THE RAFFLES BULLETIN OF ZOOLOGY 1998 **46**(1): 139-150

NEOSTETHUS DJAJAORUM, NEW SPECIES, FROM SULAWESI, INDONESIA, THE FIRST PHALLOSTETHID FISH (TELEOSTEI: ATHERINOMORPHA) KNOWN FROM EAST OF WALLACE'S LINE

Lynne R. Parenti

Division of Fishes, NHB MRC 159, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, U. S. A.

Kristina D. Louie

Department of Biology, University of California, Los Angeles, CA 90095-1606, U. S. A.

ABSTRACT. - *Neostethus djajaorum*, new species, is described from specimens from the Gowa District near Ujung Pandang, Sulawesi. It is hypothesized to be most closely related to *Neostethus robertsi* from Luzon I., and *Neostethus palawanenis* from Palawan and Cuyo Is., the Philippines, with which it shares a distinctive, bifid or claw-shaped second ctenactinial bone in the intromittent organ of males. *Neostethus djajaorum* is distinguished from its closest relatives by the shape of the claw and extent of a bony projection and fleshy profile on the ventral margin of the first ctenactinium that abuts the claw. It is the first species in the distinctive atherinomorph fish family Phallostethidae known from east of Wallace's Line and from Sulawesi. The inferred ancestral distribution of the new species and its close relatives is coincident, in part, with limits of a now geographically dispersed ancient island-arc system, the Sumba block or terrane, that comprises west Mindanao, northern Borneo (plus Palawan), east Kalimantan, the southwestern arm of Sulawesi and part of Java and the lesser Sunda Islands. The coastal and freshwater Phallostethidae and its sister taxon, the marine shorefish Dentatherinidae, have largely complementary (allopatric) distribution patterns that overlap (are sympatric) in northeastern Borneo and the Philippines, including portions of the Sumba terrane.

KEYWORDS. - Phallostethidae, Sulawesi, Wallace's Line, Dentatherinidae

Received 15 Oct 1997 Accepted 22 Jan 1998

INTRODUCTION

Complexity of the biota of the Indo-Australian archipelago was recognized by Alfred Russel Wallace (1869) who identified an Asian biota on the western portion of the archipelago and an Australian biota on the eastern portion. One imaginary line drawn vertically between islands, known as Wallace's Line, separates the two regions (Fig. 1). Early renditions of the line passed to the west of Sulawesi (formerly the Celebes); later renditions to the east. Other lines, such as Weber's Line, Lydekker's Line, or Huxley's modification of Wallace's Line (Fig. 1), were drawn as it became clear that not all taxa followed Wallace's Line precisely (viz. Simpson, 1977: fig.1).

Interpretations of the geology of the entire region explicitly within a plate tectonic framework, first by Hamilton (1979, 1988) and subsequently by others, such as Audley-Charles (1987), Daly et al. (1991), and Metcalfe (1991), demonstrated its extreme complexity, including that modern, large islands, such as Borneo, Sulawesi and New Guinea, are geological composites. Corresponding developments in the theory of historical biogeography support

