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Phylogenetic Systematics and Biogeography of Phallostethid Fishes (Atherinomorpha, Phallostethidae) of Northwestern Borneo, with Description of a New Species

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Until recently, the distinctive phallostethid genus *Phallostethus* was known from a single collection made in 1902 from Johor on the Malay Peninsula, described in 1913 by Regan as *Phallostethus duncheri*. In 1991 and 1993, specimens of *Phallostethus* were collected from disjunct coastal localities in Sarawak and Brunei, northwestern Borneo. These Borneo specimens differ from *Phallostethus duncheri* in morphology of the priapium (a complex, bilaterally asymmetric, subcephalic copulatory organ), pigmentation, and paradentary bone dentition. They are described herein as *Phallostethus lehi*, bringing the number of recognized phallostethid species to 20. *Phenacostethus smithi* Myers, 1928, previously unknown from Borneo has been collected from Sarawak, Brunei, and Kalimantan, bringing the total number of Bornean phallostethid species recognized currently to six. The phallostethids of Borneo do not form a monophyletic group but, instead, have complex, repeated sets of relationships with species on the Malay Peninsula and in the Philippines. Components of their biogeographic relationships are shared with other members of the stream biota. Composite biotic relationships are consistent with a composite geological origin of modern Borneo.

DESPITE two comprehensive monographs on Bornean freshwater fishes, one on the former North Borneo, now Sabah (Inger and Chin, 1962, 1990), and the second on the Kapuas River, Kalimantan Barat, Indonesian Borneo (Roberts, 1989), the freshwater and coastal fishes of a large, distinctive region of Borneo, including Sarawak and Brunei, are poorly collected, hence poorly known (Fig. 1). A neglected, but prominent, segment of the Bornean coastal and stream fish fauna includes small gobioids, cypriniforms, and silversides. One representative of the last group, the atherinomorph Phallostethidae, is a monophyletic (Hennig, 1966) family of 20 species classified in four genera grouped into two subfamilies, Phallostethinae (*Phallostethus* Regan, 1913, *Phenacostethus* Myers, 1928, and *Neostethus* Regan, 1916) and Gulaphallinae (*Gulaphallus* Herre, 1925), following the most recent revision (Parenti, 1989) and including the new species described herein (Table 1). Phallostethids are distinguished readily from all other teleost fishes by the presence in males of a complex, bilaterally asymmetric, subcephalic copulatory organ, called the priapium, and numerous other autapomorphies associated with maturation at a small size and internal fertilization (Roberts, 1971a, 1971b; Parenti, 1989).

Phallostethids are distributed broadly throughout coastal and freshwater habitats in southeast Asia, including Thailand, peninsular Malaysia, Singapore, northwestern Borneo, central Kalimantan, the Philippines and Sumatra (see Parenti, 1989, fig. 1; Kottelat et al., 1993). They are small (maximum-size recorded 37 mm SL), transparent to opaque, surface-feeding, schooling fishes. Phallostethids have been collected in relatively large numbers at certain localities (see materials in Roberts 1971a, 1971b; Parenti, 1989; and herein) but are rare in general collections. Scientific collections of the tribe Phallostethini (Table 1) from Borneo were first made in 1982 by the Royal Ontario Museum. I described that material from the Baram River, Sarawak, as a new species, *Phenacostethus trewavasae* Parenti (1986a).

In 1991, I began a survey of freshwater, coastal, and mangrove fishes of northwestern Borneo, defined here for the purpose of discussion as comprising Sarawak, Sabah, and Brunei (Fig. 1). Need for continued, comprehensive surveys of fishes in this region of Borneo was underscored by discovery that year of the highly autapomorphic *Phallostethus* in widely separated coastal localities in Sarawak and Brunei (Fig. 2). *Phallostethus* had been known previously from a single collection made in 1902 from Johor on the Malay Peninsula (Duncker, 1904) comprising the type series of *Phallostethus duncheri* Re-

Fig. 1. Major political divisions of Borneo and some major rivers discussed in the text. Dotted line, political boundary of Brunei; dotted and dashed line, political boundaries of Sarawak and Sabah. Lengths of rivers and tributaries are not precise.

