
BISHOP MUSEUM OCCASIONAL PAPERS

TAXONOMY, PHYLOGENY, AND ZOOGEOGRAPHY
OF THE GENUS *CYLINDROSTETHUS* FIEBER
IN THE PALEOTROPICAL REGION
(HETEROPTERA: GERRIDAE)

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TAXONOMY, PHYLOGENY AND ZOOGEOGRAPHY OF THE GENUS *CYLINDROSTETHUS* FIEBER IN THE PALEOTROPICAL REGION (HETEROPTERA: GERRIDAE)

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ABSTRACT. The genus *Cylindrostethus* is reviewed for the Paletropical Region. Two new species are described, *C. samarinda* from eastern Borneo and *C. malayensis* from the Malay Peninsula and northern Sumatra, and *C. brachykanthinos* Chen and Nieser is synonymized under *C. persephone* Kirkaldy. A phylogeny of all species occurring in the Paletropical region is presented based on morphological characters. Three distinct monophyletic species groups, the *sumatranus*, *costalis*, and *scrutator* groups, are recognized. These groups are further defined on the basis of ecological characters. A key to all Paletropical species is provided, accompanied by illustrations of key characters for the new Asian species and distribution maps for all Paletropical species. A character analysis and phylogeny are presented, followed by a discussion of the historical zoogeography of the genus.

INTRODUCTION

Members of the genus *Cylindrostethus* are large, elongate water striders inhabiting smoothly flowing tropical rain forest streams. The group contains distinctive and disjunct monophyletic species assemblages in the Neotropical and Paletropical regions¹, which appear to have evolved in relative isolation. The Paletropical component was treated by Hungerford and Matsuda (1962), but since that time two new species have been discovered in Southeast Asia, necessitating a review of the tropical Asian fauna.

Hungerford and Matsuda (1962) provided complete synonymies, detailed descriptions and excellent illustrations for all Paletropical *Cylindrostethus* species, excepting the two new species described herein. For the sake of brevity this information has not been repeated, and readers desiring such details should refer instead to the above work. The present report, by contrast, provides a character analysis and species level phylogeny for the Paletropical species, along with much new information on individual species distributions in Southeast Asia. Maps are provided detailing the ranges of all Southeast Asian species, accompanied by a zoogeographical synthesis presenting hypotheses on the faunal evolution of the genus, with particular reference to tropical Asia.

¹ I have used the term Paletropical herein to refer to the totality of the Old World tropics, including Africa, Asia, northern Australia and the Pacific islands. Despite obvious regional differences, these areas are all united by many elements common to their tropical biotas and form a natural biogeographic entity. Paletropical has precedence in the botanical literature, and stands in logical contrast to Neotropical, which has become the widely accepted regional term for the New World tropics. This same symmetry of terminology is also seen in the boreal regions, where Nearctic and Palearctic have enjoyed long usage.

ECOLOGY

Despite their large size and relative abundance, no ecological or life history studies are available for Asian *Cylindrostethus* species. The following ecological notes are therefore of necessity anecdotal, but do provide basic insights into the behavior of these insects.

Cylindrostethus species are swift and elegant skaters, occurring primarily on the smoother portions of rainforest streams. Their typical mode of locomotion is a strong kick followed by a long glide, with turns accomplished during the kick phases and the subsequent glides essentially straight. This motion on the water is extremely distinctive and stands in marked contrast to the type of movement seen in other large Asian gerrids of the genus *Ptilomera*, which tend to row more continuously and do not employ a long gliding motion. It is on the other hand similar in some respects to the motions used by another large Asian genus, *Limnometra*, except that the *Limnometra* species do not seem to have the same efficiency of gliding displayed by *Cylindrostethus*, and thus cannot generate comparable speed on the water.

Populations of *Cylindrostethus* generally contain a mixture of winged and wingless morphs, with the latter usually predominating. This frequency of winged morphs is intermediate between the situation seen among *Ptilomera* species, wherein the populations are composed almost entirely of wingless morphs with winged individuals only rarely encountered, and *Limnometra*, wherein nearly all individuals are winged and wingless forms are quite rare. A greater frequency of winged individuals probably conveys a greater potential for dispersal and inhibits the establishment of locally isolated populations. In support of such a hypothesis one might note that the predominantly wingless *Ptilomera* have diversified into a confusing array of regionally precinctive species, while the primarily winged *Limnometra* include many species with broad distributions covering most of the Malay Archipelago. *Cylindrostethus*, with its intermediate frequency of winged morphs, shows a limited degree of regional allopatry and thus falls between the two extremes discussed above.

Two ecologically distinct sets of *Cylindrostethus* species presently occur in Southeast Asia, roughly corresponding to what I have defined below as the *scrutator* and *costalis* species groups. These groups are easily distinguished morphologically, as given in the key and phylogeny, and are also separable on the basis of their habitat preferences. The species of the *scrutator* group usually occur on rocky upland streams, skating on smoothly flowing pools, while members of the *costalis* group frequent streams in lowland swamp forests. These ecological divisions are not absolute, since *C. costalis* was found on a rocky stream at Mae Sa waterfall in northern Thailand, and *C. scrutator* was occasionally encountered on lowland streams in peninsular Malaysia, but in general this pattern of habitat preferences seems to provide a useful character in defining these two groups.

The species of the *costalis* group, which are larger in body size than those of the *scrutator* group, appear to replace species of another large gerrid genus, *Ptilomera*, in the lowland swamp forest habitats. On smoothly flowing streams in such areas the two genera are almost never encountered in sympatry. *Ptilomera* species as a whole seem to require areas of turbulent flow, and this ecological factor may account for their absence on the slow, slick swamp forest streams of the lowlands. In addition, since the

Cylindrostethus species of the *costalis* group are nearly the same size as *Ptilomera* and appear better suited to skating on pools or in smoothly flowing areas an element of competitive displacement may be involved, but this is unproven.

By contrast, the smaller bodied *Cylindrostethus* species of the *scrutator* group frequently do co-occur with *Ptilomera* on more turbulent rocky upland streams. This pattern was evident at the Kota Tinggi waterfall in Johor, where *C. scrutator* and *P. tigrina* were sympatric, and on the Tumpah River in northern Celebes, where *C. persephone* and *P. dorceus* were both present. On upland streams where the two genera are sympatric there is a clear partitioning of habitat, with *Ptilomera* in the riffles and *Cylindrostethus* on the flowing pools.

Another species that does not fall into either of the above taxonomic groupings is also present in Southeast Asia: *C. sumatranus* Lundblad. This is a poorly known *Cylindrostethus* from southern Sumatra, and is the only species in the region that I have not collected or observed in the wild. Although no ecological information is available for *C. sumatranus*, I suspect from its relatively small size and robust body structure that it, like the members of the *scrutator* group, is an inhabitant of rocky upland streams.

METHODS

All descriptonal observations, including color, were made from dry pinned specimens. Measurements are given in millimeters, and represent the dimension of a specimen of average size. Measurements of leg segments on the middle and hind legs should be treated as approximate, since these legs often curl in dried specimens and their lengths are thus difficult to determine with precision; in addition, the lengths of these leg segments often display a degree of intraspecific variation.

The synonymies provided for previously described species are nomenclatural only. CL numbers following localities refer to a coding system used to cross-reference ecological notes and habitat photos. Localities in the material examined sections have been assigned to their modern states or provinces within countries, even though these data are often not present on the original labels. In addition, modern place names or references to nearby landmarks depicted on currently available maps have been added in brackets following certain localities in order to assist in the interpretation of older label data. On the distributional maps localities in close proximity are represented by a single symbol. Collection repository codes for specimens are provided in the acknowledgements.