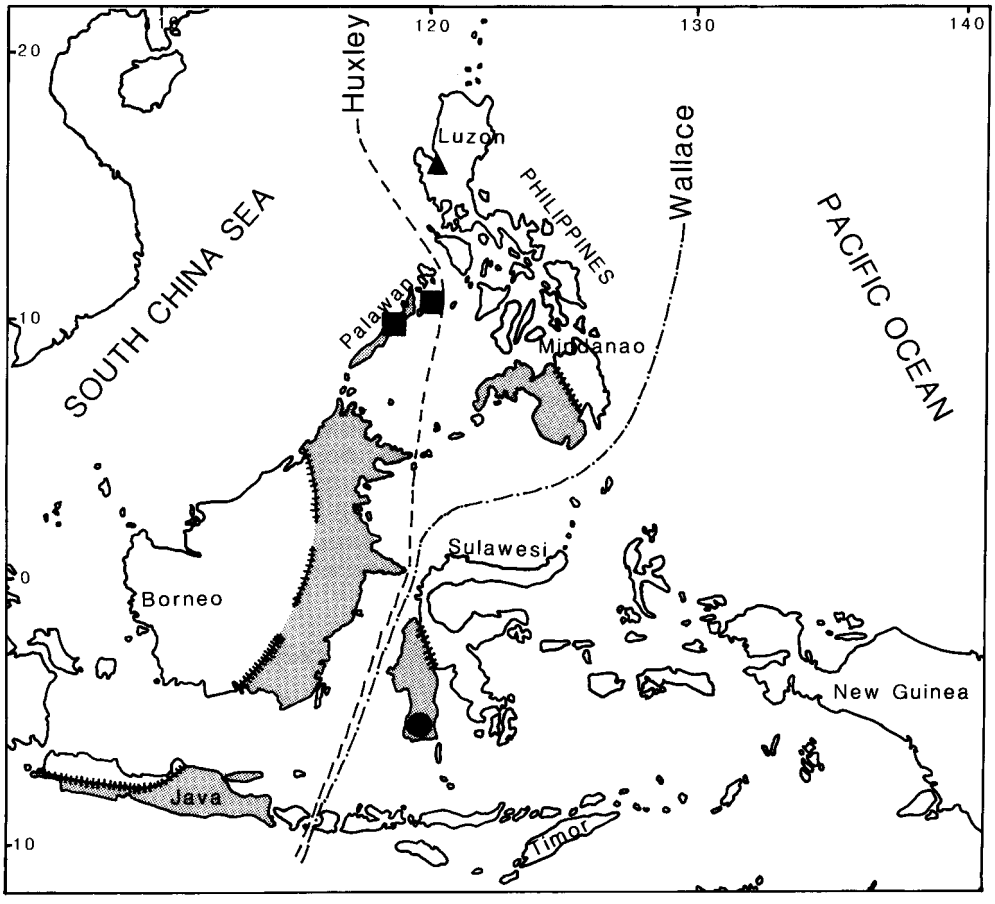

Fig. 1. Distribution of *Neostethus djajaorum* (circle, Sulawesi), *N. robertsi* (triangle, Luzon) and *N. palawanensis* (squares, Palawan). Wallace's Line (dotted and dashed), Huxley's Line (dashed) after Simpson (1977:fig. 1). Hatched lines represent approximate limits of some suture and fault lines delimiting Sumba block or terrane, the major portions of which are shaded, following Rangin et al. (1990), Michaux (1996), and herein.

the idea that distributions of plants and animals are explained best by the extent to which they conform to a generalized pattern, rather than by individual episodes of long-distance dispersal (viz. Croizat, 1958; Nelson & Platnick, 1981) and, further, that these generalized patterns may be explained by concordance with complex geological or climatic patterns. Evaluations of the biogeography of Sulawesi within a cladistic or vicariance biogeographic framework (e.g., water striders, Polhemus & Polhemus, 1990; butterflies, Vane-Wright, 1991) have confirmed that the biota of Sulawesi is composite, that is, neither wholly Asian nor wholly Australian, although the ratio of Asian to Australian taxa varies from group to group. In a summary of the cladistic relationships among mirid insects, Schuh & Stonedahl (1986:fig. 11) depicted Sulawesi in an unresolved position between western (or Asian) and eastern areas. An imaginary line could pass through the islands rather than between them to reflect their geological and biological complexity (viz. Parenti, 1991).

Phallostethids are small, transparent to opaque, surface-feeding, schooling fishes readily distinguished from all other bony fishes by a complex intromittent organ in males, called the priapium (Regan, 1913, 1916). The family Phallostethidae sensu Parenti (1984), comprising twenty-one species including the new species described herein, was known previously to be distributed broadly throughout coastal and freshwater habitats in Southeast Asia entirely west of Wallace's Line, including Thailand, peninsular Malaysia, Singapore, Borneo, the Philippines and Sumatra (see Parenti, 1989, 1996; Kottelat et al., 1993). The marine shorefish silverside genus *Dentatherina* Patten & Ivantsoff (1983), was recognized as the closest living relative of phallostethids by Parenti (1984) and placed in its own family, the Dentatherinidae, sister to the Phallostethidae in the atherinomorph superfamily Phallostethoidea. This sister-group relationship was corroborated by Dyer & Chernoff (1996) who classified *Dentatherina* in the Phallostethidae. *Dentatherina* is broadly distributed throughout coral reef habitats from off Java, northeastern Borneo, the Philippines, the Moluccas and across the Indo-Australian archipelago to eastern New Guinea, northeastern Australia and Fiji (Patten & Ivantsoff, 1983; Fig. 2). Our discovery in 1995 of a phallostethid species in southwestern Sulawesi, described herein as new, has prompted reinterpretation of some aspects of phallostethid biogeography as well as a search for distribution patterns of other taxa that may conform to that of phallostethids and their close relatives (Fig. 2).

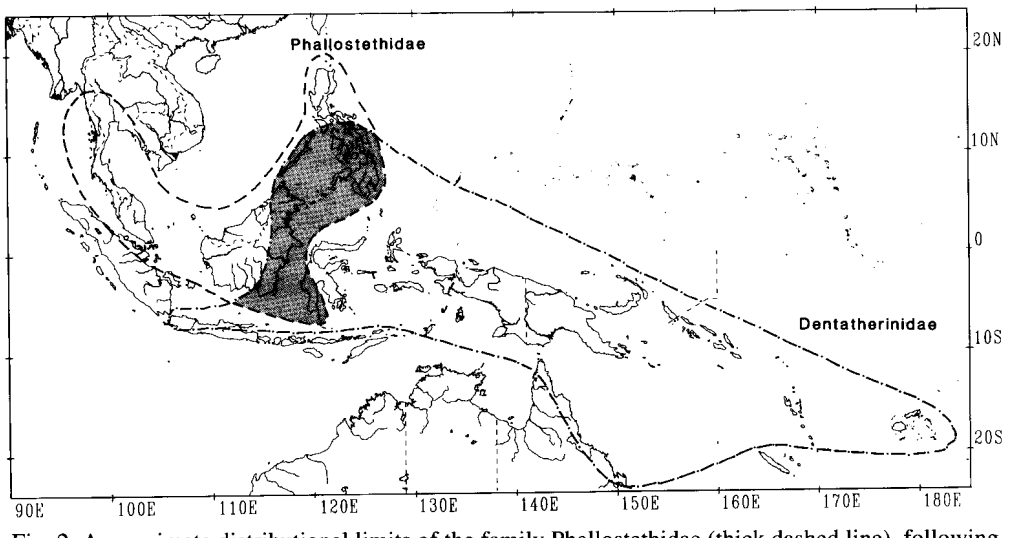

Fig. 2. Approximate distributional limits of the family Phallostethidae (thick dashed line), following Parenti (1989, 1996), and the family Dentatherinidae (dotted and dashed line), material listed herein. Approximate area of overlap is shaded.

