Brunei Darussalam. The widespread *Neostethus bicornis* was described from Kuala Langat, Selangor, Peninsula Malaysia, and is known also from Thailand, Singapore, Palawan Island, Philippines, as well as northwestern Borneo and Kalimantan, Indonesian Borneo; it is redescribed based on material from throughout its range. The two species are abundant in collections from Brunei, but were not taken at the same locality.

Key words. *Neostethus geminus*, *Neostethus bicornis*, South China Sea, priapiumfishes, allopatry

INTRODUCTION

One hundred years ago, British ichthyologist C. Tate Regan's (1913) description of the diminutive *Phallostethus dunckeri* from Muar, Peninsula Malaysia, introduced a peculiar group of living teleost fishes to science. The name of the new genus described the position of an intromittent organ or phallus on the “chest”—anteroventrally on the body—of adult males. The priapium, as Regan (1913) called it, is a complex diagnostic feature of some 23 species of atherinomorph fishes distributed throughout coastal and freshwater habitats of Southeast Asia. Four genera of priapiumfishes, as they are known commonly in English, are classified in the subfamily Phallostethinae, and with their sister group, the monotypic subfamily Dentatherininae, comprise the atheriniform family Phallostethidae (Parenti & Louie, 1998: fig. 2; Table 1).

Priapiumfishes are small (maximum size recorded is 37 mm SL for an adult female of the Philippine *Gulaphallus eximius*; Herre, 1942:144), transparent to opaque, surface-feeding fishes (Parenti, 1989). Although they move in schools and

are often collected in large numbers, priapiumfishes are overlooked by scientists and local people alike who may consider them the larvae of other more conspicuous species, if they notice them at all (Herre, 1940:16, 1942:139; personal observation).

Unlike many other atherinomorph fishes with intromittent organs, priapiumfishes are not livebearers. Males transfer sperm bundles to females and fertilisation is internal. Females then lay fertilised eggs that attach via elongate adhesive filaments to plants or other objects (Smith, 1927; Villadolid & Manacop, 1935; Grier & Parenti, 1994). Male phallostethids are bilaterally asymmetric: the anus is offset to one side of the body midline, the proctal side, and the seminal papilla is offset to the opposite side of the body midline, the aproctal side (Regan, 1916). Sinistral males are those with the aproctal side the left; dextral males are those with the aproctal side the right. Dextral and sinistral males occur in about equal numbers in collections except for three species in which males are exclusively sinistral or dextral (Parenti, 1986a). The anus and urogenital pores of female phallostethines are anterior on the body and lie just ventral to the pectoral-fin base (TeWinkel, 1939), as in males. Unlike males, females are not asymmetric with the single exception of the Philippine *Gulaphallus falcifer* (see Parenti, 1986b).

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A series of publications over a brief seven-year period (e.g., Bailey, 1936; Aurich, 1937; TeWinkel, 1939; Woltereck, 1942 a, b) documented intensive study of the comparative morphology and development of the priapium. Taxonomy of priapiumfishes grabbed the attention of American ichthyologists Albert W. C. T. Herre and George S. Myers and their students and colleagues at Stanford University who by 1942 recognised eighteen species (Herre, 1942). After a nearly 30-year hiatus, a nineteenth species, *Phenacostethus posthon*, was described from coastal Thailand by Tyson R. Roberts (1971a). I described *Phenacostethus trewavasae* from Sarawak, eastern Malaysia (Parenti, 1986a) and then *Neostethus robertsi* from Luzon, the Philippines, as part of a phylogenetic systematic revision of priapiumfishes; synonymy of two species brought the total then to 19 species (Parenti, 1989).

Subsequent fieldwork throughout the Indo-Australian Archipelago exposed further details of phallostethine systematics and distribution: I collected and described the first species of *Phallostethus* known from Borneo (*Phallostethus lehi* Parenti 1996) and the first phallostethine known from Sulawesi (*Neostethus djajaorum* Parenti & Louie, 1998). Description of *P. lehi* from northwestern Borneo bolstered the idea that there is a coherent biota throughout the South China Sea and that we might expect to discover new phallostethine taxa distributed around the southern portion of the sea that includes the Sunda Shelf (Parenti, 1991; 1996). The recent discovery and description of a third species of *Phallostethus*, *P. cuulong*, directly across the South China Sea in coastal Vietnam (Shibukawa et al, 2012; Fig. 1), as well that of the new species of *Neostethus* described herein, corroborates that prediction.

Neostethus borneensis Herre, 1939, is the first phallostethid species reported and described from Borneo which harbors a rich priapiumfish biota: seven of the 23 species in the subfamily Phallostethinae live in northwestern Borneo and three of those, including *N. geminus*, are endemic (Table 1). *Neostethus bicornis* Regan, 1916, with its two elongate ctenactinia, has been one of the most distinctive and readily identifiable of the phallostethids, especially since publication of a detailed osteological review by Roberts (1971b). I reported material of this broadly distributed species from Thailand, Peninsula Malaysia, Singapore, northwestern Borneo, and the Philippines (Parenti, 1989:270). Further study of specimens identified initially as *N. bicornis* collected in coastal localities in Brunei in 1997 led to the discovery of this new species. *Neostethus bicornis* and *N. geminus* are hypothesized to be sister species that share the unique synapomorphy of two elongate ctenactinia (Parenti, 1989; Fig. 2). They are readily distinguished from each other by a series of reproductive morphological characters of males and females described herein.

Modern detailed faunal surveys of segments of the freshwater fish biota of northwestern Borneo by river or region include those by Inger & Chin (1962, 1990; Sabah), Kottelat & Lim (1995; Sarawak and Brunei), Parenti & Meisner (2003; Sg. Belait, Brunei) and Parenti & Lim

(2005; Sg. Rajang, Sarawak). Broader systematic revisions of fish taxa from northwestern Borneo include those on phallostethines (Parenti, 1989), viviparous halfbeaks of the genera *Dermogenys* and *Nomorhamphus* (Meisner, 2001), and balitorid suckers of the genera *Gastromyzon*, *Hypergastromyzon*, and *Neogastromyzon* (Tan, 2006). Taken together, these and other compilations provide detailed systematic data on the freshwater fishes of northwestern Borneo, although most are unfortunately deficient in their coverage of coastal and mangrove fishes. Data on these fishes are divided between freshwater and marine reviews. A checklist of the fishes of the South China Sea, understood to be a compilation of marine species, included 10 of the then 11 known species of *Neostethus*; it excluded Philippine freshwater species of the genus *Gulaphallus* (Randall & Lim, 2000). A notable segment of the Sabah fish biota was omitted by Inger & Chin (1990: 12) who included “Only those [taxa] for which positive freshwater records in North Borneo [Sabah] are available...” They did not report on their collections of *Neostethus* from coastal habitats made in 1950 as part of the North Borneo survey; some of these specimens held in the collections of the Field Museum, Chicago, are included here as comparative material of *N. bicornis*. Thus, as well as to describe a new species of *Neostethus* based on comparative morphology, an equally important purpose of this report is to spotlight the understudied yet diverse coastal and mangrove fish fauna around the southern South China Sea.