SYSTEMATICS

KEY TO PALEOTROPICAL SPECIES OF *CYLINDROSTETHUS*

Note: in certain couplets where color characters are employed, care must be taken in using such characters with older dried specimens. Certain species which are black in life may turn brown over time when pinned; these are known to include *C. persephone* and *C. samarinda*. Dry pinned specimens collected within the last 20 years or fluid preserved specimens should not present this problem.

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1. Dorsal length of abdomen of both sexes shorter than or equal to dorsal length of thorax; female connexiva folded inward over apical abdominal tergites; coloration brown; males and females of relatively equal length; Africa and Sumatra 2 (*sumatranus* group)
- Dorsal length of abdomen in females always exceeding dorsal length of thorax, that of males often longer than thorax as well, if dorsal length of male abdomen subequal to length of thorax then males much shorter than females and black in coloration; female connexiva not folded inward over apical abdominal tergites; coloration usually black, but brown in a few species; Asia only 3
2. Prosternum with large rounded tumescence anteromedially; male proctiger with anteriorly directed process on left wing as viewed from above; west Africa *quadrivittatus* Bergroth
- Prosternum lacking rounded tumescence anteromedially; male proctiger lacking anteriorly directed process on left wing as viewed from above; Sumatra *sumatranus* Lundblad
3. Smaller species, length of wingless forms 16 mm. or less; sexually dimorphic, males smaller and more slender than females; male proctiger symmetrical or nearly so, shape as in fig. 8; dorsal coloration black, wingless forms with a narrow median longitudinal yellowish stripe on pronotum only 4 (*scrutator* group)
- Larger species, length of wingless forms exceeding 18 mm.; lacking sexual dimorphism, males and females close to equal in size; male proctiger strongly asymmetrical, shape as in figs 5-7; dorsal coloration variable, brown to black, but wingless forms always with broad median longitudinal brown stripe on pronotum and anterior part of mesonotum 6 (*costalis* group)
4. Connexival spines in both sexes attaining or exceeding posterior margin of first genital segment; abdominal segments I-VII in both sexes with numerous black spinules ventrally *scrutator* (Kirkaldy)
- Connexival spines in both sexes not attaining posterior margin of first genital segment; both sexes with scattered black spinules ventrally on abdominal segments IV-VII only, or spinules absent. 5
5. Mesothorax of wingless female with a pair (1 + 1) of raised longitudinal hair patches to either side of midline on posterior half, lacking raised carinate knobs; connexival margins in females broadly bordered with white; upper portion of female mesopleuron with a longitudinal stripe of silvery hairs as broad as the width of the fore femur; silvery hairs along upper metapleuron extending dorsally to intersegmental suture bordering abdominal tergites; abdomen of both sexes with scattered spinules ventrally on segments IV-VII; Philippines *vittipes* Stål
- Mesothorax of wingless female lacking longitudinal hair tufts on mesothorax, but with a pair (1 + 1) of raised carinate knobs near posterior margin; connexival margin in females black, or narrowly margined with pale brown clouded with black; female mesopleuron with a longitudinal stripe of silvery hairs only half as wide as the width of the fore femur; silvery hairs along the sides of the metapleuron restricted to the region of the metacetabulae, not attaining the intersegmental suture dorsally; abdomen of both sexes lacking spinules ventrally; Celebes *persephone* Kirkaldy
6. Mesosternum lacking black spinules ventrally (fig. 4); male proctiger distinctive (fig. 1); Indochina *costalis* Schmidt
- Mesosternum with at least a few black spinules ventrally (figs. 2,3) 7

7. Dorsal coloration predominantly reddish brown, longitudinal black markings often present on mesonotum to either side of midline but lateral portions of mesonotum always brown; mesosternum with only a few spinules ventrally near posterior margin (fig. 2); male proctiger distinctive (fig. 6); Malay Peninsula below the Isthmus of Kra, and northern Sumatra *malayensis* n.sp.
- . Dorsal coloration black, with narrow longitudinal brown line medially on thoracic dorsum, lateral portions of mesonotum always black; mesosternum with numerous spinules ventrally on posterior half (fig. 3); Ceylon or Borneo 8
8. Connexival spines exceeding tip of proctiger in male; first antennal segment reaching to distal end of fore femur when both are directed anteriorly; dorsal surface of fore femur in both sexes bearing black spinules along its entire length; male proctiger distinctive (see Hungerford and Matsuda, 1962, fig. 4f); Ceylon *productus* Spinola
- . Connexival spines not exceeding tip of proctiger in male; first antennal segment not reaching to distal end of fore femur when both are directed anteriorly; dorsal surface of fore femur in both sexes with black spinules only at extreme distal end; male proctiger distinctive (fig. 7); Borneo *samarinda* n.sp.

Genus *Cylindrostethus* Fieber

Type species: *C. fieberi* Mayr 1865, by subsequent monotypy (= *Gerris productus* Spinola 1840).

Hydrobates Erichson, 1848. Fauna Brit. Guiana 3: 614. [Generic name preoccupied by *Hydrobates* Boie in Aves].

Cylindrostethus Fieber, 1860. Europ. Hemip.: p. 33. [No species mentioned].

Cylindrostethus Mayr, 1865. Verh. Zool.-Bot. Ges. Wien 15: 444. [Described *C. fieberi*, a synonym of *C. productus* (Spinola), 1840 (as *Gerris producta*).

Janais Distant, 1910. Ann. Mag. Nat. Hist. (8) 5: 145. Syn. by Torre-Bueno, 1925: 228.

Redescription

Large elongate water striders (fig. 1), general coloration black to brown, frequently with yellowish stripes on pronotum and longitudinal band of silvery pubescence on mesopleuron; mesonotum often bearing paired longitudinal stripes.

Body elongate and cylindrical; head vertex with inner margins of eyes strongly convergent anteriorly, anterior interocular space much narrower than posterior interocular; eyes large, protrusive; antennae thick and relatively short, length of segment I greater than combined lengths of segments II and III, length of segment IV greater than length of segment III; antennal tubercles divergent anteriorly. Clypeus with basal margin absent; mandibular and maxillary plates poorly defined; rostrum reaching to posterior margin of head, length of third rostral segment 1.5–2.0 times greater than that of the fourth.

Pronotum roughly hexagonal in shape, length (midline) shorter than head, posterior margin straight, posterolateral margins oblique. Mesonotum long, posterior margin rounded and weakly indented medially, midline with incipient longitudinal sulcus. Mesosternum with length 2.0–3.5 times that of metasternum, posterior margin simple and concave. Metanotum with distinct longitudinal sulcus along midline. Metasternum subequal in length to abdominal ventrite II.

Abdomen long, usually parallel sided; tergite I shorter than tergite II, with sinuate anterior margin; tergites II–VI subequal in length; connexiva usually reflexed, in some cases folded inward over

distal tergites; connexival segment VII usually with a distinct posteriorly directed spine in both sexes; male abdominal segment IX lacking rotation; male proctiger narrowed apically, form variable, often with lateral projections, tip acuminate in New World species; male pygophore with apex rounded; male parameres small, symmetrical.

Fore femur enlarged, usually slightly longer than fore tibia, apical margin notched, bearing a few small teeth at inner apical angle; fore tarsal segment II 2.0–4.0 times as long as fore tarsal segment I; fore claws weakly subapical. Middle leg longer than hind leg; middle femur with length subequal to or shorter than length of body; middle tibia shorter than middle femur, length 2.0–3.0 times that of middle tarsal segment I; middle tarsus flattened, segment I at least 3.0 times longer than segment II. Hind femur at least 1.2 times as long as hind tibia; hind tibia at least 5.0 times as long as hind tarsi; hind tarsal segment I with length 1.0–2.0 times greater than hind tarsal segment II. Claws on middle and hind legs small, inconspicuous and subapical in Old World species, absent in New World species.