METHODS

Anatomical description follows Roberts (1971) and Parenti (1989). Male phallostethids are bilaterally asymmetric: the anus is offset to the so-called proctal side of the body, and the seminal papilla is offset to the opposite or aproctal side. Males with the aproctal side the left are termed sinistral; males with the aproctal side the right are dextral. Males have a prominent, external priapial bone, the first ctenactinium, and a smaller bone, the second ctenactinium, arising on the aproctal side in *Neostethus*. Counts were made from cleared and stained preparations, radiographs, and alcohol specimens. Counterstained specimens were prepared according to Dingerkus and Uhler (1977). The generic citation is abbreviated from the complete synonymy in Parenti (1989). Institutional abbreviations: AMS, Australian Museum, Sydney; CAS, California Academy of Sciences, San Francisco; CAS-SU, Stanford University, at California Academy of Sciences, San Francisco; CMK, private collection of Maurice Kottelat, Switzerland; FMNH, Field Museum of Natural History, Chicago; MZB, Muzium Zoologicum Bogoriense, Bogor; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.; and ZRC, Zoological Reference Collection, National University of Singapore. Select abbreviations: SL, standard length; Sg., sungei or sungai (stream); trib., tributary; juv., juvenile. Locality coordinates are approximate.

SYSTEMATIC ACCOUNTS

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* (coincident with the tribe Neostethini) differs from other phallostethids in having a priapium with an inner pulvinular bone (as opposed to lacking the bone), and thin bony projections on the papillary bone that may number 80 or more (as opposed to lacking bony projections). Males lack a large, fleshy seminal papilla, and there is no translucent, membranous dome on the dorsal surface of the head as in the tribe Phallostethini. Males also lack a perforated gular flap of skin through which anterior end of the first ctenactinium projects and lack an aproctal axial bone projecting beyond ventral body profile as in the subfamily Gulaphallinae.

Composition and Distribution. - Eleven species: *N. lankesteri* Regan, 1916, Thailand, peninsular Malaysia, Singapore, and Borneo; *N. bicornis* Regan, 1916, peninsular Malaysia, Singapore, Thailand, Borneo, and Palawan, Philippines; *N. palawanensis* (Myers, 1935), Palawan, Philippines; *N. amaricola* (Villadolid and Manacop, 1935), throughout Philippines; *N. thessa* (Aurich, 1937), Mindanao, Philippines; *N. ctenophorus* (Aurich, 1937), Luzon, Philippines; *N. borneensis* Herre, 1939, Borneo and Coron, Philippines; *N. zamboangae* Herre, 1942, Mindanao and Luzon, Philippines; *N. villadolidi* Herre, 1942, throughout Philippines; *N. robertsi* Parenti, 1989, Luzon, Philippines; and *Neostethus djajaorum*, new species, Sulawesi Selatan, Indonesia, described below.

Neostethus djajaorum, new species
(Figs. 3,4)

Material examined. - Holotype- sinistral male (18.0 mm SL) (MZB.6730, ex. USNM.340426), Indonesia: Sulawesi Selatan: Ujung Pandang (approx. 5°07' S 119°24'E): Gowa District: irrigation

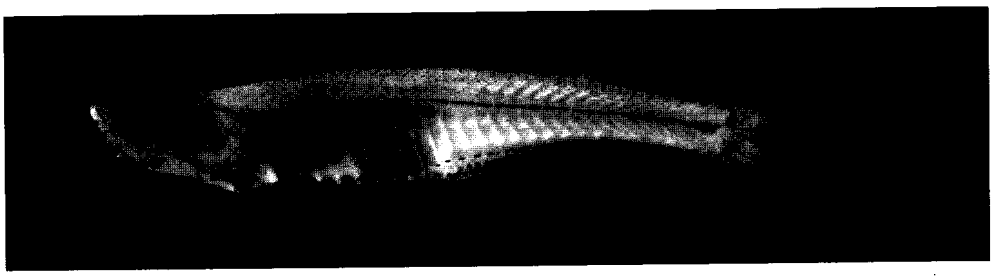

Fig. 3. *Neostethus djajaorum,* holotype, MZB 6730, sinistral male, 18.0 mm SL.

ditch approximately 5 Km SE of road from Ujung Pandang to Patalasang, coll. L. R. Parenti, K. D. Louie, and T. Amos, 3 Aug.1995.

Paratypes - sinistral male, 3 dextral males, 5 adult females (15.5-18.5 mm SL) (MZB.6731, ex. USNM.340426); 3 sinistral males, 2 dextral males, 2 females, juv. (10.0 - 19.0 mm SL, of which one sinistral male and a female were counterstained for bone and cartilage) (USNM.340426); sinistral male, dextral male (18.0 - 18.4 mm SL),(ZRC.41745, ex. USNM.340426); sinistral male (18.0 mm SL; female, 18.5 mm SL, preserved in ethanol), (USNM.345483), all collected with holotype.

Differential Diagnosis. - *Neostethus djajaorum*, like *N. robertsi* and *N. palawanensis*, has a large second ctenactinium that is bifid distally, but distinguished from those species by having that bone larger and more distinctly claw-shaped (Fig. 4a), and extent of a bony projection and fleshy profile on the ventral margin of the first ctenactinium that abuts the claw (Fig. 4b) (See Relationships, below).