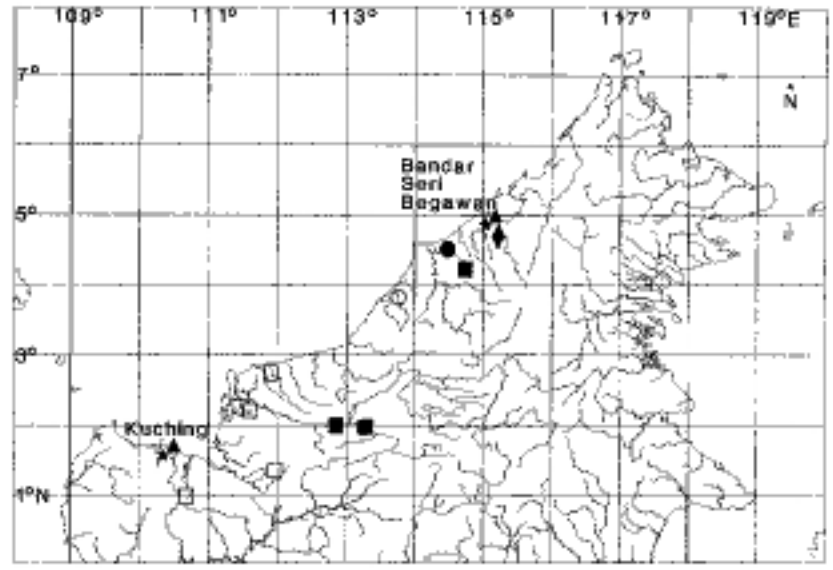

Fig. 2. Approximate localities of 1991, 1993, and 1994 collections of phallostethins from northwestern Borneo; each symbol may represent more than one collection. For description of a locality, see materials; USNM and Muzium Brunei material, solid symbols, CMK material, open symbols. *Phallostethus lehi*, stars; *Phenacostethus trewavasae*, circle, *Phenacostethus smithi* and *Phenacostethus* cf. *smithi*, squares; *Neostethus borneensis*, diamond, *Neostethus bicornis*, triangles.

gan, 1913, now in the ZMH and BMNH (see material below). During the past several years, *Phallostethus* has been searched for in the streams of Johor, but the only phallostethid found in those scientific collections is *Phenacostethus smithi* (see Additional Study Material); *P. dunckeri* is possibly extinct. The Borneo *Phallostethus* specimens differ in pigmentation, morphology of the priapium, and paradentary bone dentition (Parenti, 1986b) from the type series of *P. dunckeri* and are described herein as a new species, *Phallostethus lehi* (Fig. 3). In addition to *Phallostethus*, *P. smithi* Myers, 1928, was collected in 1991 from a tributary of the Rajang River near the town of Kapit, Sarawak, a species collected by T. R. Roberts that same year from Kalimantan Tengah, bringing the number of phallostethin species known from Borneo to three. I collected these three phallostethin species in northwestern Borneo again in 1993. Material of a possibly undescribed taxon is listed here as *Phenacostethus* cf. *smithi*. The tribe Neostethini is represented in Borneo by three species: *Neostethus bicornis* Regan, 1916, *N. borneensis* Herre, 1939, and *N. lankesteri* Regan, 1916, the first two of which were collected in Brunei in 1991. *Gulaphallus* is known only from the Philippines (Parenti, 1989).

The phallostethids of Borneo do not form a monophyletic group but, instead, have complex, repeated sets of relationships with species on the Malay Peninsula and in the Philippines (Parenti, 1986a, 1989, 1991; and below). In addition to supporting a distinctive fauna with numerous endemics, northwestern Borneo is geologically and hydrographically distinct from southeastern Borneo and should be recognized as an area of endemism in a historical biogeographic analysis (see Sengör, 1985; Michaux, 1991; and Discussion below).

TABLE 1. CLASSIFICATION OF FAMILY PHALLOSTETHIDAE, FOLLOWING PARENTI (1989).

Family Phallostethidae
Subfamily Phallostethinae
Tribe Phallostethini
Genus *Phallostethus*
Genus *Phenacostethus*
Tribe Neostethini
Genus *Neostethus*
Subfamily Gulaphallinae
Tribe Gulaphallini
Genus *Gulaphallus*

METHODS

Anatomical descriptions follow Parenti (1984, 1989). Osteology of *P. dunckeri* was illustrated by Parenti (1984) and that description will suffice for the genus, except as noted and figured herein for the new species. Male phallostethids

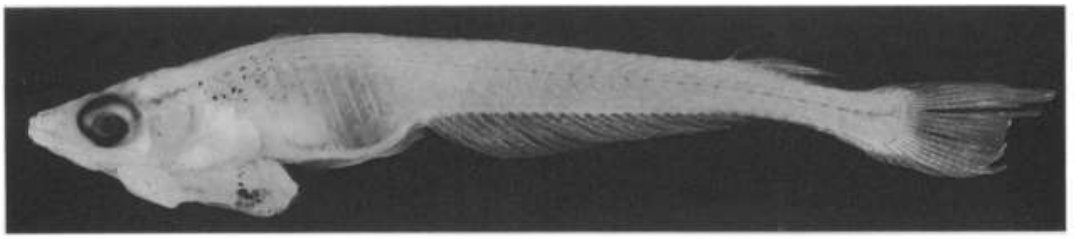

Fig. 3. *Phallostethus lehi*, new species. Holotype, USNM 329349, sinistral male, 27.1 mm SL, Sarawak River at Kuching, Sarawak, East Malaysia.

are bilaterally asymmetric: the anus is offset to one side of the body midline, termed by Regan (1916) the proctal side, and the seminal papilla is offset to the opposite side of the body midline, the aproctal side. Males with the aproctal side on the left are termed sinistral; hence, males with the aproctal side on the right are dextral. Males also have a prominent, external priapial bone, a toxactinium arising on the proctal side in *Phallostethus* and *Phenacostethus*, or a ctenactinium arising on the aproctal side in *Neostethus* and *Gulaphallus*. Counts were made from cleared-and-stained preparations, radiographs, and alcohol specimens. Counterstained specimens were prepared according to Dingerkus and Uhler (1977). The phylogenetic systematics computer program Hennig86 (J. S. Farris, 1988, distributed by the author) was used to generate a phylogenetic hypothesis, expressed as a cladogram. The length of a cladogram is the total number of character state changes. The consistency index (CI) is a ratio of the minimum possible number of character state changes to the actual number of changes; the retention index (RI) is a ratio of the number of maximum possible changes minus the number of observed changes to the number of maximum possible changes minus the number of minimum changes (Farris, 1989).