Discussion

The genus *Cylindrostethus* as presently accepted consists of two morphologically distinct components inhabiting the New World and Old World tropics respectively. The New World species are distinguished by the absence of claws on the middle and hind legs, and by the acuminate prolongation of the terminal genital segment in both sexes. Matsuda (1960) created the tribe Cylindrostethini to hold *Cylindrostethus* and two related Neotropical genera, *Potamobates* and *Platygerris*. Andersen (1982) treated this grouping as the subfamily Cylindrostethinae, defined by the synapomorphies of a flattened middle tibia and tarsus, and heavily sclerotized gonapophyses. The congeneric status of the Neotropical and Paletropical components of *Cylindrostethus* is open to question, but resolution of this issue is deferred herein.

The characters discussed in the foregoing generic description are essentially uniform in all *Cylindrostethus* species and are not repeated in the individual species descriptions below.

Cylindrostethus samarinda Polhemus, new species

Figs. 1, 3, 7, 9

Description

APTEROUS MALE. Large for genus, elongate, dorsal coloration black with dark yellow markings on posterior portion of head, longitudinal midline of thorax, and connexival margins; stripe of silvery hairs running longitudinally along each side of thorax and abdomen; entire dorsal surface covered with very short recumbent gold setae. Length 20.50 mm.; width of head across eyes 2.09 mm.; width of thorax across mesoacetabula 2.97 mm.

Head blackish brown anteriorly, dark yellow on vertex, behind eyes, and ventrally; antennae black, lengths of antennal segments I–IV = 2.77; 1.36; 0.86; 1.14; rostrum black, glabrous, barely attaining anterior margin of prosternum; patches of silvery hairs present on clypeus and near bases of antennae.

Pro-, meso- and metanotum black, narrow longitudinal yellow line present medially on pronotum and anterior portion of mesonotum; side of thorax with longitudinal band of silvery hairs, beginning on posterior half of propleura and extending along meso- and metapleura; silvery hair patches also present on fore, meso-, and metacetabulae and on pronotum behind eyes; pronotum with shallow longitudinal depression medially; mesonotum with very fine depressed longitudinal line medially, posterior margin weakly bilobate; metanotum depressed anteriorly, weakly swollen posteriorly, posterior margin bilobate.

Abdomen black, shining, connexival margins dark yellow; connexiva approximately half as wide as abdominal tergites, bearing numerous fine black spinules along margins, connexival spines approaching but not exceeding tip of proctiger; proctiger asymmetrical, left lobe as viewed from above more highly produced, lateral margin of left lobe straight (fig. 3); parameres slender, symmetrical, tips rounded.

Ventral surface pale yellowish white, bearing very short recumbent pale setae; numerous tiny black spinules present on meso- and metasternum and on abdominal ventrites I–VII (fig. 7); abdomen with weak lightly embrowned longitudinal carina medially; length of metasternum exceeding combined lengths of abdominal ventrites I and II (2.16/1.98); first genital segment longer than abdominal ventrite VII (1.73/1.08). Legs dark yellow, becoming brown distally, fore femur with lightly embrowned longitudinal spot on centrally on dorsal face, ventral faces of fore femur and tibia black; legs with following measurements: fore femur/tibia/tarsal I/tarsal II = 4.70/4.56/0.20/0.66; middle femur/tibia/tarsal I/tarsal II = 18.52/11.33/6.05/1.01; hind femur/tibia/tarsal I/tarsal II = 21.60/11.23/0.68/0.40.

APTEROUS FEMALE. Similar to male in general structure and coloration but slightly larger, length 21.75 mm.; width of head across eyes 2.15 mm. (fig. 1); width of thorax across mesoac-
etabulae 3.26. Connexival spines clearly exceeding posterior tip of abdomen.

MACROPTEROUS FORM. Unknown.

Diagnosis. *Cylindrostethus samarinda* n.sp. may be recognized by its predominantly black coloration, the presence of numerous black spinules on the posterior half of the mesosternum (fig. 3), and the straight lateral margin on the expanded left lobe of the male proctiger (fig. 7). This species is the only member of the *costalis* group known to occur on Borneo.

Ecological Notes. The type series was taken on a deep, smoothly flowing stream below a waterfall and plunge pool in the hills north of Samarinda, a port on the Mahakam River in eastern Borneo. The surrounding vegetation appeared to have originally been swamp forest but was seriously disturbed due to the effects of a sweeping forest fire in 1984 and subsequent encroaching rice cultivation. Other individuals of what were presumed to be *C. samarinda* were seen from boats in the swamp forest channels bordering the Mahakam about 100 kilometers farther upriver near Kota Bangun, but none could be captured to verify their identity.

Distribution. Central and eastern Borneo.

Material examined. Holotype, male, and allotype, female: INDONESIA, Borneo, Kalimantan Timur Prov., waterfall and stream 11 km. NE of Samarinda, CL 2091, 27 August 1985 (J. T. and D. A. Polhemus) (USNM). Paratypes: INDONESIA, Borneo, Kalimantan Timur Prov.: many males and females, same data as types (JTFC, BPBM, MZB); 3 males, 5 females, C. Borneo, Sungai Pajau [Payau], 1925 (Mjoberg) (ZMA); 4 males, 6 females, C. Borneo, Mt. Tibang [Mt. Batu Tibang], 1925 (Mjoberg) (ZMA).

Etymology. The name "samarinda" is a noun in apposition and refers to the type locality, near the river port of Samarinda in eastern Borneo.

Cylindrostethus malayensis Polhemus, new species

Figs. 2, 6, 9

Description. **APTEROUS MALE.** Large for genus, elongate, dorsal coloration brown with black markings on anterior portion of head, longitudinally on either side of midline on thorax, and variably on abdominal tergites; stripe of silvery hairs running longitudinally along each side of thorax and abdomen; entire dorsal surface covered with very short recumbent gold setae. Length 20.00 mm.; width of head across eyes 2.09 mm.; width of thorax across mesoacetabulae 2.90 mm.

Head black anteriorly, brown on vertex, behind eyes, and ventrally; antennae black, lengths of segments I–VI = 3.03; 1.41; 0.88; 1.14; first antennal segment not attaining tip of fore femur; rostrum brown basally, black apically, glabrous, barely attaining anterior margin of prosternum; patches of silvery hairs present on clypeus and near bases of antennae.

Pro-, meso-, and metanotum brown laterally, with broad longitudinal black markings to either side of midline, longitudinal midline stripe yellowish and broad on prothorax, brown and narrower on meso- and metanotum; side of thorax with longitudinal band of silvery hairs, beginning near posterior margin of propleura and extending along meso- and metapleura; silvery hair patches also present on fore, meso- and metacetabulae and on pronotum behind eyes; pronotum with broad, shallow longitudinal depression medially; meso- and metanotum with very fine depressed longitudinal line medially, posterior margins bilobate; metanotum slightly depressed anteriorly.

Abdomen brown, central portions of tergites often blackish, connexival margins dark yellow; connexiva approximately half as wide as abdominal tergites, margins bearing numerous black spinules, connexival spines exceeding tip of proctiger; proctiger asymmetrical, left lobe as viewed from above more highly produced, lateral margin of left lobe irregular (fig. 2); parameres slender, symmetrical, tips rounded.