Description. - A small, laterally compressed species, our largest specimen only 19.0 mm SL. Skull and jaws like those illustrated for *Neostethus bicornis* by Roberts (1971), with little modification. Jaw teeth small, conical, in a single uneven row or grouped together in indistinct rows. Paradentary bone edentulous. Eye-lens large, just smaller than eye. Ventral dermal keel extending from posterior extent of priapium in males or urogenital opening in females, to anal fin origin. Scales on body of moderate size, deciduous.

No vestigial pelvic fin rays or bones in adult females; males with pelvic and parts of pectoral fin modified into priapium that is either sinistral (holotype, 5 male paratypes) or dextral (6 male paratypes). Prominent externalized subcephalic bone a first ctenactinium, arising on either left or right side of body and articulating with posterior extent of left or right (proctal) axial bone, curving gently along the left or right side of the head and the tip lying just ventral to lower jaw. First ctenactinium with bony projection covered by a fleshy, ventral ridge that nearly abuts the second ctenactinium. Large, well-developed, claw-shaped second ctenactinium (Fig. 4). Fibrous pulvinulus lateral to, and covering articulation point of, inner pulvinular and proctal axial bones. Papillary bone with numerous thin, bony segments that are not separated from each other and cannot be counted accurately. Pleural ribs of fourth vertebra in males expanded anteroposteriorly, their distal tips meeting 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 fourth vertebra in females.

Pectoral fin narrow and elongate, with 12 rays. Two dorsal fins, the first with two spines or thickened rays supported by a single pterygiophore, the second with 6 rays, the second through fifth branched, the first and last articulated, but not branched. Caudal skeleton with two epurals, autogenous parhypural, and a dorsal and a ventral hypural plate; a ventral

accessory or y-bone in one female. Principal caudal fin rays 14. Anal-fin rays 15. Vertebrae 33-35 (counterstained specimens: 15+20=35, male, 14+19=33, female), scales in a lateral series 30-32 (estimated), branchiostegal rays 5.

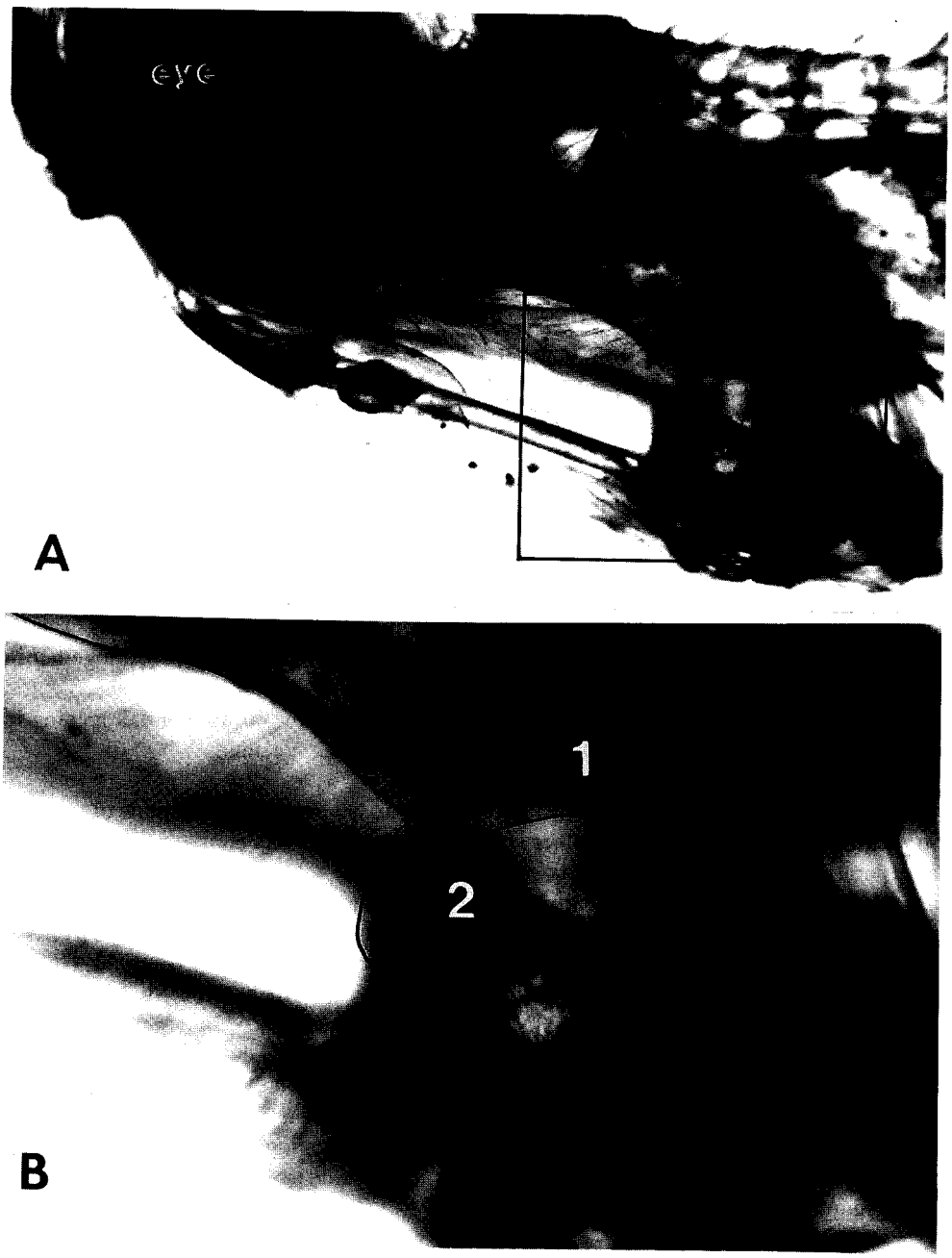

Fig. 4. *Neostethus djajaorum,* paratype, USNM 340426, photomicrographs of counterstained sinistral male, A) head, anterior portion of the body and the priapium. Area in square is enlarged in B. B) Posterior portion of the priapium. 1, first ctenactinium, 2, second ctenactinium, bony and fibrous margins of which have been outlined in ink.