MATERIAL AND METHODS

The fine osteology of *Neostethus bicornis* specimens from Thailand by Roberts (1971b) is representative of species of

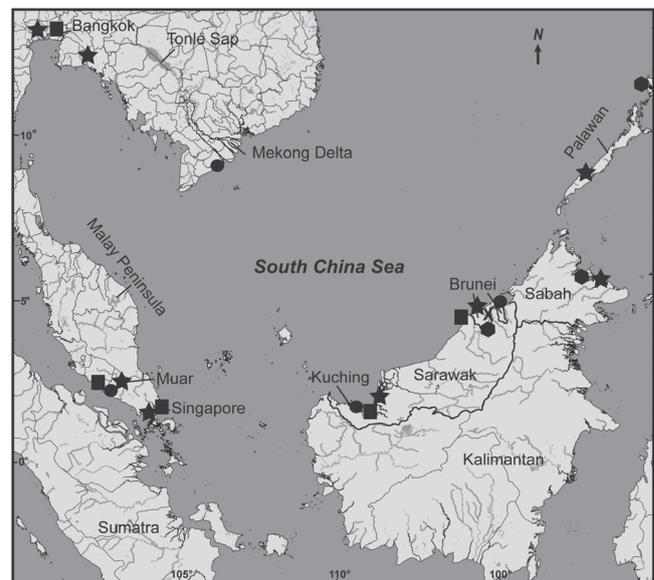


Figure 1. Localities of some phallostethines discussed herein. The genus *Phallostethus* (circles) comprises three species: *P. dunckeri* (Muar), *P. lehi* (Sarawak and Brunei), and *P. cuulong* (Vietnam). *Neostethus lankesteri* (squares): Muar, Singapore, Bangkok, Kuching, and Brunei. *Neostethus bicornis* (stars): type locality, Muar, and collections examined here from Singapore, Thailand, Kuching, Brunei, Sabah, and Palawan. *Neostethus borneensis* (hexagon): Brunei, Sabah and Coron Is. *Neostethus geminus*, Brunei (cross). Each symbol may represent more than one locality. Details on the collection localities of *N. geminus* are in the text and Figure 7.

Neostethus with two elongate ctenactinia, except as noted herein for the new species. Parenti (1989:269) provided a detailed generic synonymy for *Neostethus* Regan, 1916, abstracted below. A synonymy and homology assessment of the priapial bones and muscles by Parenti (1989) is followed here.

Specimens reported on herein are housed in the Brunei Museum, Brunei Darussalam; National Museum of Natural History, Washington, D.C. (USNM); Zoological Reference Collection of the Raffles Museum of Biodiversity Research, National University of Singapore (ZRC); Field Museum, Chicago (FMNH); Natural History Museum, London (BMNH); the Museum of Comparative Zoology, Harvard University, Cambridge (MCZ); California Academy of Sciences, San Francisco (CAS), and the former Stanford University collection now at the California Academy of Sciences (CAS-SU), San Francisco. Counts were made from cleared and stained preparations, radiographs, and alcohol specimens; they are most accurate in cleared and stained material. A computed tomography (CT) micrograph of a male *N. bicornis* was prepared by Andrew Williston (MCZ) at the facilities of Harvard University's Center for Nanoscale Systems and the National Science Foundation's National Nanotechnology Infrastructure Network. I describe some characters of body shape with landmarks rather than measurements because landmarks are more reliably observed in priapiumfish specimens which may be distorted or dehydrated. The pectoral fins of nearly all individuals of *N. geminus*, and some *N. bicornis*, rotated anteroventrally when placed in fixative (Figs. 2, 5). Pectoral-fin rays were removed from select male and female specimens for photographs (Figs. 3, 4, 6). Data for the holotype of *N. geminus* are given in brackets.

Solely alcian blue, solely alizarin, and counterstained specimens were prepared according to the protocol of Dingerkus & Uhler (1977) and other methods unspecified in collection records. Abbreviations: SL, standard length; Sg., sungai (Bahasa Malaysia for river); Dist., district; Prov., province; R., river; trib., tributary; imm., immature. Other abbreviations are clear in context or defined in the figure captions.

TAXONOMY

Neostethus Regan, 1916

Neostethus Regan, 1916:1, 2

Type species. *Neostethus lankesteri* Regan, 1916 by original designation (use of "gen. et sp. n." for one of two included new species).

Differential diagnosis. (modified from Parenti, 1989:269) *Neostethus* differs from all other phallostethines in having a priapium with an inner pulvinular bone (vs. lacking the bone), thin bony projections on the papillary bone that may number 80 or more (vs. lacking such bony projections)

(Parenti, 1989: fig. 3) and two ctenactinia (vs. just a single short or rudimentary second (and no first) ctenactinium in *Phallostethus* and *Phenacostethus* and one elongate first (and no second) ctenactinium in *Gulaphallus*). Males lack an enlarged, fleshy seminal papilla and there is no translucent, membranous dome on the dorsal surface of the head as in *Phallostethus* and *Phenacostethus*. Males also do not have a perforated gular flap of skin through which the anterior end of the first ctenactinium projects or an aporoctal axial bone that projects beyond the ventral body profile (Parenti, 1989: fig. 4) which diagnoses *Gulaphallus*.

Composition. Twelve species, including the new species described herein (Table 1).

Neostethus geminus, new species (Figs. 1, 2A, 3A, 4C, 5A, 6A, 7)

Material examined. All specimens collected in Brunei Darussalam. Holotype: USNM 409956 (sinistral male, 23.3 mm SL), Tutong Dist., Sg. Birau, trib. of Sg. Tutong, just above where it enters Sg. Tutong, E of Bandar Tutong, 4°48'0" N, 114°40'38" E, coll. L. R. Parenti, H. K. Larson, Hj. Ramlee, Hj. Bahrin, Abu Bakar & Bujong, 25 August 1997. Paratypes: Brunei Museum/USNM 409980 (40, 10 sinistral males, 10 dextral males, 10 females, 10 imm., 16.8–23.0 mm SL), USNM 409963 (95, 14 sinistral males, 12 dextral males, 27 females, 42 imm., 11.3–25.7 mm SL, of which one sinistral male, one adult female and one imm. male were cleared and stained solely with alcian blue and one sinistral male was cleared and stained solely with alizarin), BMNH 2013.5.10.2-4, sinistral male, 23.8 mm SL, dextral male, 23.5 mm SL, female, 18.8 mm SL; CAS 235597, sinistral male, 23.7 mm SL, dextral male, 23.0 mm SL, female, 19.5 mm SL; FMNH 121800, sinistral male, 23.4 mm SL, dextral male, 23.8 mm SL, female, 19.8 mm SL; MCZ 170559, sinistral male, 22.4 mm SL, dextral male, 24.5 mm SL, female, 18.3 mm SL; ZRC 54117, sinistral male, 23.8 mm SL, dextral male, 24.5 mm SL, female, 18.8 mm SL, all collected with the holotype. USNM 409957 (133, 17 sinistral males, 15 dextral males, 25 females, 76 imm., 12.5–24.8 mm SL, of which one dextral male, one sinistral male, and two adult females were cleared and counterstained), Belait District, Sg. Dalit, just above where it enters Sg. Belait, 4°34'0" N, 114°12'0" E, coll. L. R. Parenti, H. K. Larson, Hj. Ramlee, Hj. Bakana, Hj. Bahrin, M. Wong & Yussof, 27 August 1997; USNM 356847 (10, 13–24 mm SL), Tutong Dist., Sg. Tutong, upstream from Bandar Tutong near Kampung Panchor Dulif, 4°46'04" N, 114°36'12" E, coll. L. R. Parenti, H. K. Larson, Hj. Ramlee, Zainal & Hj. Ariffin, 23 August 1997; USNM 409958 (10, 9–24.8 mm SL), Belait Dist., Sg. Teraban, trib. of Sg. Belait, just above where it enters main river channel, and in main channel, 4°34'41" N, 114°10'59" E, coll. L. R. Parenti, H. K. Larson, Hj. Ramlee, Hj. Bahrin & Yussof, 26–27 August 1997; USNM 409960 (adult female, 19 mm SL), Tutong Dist., Sg. Gandang, trib. of Sg. Penyatang, coll. L. R. Parenti, H. K. Larson, Hj. Ramlee, Hj. Bakana, Hj. Bahrin, Abu Bakar & Hj. Ariffin, 24 August 1997; USNM 365135 (47, 10–20.5 mm SL), Belait Dist., Sg. Limatak, just above where it enters Sg. Belait, 4°34'20" N, 114°11'33" E, coll. L. R. Parenti, H. K. Larson, Hj. Ramlee, Hj. Bakana, Hj. Bahrin, M. Wong & Yussof, 27 August 1997.