Ventral surface pale yellowish white, bearing very short recumbent pale setae; meso- and metasternum with a few scattered black spinules near posterior margins (fig. 6); abdominal ventrites I–VII with numerous tiny black spinules, ventrites II–VII with weakly embrowned longitudinal median carina; length of metasternum exceeding combined lengths of abdominal ventrites I and II (2.02/1.72); first genital segment longer than abdominal ventrite VII (1.21/0.76). Legs brown, suffused with yellowish basally; fore femur dark yellow, bearing longitudinally ovate black spot centrally on dorsal face, length of spot over half the length of the femur; ventral faces of fore femur and tibia black; legs with following proportions: fore femur/tibia/tarsal I/tarsal II = 4.99/4.61/0.25/0.66; middle femur/tibia/tarsal I/tarsal II = 18.50/11.71/5.52/0.96; hind femur/tibia/tarsal I/tarsal II = 20.10/11.32/0.61/0.35.

APTEROUS FEMALE. Similar to male in general structure and coloration, length 21.00 mm.; width of head across eyes 2.09 mm.; width of thorax across mesoacetabulae 2.93 mm. Connexival spines clearly exceeding posterior tip of abdomen; abdominal tergites often entirely black.

MACROPTEROUS MALE. Length 20.25 mm; width of head across eyes 2.02 mm.; width of thorax across mesoacetabulae 3.08 mm. Similar to apterous form in general structure and coloration with following exceptions: posterior lobe of pronotum produced, brown, posterior margin dark yellow, slightly reflexed, humeral angles weakly protruberant, rounded, length of posterior lobe over 3 times that of anterior lobe (4.42/1.26), a low narrow longitudinal carina present medially. Wings complete, extending to abdominal tergite VII, dull brown with costal margin yellowish.

MACROPTEROUS FEMALE. Length 20.60 mm.; width of head across eyes 2.07 mm.; width of thorax across mesoacetabulae 3.33 mm.

Diagnosis. *Cylindrostethus malayensis* n.sp. may be distinguished from other members of the *costalis* group by its brownish coloration, distinctively shaped male proctiger (fig. 6), and the presence of black spinules in small numbers near the posterior margins of the meso- and metasternum (fig. 2).

Ecological Notes. *Cylindrostethus malayensis* appears to dwell primarily in the lowland swamp forests of north Sumatra and the Malay Peninsula south of the Isthmus of Kra; I have no records of it from elevations above 100 meters. The species frequents the shaded, smoothly flowing streams characteristic of such forests, and was listed by Cheng and Fernando (1969) as a typical inhabitant of slow flowing forest streams, peaty acidic black-water streams, and non-acidic lowland streams. The type series was collected from one of the numerous deep channels that drain the swamp forests along the road to Mersing in eastern Johor, with most taken on a pool created behind a fallen log.

This species has been previously treated in the literature as *C. costalis* (Cheng and Fernando, 1969), and is the species that Fernando and Cheng (1974) reported as occurring by the thousands on a stream in the vast swamp of Tasek Berah, in southern Peninsular Malaysia.

Distribution. Northern Sumatra, and the Malay Peninsula below the Isthmus of Kra.

Material examined. Holotype, male, and allotype, female: WEST MALAYSIA, **Johor**, swamp forest stream 61 km. NE of Johor Bharu on Mersing hwy., CL 2220, 16 October 1986 (J. T. and D. A. Polhemus) (USNM). Paratypes: WEST MALAYSIA, **Johor**: 11 males, 5 females, same data as types; 3 males, 1 female, swamp forest stream 15 km. W. of Sedili Besar, 20 m., CL 2218, 16 October 1986 (J. T. and D. A. Polhemus) (JTPC, BPBM); 2 males, 4 females, stream 27 km. SW of Mersing, CL 2058, 14 August 1985 (J. T. and D. A. Polhemus) (JTPC, BPBM); 12 males, 12 females, stream 12 km. N. of Labis, nr. Ayer Panas, CL 2087, 22 August 1985 (J. T. and D. A. Polhemus) (JTPC, BPBM). **Pahang**: many males and females, Tasek Berah, S. of Ft. Iskander [Pos Iskandar], 29 March 1963 (NUS). SINGAPORE: 1 male, Seletar [River], 10.5 mi. Mandai Rd., 16 April 1964 (L. Cheng) (JTPC). THAILAND, **Trang Prov.**: 3 males, 3 females, Krachong Forest, E. of Trang, 100 m., 2 July 1962 (E. S. Ross and D. Q. Cavagnaro) (JTPC, CAS). INDONESIA, Sumatra, **Sumatera Utara Prov.**: 8 males, 3 females, Sumatra, N. O., Tandjong Morawa [Tanjung Morawa, E. of Medan], Serdang [Deli Serdang district] (B. Hagen) (RMNH).

Etymology. The name "malayensis" refers to the Malay Peninsula, where this species occurs abundantly.

Cylindrostethus costalis Schmidt

Figs. 4, 5, 9

Cylindrostethus costalis Schmidt, 1915. Stett. Ent. Zeit. 76: 364.

Diagnosis. *Cylindrostethus costalis* may be recognized by its dark coloration, the lack of black spinules on the mesosternum (fig. 4), and the shape of the male proctiger (fig. 5). A series of specimens from Phuket Island contains individuals in which the left wing of the proctiger as viewed from above has the angles slightly more rounded than the example shown in fig. 5, so this character may prove to be slightly variable.

Discussion. Schmidt's types of *C. costalis* came from an unspecified locality in Cambodia, probably in the swamp forests bordering the Mekong. Hungerford and Matsuda (1962) reported the species from Thailand and Burma and I now have records from Laos and Vietnam, so the species appears to be widely distributed across Indochina (fig. 9).

Material examined. VIETNAM, **Quang Tri Prov.:** 13 males, 12 females, 1 mi. N. of Quang Tri, 7 June 1970 (A. R. Gillogly) (JTPC). LAOS, **Vientiane Prov.:** 4 males, 3 females, Ban Van Eue, 16 March 1966 (native collector) (JTPC, BPBM). THAILAND, **Chiang Mai Prov.:** 6 males, 5 females, Mae Sa waterfall, 7 km. W. of Mae Rim, CL 2203, 18 November 1985 (J. T. and D. A. Polhemus) (JTPC); 3 males, stream 10 km. NW of Mae Rim, CL 2204, 19 November 1985 (J. T. and D. A. Polhemus) (JTPC). **Loei Prov.:** 1 male, 40 km. S. of Loei, 12 July 1966 (R. R. Pinger) (CAS). **Nakhon Ratchasima Prov.:** 18 males, 21 females, 60 km. S. of Nakhon Ratchasima, Sakaerat Experiment Station, 14°30' N, 101°55' E, 300–600 m., 2–4 March 1971 (P. Spangler and P. Spangler) (USNM). **Phuket Prov.:** 3 winged males, 3 winged females, Phuket Is., Tone Sai waterfall area, 25 January 1987 (N. M. Andersen) (USNM). **Sakon Nakhon Prov.:** 9 winged males, 9 winged females, Phu Phan, 27 June 1954 (R. E. Elbel) (USNM). BURMA: 1 male, Burmah (Alfd. Hough) (BMNH).