Colouration. - Preserved (formalin-fixed) specimens (Fig. 3) with ground colour pale yellow or brown. Dark brown melanophores scattered on dorsal surface of head, along midlateral intermuscular septum, on operculum and priapium, along basal portion of anal fin, pectoral fin, dorsal and ventral midline, and scattered on abdomen. Dorsal scales with faint dark brown margins.

Habitat. - *Neostethus djajaorum* was collected with a seine and dip nets over a muddy substrate that was thick with leaves and fallen branches, in a slightly turbid irrigation ditch relatively near (approx. 5 km from) the sea (Fig. 5). Other fish taxa taken at the locality were the atherinomorphs *Aplocheilus panchax* and *Oryzias celebensis*, and the introduced cyprinid *Osteochilus hasseltii*.

Distribution. - Known only from the single collection from the type locality, Gowa District, Ujung Pandang (approx. 5°07' S 119°24'E), Sulawesi Selatan, Indonesia.

Etymology. - *djajaorum,* to honor the contributions of the Djaja family, Rachmat, Jootje and their children, Ike, Yuni, and Andi, for their kindness and extraordinary support of our fieldwork in Sulawesi.

Relationships. - The monophyletic *Neostethus* comprises eleven species distributed broadly throughout much of the range of Phallostethidae sensu Parenti, 1984, including peninsular Malaysia, Singapore, northwestern Borneo, the Philippines (see Parenti, 1989:fig. 1), and Sulawesi. A cladogram of relationships and an area cladogram for the then ten known *Neostethus* species were given by Parenti (1989, 1991:figs. 6,7). *Neostethus djajaorum* has the diagnostic characters of *Neostethus*: presence of an inner pulvinular bone and papillary bone with numerous thin, bony segments. The segments are not separated from each other

Fig. 5. Type locality of *Neostethus djajaorum.* Tony Amos and Kristina Louie seining in irrigation ditch approximately 5 Km SE of road from Ujung Pandang to Patalasang, Gowa District, Sulawesi Selatan.

Table 1. Frequency distribution of vertebral number and position of first pleural rib in males and females of selected species of *Neostethus*.

Species	Vertebral Number	Position of First Pleural Rib
Neostethus djajaorum		
males	15+19 = 34(3)	4th vertebra (1)
	15+20 = 35(2)	
females	14+19 = 33(3)	4th* vertebra (1)
	14+20 = 34(2)	
Neostethus palawanensis		
males	16+19 = 35(2)	4th vertebra (2)
females	15+19 = 34(2)	3rd vertebra (2)
Neostethus robertsi		
males	17+19 = 36(2)	4th vertebra (2)
female	17+19 = 36(1)	3rd vertebra (1)
Neostethus lankesteri		
males	17+19 = 36(2)	4th vertebra (2)
	16+19 = 35(2)	4th vertebra (2)
female	16+18 = 34(1)	4th* vertebra (1)

* - remnant of pleural rib associated with third vertebra; pleural rib on fourth vertebra complete.

as thin bony projections as in other *Neostethus* species; this difference may be due to state of maturity of our specimens, the largest of which is a 19.0 mm SL adult male. *Neostethus djajaorum* appears to be most closely related to the clade comprising *N. robertsi,* from Luzon I., and *N. palawanensis,* from Palawan and Cuyo Is., Palawan Prov., with which it shares a bifid or claw-shaped second ctenactinium in the priapium. *Neostethus djajaorum* and *N. robertsi* differ from *N. palawanensis* in having two, rather than one, first dorsal-fin rays. *Neostethus djajaorum* and *N. palawanensis* both have a fleshy ventral margin of the first ctenactinium that is thicker in *N. palawanensis,* and both have sexually dimorphic vertebral counts, with usually one more precaudal vertebra in males than in females, although these numbers may be highly variable (Table 1). Also, accurate counts were obtained only from cleared and stained material. Sexually dimorphic vertebral counts were also found in *N. lankesteri* (Table 1) and have also been reported in the poeciliid *Tomeurus gracilis*, another internally fertilized atherinomorph cyprinodontiform fish in which a male was reported to have 16+21=37 vertebrae and a female 13+25=38 vertebrae (Parenti and Song, 1996:table 1). Distribution and phylogenetic significance of sexually dimorphic vertebral counts in atherinomorph fishes has not been investigated.

Neostethus lankesteri and *N. djajaorum* share one derived character of questionable homology: a projection on the ventral margin of the first ctenactinium, fibrous in *N. djajaorum* (Fig. 4b), ossified in *N. lankesteri* (Parenti, 1989: fig. 3). *Neostethus lankesteri* has a small, pointed second ctenactinium, however, unlike *N. djajaorum*, *N. palawanensis* and *N. robertsi.*

Comparative material examined. - Phallostethidae
Neostethus robertsi:
Philippines: holotype, dextral male (22.3 mm SL) (CAS.50723), Calasiao R., about 12 km N of San Carlos City, Pangasinan Prov., Luzon, coll. T. R. Roberts, 16.Mar.1976; paratypes, 12 sinistral males, 9 dextral males, 10 females, 9 juv. or sex undet., (9.0 - 23.0 mm SL; sinistral male, dextral male and female counterstained for bone and cartilage)(CAS.64254), collected with holotype.