Nontype specimens (all poorly preserved or distorted): USNM 409959 (90, 7–24 mm SL), from the type locality; USNM 389677 (4, alcohol fixed), USNM 389674 (2, alcohol fixed), Belait District, Sg. Dalit, just above where it enters



Figure 2. A, *Neostethus geminus*, new species. Holotype, USNM 409956, sinistral male, 23.3 mm SL; B, *Neostethus bicornis*, USNM 409961, sinistral male, 27.0 mm SL.

Table 1. Classification of family Phallostethidae, following Parenti (1989) and Dyer & Chernoff (1996). Species of subfamily Phallostethinae recorded from northwestern Borneo are marked with an asterisk (*).

Family Phallostethidae
Subfamily Denatherininae
Genus <i>Dentatherina</i> Patten & Ivantsoff 1983
<i>Denatherina merceri</i> Patten & Ivantsoff 1983
Subfamily Phallostethinae
Tribe Phallostethini
Genus <i>Phallostethus</i> Regan, 1913
<i>Phallostethus dunckeri</i> Regan, 1913
<i>Phallostethus lehi</i> Parenti, 1996*
<i>Phallostethus cuulong</i> Shibukawa et al., 2012
Genus <i>Phenacostethus</i> Myers, 1928
<i>Phenacostethus smithi</i> Myers, 1928*
<i>Phenacostethus posthon</i> Roberts, 1971a
<i>Phenacostethus trewavasae</i> Parenti, 1986*
Tribe Neostethini
Genus <i>Neostethus</i> Regan, 1916
<i>Neostethus lankesteri</i> Regan, 1916*
<i>Neostethus bicornis</i> Regan, 1916*
<i>Neostethus amaricola</i> (Villadolid & Manacop, 1935)
<i>Neostethus palawanensis</i> (Myers, 1935)
<i>Neostethus thessa</i> (Aurich, 1937)
<i>Neostethus ctenophorus</i> (Aurich, 1937)
<i>Neostethus borneensis</i> Herre, 1939*
<i>Neostethus villadolidi</i> Herre, 1942
<i>Neostethus zamboangae</i> Herre, 1942
<i>Neostethus robertsi</i> Parenti, 1989
<i>Neostethus djajaorum</i> Parenti & Louie, 1998
<i>Neostethus geminus</i> , new species*
Tribe Gulaphallini
Genus <i>Gulaphallus</i> Herre, 1925
<i>Gulaphallus eximius</i> Herre, 1925
<i>Gulaphallus mirabilis</i> Herre, 1925
<i>Gulaphallus falcifer</i> Manacop, 1936
<i>Gulaphallus bikolanus</i> (Herre, 1926)
<i>Gulaphallus panayensis</i> (Herre, 1942)

Sg. Belait, 4°34'0" N, 114°12'0" E, coll. L. R. Parenti, H. K. Larson, Hj. Ramlee, Hj. Bakana, Hj. Bahrin, M. Wong & Yussof, 27 August 1997.

Differential diagnosis. *Neostethus geminus* and *N. bicornis* are distinguished from all other phallostethid fishes by mature males with two elongate ctenactinia (vs. one elongate and one short ctenactinium in other *Neostethus*), immature males with a brown blotch on the pelvic fin rays of the proctal side, which fades with growth and maturity, and females with a fleshy, hoodlike fold or flap that includes the anus, genital pore and urinary pore. These characters were considered diagnostic of *N. bicornis* by Parenti (1989). *Neostethus geminus* differs from *N. bicornis* in being smaller (reaching no more than 25.7 mm SL vs. 31 mm SL) and having a relatively compact priapium with a foreshortened, broad aproctal axial bone that meets but does not overlap the pulvinular appendage (vs. a relatively elongate priapium with a long and narrow aproctal axial bone that overlaps the pulvinular appendage medially; Figs. 3, 4), thin, nearly translucent, broad papillary bone expanded distally into a tab (vs. a short papillary bone; Figs. 3,4), thin, nearly translucent, broad papillary bone expanded distally into a tab (vs. a short papillary bone; Figs. 3,4), and females with a thickened fleshy, hoodlike fold that includes the anus, genital pore and urinary pore (vs. a thin fold of skin; Fig. 6), and a thickened ridge just posterior to the fold and separated from it by a gap (vs. lacking a ridge and a gap; Fig. 6).

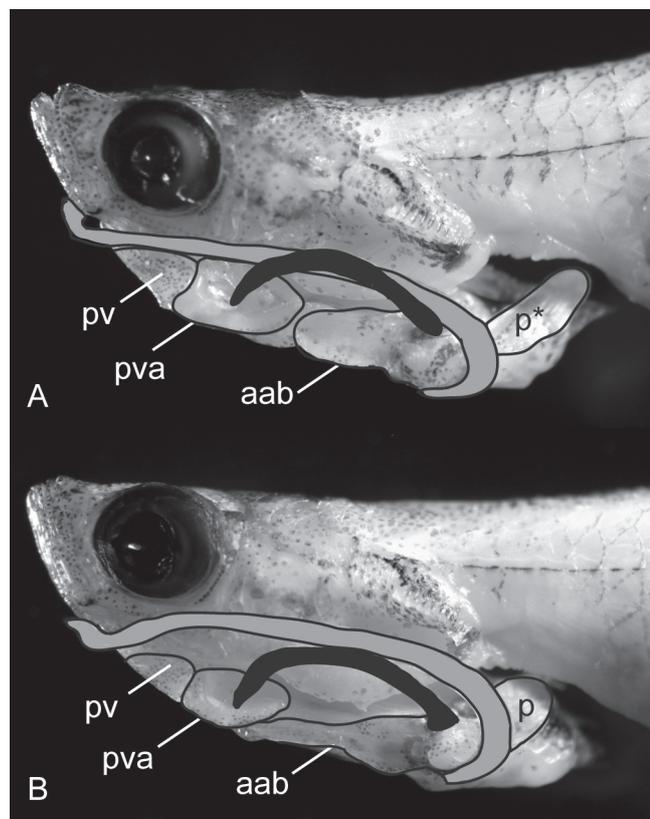


Figure 3. Comparison of external form of priapium in adult males. A, *Neostethus geminus*, Brunei Museum/USNM 409963, sinistral male, 25.2 mm SL; B, *Neostethus bicornis*, USNM 409964, sinistral male, 27.0 mm SL. First ctenactinium, gray; second ctenactinium, black. Abbreviations: aab, aproctal axial bone; pv, pulvinulus, pva, pulvinular appendage, p, seminal papilla, p*, seminal papilla and enlarged papillary tab.