Cylindrostethus productus Spinola

Fig. 12

Gerris productus Spinola, 1840. Essai sur les insectes hémiptères, rynchotes ou hétéroptères, p. 64. *Cylindrostethus fieberi* Mayr, 1865. Verh. Zool.-Bot. Ges. Wien 15: 444. Syn. by Distant, 1904: 184. *Cylindrostethus productus* Distant, 1904. Fauna British India, Rhynchota, 2: 184. *Janais elegantulus* Distant, 1910. Ann. Mag. Nat. Hist. (8) 5: 145. Syn. by Torre-Bueno, 1925: 228. *Cylindrostethus bituberculatus* Schmidt, 1915. Stett. Ent. Ztg. 76: 364. Syn. by Hungerford and Matsuda, 1962: 84. *Cylindrostethus neitneri* Schmidt, 1915. Stett. Ent. Zeitt. 76: 363. Syn. by Hungerford and Matsuda, 1962: 84.

Diagnosis. *Cylindrostethus productus* is a very large, dark, elongate *Cylindrostethus* that may be recognized by its long connexival spines and distinctive male proctiger with a prolonged median lobe (see figures in Hungerford and Matsuda 1962).

Discussion. This species is very common on Ceylon, and I have examined numerous specimens from that island; localities for these were listed by Hungerford and Matsuda (1962) and J. Polhemus (1979) and are not repeated here. Hungerford and Matsuda (1962) also reported this species from southern peninsular India and west Bengal. Additional material that I have examined from the British Museum shows that *C. productus* has a much wider range in peninsular India than previously realized, occurring northward to the Himalayan foothills in Punjab and Uttar Pradesh. Dr. N. M. Andersen of Copenhagen (pers. comm.) has also provided records from Nepal and Karnataka, south India. These new records are listed below to clarify the range of the species.

Material examined. INDIA, **Punjab:** 1 male, Narpur, Kangra, 3300 ft. (H. G. Champion) (BMNH). **Uttar Pradesh:** 1 female, Dehra Dun (H. G. Champion) (BMNH). **Kerala:** 1 male, Tenmalai, Western Ghats (west side), Travancore, 22 November 1908 (Annandale) (BMNH). **West Bengal:** 2 females, Manbhum (K. A. Hallows) (BMNH). **Madhya Pradesh:** 9 males, 5 females, 4 mi. S. of Kanker, 360 m., 31 January 1962 (E. S. Ross and D. Q. Cavagnaro) (JTPC, CAS). **Karnataka:** 1 male, 1 female, Bangalore, Bannerghata, 900 m., 27–31 October 1977 (N. M. Andersen) (ZMUC). NEPAL: 1 male, 1 female, Amaha Terai jungles, February–April 1959 (K. Becker Larsen) (ZMUC). SRI LANKA, **Uva:** 5 males, 5 females, Belihuloya, 14 April 1962 (K. L. A. Perera) (KU). **Central:** 2 males, 3 females, Kandy District, Katugastola, 1600 ft., 28 January 1966 (P. B. Karunaratne) (CAS).

Cylindrostethus quadrivittatus Bergroth

Fig. 11

Cylindrostethus quadrivittatus Bergroth, 1916. Proc. U.S. Natl. Mus. 51: 237.

Diagnosis. *Cylindrostethus quadrivittatus* is the only *Cylindrostethus* species occurring in Africa, and may be easily recognized by its yellowish brown coloration with prominent longitudinal black stripes on the thorax, the tumid prosternum, the modified female gonocoxae whose tips cross over each other and project beyond the sides of the abdomen, and the distinctive male proctiger which bears a forward curving prong on the left side as viewed from above; this latter structure was illustrated by Hungerford and Matsuda (1962, pg. 111).

Discussion. The species was described from Liberia, and appears to be confined to the tropical portions of western Africa, but little is known of its ecology.

Material examined. CAMEROON: 4 males, 3 females, Muyuka, Victoria, 27 June 1949, B. Malkin (JTPC). LIBERIA: 1 male, 2 females, Mt. Coffee, February 1897, R. P. Currie (JTPC); 1 male, Genewoday, Cape Mount, 2-18-53-32, O. Blickenstaff (JTPC).

Cylindrostethus sumatranus Lundblad

Fig. 9

Cylindrostethus sumatranus Lundblad, 1933. Arch. Hydrobiol. Suppl. 12: 392.

Diagnosis. Among Asian species *sumatranus* may be immediately recognized by its relatively broad form, brown coloration, modified female gonocoxae, raised abdominal tergite I, and asymmetrical male proctiger (see key).

Discussion. This is the only species in Southeast Asia that I have not collected or studied in the wild, but I have examined Lundblad's type, a female specimen in good condition now housed in the Naturhistoriska Riksmuseet, Stockholm. The male of this species, which I have not seen, was described and illustrated by Hungerford and Matsuda (1962).

The few known specimens of *C. sumatranus* have all come from the Musi River basin in southern Sumatra (fig. 9), and I did not encounter the species while working in the northern portion of the island in 1985. A visit to the Curup type locality in 1991 failed to produce further specimens of this elusive insect, but did indicate that the habitat will prove to be rocky upland streams, since no lowland streams are present in the area.

Material examined. INDONESIA, Sumatra, Bengkulu Prov.: 1 female, Curup, FM 12, 10 May 1929 (A. Theinemann) (holotype, NHRM). Sumatera Seletan Prov.: 1 female, Kloempang [Kloempang River, trib. to Rawas River below Muararupit], August 1878 (JTPC).

Cylindrostethus scrutator (Kirkaldy)

Figs. 8, 10

Gerris scrutator Kirkaldy, 1899. Rev. Ent. 18: 90.*Cylindrostethus scrutator* Distant, 1904. Fauna British India, Rhychocha 2: 184.*Cylindrostethus naiades* Kirkaldy, 1909. Canadian Entomol. 41: 389. Syn. by Hungerford and Matsuda, 1962: 85.*Cylindrostethus flaviventer* Schmidt, 1915. Stett. Entomol. Zeit. 76: 363. Syn. by Lundblad, 1933: 372.

Diagnosis. Among the species in the *scrutator* group, *C. scrutator* is the most widely distributed, and may be recognized by the length of the connexival spines, which attain or exceed the posterior margin of the first genital segment in both sexes, the presence of numerous black spinules on the venter of both sexes, and the absence of longitudinal hair tufts or raised carinate knobs laterally on the mesothorax (see key).

Discussion. Hungerford and Matsuda (1962) reported this species from the Asian mainland, Java, and the Mentawai Archipelago (Simeulue and Sipora islands). Material is now at hand from many localities in Sumatra, Borneo and Bali as well, showing that the species occurs on all the Greater Sunda Islands (fig. 9). Hungerford and Matsuda (1962) listed specimens from an unspecified locality in India, but I have seen no specimens from peninsular India and suspect instead that these may have been specimens collected in Assam.