Abbreviations: SL, standard length; Sg., sungai or sungei (Malay or Indonesian, respectively, for river); trib., tributary; juv., juvenile. Other abbreviations are clear in context. Institutional abbreviations are as in Leviton et al. (1985); CMK is the private collection of M. Kottelat, Switzerland. Material in the Muzium Brunei is not cataloged formally and is identified by an entry in the Natural History Section logbook. Coordinates of localities are approximate.

Phallostethus Regan, 1913

Phallostethus Regan, 1913:548–550 (type species: *P. dunckeri* Regan, 1913, by monotypy).

Differential diagnosis.—(Modified from Parenti, 1989:267) Anal fin longer (26–28 rays, as opposed to 13–22) and vertebral number higher (40, as opposed to 31–37) than in all other phallostethids. Males are readily separable from those of *Phenacostethus* by a serrated ctenactinium (Fig. 4, compare with Parenti, 1986a, fig. 4). Both sexes differ from *Phenacostethus* by lacking the first dorsal fin and having a second dorsal fin with 8–10, rather than 5–7, rays.

Composition and distribution.—Two species, *P. dunckeri* Regan, 1913, Johor, West Malaysia, and *P. lehi*, new species, Sarawak, East Malaysia, and Brunei, described below.

Phallostethus lehi, n. sp.
Figures 3–4

Differential diagnosis.—*Phallostethus lehi* is distinguished from its sister species, *P. dunckeri*, by having more serrae on the second ctenactinium (eight as opposed to five), females with a few minute melanophores posterior to the urogen-

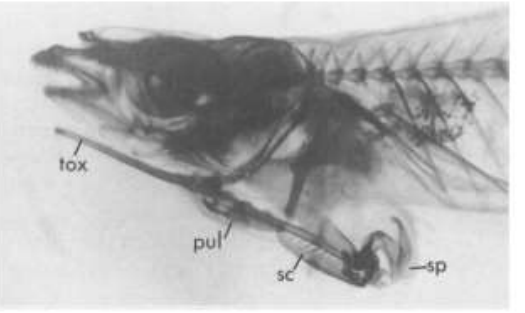

Fig. 4. *Phallostethus lehi*, new species. Photomicrophotograph of head and anterior portion of body of cleared-and-counterstained sinistral male paratype, USNM 325054 (focused on second ctenactinium). Anterior to the left. Abbreviations: tox = toxactinium; pul = fibrous pulvinular pad; sc = second ctenactinium; sp = seminal papilla.

ital openings (as opposed to having many large melanophores), and a high number of uniserial, unicuspid teeth on the paradentary bone (28 or more as opposed to approximately 15–20). Further, the four known adult males of *P. lehi* are sinistral; therefore, it is possible that males of this species are exclusively sinistral. *Phallostethus dunckeri* is known from a total of 25 specimens, including one sinistral and two dextral males.

Description.—A moderately large phallostethin species as diagnosed by Parenti (1989:257) reaching a recorded 27.5 mm SL. Anus and urogenital openings anterior, ventral to pectoral-fin base, in both sexes. A median, abdominal, slightly frayed, fleshy ridge or keel from urogenital openings to anterior anal-fin rays. Anal-fin rays 25–27. First dorsal fin absent. Dorsal-fin rays 8–9. Pectoral-fin rays 12. Pelvic fin vestigial in adult females, represented by pelvic bone and one to three rays. Caudal fin emarginate, symmetrical, forming incipient lobes, branched caudal-fin rays 6/6. Vertebrae 40 (12 + 28). First pleural rib on fourth vertebra in females, fifth vertebra in males. No epineural bones.

Eye-lens large. Dorsal surface of head without membranous dome in alcohol. Outer jaws highly protractile, with elongate premaxillary ascending process and submaxillary bone between maxilla and vomer. Unicuspid teeth biserial on premaxilla and dentary, teeth relatively small medially, larger on lateral ramus of premaxilla. Paradentary bone robust in adults, with approximately 28 small, uniserial, unicuspid teeth. Hyobranchial apparatus reduced relative to that of other atherinoids; small tooth patch on fourth ceratobranchial bone. Gillrakers on first arch elongate, 14. Four branchiostegal rays, a rudimentary, anterior fifth ray in some specimens.