Description. Meristic data for the new species are summarised in Table 2. A small, laterally compressed species, maximum size recorded 25.7 mm SL. No vestigial pelvic-fin rays or bones in adult females; males with parts of pelvic and pectoral fins modified into priapium that is either sinistral (holotype, 46 male paratypes) or dextral (42 male paratypes). Two prominent externalised subcephalic bones: an elongate first ctenactinium arises on either left or right side of body and articulates with posterior extent of left or right (proctal) axial bone, curves gently along the left or right side of the head and the somewhat expanded tip lies just ventral to the lower jaw (Figs. 2A, 3A). A curved second ctenactinium about one-half the length of the first arises on the same side of the

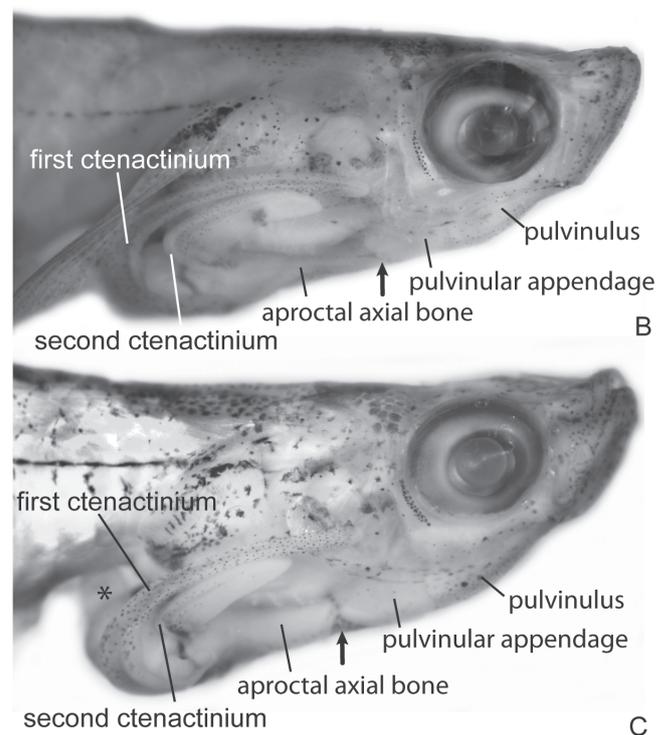
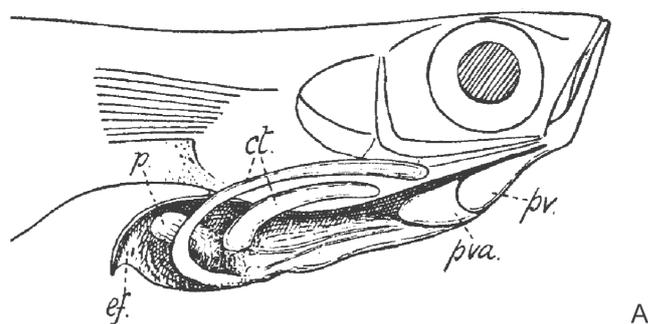


Figure 4. Comparison of external form and extent of development of the priapium in immature males. A, *Neostethus bicornis*, modified from Regan (1916: fig. 11 B) of a dextral male, 25 mm TL. Abbreviations: pv., pulvinulus, pva., pulvinular appendage, ct., ctenactinia, p., seminal papilla, ef., efferent groove; B, *Neostethus bicornis*, USNM 409964, immature sinistral male, 24 mm SL (photo is reversed); C, *Neostethus geminus*, Brunei Museum/USNM 409963, immature dextral male, 23 mm SL. Pectoral-fin rays were removed from specimen in bottom photo. Arrows point to where anterior extent of aproctal axial bone and posterior extent of pulvinular appendage overlap (B) or meet (C). An asterisk (*) marks the broad papillary tab.

Table 2. Meristic data for holotype and select paratypes of *Neostethus geminus*. Mean includes holotype.

Character	Holotype	Paratypes	Mean
First dorsal-fin rays	2	1–2 (n=9)	1.6
Second dorsal-fin rays	6	6–7 (n=9)	6.1
Anal-fin rays	15	15–16 (n=9)	15.3
Pectoral-fin rays	11	10–11 (n=9)	10.8
Principal caudal-fin rays	i,7/7,i	i,7–8/7–8,i (n=9)	i,7.2/7.4,i
Vertebrae	37 (17+20)	35–37(16–18+19–20) (n=9)	36.4(17.2+19.2)
Branchiostegal rays	5	5 (n=8)	5
Scales in a transverse series	34	35–36 (n=10)	35.1
Standard length (mm)	23.3	18.0–23.7 (n=19)	21.5

body and articulates with the posterior extent of left or right (proctal) axial bone (Figs. 3A, 4C) reaches the fibrous, oval pulvinulus which is lateral to, and covers articulation point of, inner pulvinular and proctal axial bones. Papillary bone with numerous thin, bony segments, confluent posteriorly to form a broad, elongate, translucent tab with faint striations. Aproctal axial bone short and broad, meets posterior extent of pulvinular appendage (Figs. 3A, 4C). Immature males with a small pelvic fin or fins on the proctal side of the body. Mature males with two small bundles of rudimentary pelvic-fin rays in the wall of the membranous sac at the posterior extent of the priapium. Pleural ribs of fourth vertebra in males expanded anteroposteriorly, their distal tips meet on right side of proctal axial bone in sinistral males and left side in dextral males; parapophysis on right side greatly expanded and oriented anteriorly in sinistral males, on left side in dextral males. First pleural rib on third vertebra in females.

Females with a thickened fleshy, hoodlike fold that includes the anus, genital pore and urinary pore and a thickened ridge just posterior to the fold (Fig. 6A). Ventral dermal keel extends from body just posterior to thickened ridge in females or

constricted body just posterior to the priapium in males, to just before the anal-fin origin (Fig. 5). Swim bladder spans four to five body segments anterior to anal-fin base.

Neurocranium and jaws like those illustrated for *Neostethus bicornis* by Roberts (1971b), with little modification. Posttemporal bone forked, lower limb short and connected via a ligament to the basicranium. Jaw teeth conical, in a single uneven row, small medially and progressively larger distally. Paradentary bone edentulous. Caudal fin forked. Caudal skeleton with two thin epurals, autogenous parhypural, and a dorsal and a ventral hypural plate. Principal caudal-fin rays i,7–8/7–8,i [i,7/7,i]. Pectoral fin narrow and elongate, with 10–11 [11] rays. Two dorsal fins, the first with one short, thickened ray followed by a thinner second ray in males, both supported by a single, elongate pterygiophore; the second fin with 6–7 [7] rays, the second through fourth or fifth branched, the first and last articulated, but not branched. Anal-fin rays 15–16 [15], the first ray short and unsegmented. Vertebrae 35–37 [37] (precaudal 16–18 + caudal 19–20, including half centrum). Branchiostegal rays 5. Scales on body of moderate size, deciduous, 34–36 [34] in a transverse series.



Figure 5. A, *Neostethus geminus*, new species. Paratype, Brunei Museum/USNM 409963, adult female, 22.7 mm SL; B, *Neostethus bicornis*, USNM 409961, adult female, 25.0 mm SL.

Colour in life. Body largely translucent with melanophore pigmentation pattern as in preservative, below. Specimens from the type locality at capture had a bright orange blotch on the caudal peduncle and a bright orange band at midbody, just anterior to the anal fin (see Remarks, below).

Colour in preservative. Preserved, formalin-fixed, specimens (Figs. 2, 5) with ground colour pale yellow. Dark brown melanophores scattered on dorsal surface of head, just ventral to the midline, on operculum and priapium, along basal portion of anal fin, pectoral fin, dorsal and ventral midline, and abdomen where they are concentrated into a blotch in some specimens. An arc of small brown melanophores on the posteroventral rim of the orbit. All fin rays with thin, black, interrupted to complete line of melanophores on margin. A discrete, thin black line along midlateral, intermuscular septum from pectoral fin to caudal fin base. Dorsal and ventral extent of hypural plates with indistinct black blotch. Body scales with a posterior margin of small brown melanophores. Immature males with a brown blotch on the pelvic-fin rays of the proctal side and a line of brown melanophores on the ventral surface of the body from about the position of the first through third pleural rib. Medial portions of membranous sac at the posterior extent of the priapium in mature males dark brown.