Material examined. WEST MALAYSIA, **Johor:** 9 males, 10 females, stream 27 km. SW of Mersing, CL 2058, 14 August 1985 (J. T. and D. A. Polhemus) (JTPC); 5 males, 4 females, Kota Tinggi waterfall, 16 km. N. of Kota Tinggi, 60 m., CL 2217, 15 October 1986 (J. T. and D. A. Polhemus) (JTPC). **Pahang:** 4 males, 3 females, Cheroh River, 6 km. E. of Tapah, CL 2072, 18 August 1985 (J. T. and D. A. Polhemus) (JTPC). **Perak:** 8 males, 7 females, stream 58 km. S. of Grik, CL 2077, 19 August 1985 (J. T. and D. A. Polhemus) (JTPC). EAST MALAYSIA, Borneo, **Sabah:** 10 males, 10 females, trib. to Moyog River nr. km. 12 on Keningau Hwy., CL 2039, 6 August 1985 (J. T. and D. A. Polhemus) (JTPC); 5 males, 5 females, stream 40 km. NE of Kota Belud, CL 2032, 5 August 1985 (J. T. and D. A. Polhemus) (JTPC). **Sarawak:** 2 females, Sematan River, 2 km. SW of Tubeh, CL 2047, 9 August 1985 (J. T. and D. A. Polhemus) (JTPC); 8 males, 8 females, Pided River, 5 km. SW of Bau, CL 2053, 10 August 1985 (J. T. and D. A. Polhemus) (JTPC); 2 males, Sadong, Kampong Tepuh, 300–450 m., 10 July 1958 (T. C. Maa) (ZMUC). VIETNAM: 3 males, 3 females, 6 km. S. of Dalat, 1400–1500 m., 9 June–7 July 1961 (N. R. Spencer) (JTPC). THAILAND, **Kanchanaburi Prov.:** 1 male, 1 female, Kanchanaburi, Sai Yok waterfall, 21–22 December 1981 (N. M. Andersen) (ZMUC). **Trang Prov.:** 1 male, Khaophappa, Khaochang, 200–400 m., 10 January 1964 (G. A. Samuelson) (JTPC, BPBM); 2 males, 2 females, Trang Ramo, stream behind temple, 16 April 1960 (M. Griffith) (USNM). **Province uncertain:** 1 female, 1 immature, mouth of Tharn Mayom stream, N. side of Ko Chang Island, Gulf of Thailand, 28 October 1957 (R. R. Rofen) (CAS). INDONESIA, Java, **Jawa Barat Prov.:** 3 males, 3 females, Tjibarangbang, Gunung Salak [above Bogor], July 1936 (E. Le Moul) (RMNH); 1 male, 1 female, Batavia [Jakarta], December 1814 (ZMUC). **Jawa Tengah Prov.:** 1 male, Pekalongan (F. Muir) (CAS); 1 female, Roban, (F. Muir) (CAS). **Jawa Timur Prov.,** 2 females, Malang, December 1910 (P. Brutendyk) (RMNH). Bali, **Bali Prov.:** 6 males, 2 females, Sangsang River, W. of Bangli, 400 m., CL 2171, 17 October 1985 (J. T. and D. A. Polhemus) (JTPC). Borneo, **Kalimantan Timur Prov.:** 8 males, 6 females, C. Borneo, Mt. Tibang [Mt. Batu Tibang], 1925 (Mjoberg) (ZMA); 3 males, 3 females, C. Borneo, Sungai Birang [trib. to Berau River, N. of Tanjung Redeb], 1925 (Mjoberg) (ZMA). Sumatra, **Aceh Prov.:** 1 male, 1 female, Seumanjam [Seumanyam], Menlabok, 20 October 1953, R. Straatman (RMNH). **Bengkulu Prov.:** 10 males, 5 females, Sungai Airputih at Kerinci-Seblat National Park, 10 km. W. of Muaraaman, 450 m., water temp. 23 °C., 7 September 1991, (J. T. and D. A. Polhemus) (JTPC); 3 males, 3 females, Pauh River, 25 km. SE of Muaraaman, 600 m., water temp. 23 °C., 8

September 1991, (J. T. and D. A. Polhemus) (JTPC). **Sumatera Utara Prov.:** 2 males, 1 female, Medan (Mjoberg) (RNHL); 13 males, 10 females, Soengai Bohorok [Sungai Bohorok, W. of Binjai], Boven - Langkat, S. O., Sumatra, 13 July 1917 (J. E. A. den Doop) (ZMA); 1 male, 1 female, Sumatra, tusschen Serdang, en het Toba-meer [Lake Toba] (B. Hagen) (RMNH). Mentawai Archipelago, **Sumatera Barat Prov.:** 1 female, Sereinu, Sipora Island, May-June 1894 (Modigliani) (JTPC).

Cylindrostethus persephone Kirkaldy

Fig. 10

Cylindrostethus persephone Kirkaldy, 1899. Ann. Soc. Ent. Belg. 43: 508.

Cylindrostethus brachyakanthinos Chen and Nieser, 1992. Tijdschr. Entomol. 135: 151. **New synonymy.** [The spelling *akanthinos* on p. 145 is clearly a lapsus for *brachyakanthinos*.]

Discussion. *Cylindrostethus persephone* is endemic to Celebes, and may be easily recognized by the presence of a pair of raised carinate knobs near the posterior margin of the mesothorax in females (a character not mentioned by Hungerford and Matsuda 1962, and not well shown in their plate 3, fig. E), and the absence of black spinules on the abdominal venter in both sexes.

I have examined paratype specimens of *C. brachyakanthinos* Chen and Nieser, and find them to be indistinguishable from *C. persephone* Kirkaldy, differing only in minor structural details that fall easily within the range of intraspecific variation displayed by the latter species.

Ecological Notes. *Cylindrostethus persephone* was originally described from the southern peninsula of Celebes but seems to be widespread throughout the island, since it also occurs abundantly on rocky streams in the Minahasa region at the far tip of the northern peninsula, and in the central ranges near Rantepao (fig. 9). I found *C. persephone* to be present in enormous numbers on the permanent pools of the Pattunuang River in southern Celebes during October of 1985. This portion of the island experiences a pronounced dry season from July to November, and it appeared that the spring fed limestone channels at this locality provided a refugium into which *Cylindrostethus* and many other water striders had retreated, resulting in their aggregation in abnormally high densities.

Material examined. INDONESIA, Celebes, **Sulawesi Utara Prov.:** many males and females, Tumpah River, Dumoga-Bone Nat. Park, 60 km. SW of Kotamobagu, 222 m., 0°34'N, 123°54'E, CL 2099, 3 September 1985 (J. T. and D. A. Polhemus) (JTPC); 10 males, 7 females, Metalanga River, 5 km. S. of Doloduo, CL 2111, 7 September 1985 (J. T. and D. A. Polhemus) (JTPC); 7 males, 6 females, Pononontuna River at Tapakulintang, 200 m., CL 2121; 15 September 1985 (J. T. and D. A. Polhemus) (JTPC); 2 males, 2 females, stream at Dimembe, NE of Manado, CL 2126, 19 September 1985 (J. T. and D. A. Polhemus) (JTPC); 4 males, 4 females, Tondano River trib., S. of Airmadidi, CL 2127, 20 September 1985 (J. T. and D. A. Polhemus) (JTPC). **Sulawesi Selatan Prov.:** many males and females, Pattunuang River at Biseang Labboro Rec. Area, 7 km. SW of Bantimurung, 50 m., CL 2165, 13 October 1985 (J. T. and D. A. Polhemus) (JTPC); 5 males, 5 females, Marana River nr. Laiya, 50 km. E. of Maros, 450 m., CL 2167, 14 October 1985 (J. T. and D. A. Polhemus) (JTPC); 2 males, 2 females, Nanggala, E. of Rantepao, 900 m. (F. C. Dreschler) (MZB). **Sulawesi Tengah Prov.:** 1 male, 1 female, Batui River at Singsing Camp, SW of Luwuk, 1°09'S, 122°31'E, 90 m., 14-17 October 1989, middle sized stream in lowland rain forest, J. P. Duffels (JTPC).

Cylindrostethus vittipes Stål

Fig. 10

Hydrobates vittipes Stål, 1870. Ofv. Kongl. Svenska Vet. Akad. Förh. 7: 705.*Cylindrostethus vittipes* Kirkaldy, 1909. Can. Entomol. 41: 389.

Diagnosis. This is the only species of *Cylindrostethus* known to occur in the Philippine archipelago, and may be recognized by the presence in females of a pair of longitudinal hair patches on either side of the midline on the posterior half of the mesonotum, and by the broad white margins on the female connexiva. The lateral silvery hair stripes running along the meso- and metapleura are broader in this species than in either *persephone* or *scrutator*.