Males bilaterally asymmetric, sinistral: anus and seminal papilla offset to opposite sides of the body midline, proctal (right) and aproctal (left), respectively. The proctal axial bone is the main bony priapial support. Main external bones are a long, curved toxactinium and a short, stout ctenactinium with eight serrae in mature males, not counting the anterior hook. Anterior ramus of cleithrum not elongate. Postcleithra absent. First pair of pleural ribs in males expanded anteroposteriorly and dorsoventrally, ventral tips meeting and enclosed in block of cartilage. Large, fibrous pad, the pulvinulus, covers articulation point of toxactinium and proctal axial bone.

Color in life.—As in other phallostethins, body and fins nearly transparent in life and caudal peduncle with small, orange blotch. Eye silvery above. Other pigmentation as in alcohol specimens, below.

Color in alcohol.—Ground coloration a uniform pale cream to yellow, with small melanophores on dorsal surface of head and body, midlateral intermuscular septum, anal-fin base, and dorsal and ventral midline. Large, black blotches on interradial membranes of dorsal portion of pectoral fin. Dorsal scales with faint brown to black margins. Seminal papilla and surrounding basal portion of priapium with a large black blotch.

Etymology.—*lehi*, in honor of Dr. Charles Leh, Muzium Sarawak and the Ministry of Environment and Tourism, who aided the first scientific collection of *Phallostethus* in Borneo.

Habitat.—*Phallostethus lehi* was collected at the surface using a dip net or scoop net from a boat in mangroves and tidal portions of rivers. In Kuching, it was found near shorelines dense with nipah palm as well as near the concrete boat launch at the fish market.

Study material.—*Phallostethus lehi*: HOLOTYPE, USNM 329349, sinistral male, 27.1 mm SL, East Malaysia: Sarawak: Kuching: tidal portion of Sg. Sarawak between boat launch at fish market and just past State Mosque (1°33′N, 110°25′E), 2 July 1993, L. R. Parenti, A. L. Downing, and party from Muzium Sarawak. PARATYPES, USNM 334043 (ex. USNM 329349; 8: 1 sinistral male, 7 females), collected with holotype. Brunei: Muzium Brunei Natural History Section NH/91-81, adult female, 18.5 mm SL, USNM 325052, adult female, 25.5 mm SL, Sg. Dolhakim, trib. of Sg. Brunei, near Bandar Seri Begawan (4°50′N, 115°00′E), 17 Aug. 1991, L. R. Parenti, M. Wong, and party from Muzium Brunei. USNM 325044, sinistral male, 25.5 mm SL, Sg. Dolhakim, trib. of Sg. Brunei, near Bandar Seri Begawan (4°50′N, 115°00′E), 19 Aug. 1991, L. R. Parenti, M. Wong, and party from Muzium Brunei. Malaysia: Sarawak: USNM 325050, adult female, 27.5 mm SL, Kuching, Sg. Sarawak, N shore at Kampung Tupong (1°33′N, 110°25′E), 20 July 1991, L. R. Parenti, M. Zakaria-Ismail, and party from Muzium Sarawak. USNM 325054, 17 (sinistral male, 4 females, 12 juv., 9.0–26.1 mm SL, of which the sinistral male, a female and a juv. have been cleared and counterstained with alcian blue and alizarin), Kuching, Sg. Sarawak, N shore at Kampung Tupong (1°33′N, 110°25′E), 13 Aug. 1991, L. R. Parenti and party from Muzium Sarawak.

TABLE 2. DATA MATRIX FOR 18 CHARACTERS OF FIVE SPECIES OF PHALLOSTETHINS. Autapomorphies not included. Characters 8 through 18 were used in the parsimony analysis.

	Character																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Neostethus lankesteri	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phallostethus lehi	1	1	1	1	1	1	?	0	0	0	2	1	1	2	1	1	1	0
Phallostethus dunckeri	1	1	1	1	1	1	1	0	0	0	2	1	0	2	1	1	1	0
Phenacostethus smithi	1	1	1	1	1	1	1	1	1	0	0	1	0	1	0	0	0	1
Phenacostethus trewavasae	1	1	1	1	1	1	?	1	1	1	1	2	1	1	0	0	0	1
Phenacostethus posthon	1	1	1	1	1	1	1	1	1	1	1	2	1	1	0	0	0	1

Characters: 1. body robust, fully scaled (0), slender, scales deciduous (1); 2. body opaque (0), translucent (1); 3. main external bone of priapium a ctenactinium (0), toxactinium (1); 4. fleshy seminal papilla absent (0), present (1); 5. pelvic rays fully formed (0), reduced or absent (1); 6. vas deferens relatively short and straight (0), long and highly coiled (1); 7. spermatozeugmata formed (0), not formed (1), unknown (?); 8. dorsum of head without membranous dome (0), with dome (1); 9. upper and lower jaws relatively equal in length (0), lower jaw protrudes beyond upper jaw (1); 10. penial bone present (0), absent (1); 11. ctenactinium robust and smooth (0), small or absent (1), large and serrated (2); 12. toxactinium absent (0), relatively straight (1), distinctly curved (2); 13. males either sinistral or dextral (0), only sinistral or only dextral (1); 14. anal-fin rays 16–17 (0), 14–15 (1), 26–28 (2); 15. vertebrae 34–35 (0), 40 (1); 16. first dorsal fin present (0), absent (1); 17. second dorsal-fin rays 5–7 (0), 8–10 (1); 18. adults small, mature at 20 mm SL or more (0), miniature, mature at about 15 mm SL (1).