Distribution and habitat. *Neostethus geminus* was collected from six localities in the Belait and Tutong districts of Brunei, clustered near Kuala Belait and Kuala Tutong (Fig. 7). At the type locality, *N. geminus* was collected using dip nets and a scoop net along with other fish species representative of a Southeast Asian nipah forest biota including *Ambassis* sp., *Scatophagus argus*, *Tetraodon leiurus*, *Gobiopterus brachypterus*, and *Brachygobius doriae*; a mangrove colubrid snake, *Cerberus* sp., was also seen. *Neostethus borneensis* was the only other phallostethid species collected with *N. geminus*. The brackish water was clear and brown with a temperature of 27°C.

Etymology. *geminus*, Latin for twin or double referring to the close morphological similarity of the new species to its inferred sister species, *N. bicornis*, and to the paired or double ctenactinia in both species.

Remarks. Collections examined here of both *N. bicornis* and *N. geminus* contain roughly even numbers of sinistral and dextral males that, together, number somewhat more than the total number of females (see Material Examined).

A bright orange blotch on the caudal peduncle in freshly caught specimens of *Phallostethus cuulong* was illustrated by Shibukawa et al. (2012: fig. 1). Bright orange-yellow markings on the caudal peduncle and, rarely, at the base of the anal fin were reported by Roberts (1971a) for *Phenacostethus posthon* and *P. smithi*; he noted that such markings were unknown in *Neostethus*. There are few photographs of live or freshly caught *Neostethus*; a freshly-caught dextral male *N. bicornis* from Singapore has orange-yellow blotches at the base of the caudal-fin rays (see below). Other atherinomorph fishes may have orange markings on the caudal fin; the

North American Desert Pupfish, *Cyprinodon macularius* has a lemon yellow to orange caudal peduncle (Page & Burr, 2011). These markings fade rapidly upon formalin-fixation and preservation in alcohol. The distribution of the caudal peduncle and mid-body orange markings in atherinomorphs is unknown and, therefore, I do not include the markings as diagnostic of the new species.

Neostethus bicornis Regan, 1916
(Figs. 1, 2B, 3B, 4A,B, 5B, 6B, 8)

Neostethus bicornis Regan, 1916:14–15, text figure 11A, B, original description.

Ceratostethus bicornis (Regan, 1916). – Myers, 1937, description of new monotypic genus.

Ceratostethus bicornis (Regan, 1916). – Herre, 1942, characters, distribution.

Ceratostethus bicornis (Regan, 1916). – Roberts, 1971b, osteological description.

Neostethus bicornis Regan, 1916. – Parenti, 1989, meristic data, comparative anatomy and phylogenetic analysis.

Differential diagnosis. *Neostethus bicornis* and *N. geminus* are distinguished from all other phallostethid fishes by mature males with two elongate ctenactinia (vs. one elongate and one short ctenactinium as in other *Neostethus*), immature males with a brown blotch on the pelvic-fin rays of the proctal side which fades with growth and maturity, and females with a fleshy, hoodlike fold that includes the anus, genital pore and urinary pore. I (Parenti, 1989) considered these characters diagnostic of *N. bicornis* which differs from the new species, *N. geminus*, in being larger (reaching 31 mm SL vs. no more than 25.7 mm SL), having a priapium with a relatively long and narrow aproctal axial bone that overlaps the pulvinular appendage medially (vs. relatively compact priapium with a foreshortened, broad aproctal axial bone that meets but does not overlap the pulvinular appendage; Figs. 3, 4), a short, translucent papillary bone (vs. a thin, nearly translucent, broad papillary bone expanded distally into a tab; Figs. 3, 4), and females with a thin fleshy, hoodlike fold that includes the anus, genital pore and urinary pore (vs. a thick fold; Fig. 6), and no thickened ridge just posterior to the fold (vs. having a ridge; Fig. 6).

Description. A small, laterally compressed species, maximum size recorded 31 mm SL. No vestigial pelvic fin rays or bones in adult females; males with parts of pelvic and pectoral fins modified into priapium that is either sinistral or dextral. Two prominent externalised subcephalic bones: an elongate first ctenactinium arises on either left or right side of body and articulates with posterior extent of left or right (proctal) axial bone, curves gently along the left or right side of the head and the somewhat expanded tip lies just ventral to the lower jaw (Figs. 2B, 3B). A curved second ctenactinium about one-half the length of the first arises on the same side of the body and articulates with the posterior extent of left or right (proctal) axial bone (Figs. 3B, 4A, B) reaches the fibrous, oval pulvinulus which is lateral to, and covers articulation point of, inner pulvinular and proctal axial bones. Papillary bone with numerous thin, bony segments, confluent posteriorly, not forming an elongate tab. Aproctal axial bone

long and narrow, overlaps the pulvinular appendage medially. Immature males with a small pelvic fin or fins on the proctal side of the body. Mature males with two small bundles of rudimentary pelvic-fin rays in the wall of the membranous sac at the posterior extent of the priapium. Pleural ribs of fourth vertebra in males expanded anteroposteriorly, their distal tips meet on right side of proctal axial bone in sinistral males and left side in dextral males; parapophysis on right side greatly expanded and oriented anteriorly in sinistral males, on left side in dextral males. First pleural rib on third vertebra in females.

Females with a thin fleshy, hoodlike fold that includes the anus, genital pore and urinary pore and no thickened ridge just posterior to the fold (Fig. 6B). Ventral dermal keel extends from body just posterior to thickened ridge in females or constricted body just posterior to the priapium in males, to just before the anal-fin origin (Fig. 5).

Neurocranium and jaws as illustrated by Roberts (1971b). Post-temporal bone forked, lower limb short and connected via a ligament to the basicranium. Jaw teeth conical, in a single uneven row, smaller medially and progressively larger distally. Paradentary bone edentulous. Caudal fin forked. Caudal skeleton with two thin epurals, autogenous parhypural, and a dorsal and a ventral hypural plate. Principal caudal-fin

rays $i, 7-8/7-8, i$. Pectoral fin narrow and elongate, with 10–11 rays. Two dorsal fins, the first with one short, thickened ray followed by a thinner second ray in most adult males and females, both supported by a single, elongate pterygiophore; the second fin with 5–6 rays, the second through fourth or fifth branched, the first and last articulated, but not branched. Anal-fin rays 13–16, the first ray short and unsegmented. Vertebrae 36–37 (precaudal 17–18 + caudal 18–20, including half centrum). Branchiostegal rays 5–6. Scales on body of moderate size, deciduous, 31–37 in a transverse series.

Colour in life. Body and fins nearly transparent in life. Other pigmentation as in alcohol specimens described below. A fresh specimen of a dextral male captured during the October 2012 Straits of Johore Biodiversity Survey, Singapore, photographed by Arthur Anker (http://www.flickr.com/photos/artour_a/8147112311; Accessed 12 December 2013) has yellow blotches at the base of the caudal-fin rays. Dark brown melanophores that line the dorsal portion of the body cavity and anterior portion of the testis and gut are also visible. The reddish colour of the gills in this specimen is an exaggeration, the result of its being placed on ice.