Neostethus palawanensis:
Philippines: holotype, sinistral male (22.5 mm SL), (USNM.93421), mouth of Caiholo R., Ulugan Bay, west coast of Palawan I., Palawan Prov., coll. U.S.S. ALBATROSS, 29.Dec.1908; paratype, female (19 mm SL), (USNM.93422); paratypes, 5 dextral males, 3 females, (USNM.93423), collected with holotype; 5 sinistral males, 4 dextral males, 8 females; 4 ex. cleared and stained (CAS.63200), Cuyo I., Palawan Prov.

Neostethus borneensis:
Brunei (Borneo): 11 ex.(USNM.325046), Sg. Dolhakim, trib. of Sg. Brunei, near Bandar Seri Begawan (4°50'N, 115°00'E), coll. L. R. Parenti, M. Wong, and party from Muzium Brunei, 17.Aug.1991; 162 ex.(USNM.321316), same locality, 19.Aug.1991.
Sabah (Borneo): paratypes, 6 ex. (FMNH.51537), 6 ex. (FMNH.51538) paratypes, Sg. Kabili, Sanadakan, Dist., East Coast Residency, coll. A. W. C. T. Herre, Jan.1937.

Neostethus bicornis:
Brunei (Borneo): 7 ex. (USNM.325051), Sg. Dolhakim, trib. of Sg. Brunei, near Bandar Seri Begawan (4°50'N, 115°00'E), coll. L. R. Parenti, M. Wong, and party from Muzium Brunei, 19.Aug.1991.
East Malaysia (Borneo): 30 ex. (USNM.325053), Kuching, Sg. Sarawak, N shore at Kampung Tupong (1°33'N, 110°25'E), coll. L. R. Parenti and party from Muzium Sarawak, 13.Aug.1991.
Indonesia (Borneo): 14 ex. (CMK.9482), 2 adult males cleared and stained solely with alcian blue, (CMK.11024), Kalimantan Timur, Sg. Sebuku basin, Sg. Tulit, about 1 km downriver from confluence of Semunad and small tributary creek.

Neostethus lankesteri:
Singapore: 105 ex. (5 ex. cleared and counterstained),(CAS-SU.67162), Sg. Seletar.

Locality records- Dentatherinidae (compiled from USNM catalog records and Patten & Ivantsoff, 1983:331-332)

Dentatherina merceri:
Australia: Queensland: 15 ex.(USNM.230378), 5 ex.(USNM.230379), One Tree I.; 2 ex. (AMS.I 22653-001), Lizard I.
Fiji: 1 ex. (USNM.261618), Malolo Lailai, large rock (islet) on SW corner; 2 ex.(USNM 261622): Kandavu, Dawson Reef.
Indonesia: Moluccas: Haruku I.: 1 ex. (USNM.209578), 3 ex. (USNM.230376): Point E of Tandjung Naira; Nusa Laut I.: 1 ex. (USNM.209883), N shore at Tandjung Tala (Tolo); Ceram: holotype (USNM.210180), 33 ex. (USNM.230374), 7 ex. (USNM.230364): Tandjung Liang, E shore, Piru Bay; Saaro I.: 1 ex. (USNM.211044), bay off Tuhaha Saparua. Seribu I.(off NW coast of Java): 1 ex. (USNM.220145), 1 ex. (USNM.230372), 4 ex. (USNM.230373): off W side of Pulau Ajer.
Malaysia: Borneo: 1 ex. (USNM.220136), Pulau Bohidulong, (island next to Pulau Gaya) Darvel Bay, coral fringing reef on E (outer) side of island.
Papua New Guinea: 3 ex. (USNM.230179), 4 ex. (USNM.230180):coral reef 0-3 m deep at Harvey Bay, 33 Km ESE of Popondetta; Basilaki I.: 2 ex. (USNM.230368), 1 ex. (USNM.230369), Milne Bay Dist., coral reef; Trobriand Is.: 4 ex. (USNM.230365), 3 ex. (USNM.230366), 9 ex. (USNM.230367), coral reef on W side of Kiriwina I., 3 ex. (USNM.230375), Kiriwina (Labai) on N. Coast off Towai Pt., NW part of island.
Philippines: Negros Oriental: 2 ex. (USNM.220142), 5 ex. (USNM.230377), near Port Siyt;

Palawan Prov.: 42 ex. (USNM.230181), 4 ex. (USNM.230370), 5 ex. (USNM.230371), Putic I., NW side (Cuyo I.).

DISCUSSION

Significance of the discovery and description of *Neostethus djajaorum*, the first phallostethid fish known from Sulawesi, may be considered from the family to the species level. Distribution of the Phallostethidae and its sister taxon, *Dentatherina*, are largely complementary or allopatric, phallostethids living in the western portion of the Indo-Australian archipelago, *Dentatherina* living in the eastern portion of the archipelago and the western Pacific (Parenti, 1991). As expected for sister taxa (viz. Croizat, Nelson & Rosen, 1974), there is an area of overlap, or sympatry, in northeastern Borneo and the Philippines, indicating that once separation between the sister lineages occurred, there was hypothesized dispersal of some members of one or both lineages into the range of the other (Fig. 2). Such dispersal cannot be recognized without a phylogenetic hypothesis of relationships among taxa, at the minimum knowing that the monophyletic Phallostethidae and Dentatherinidae are sister taxa. One may suppose that *Dentatherina*, a shorefish genus, would have been more likely than its sister group phallostethids, largely coastal and freshwater taxa, to have dispersed; however, that is a probability argument that receives no particular support from, and cannot be tested by, the distribution patterns of Figure 2.