Phylogenetic relationships and distribution of Borneo phallostethids.—Parenti (1986a, fig. 5) hypothesized phylogenetic relationships among phallostethin species, and summarized them in a cladogram that was calculated by hand. Characters from that paper, Parenti (1989), Grier and Parenti (1994), and data presented herein for *P. lehi*, have been coded in a data matrix (Table 2). Characters in the matrix are not necessarily numbered as in Parenti (1986a, 1989).

Phallostethin monophyly is well supported by characters 1 through 6, and possibly 7. The implicit enumeration option of Hennig86 found a single shortest tree (Fig. 5) for characters 8 through 18 in Table 2. Multistate characters were treated as unordered. Characters for a plesiomorphic *Neostethus* species, *N. lankesteri*, were used to root the tree, following Parenti (1989).

Phallostethus lehi is the hypothesized sister species of *P. dunckeri*, Malay Peninsula, its only congener. *Phenacostethus*, the sister genus of *Phallostethus*, comprises three species, *P. posthon*, Malay Peninsula and Sumatra; its sister species, *P. trewavasae*, Brunei and Sarawak; and their closest relative, *P. smithi*, from Malay Peninsula, Sarawak, Brunei, Sumatra, and Kalimantan. The cladogram of relationships (Fig. 5) may be converted into an area cladogram (Fig. 6) by substituting the name of the species by the name of the area in which it lives, following Nelson and Platnick (1981).

The monophyletic *Neostethus* is distributed broadly throughout much of the range of phallostethids including peninsular Malaysia, Singapore, northwestern Borneo, and the Philippines. The three Borneo species, *N. bicornis*, *N. borneensis*, and *N. lankesteri*, do not form a mono-

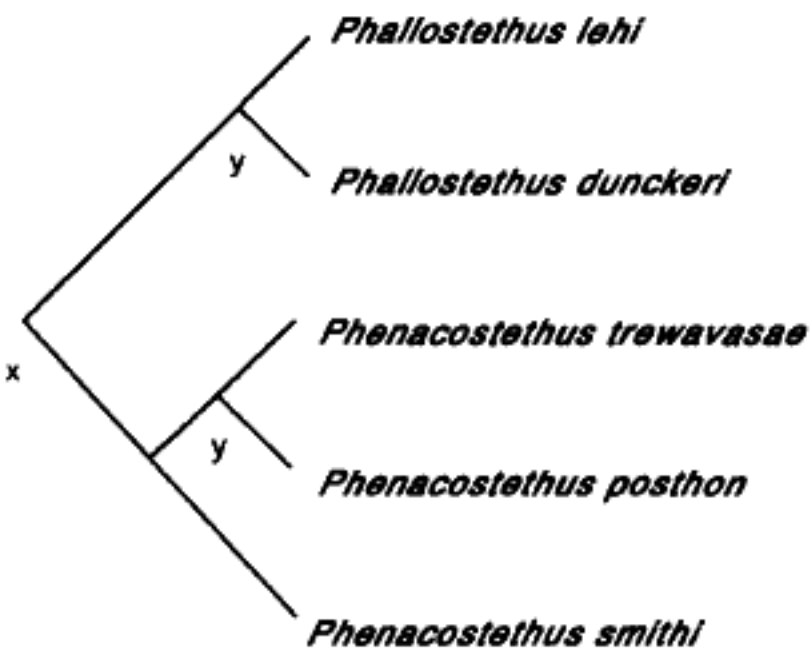

Fig. 5. Cladogram of phallostethin species calculated from characters 8 through 18 of data matrix in Table 2 using implicit enumeration option of Hennig86. Length = 15 steps; CI = 0.93; RI = 0.93.