Colour in preservative. Preserved, formalin-fixed specimens with ground colour pale yellow, brownish in specimens from Sabah. Dark brown melanophores scattered on dorsal surface of head, just ventral to the midline, on operculum and priapium, along basal portion of anal fin, pectoral fin, dorsal and ventral midline, and abdomen where they are concentrated into a blotch in some specimens. An arc of small brown melanophores on the posteroventral rim of the orbit. All fin rays with thin, black, interrupted to complete line of melanophores on margin. A discrete, thin black line along midlateral, intermuscular septum from pectoral fin to caudal fin base. Dorsal and ventral extent of hypural plates with indistinct black blotch. Body scales with a posterior margin of small brown melanophores. Immature males with a brown

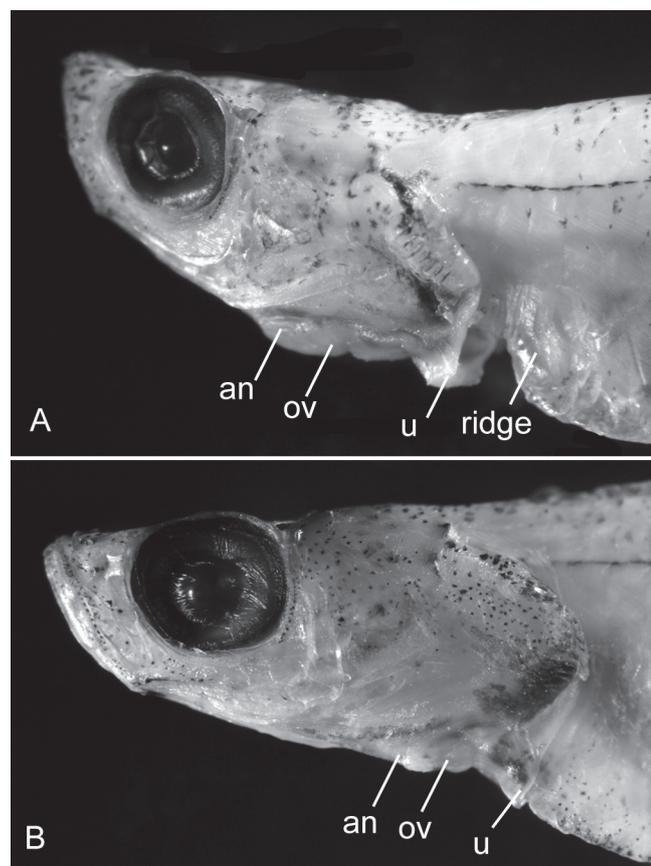


Figure 6. Comparison of position of the anus and urogenital openings in mature females. A, *Neostethus geminus*, new species, paratype, Brunei Museum/USNM 409963, adult female, 20.9 mm SL. B, *Neostethus bicornis*, USNM 409964, adult female, 26.3 mm SL. Abbreviations: an, anus; ov, oviduct aperture or genital pore, u, urinary pore. Pectoral-fin rays have been removed in both specimens.

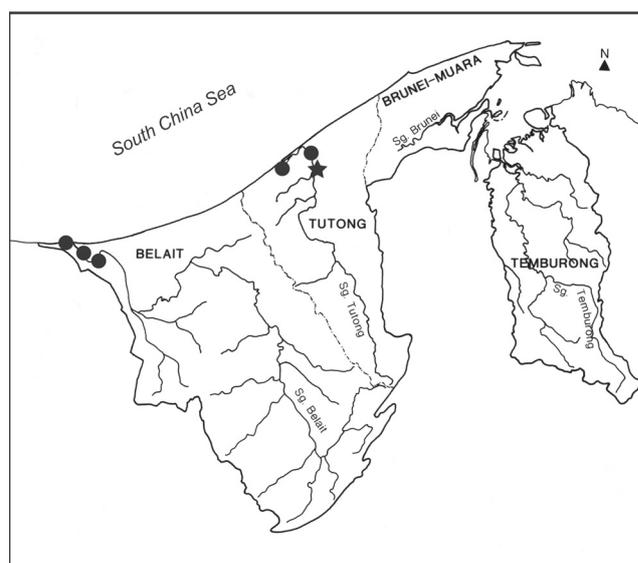


Figure 7. The six localities at which *Neostethus geminus* was collected in 1997 in the Belait and Tutong districts of Brunei, clustered near Kuala Belait and Kuala Tutong. The type locality is marked with a star.

blotch on the pelvic-fin rays of the proctal side and a line of brown melanophores on the ventral surface of the body from about the position of the first through third pleural rib. Medial portions of membranous sac at the posterior extent of the priapium in mature males medium to dark brown.

Distribution and habitat. Widespread in coastal, brackish water habitats from Thailand, Peninsula Malaysia, Singapore, East Malaysia (Sarawak and Sabah), Kalimantan, Indonesia (see Parenti & Louie, 1998), Brunei, and Palawan Is., Philippines (Fig. 1).

Material examined. **Peninsula Malaysia:** Lectotype: BMNH 1937.2.9:4 (imm. dextral male, 20.9 mm SL), designated by Parenti (1989); Paralectotypes: BMNH 1937.12.9:5–6 (female, 16.7 mm SL; imm. male, 19.1 mm SL), Kuala Langat, Selangor, coll. G. Duncker. **Thailand:** Central Thailand: brackish fish farming ponds in area of Samut Sakhon, ca. 25 km S of the center of Bangkok, USNM 358614 (5, 20–23.5 mm SL), coll. A. Whitehouse, 1 December 1997. Chanthaburi: ca. 1/2 km up from mouth of Chantiburi R. (near Tah Chalap), MCZ 47306 (adult sinistral male, CT micrograph), coll. T. R. Roberts & P. Wongrat, 5 May 1970. Chumporn Prov., Klong Panangtak in vicinity of Banthup Tanhot ca. 5 km from Chumporn town, CAS 63196 (2, sinistral male, sinistral female, 22 mm SL), coll. H. A. Fehlmann, 22 May 1960. **Singapore:** CAS-SU 31133 (10, 3 sinistral males, 7 dextral males, 26–28 mm SL), coll. A. W. C. T. Herre, 1934. USNM 102142 (8, sinistral male, 4 dextral males, 3 females; 21.0–28.0 mm SL), coll. A. W. C. T. Herre, 18 March 1934. Kranji R., CAS-SU 35783 (52, 13 sinistral males, 9 dextral males, 27 females, 3 imm., 15–28 mm SL, of which 2 sinistral male, 2 dextral male and 6 females have been cleared and stained solely with alizarin), coll. A. W. C. T. Herre, March 1937. Seletar R., CAS-SU 67161 (10, 2 sinistral males, 6 dextral males, 1 female, 1 imm, 18.1–27.8 mm SL), coll. E. Alfred, 11 February 1966. Sg. Buloh just outside of nature reserve, small stream entering Straits of Johore, USNM 348392 (50+, sinistral male, dextral male, female cleared and stained solely with