Interestingly, the area of overlap or sympatry is coincident, in part, with limits of an hypothesized ancient island-arc system called the Sumba block or terrane (Rangin et al., 1990; Figs. 1, 2). The southwestern arm of Sulawesi, west Mindanao, northern Borneo (interpreted to include Palawan), east Kalimantan, and part of Java and the lesser Sunda Islands comprise an island-arc system recognized by Rangin et al. (1990) that became sutured to continental margins in the late Cretaceous or early Tertiary (Michaux, 1996). This suggests that Phallostethidae and Dentatherinidae had diverged prior to the suturing of the exotic terranes, an event that would have facilitated dispersal of either or both phallostethids and *Dentatherina* into the range of the other.

One benefit of historical biogeography is its predictive value; what is true for one group of taxa in a biota may be true for another. Distributions of birds and moths coincident with the limits of the Sumba terrane were tabulated by Michaux (1996) who proposed that these now diverse geological fragments share a closer biotic relationship than they do with any other areas. *Neostethus djajaorum* is hypothesized to be part of a monophyletic group that also includes two *Neostethus* species that live in the Philippines, *N. robertsi,* known only from a single collection from Luzon I., and *N. palawanensis,* from Palawan and Cuyo Is. (Fig. 1) in the area of phallostethid- *Dentatherina* sympatry. This further suggests that *N. djajaorum, N. robertsi* and *N. palawanensis* have an ancestral distribution pattern that is coincident, in part, with limits of the now geographically dispersed Sumba terrane.

Neostethus djajaorum lives in the southwestern arm of Sulawesi. It is not likely to be found in Sulawesi outside of the southwestern arm because southwestern Sulawesi did not join the other two geologically distinct portions of the large island until an estimated 5 to 10 mya (Hall, 1996; Fig. 1), having been rifted from eastern Kalimantan, opening the Makassar Strait for the first time in the Miocene. *Neostethus djajaorum* or another as yet undiscovered close relative, if either lives outside of Sulawesi, is most likely living in the drainages of eastern Kalimantan that empty into the Makassar Strait, such as the Mahakam River.

Published surveys of the Mahakam ichthyofauna have concentrated on relatively large species important for fisheries (Christensen, 1992) or on portions of the river (Kottelat, 1994) where *Neostethus,* generally a coastal genus, is not expected. This emphasizes the need for continued surveys of coastal, estuarine and mangrove habitats throughout the Indo-Australian archipelago, which continue to reveal new fish taxa (e.g., Kottelat, 1994; Parenti, 1996, and herein) that may lead to reinterpretation of distribution patterns.

ACKNOWLEDGMENTS

Permission to collect freshwater fishes in Sulawesi was granted by the Lembaga Ilmu Pengetahuan Indonesia (LIPI). Logistical support from Bambang Soerto and the Department of Fisheries, Universitas Sam Ratulangi, Manado, Massud and Tony Amos, Department of Fisheries, Universitas Hassannudin, Ujung Pandang, and Soetikno Wirjoatmodjo (LIPI) and Mohd. Amir (MZB) is gratefully acknowledged. Fieldwork was supported by the National Museum of Natural History Research Opportunities Fund, the Leonard P. Schultz Fund of the Department of Vertebrate Zoology (to LRP), and the Richter Fellowship and the Undergraduate Scholarship for Asia/Pacific Study of the Institute of International Education, Occidental College, California (to KDL). Loan of specimens, access to collections, and other information was provided by William N. Eschmeyer, Tomio Iwamoto, David Catania and Carl Ferraris (CAS), Maurice Kottelat (CMK), Barry Chernoff and MaryAnne Rogers (FMNH), and Daisy Wowor (MZB). Theophilus Britt Griswold photographed the holotype. Jeffrey Clayton (USNM) provided valuable technical assistance. Bruce B. Collette (Systematics Laboratory, National Marine Fisheries Service, Washington, D.C.) read and commented on an earlier draft of the manuscript, and in many other ways supported and encouraged our research on Sulawesi fishes. We are indebted to the Djaja family of Ujung Pandang for their extraordinary logistical support.

LITERATURE CITED

Audley-Charles, M. G., 1987. Dispersal of Gondwanaland: relevance to evolution of the angiosperms. In: T. C. Whitmore (ed.), *Biogeographical evolution of the Malay Archipelago.* Oxford University Press Monographs on Biogeography, No. 4, Oxford. Pp. 5-25.

Christensen, M. S., 1992. Investigations on the ecology and fish fauna of the Mahakam River in East Kalimantan (Borneo), Indonesia. *Intl. Rev. Hydrobio.*, **77**:593-608.

Croizat, L., 1958. *Panbiogeography, or, an introductory synthesis of zoogeography, phytogeography, and geology; with notes on evolution, systematics, ecology, anthropology, etc.* Published by the author, Caracas. Vol. 1, The New World, xxxi+1018 pp., vol. IIA, The Old World, pp. 1-771, vol. IIB, the Old World (continuation), pp. 772-1731.

Croizat, L., G. Nelson & D. E. Rosen, 1974. Centers of origin and related concepts. *Syst. Zool.,* **23**(2):265-287.