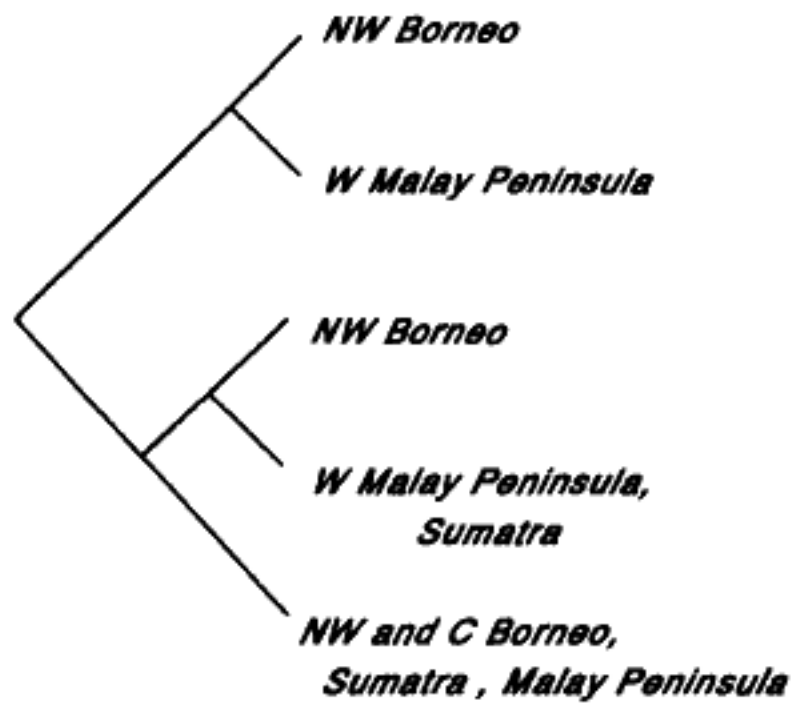

Fig. 6. Area cladogram of phallostethin species derived from Figure 5.

Fig. 7. Accretionary complex of northwestern Borneo, following Sengör (1985) and Daly et al. (1991). Stippled area, accretionary complex; hatched line, Sabah and Sibu sutures.

phyletic group (Parenti, 1989, fig. 8). *Neostethus bicornis* and *N. lankesteri* have broad distributions nearly coincident with that of the genus *Neostethus*; *N. borneensis* is known from northwestern Borneo and Coron I., Philippines. A cladogram of relationships and an area cladogram for *Neostethus* species were presented by Parenti (1991, figs. 6–7).

Discussion

Borneo is treated in historical biogeographic studies as part of Sundaland, comprising the Malay Peninsula, Sumatra, Borneo, and Java, a contiguous, continental land mass during periods of lowered sea-level that was drained by the Sunda River, flowing south into the Indian Ocean (Ollier, 1985). The history of Borneo is often included within the history of Sundaland without clarification (Audley-Charles, 1987). Exact limits of Sundaland are unknown, however, and evidence that it functioned as a geological unit throughout the Cenozoic is lacking (Schmidtke et al., 1990; Daly et al., 1991). Furthermore, northwestern Borneo (Sabah, Sarawak, and Brunei) was not drained by the Sunda River (Ollier, 1985), and, today, rivers of northwestern Borneo flow northwest, north, and east into the South China, Sulu, and Celebes seas, respectively (Fig. 1).

The independent drainage pattern of northwestern Borneo is consonant with its independent geological history. Each modern large island in the Indo-Australian archipelago (Borneo, Sulawesi, New Guinea) is a geological composite (Hamilton, 1979, 1988). Identification of the distinct components of each island, the component's age, and age of formation of the modern island will help eliminate incongruence from historical biogeographic studies that results when composite areas are treated as a single area with a single age of origin (see New Guinea example in Parenti, 1991). Recognition of the distinct geological and biological history of the composite areas of Borneo may be useful in other biogeographic studies in which Borneo is usually treated as a single area (e.g., Cracraft, 1988, for birds).

Hamilton (1979, 1988) interpreted geology of the Indo-Australian region explicitly within a plate tectonic model and confirmed the extreme complexity of landmass relationships throughout geological history. Assembly of continental southeast Asia from allochthonous (to Eurasia) Gondwanian terranes between the late Paleozoic and Mesozoic periods is detailed by Metcalfe (1991). Daly et al. (1991) provide a comprehensive summary of plate tectonics and basin evolution in southeast Asia during the Cenozoic, from 70 MYA to the present. They identify seven major tectonic events in the Indonesian region during this period, two of which pertain directly to Borneo (Daly et al., 1991:7): 32 MYA, ocean-floor spreading began in the South China Sea, with subduction in northwestern Borneo; and by 17 MYA, that ocean-floor spreading ceased as Palawan and the allochthonous Reed Bank terrane collided with Borneo. Collision with Borneo of this mixture of continental fragments and volcanic material created an accretionary wedge composed of oceanic flysch or mélange fill (Sengör, 1985; Daly et al., 1991), called the Eocene accretionary complex (Hamilton, 1979). The accretion, outlined by a suture in two named segments, Sabah and Sibu, marks the boundary between the allochthonous terrane and the rest of Borneo (Fig. 7).

Correspondingly complex relationships of the Bornean biota to that of the rest of the Indo-Australian archipelago were recognized by Croizat (1958) who drew five biogeographic tracks or lines from Borneo representing biotic similarity: from SE Kalimantan to Sumatra and Sulawesi; from W Kalimantan to the Malay Peninsula; from NW Borneo to Palawan; from NW Borneo to Mindanao; and from NW Borneo, across the South China Sea, to mainland China. Croizat's (1958) summary implies a polyphyletic Bornean biota, including close relationship of

some northwestern Borneo taxa to those in the Philippines and subtropical China.