alizarin), USNM 373890 (4 pres. in ethanol), coll. L. R. Parenti, H. K. Larson, K. Lim & N. Sivasothi, 5 September 1997. **East Malaysia, Sarawak:** Kuching, Sarawak R., N. bank at Kampung Tupung, USNM 325053 (30, imm. 5–16.5 mm SL). **Brunei:** Tutong Dist.: Kuala Tutong at Tg. Tanah Palang, USNM 409961 (45, 9 sinistral males, 10 dextral males, 14 adult females, 9 imm., from which one dextral male and one female were cleared and stained solely with alcian blue and one dextral male was cleared and stained solely with alizarin; 12–29 mm SL), coll. L. R. Parenti, H. K. Larson, Hj. Ramlee, Hj. Bahrain, Abu Bakar & Zainal, 23 August 1997. Kuala Tutong, small stream that enters main river (4°47'09" N, 114° 36'56" E), USNM 409964 (317, of which one sinistral male, one dextral male, and 2 adult females were cleared and counterstained), coll. L. R. Parenti, H. K. Larson, Hj. Ramlee, Hj. Bahrain, Abu Bakar & Bujang, 25 August 1997. Lubok api-api, Kuala Tutong (4°45'12" N, 114° 35'18" E), USNM 356849 (50+, 10–25 mm SL), coll. L. R. Parenti, H. K. Larson, Hj. Ramlee, Hj. Bahrain, Abu Bakar, & Hj. Ariffin, 24 August 1997. Sg. Penabai, trib. of Sg. Tutong where it enters Sg. Tutong (4°46'29" N, 114° 36'16" E), USNM 356846 (50+, 12–29.5 mm SL), coll. L. R. Parenti, H. K. Larson, Hj. Ramlee, Hj. Bahrain, Abu Bakar & Zainal, 23 August 1997. Temburong Dist.: Sg. Mataiang on Hutan Simpan Selirong at Forest Dept. jetty, (4°53'26" N, 115°07'06" E), USNM 364887 (30, 7–28.5 mm SL), coll. L. R. Parenti, H. K. Larson, Hj. Ramlee, Hj. Ahmad & Pinde, 30 August 1997. Sg. Raya, Trib. of Sg. Temburong (4°48'11" N, 115°03'47" E), USNM 409934 (8, 8.5–28.7 mm SL), coll. L. R. Parenti, H. K. Larson, Hj. Ramlee, Hj. Bakaria, Hassan & Pinde, 21 August 1997. Pulau Pitu at sg. that enters Sg. Temburong just downstream from confluence with Sg. Labu (4°45'57" N, 115°04'44" E), USNM 365125 (2, 13.5–14.5 mm SL), coll. L. R. Parenti, H. K. Larson, Hj. Ramlee, Hj. Bakaria, Hassan & Pinde, 21 August 1997. Brunei-Muara Dist.: Sg. Kalmasi, trib. of Sg. Brunei, (4°50'44" N, 114°57'18" E), USNM 378045 (21, 11.2–28.6 mm SL), coll. L. R. Parenti, H. K. Larson, Hj. Ahmad & Hj. Junggal, 16 August 1997. Sg. Pulau Berambang, Tg. Bakaka, shore and stream that enters Brunei Bay, (4°54'04" N, 115°01'25" E), USNM 356128 (27, 10–28.2 mm SL), coll. L. R. Parenti, H. K. Larson, Hj. Ramlee, Hj. Ahmad & Pinde. 30 August 1997. Sg. Mambangan, trib. of Sg. Brunei, from above to where it enters Sg. Brunei, opposite Kampung Dato Gandi, USNM 356848 (61, 8–28.6 mm SL), USNM 389678 (5 pres. in ethanol), coll. L. R. Parenti, H. K. Larson, Hj. Ahmad & Hj. Junggal, 15 August 1997. Sg. Dolhakim, trib. stream of Sg. Brunei, USNM 364888 (17, 9.5–27.5 mm SL), coll. L. R. Parenti, H. K. Larson, Hj. Ahmad & Hj. Junggal, 17 August 1997. Main wharf [Bandar Seri Begawan], CAS-SU 61764 (dextral male, 24 mm SL), coll. J. A. Tubb, 30 July 1948. **East Malaysia, Sabah:** East Coast Residency, Kinabatangan Dist., Little Kretam R., winding embayment into nipah swamp, mouth of Ayer Terjun, FMNH 51726 (87, 8 dextral males, 7 sinistral males, 53 adult females, 29 imm., 8.5–26 mm SL), coll. R. F. Inger, 10 May 1950; near mouth of Kretam Kechil R., FMNH 51727 (6, dextral male, 2 sinistral males, 3 adult females, 20–24.5 mm SL), coll. R. F. Inger, 25 May 1950; fork of East and West Gaja, in West Fork, 100 yds.; trib. of Kretam Kechil R., FMNH 51728 (41,

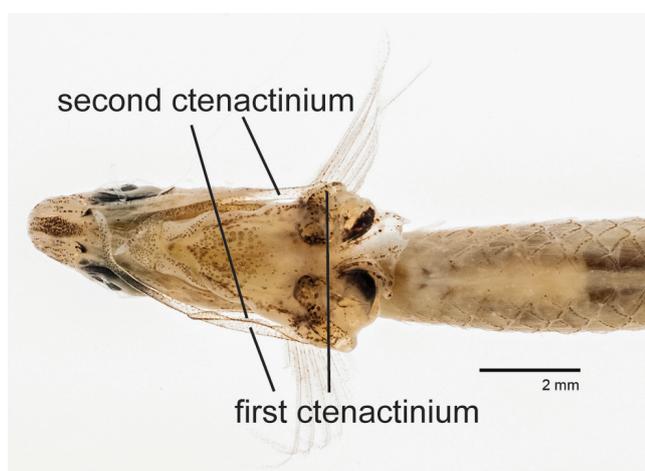


Figure 8. *Neostethus bicornis*. USNM 409961, adult male, 28.5 mm SL, with two priapia, one on the left side of the body, the other on the right side. Priapium on the right side appears complete; that on the left side has an incompletely formed first ctenactinium.

10 dextral males, 15 sinistral males, 14 adult females, 2 imm., 15.5–25 mm SL), coll. R.F. Inger, 22 May 1950; mouth of Pinang R. (trib. of Little Kretam R.), FMNH 51729 (26, 8 dextral males, 10 sinistral males, 6 adult females, 2 imm., 10–27 mm SL), coll. R. F. Inger, 10 June 1950. **Philippines:** Palawan, Nakoda Bay, USNM 98838 (3, sinistral male, 2 adult females, 26–29 mm SL), USNM 98839 (3, sinistral male, 2 adult females, 27–31 mm SL), unnamed river SE of Maricaban Is., USNM 150632 (2, dextral male, sinistral male, 30.0 mm SL), coll. Albatross, 31 December 1908; Malampaya Sound, Malampaya R., USNM 98840 (1 sinistral male, 30.0 mm SL), coll. Albatross, 26 December 1908.

Remarks. Although Regan (1916) did not report first dorsal-fin rays in his description of *N. bicornis*, a single first dorsal-fin ray was found subsequently in his type material (Myers, 1937: 141). All specimens examined here have at least one thickened first dorsal-fin ray. The small, second dorsal-fin ray is absent in female *N. geminus* and some females and males of *N. bicornis* examined here. Number of fin rays could be verified only in cleared and stained specimens.

One 28 mm SL adult male specimen of *N. bicornis* from Brunei has two priapia (Fig. 8), a rare condition that has been reported previously as a developmental anomaly (Roberts, 1971b: 417). Either one or both or neither of the priapia may have been functional in life; the first ctenactinium on the left side of the specimen illustrated here is incomplete either due to developmental arrest or damage. No parts of the specimen, other than those of reproductive morphology, are obviously duplicated. Such individuals may represent monozygotic twins—one sinistral and one dextral male—a hypothesis supported by the observation that sinistral and dextral males have been collected in about equal numbers (see FMNH material, above).

A 215 bp fragment of the mitochondrial cytochrome *c* oxidase subunit 1 (COI), the DNA barcode (Ward et al., 2005), for *N. bicornis* from Thailand was sequenced as part of a study by Sparks & Smith (2004).

COMPARATIVE MORPHOLOGY

Meristic and morphometric data. Meristic data contrast sharply among many species of phallostethines (e.g., Parenti, 1989: table 2), but not between *N. bicornis* and *N. geminus*. The sister species have overlapping ranges of fin rays, vertebral counts, branchiostegal rays, and scales in a transverse series. One measurable character that distinguishes them is adult size: *N. bicornis* reaches a maximum recorded size of 31 mm SL, whereas *N. geminus* specimens are no larger than 25.7 mm SL (Fig. 2). This size difference is not reflected in vertebral counts even though among other phallostethid species SL is correlated roughly with total number of vertebrae: the smallest species of *Neostethus*, *N. borneensis*, has 31–32 vertebrae, whereas the largest phallostethine species, *Gulaphallus eximius*, has 36–37 vertebrae (Parenti, 1989: table 2).