Discussion. Hungerford and Matsuda reported this species only from Mindanao, but additional specimens are present from Leyte, Samar, and Luzon, showing that it occurs throughout the Philippine archipelago (fig. 10). Personal observations indicate that this species prefers rocky rivers, where it skates on open pools, and the species as a whole seems to be more commonly encountered on Mindanao and the Visayas than on Luzon.

Material examined. PHILIPPINES, Luzon, **Pangasinan Prov.**: 1 female, 1 km. W. of Sual, stream in rice paddies, CL 1955, 6 July 1985 (J. T. and D. A. Polhemus) (JTPC). **Leyte, Leyte Prov.**: many males and females, Lusig River at Hilusig, CL 1979, 15 July 1985 (J. T. and D. A. Polhemus) (JTPC, BPBM); 7 males, 10 females, Makhinas River at Makhinas, 12 km. SE of Bay Bay, CL 1984, 16 July 1985 (J. T. and D. A. Polhemus) (JTPC). **Mindanao, South Cotabato Prov.**: 11 males, 11 females, Seven Falls, nr. Lake Sebu, SW of Surallah, 1100 m., CL 1992, 19 July 1985 (J. T. and D. A. Polhemus) (JTPC). **Lanao del Sur Prov.**: 4 females, Dansalan [Marawi] (G. Böttcher) (BMNH). **Samar, Samar Prov.**: 6 males, 10 females, Mt. Concord, nr. Hinabangan (Alasar) (JTPC).

PHYLOGENY

Characters

Species of *Cylindrostethus* are conservative in their external morphology, differing primarily in small details of the male and female genital and pregenital structures. A careful analysis was performed to discover characters that would be useful in a phylogenetic reconstruction of the genus, and these are listed in the character state matrix below. The matrix contains 13 characters, numbered 1 to 13. For each character, two or more discrete states were defined and symbolized by numbers. Based on outgroup comparisons, the most primitive (plesiomorphic) state was assigned a zero (0) value, and each successive derived (apomorphic) state a value of 1 or greater using successive integers. Multistate characters (those with more than two states) were ordered in linear transformation series, with 0 the most plesiomorphic state and each subsequent state assumed to be more apomorphic.

The characters used were as follows:

1. Claws on middle legs: 0 = present, 1 = absent.
2. Tip of male proctiger: 0 = short and rounded, 1 = prolonged and acuminate.
3. Projections on wings of male proctiger: 0 = absent, 1 = produced posteriorly, 2 = produced posteriorly with secondary anterior prong on left side as viewed from above.
4. Black spinules on abdominal venter: 0 = absent, 1 = present on abdomen only, 2 = present on abdomen and metasternum, 3 = present on abdomen, metasternum and mesosternum.

5. Connexiva of female abdomen folded inward over apical abdominal tergites: 0 = no, 1 = yes.
6. Wings of male proctiger: 0 = symmetrical, 1 = asymmetrical.
7. Length of abdomen in females: 0 = less than or equal to length of thorax, 1 = exceeding length of thorax.
8. Length of abdomen in males: 0 = less than or equal to length of thorax, 1 = greatly exceeding length of thorax.
9. Male connexival spines: 0 = short and not attaining tip of proctiger, 1 = moderately long and reaching to tip of proctiger, 2 = very long and greatly exceeding tip of proctiger.
10. Sexual dimorphism: 0 = absent, both sexes of relatively equal size, 1 = present, males much smaller than females.
11. Lateral knobs on mesothorax: 0 = absent, 1 = present near posterior margin.
12. Female connexival spines: 0 = short and not reaching to tip of genital segments, 1 = moderately long and reaching to tip of genital segment but not far beyond, 2 = very long, greatly exceeding tip of genital segment.
13. Female first gonocoxae: 0 = unmodified, 1 = with small angular projections at posterolateral margins.

Discussion of characters

The polarities of the characters used in the phylogenetic analysis were determined by comparison to members of the genus *Aquarius*. This was chosen as an outgroup on the basis of Andersen's (1982) phylogeny of gerrid subfamilies, being among the most generalized members of the Gerrinae, which Andersen interpreted as being the plesiomorphic sister group to a clade containing the *Cylindrostethinae*, *Ptilomerinae*, and *Halobatinae*. The polarization of individual character systems is discussed below (character numbers are the same as those in the foregoing discussion).

1. *Claws on middle legs*—It is clear that the possession of claws on all legs is the plesiomorphic state in both *Cylindrostethus* and Gerridae as a whole. Their absence on the middle legs of all South American species is therefore treated as an apomorphic secondary loss.

2–3, 6. *Male proctiger*—In its primitive form the male proctiger in Gerromorpha is small and unmodified, forming a compact lid over the top of the genital complex. In all species of *Cylindrostethus* the proctiger possesses lateral wings, which may be modified in various ways. The plesiomorphic state is interpreted to be one in which the lateral wings are symmetrical and bear posteriorly directed spines at their posterolateral angles. This basic plan is then modified by the wings becoming asymmetrical, with the left wing as viewed from above becoming enlarged, but with both wings retaining posteriorly directed projections. Finally, an anteriorly directed spur may arise from the anterior margin of the enlarged left wing. These modifications are interpreted as being progressively more apomorphic. The tip of the male proctiger is interpreted to be rounded in the plesiomorphic state, and the acuminate prolongation seen in all South American species is considered an apomorphy.

4. *Ventral abdominal and thoracic spinules*—The absence of black spinules on the abdominal and thoracic ventrites is considered plesiomorphic within *Cylindrostethus*. The acquisition of such spinules is considered an apomorphic trait with several different

states. The spinules appear first on the abdomen, and then progressively more anterad on the meta- and mesosterna. This transformation series is best illustrated in the large species of the *costalis* group, where the distribution of the spinules provides a useful character for species separation (figs. 2–4). These spinules are absent in *C. persephone* from Celebes, and this is interpreted to be a secondary loss.

5, 9, 12. *Connexiva*—The primitive condition of the connexiva in *Cylindrostethus* is interpreted to be one in which the posterolateral angles lack spines or are at most weakly developed. In many species these angles have become prolonged, with the resultant spines in the most extreme cases greatly exceeding the tip of the genital segment. The progressive prolongation of the connexival spines is considered apomorphic, and the character has been broken into three states depending on whether these spines are shorter than, equal to, or longer than the tip of the genital segment. In addition, the possession of elongate connexival spines in both sexes is considered more apomorphic than their presence in only a single sex.

Widely separated connexival margins are considered to represent the plesiomorphic state, and the inward folding of these margins seen in the females of species in the *sumatranus* group is considered to be apomorphic.

7–8. *Abdominal length*—Andersen (1982 and pers. comm.) has noted that among Gerridae as a whole the apomorphic trend appears to be towards the shortening of the abdomen. In *Cylindrostethus* however, it appears that the progressive prolongation of the abdomen is an apomorphic character correlated with an overall elongation of the body plan for streamlining and speed. This is particularly obvious in the large and slender species in the *costalis* species group. The prolongation of the abdomen in one or both sexes is thus treated as an apomorphy.

10. *Sexual dimorphism*—The primitive trait among Gerridae is for sexes of equal body size, and this is also seen in most species of *Cylindrostethus*. In the *scrutator* group, however, the males are significantly smaller than the females. This aids in locomotion when the two sexes are coupled since small males are able to ride more easily on top of females, and is treated as an apomorphy. It is worth noting that similar trends toward sexual dimorphism and the reduction of male size have arisen many times independently in many different gerrid subfamilies.