Geologically and hydrographically distinct northwestern Borneo may be considered a putative area of endemism for at least a portion of the fish fauna. An area of endemism, as defined by Harold and Mooi (1994:262) is ". . . a geographic region comprising the distributions of two or more monophyletic taxa that exhibit a phylogenetic and distributional congruence and having their respective relatives occurring in other such defined regions." This definition requires a hypothesis of phylogenetic relationships among three taxa from three different areas of endemism, analyses lacking for the bulk of the southeast Asian fish fauna. Nonetheless, statements may be made about the distribution and relationships of northwestern Borneo fishes, which include numerous endemics that have repeated, overlapping relationships to those throughout southeast Asia (Kalimantan/Malay Peninsula/Sumatra) or to the north (Philippines/China). Fish taxa with close relatives in the first category are numerous and include the goramy, *Osphronemus laticlavius*, endemic to Sabah (Roberts, 1992), the loach, *Pangio agma*, endemic to northern Sarawak and Brunei (Burridge, 1992), the halfbeak, *Hemirhamphodon kuekenthali*, endemic to Sarawak and Brunei (Anderson and Collette, 1991), the pufferfish, *Carinotetraodon salivator*, endemic to Sarawak (Lim and Kottelat, 1995), and the minnow, *Rasbora kottelati*, endemic to Sarawak and Brunei (Lim, 1995), each of which has a close relative distributed more broadly throughout southeast Asia. This distribution is duplicated in numerous fish taxa for which there are northwestern Borneo representatives but no northwestern Borneo endemic (Weber and de Beaufort, 1913). Fish taxa with close relatives in the second category include gastromyzontine loaches, distributed throughout Borneo and across the South China Sea in Viet Nam and China (Roberts, 1982). The gastromyzontine loach genus *Protomyzon* has been reported from northwestern Borneo (Inger and Chin, 1962, 1990) and China (Chen, 1980), including Hainan Island. The genus *Glaniopsis* is known from localities throughout northwestern Borneo (Roberts, 1982); its sister group is unknown.

The two endemic northwestern Borneo phallostethins have replicated distribution components. *Phallostethus lehi* and *P. trewavasae* both have their sister species in Malay Peninsula/Sumatra (Fig. 6). The phallostethin cladograms (Figs. 5–6) may be used to infer relative timing of differentiation events. The cladograms require that differentiation between the genera *Phallostethus* and *Phenacostethus* (at time x) occurred prior to an inferred vicariant event (at time y) that produced the sister-group pairs. If speciation between northwestern Borneo and Malay Peninsula/Sumatra taxa was inferred to have been caused by lowered Pleistocene sea levels (as in Polhemus and Polhemus, 1988; Bornbusch and Lundberg, 1989; and elsewhere), then differentiation between genera was caused by a relatively older vicariant event. The widespread distribution of *P. smithi* (Fig. 7) may reflect our failure to identify at the specific level or above differences among populations from northwestern Borneo, central Borneo, Sumatra, and the Malay Peninsula.

This assessment of northwestern Borneo biotic affinities is preliminary in that phylogenetic systematic revisions of most taxa have not been carried out and, when they have, not always at a taxonomic level appropriate to the question at hand. Recognition of northwestern Borneo as an area of endemism and recognition of vicariant relationships for some portion of that biota that predate Pleistocene events will aid and encourage the further discovery of underlying vicariant patterns in an area for which distributions have been explained traditionally solely by dispersal. If, for example, distribution of the northwestern Borneo biota has been affected by vicariant events associated with opening of the South China Sea, we may expect to find taxa, either freshwater or marine, distributed around the basin (viz. Parenti, 1991). The water strider, *Rhagovelia kawakamii*, lives in northwestern Borneo, Palawan, Luzon, and Taiwan, islands that today form the eastern rim of the South China basin (Polhemus and Polhemus, 1988). *Neostethus borneensis*, a northwestern Borneo phallostethid, also lives in Coron Island, the Philippines. That species is most closely related to a Philippine sister-group pair, one species of which lives in Mindanao, the other in Mindanao and Luzon (Parenti, 1989). One benefit of even such a preliminary analysis is that we may predict where to search for close relatives of northwestern Borneo endemics. Subtropical Hainan Island, across the south China Sea from northwestern Borneo, is one area that may likely contain close relatives of portions of the northwestern Borneo biota, especially the often overlooked mangrove and estuarine fishes.

Additional study material.—Phallostethus dunckeri: Lectotype (designated by Ladiges et al., 1958): ZMH 193, dextral male, mouth of Sg. Muar, Johor, Malaysia, 1902, G. Duncker. Paralectotypes: BMNH 1913.5.24:18–22 (5: 1 sin-

istral male, 3 females, 1 sex undet.) and ZMH 194–195 (19: 2 dextral males, 14 females, 3 juv.) collected with lectotype.