Males. *Neostethus geminus* and *N. bicornis* males are readily distinguished from each other by morphology of the priapium. From just two immature individuals and one not-fully-adult male available to him, Regan (1916) accurately described *N. bicornis* as having two ctenactinia, rather than one as in the other then known species of *Neostethus*, *N. lankesteri*. Regan (1916:14–15) described the differences in the priapia between the two species:

“A male of 25 mm. [total length] is not fully adult, but its priapium (text-fig. 11, B) differs from that of *N. lankesteri* in three important characters: (1) there are two ctenactinia (*ct.*), both on the aproctal side; (2) the efferent groove (*ef.*) extends downwards to the ventral surface of the posterior end of the priapium; and (3) the seminal papilla (*p.*) opens into the efferent, not the glandular groove. The ctenactinia have not attained their full development and are cartilaginous and enclosed in skin; their final shape is uncertain; the testis (*t.*) is fairly large.”

In Regan’s (1916) sketch of *N. bicornis*, as in recently collected material identified as that species from Brunei and elsewhere throughout its range, the pulvinular appendage and aproctal axial bone overlap just posterior to a vertical line drawn through the posterior margin of the preopercle (Fig. 4A, B). In contrast, in *N. geminus* the pulvinular appendage is larger and the aproctal axial bone correspondingly shorter and broader such that the two meet, but do not overlap, more posteriorly (Fig. 4C).

Neostethus geminus also uniquely has a broad, elongate papillary tab in immature as well as adult males (Figs. 2A, 3A, 4C). The tab is an extension of the papillary bone and has faint striations suggesting fusion of its thin, bony projections. It meets or extends beyond the narrow body just posterior to the priapium. Regan (1916) did not illustrate such an elongate tab in the male lectotype of *N. bicornis* (Fig. 4A) and it is not present in photographs and radiographs of the type material nor in recently collected material of that species; I conclude that it is not present.

Females. The anus and urogenital pores of female phallostethines lie just ventral to the pectoral-fin base, and are in line from anterior to posterior: anus, oviduct aperture or genital pore, and urinary pore (TeWinkel, 1939: fig. 3). Identification of these structures in female phallostethines has not been clear or consistent. Myers (1937:141–142) remarked on *N. bicornis*: “The anus of the female is surrounded by many folds of loose tissue, this area being larger than in *Neostethus lankesteri*. I do not, however, find what I am certain is a homologue of the postanal papilla of that species. The oviduct (and ureter?) appear to open at the end of a median tubelike structure some distance behind the anus. On each side of this structure is a longitudinal ridge.” Likewise, a fleshy, hoodlike fold covering the urogenital openings of adult females was considered one autapomorphy of *Neostethus bicornis*, illustrated by Parenti (1989:260). Identification of a combined urogenital opening at the end of the fold or tube of

skin was in error, as demonstrated by Mok & Munro (1997). The oviduct opens to the surface surrounded by loose folds of tissue and had been misidentified as the anus which lies just anterior to it (Fig. 6). The tube that opens posteriorly as the urinary pore of females is most prominent in the material that Myers (1937) examined from Palawan (USNM 98838).

Neostethus geminus and *N. bicornis* females are readily distinguished from each other by morphology of the transverse folds of tissue and the ventral surface of the body just posterior to the folds (Fig. 6). Females of *N. geminus* have a thickened fleshy, hoodlike fold that includes the anus, genital pore and urinary pore. Just posterior to the fold, and separated from it by a gap, there is a thickened ridge of tissue which is ossified in some larger specimens. In females of *N. bicornis*, the fold is relatively thin and there is no thickened ridge posterior to the fold.

DISCUSSION AND CONCLUSIONS

Neostethus geminus, new species, is described from coastal localities in Brunei, northwestern Borneo. The specimens of *N. geminus* reported here were collected during a 1997 survey of the coastal and mangrove fishes of Brunei. They were identified initially as *N. bicornis* because they have the characters that Parenti (1989) considered diagnostic of that species: two, elongate curved ctenactinia in mature males, a brown blotch on the pelvic-fin rays of the proctal side of immature males, and a fleshy, hoodlike fold that includes the anus, genital pore and urinary pore of females. These characters are reinterpreted here as synapomorphies of the sister species *N. bicornis* and *N. geminus*.

Neostethus bicornis and *N. geminus* are superficially similar and overlap in meristic characters, yet comparative examination of large collections from Brunei revealed distinct morphological differences between the two sister species. *Neostethus geminus* is smaller than *N. bicornis* and, correspondingly, males of *N. geminus* have a relatively compact priapium with a foreshortened, broad aproctal axial bone that meets but does not overlap the pulvinular appendage, and a thin, nearly translucent, broad papillary bone with an elongate tab that may extend posteriorly to and beyond the constricted body wall. This is in contrast to the relatively elongate priapium of *N. bicornis* with a long and narrow aproctal axial bone that overlaps the pulvinular appendage medially and a broad, yet short, papillary bone that does not extend beyond the membranous sac at the posterior extent of the priapium. Female specimens of *N. geminus* have a thickened fleshy, hoodlike fold that includes the anus, genital pore and urinary pore and a thickened ridge just posterior to the fold and separated from it by a gap. The anus, genital pore and urinary pore of females of *N. bicornis* are in the same relative position as those of *N. geminus*, but the skin is not thickened and there is no ridge on the body just posterior to the fold.

This discovery reinforces the recognition of northwestern Borneo (here Brunei and the Bornean Malaysian states of Sarawak and Sabah) as an area of endemism for freshwater

fishes which reflects its composite geological history (e.g., Hamilton, 1979; Hall, 2002, 2009). *Neostethus geminus* joins *Phenacostethus trewavasae* and *Phallostethus lehi* as northwestern Borneo endemics with close relatives living around the southern portion of the South China Sea. It is sympatric with the abundant *N. borneensis* throughout its range, yet to date has not been collected with its sister species, *N. bicornis*.

Neostethus geminus is described as an endemic species of Brunei, but its endemic status awaits clarification. Large portions of the northwest Borneo coast between Kuching and the mouth of the Belait River, Sarawak, have never been surveyed for coastal or mangrove fishes. More focused collecting along the northwest coast of Borneo is likely to reveal additional populations of the new species. Further study of material in archival collections may also reveal additional, new cryptic species.

Comparative material examined. *Neostethus borneensis*:

Brunei: Tutong Dist.: Kuala Tutong at Tg. Tanah Palang (4°46'04" N, 114°36'12" E), USNM 409945(100+), coll. L. R. Parenti, H. Larson, H. Ramlee, H. Bahrain, A. Bakar & Zainal, 23 August 1997. Kuala Tutong, small stream that enters main river (4°47'09" N, 114° 36'56" E), USNM 409943 (100+, sinistral male, dextral male, 2 adult females cleared and counterstained), coll. L. R. Parenti, H. K. Larson, Hj. Ramlee, Hj. Bahrin, Abu Bakar & Bujang, 25 August 1997. Kuala Tutong At Tg., Tanah Palang, USNM 409945 (100+), coll. L. R. Parenti, H. K. Larson, Hj. Ramlee, Hj. Bahrin, Abu Bakar & Bujang, 25 August 1997. Belait Dist: Sg. Teraban, trib. of Sg. Belait, just above where it enters main river channel, and in main channel, (4°34'41" N, 114°10'59" E), USNM 409944 (10+), coll. L. R. Parenti, H. K. Larson, Hj. Ramlee, Hj. Bahrin & Yussof, 26–27 August 1997. ***Gulaphallus eximius*:** CAS-SU 38900 (78, 1 sinistral male, 1 dextral male, 45 females, 31 imm., 12.5–37 mm SL, of which 2 males and 9 females have been cleared and stained solely with alizarin), Philippines, Luzon Is., Nueva Vizcaya Prov., Magat R., near Santa Fe, coll. A. W. C. T. Herre, 3 June 1940. ***Dentatherina merceri*:** USNM 230374 (2, cleared and counterstained with alcian blue and alizarin), Indonesia, Moluccas, Tandjung Liang, East Shore, Piru Bay, coll. V. G. Springer & M. F. Gomon, 10 January 1973.

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