Daly, M. C., M. A. Cooper, I. Wilson, D. G. Smith & B. G. Hooper, 1991. Cenozoic plate tectonics and basin evolution in Indonesia. *Mar. Petro. Geol.,* **8**:2-21.

Dingerkus, G. & L. D. Uhler, 1977. Enzyme clearing of alcian blue stained whole small vertebrates for demonstration of cartilage. *Stain Tech.*, **52**:229-232.

Dyer, B. & B. Chernoff, 1996. Phylogenetic relationships among atheriniform fishes (Teleostei: Atherinomorpha). *Zool. J. Linn. Soc.,* **117**:1-69.

Hall, R., 1996. Reconstructing Cenozoic SE Asia. In: Hall, R. & D. Blundell (eds.), *Tectonic evolution of southeast Asia. Geol. Soc. Spec. Publ. no.* **106**:153-184.

Hamilton, W. B., 1979. Tectonics of the Indonesian region. *Prof. Pap. U.S. Geol. Surv.*, **1087**:1-338.

Hamilton, W. B., 1988. Plate tectonics and island arcs. *Geol. Soc. Amer. Bull.*, **100**:1503-1527.

Kottelat, M., 1994. The fishes of the Mahakam River, East Borneo: an example of the limitations of zoogeographic analyses and the need for extensive fish surveys in Indonesia. *Trop. Biodiversity*, **2**(3):401-426.

Kottelat, M., A. J. Whitten, S. N. Kartikasari & S. Wirjoatmodjo, 1993. *Freshwater fishes of Western Indonesia and Sulawesi*. Periplus Editions Ltd., Hong Kong. Xxxviii+221 pp., 84 pls.

Metcalfe, I., 1991. Late Palaeozoic and Mesozoic palaeogeography of Southeast Asia. *Palaeogeog., Palaeoclimat., Palaeoecol.*, **87**:211-221.

Michaux, B., 1996. The origin of southwest Sulawesi and other Indonesian terranes: a biological view. *Palaeogeo. Palaeoclim. Palaeoecol.*, **122**:167-183.

Nelson, G. & N. I. Platnick, 1981. Systematics and biogeography; cladistics and vicariance. Columbia University Press, New York. xi+567 pp.

Parenti, L. R., 1984. On the relationships of phallostethid fishes (Atherinomorpha), with notes on the anatomy of *Phallostethus dunckeri* Regan, 1913. *Am. Mus. Novit.*, **2779**:1-12.

Parenti, L. R., 1989. A phylogenetic revision of the phallostethid fishes (Atherinomorpha, Phallostethidae). *Proc. Calif. Acad. Sci.*, **46**(11):243-277.

Parenti, L. R., 1991. Ocean basins and the biogeography of freshwater fishes. *Aust. Syst. Bot.*, **4**:137-149.

Parenti, L. R., 1996. Phylogenetic systematics and biogeography of phallostethid fishes (Atherinomorpha, Phallostethidae) of northwestern Borneo, with description of a new species. *Copeia,* **1996**(3):703-712.

Parenti, L. R. & J. Song, 1996. Phylogenetic significance of the pectoral-pelvic fin association in acanthomorph fishes: a reassessment using comparative neuroanatomy. In: M. L. J. Stiassny, L. R. Parenti & G. D. Johnson (eds.), *Interrelationships of Fishes*. Academic Press, San Diego. Pp. 427-444.

Patten, J.M. & W. Ivantsoff, 1983. A new genus and species of atherinid fish, *Dentatherina merceri* from the western Pacific. *Japan. J. Ichthyol.*, **29**(4):329-339.

Polhemus, J. T. & D. A. Polhemus, 1990. Zoogeography of the aquatic Heteroptera of Celebes: regional relationships versus insular endemism. In: W. J. Knight & J. D. Holloway (eds.), *Insects and the Rain Forests of South East Asia (Wallacea).* Royal Entomological Society of London, London. Pp. 73-88.

Rangin, C. & The Tethys Pacific Working Group, 1990. The quest for Tethys in the western Pacific. 8 paleogeodynamic maps for Cenozoic time. *Bull. Soc. géol. Fr.*, **6**:907-913.

Regan, C. T., 1913. *Phallostethus dunckeri*, a remarkable new cyprinodont fish from Johore. *Ann. Mag. Nat. Hist.*, **12**:548-555.

Regan, C. T., 1916. The morphology of the cyprinodont fishes of the subfamily Phallostethinae, with descriptions of a new genus and two new species. *Proc. Lond. Zool. Soc.*, **1916**:1-26.

Roberts, T. R., 1971. Osteology of the Malaysian phallostethid fish *Ceratostethus bicornis*, with a discussion of the evolution of remarkable structural novelties in its jaws and external genitalia. *Bull. Mus. Comp Zool. Harvard Univ.*, **142**:393-418.

Schuh, R.T. & G. M. Stonedahl, 1986. Historical biogeography in the Indo-Pacific: a cladistic approach. *Cladistics,* **2**:337-355.

Simpson, G. G., 1977. Too many lines; the limits of the Oriental and Australian zoogeographic regions. *Proc. Amer. Phil.Soc.*, **121**:107-120.

Vane-Wright, R. I., 1991. Transcending the Wallace Line: do the western edges of the Australian region and the Australian plate coincide? *Aust. Syst. Bot.*, **4**:183-197.

Wallace, A. R., 1869. *The Malay Archipelago: the land of the Orang-Utan and the Bird of Paradise.* MacMillan, London. 2 vols., 478, 528 pp.