Phenacostethus smithi: East Malaysia: Sarawak: USNM 325049 (5), Sg. Baleh, trib. of Sg. Rajang, Sg. Sut, first mapped trib. E of Kapit, about 2 Km S of where the Sut enters the Baleh, 24 July 1991, L. R. Parenti, M. Zakaria-Ismail, and K. Luhat. USNM 325048 (11), Sg. Kapit, just S of where it enters the Sg. Rajang, 27 July 1991, L. R. Parenti and K. Luhat. West Malaysia: Johor: ZRC 16802–16805 (4), Sg. Sayong, 5 Sept. 1990, A. D. Munro; ZRC 19342–19346 (5), stream along Kota Tinggi-Desaru Rd, 14 Aug. 1991, P.K.L. Ng and M. Kottelat; ZRC 23138–23147 (10), CMK 8541 (10), Sg. Tui, 25 km from Labis on road to Muar, 26 July 1992, K. Lim et al. Brunei: USNM 329346 (21), Muzium Brunei Natural History Section NH/95-3 (10), Ulu Belait, along bank just upstream from Kuala Ingei (4°10′N, 114°43′E), 14 July 1993, L. R. Parenti, A. L. Downing, Hj. Ramlee, M. Wong et al. USNM 329581 (73), Muzium Brunei Natural History Section NH/95-4 (30), Ulu Ingei, trib. of Ulu Belait, at base camp (4°10′N, 114°43′E), 7 July 1993, L. R. Parenti, A. L. Downing, Hj. Ramlee, Hj. Ahmad. USNM 329582 (16), Muzium Brunei Natural History Section NH/95-5 (10), Ulu Belait, just downstream from Lubok Tapah (4°10′N, 114°42′E), 13 July 1993, L. R. Parenti, A. L. Downing, Hj. Ramlee, M. Wong, et al. Indonesia: Borneo: ZRC 22455–22464 (10), Kalimantan Tengah Mentaya basin, blackwater tidal creek on left bank of Sg. Mentaya, one-half hour by speedboat upriver from Sampit, 10 June 1992, T. R. Roberts. Riau I.: USNM 326054 (10), Pulau Bintan, May 1993, ZRC field no. SS13.

Phenacostethus cf. *smithi*: Brunei: USNM 329347 (2), Ulu Ingei, trib. of Ulu Belait, at base camp (4°10′N, 114°43′E), 6 July 1993, L. R. Parenti and A. L. Downing. East Malaysia: Sarawak: CMK 10965 (18), Sg. Engkurah, 8.5 km on road from Tebakang to Mongkos above where it branches from road between Serian and Tebedu, 16 May 1994, M. Kottelat, D. Chung, H. H. Tan and S. H. Tan; CMK 10908 (8), Sg. Semanju, road from Sri Aman to Lubok Antu, 9 km above where it branches from Sri Aman-Sibu road, 10 May 1994, M. Kottelat, D. Chung and C. Leh; CMK 10983 (8), Sg. Pahlawan, about midway on road between Oya and Dalat, in sago forest, 15 June 1994, M. Kottelat, T. Tan and C. Leh; CMK 10952 (45), brown water stream 6 km S. of Durin ferry on road between Sibu and Sarikei, M. Kottelat, D. Chung, H. H. Tan, and S. H. Tan.

Phenacostethus posthon: Indonesia: Sumatra: Riau Prov.: CMK 7308 (1), Sg. Siak basin, canal connecting Sg. Siak and Sg. Siak Kecil, about 1 km upstream from confluence, 13 Feb. 1991, M. Kottelat.

Phenacostethus trewavasae: Brunei: USNM 329580 (15), Muzium Brunei Natural History Section NH/95-6 (10), trib. stream of Sg. Belait, bet. Kuala Balai and Badas (4°30′N, 114°20′N), 28 July 1993, L. R. Parenti, A. L. Downing, Hj. Ramlee, et al. East Malaysia: Sarawak: CMK 10997 (12), Sg. Niah, between Batu Niah and Niah Cave Headquarters, 16 June 1994, M. Kottelat, T. Tan and C. Leh.

Neostethus borneensis: Brunei: USNM 325046 (11), Muzium Brunei Natural History Section NH/91-183 (11), Sg. Dolhakim, trib. of Sg. Brunei, near Bandar Seri Begawan (4°50′N, 115°00′E), 17 Aug. 1991, L. R. Parenti, M. Wong, and party from Muzium Brunei; USNM 321316 (162), CAS 79340 (10), Muzium Brunei Natural History Section NH/91-215 (30), same locality, 19 Aug. 1991. USNM 325047 (7), Muzium Brunei Natural History Section NH/91-203 (4), Sg. Baung near where it enters Sg. Malais, trib. of Sg. Brunei (4°50M, 115°00′E), 19 Aug. 1991, L. R. Parenti, M. Wong, and party from Muzium Brunei.

Neostethus bicornis: Brunei: USNM 325051 (7), Muzium Brunei Natural History Section NH/91-213 (4), Sg. Dolhakim, trib. of Sg. Brunei, near Bandar Seri Begawan (4°50′N, 115°00′E), 19 Aug. 1991, L. R. Parenti, M. Wong, and party from Muzium Brunei. East Malaysia: Sarawak: USNM 325053 (30), Kuching, Sg. Sarawak, N shore at Kampung Tupong (1°33′N, 110°25′E), 13 Aug. 1991, L. R. Parenti and party from Muzium Sarawak. Indonesia: Kalimantan Timur: CMK 9482 (14), CMK 11024 (2 adult males cleared and stained solely with alcian blue), ROM 66669 (2), Sg. Sebuku basin, Sg. Tulit, about 1 km downriver from confluence of Semunad and small tributary creek. Additional material is listed in Parenti (1989).

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