11. *Mesothorax*—The absence of lateral knobs on the mesothorax is considered to be plesiomorphic in *Cylindrostethus*, and the presence of such knobs are seen in *C. persephone* is interpreted as an apomorphy.

13. *Female gonocoxae*—The plesiomorphic condition of the female gonocoxae in *Cylindrostethus* is interpreted to be one in which the two halves meet evenly along the ventral midline and lack any posterior prolongations at the posterolateral angles. In the *sumatranus* group these structures possess distinctive posteriorly directed angulations at the posterolateral angles, a trait which is considered apomorphic.

Computer Analysis

A cladistic analysis of Paleotropical *Cylindrostethus* at the species level was performed using the program PAUP 3.0.m (Swofford, 1990). This program generates phylogenies using the principle of maximum parsimony, and eliminates trees that are identical due to zero length branches. The ingroup taxa for the analysis were the 9 species of *Cylindrostethus* occurring in the Paleotropical region. The outgroup for the analysis was all of the South American species of *Cylindrostethus* taken as a whole. The species in this

latter grouping all share common synapomorphic character states for characters 1 and 2 in the character state matrix, and are thus considered to form a monophyletic unit.

Results

The PAUP analysis was carried out using the *branch and bound* option, and produced a single most parsimonious tree, depicted in figure 13. This tree has a length of 23, a consistency index of 0.87, and a retention index of 0.90.

Based on this tree, the Neotropical and Paleotropical species separate as two distinct monophyletic clades. In addition, the *sumatranus*, *costalis* and *scrutator* groups separate as a clearly distinct monophyletic units within the Paleotropical fauna. The relationships among three species in the *costalis* group fail to resolve fully, producing a terminal trichotomy.

ZOOGEOGRAPHY

Historical Zoogeography

Cylindrostethus as a whole is a circumtropical genus presently known to occur in tropical west Africa, Ceylon and India, Southeast Asia as far east as the Philippines and Celebes, and the Amazon Basin of South America. It is unknown from any of the land masses which formerly comprised the supercontinent of Laurasia in the Mesozoic, and is instead hypothesized to have arisen on the Gondwana supercontinent, with the major clades having attained their present disjunct distributions via the fragmentation of that land mass.

A fundamental basal split on the cladogram of *Cylindrostethus* species separates all Neotropical taxa from those in the Paleotropical region (figs. 13, 14). The South American *Cylindrostethus*, which may in fact represent a distinct genus, are easily distinguished from their Paleotropical sister clade by the absence of tarsal claws on the middle and hind legs and by the acute prolongation of the proctiger. Neotropical cylindrostethines have also diversified into several additional genera, *Potamobates* and *Platygerris*, which are not represented in the Paleotropical region. This basal phylogenetic bifurcation and corresponding zoogeographical segregation in the Cylindrostethinae is hypothesized to have resulted from the rifting of west Gondwana, in the form of South America, from the remainder of that supercontinent in the late Mesozoic, or from earlier vicariance events within an intact Gondwana supercontinent.

If this hypothesis of an initial Gondwana distribution and diversification is correct then ancestral *Cylindrostethus* would have reached what is now tropical Southeast Asia from the south, rafting on drifting Gondwanan continental fragments. Two competing hypotheses may be advanced in this regard. The ancestral lineage of Asian *Cylindrostethus* could have arrived in southeastern Laurasia in the middle to late Mesozoic via the collision of a rifted subcontinent or an archipelago of continental fragments which are now incorporated into portions of Sumatra, the Malay Peninsula, Burma and Indochina. Conversely, *Cylindrostethus* may have arrived much later, carried on drifting India which contacted the southern flank of Laurasia in the Eocene (Searle 1991).

Among the Paleotropical cylindrostethines, three distinct clades are indicated by the present phylogenetic analysis (figs. 13, 14). The most basal of these, the *sumatranus* group, contains two taxa, *C. quadrivittatus* from tropical west Africa, and *C. sumatranus*

from southern Sumatra. Although displaying plesiomorphic states for most characters, both of these taxa share unique modifications of the female gonocoxae. At the same time, the proctiger of *C. sumatranus* is very similar to that of the species in the tropical Asian *costalis* group, indicating that *sumatranus* and its African sister species may be relictual representatives of the original cylindrostethine stock that was widely distributed in east Gondwana and subsequently give rise to the present day Southeast Asian clades. The sister area relationship of Africa and south Sumatra is unusual, but could be accounted for by the rifting of a continental block incorporating portions of present day Sumatra, Malaya and Indochina from the northern margin of east Gondwana.

Geological evidence indicates that such rifting did indeed occur. Present continental Southeast Asia contains a mix of tectonic blocks, whose Laurasian and Gondwana affinities have been determined on the basis of the Permian paleofloras they harbor (Hutchinson 1989). The Indochina block and the Yangtze Platform preserve a Cathaysian paleoflora characterized by the genus *Gigantopteris*; western Borneo also appears to belong to this assemblage on the basis of stratigraphic correlations, but as yet there is no paleofloral information at hand. These blocks all lie to the east of a major north-south suture zone that runs southward from Yunnan through Burma, Thailand, and peninsular Malaysia. All blocks west of this suture preserve a Gondwanan paleoflora characterized by the genus *Glossopteris*, these blocks include a series of accreted terranes along the western sides of Burma and the Malay Peninsula, the Lhasa block of Tibet, and the entire Indian subcontinent. The affinities of Sumatra are equivocal; a paleoflora of apparently Laurasian affinities (but lacking the signature *Gigantopteris*) is present at Jambi in the south, but the stratigraphy of northern Sumatra is correlative with that of the Gondwana-derived terranes of western peninsular Malaysia (Hutchinson 1989). Hamilton (1979) suggested that Sumatra might be geologically composite, with the Burmese-Malayan suture zone continuing southward into the island along some presently undetermined alignment, a hypothesis consistent with the contradictory stratigraphic and paleofloral observations noted above.

Hamilton (1979) also hypothesized that an Indochina-Malaya-Sumatra subcontinent was rifted away in early Jurassic (or possibly even Triassic) time from the truncated margin of the Australian craton that now lies buried beneath the Tertiary mountains of central New Guinea. This Indo-Malayan block apparently drifted northward and collided with southern Laurasia in the middle Mesozoic along a line running from Tibet southward through the Burmese-Malayan suture. The parallel ranges of medial Burma in fact record a sequential series of no less than three Mesozoic collisions and sutures of continental blocks of this type derived from northeast Gondwana. Mitchell (1989) recognized three major accreted terranes in this region, which he referred to, in order of decreasing age, as the Shan-Thai, Lhasa, and Mt. Victoria Land blocks. The Shan-Thai block, the oldest of the three, rifted from Gondwana in the late Paleozoic and collided with Indochina in the middle Triassic (Mitchell 1989); portions of this block are now incorporated into eastern Burma, western Thailand, western peninsular Malaysia, and Sumatra. The Lhasa block rifted from Gondwana in the late Triassic, and collided with south China, Tibet, and possibly Indochina (although evidence along the southern end of the suture is inconclusive) in the late Jurassic or early Cretaceous. The Mt. Victoria Land block rifted from Gondwana in the middle to late Jurassic, and collided with Burma in the early Cretaceous; Mitchell (1989) felt that portions of this block might also be present in Tibet south of the

Zangbo ophiolite sheet. The continuity and correlation of the ophiolite slivers found in the suture zones between these blocks is still poorly understood; they may represent either the remains of island arcs formed along the leading edges of the continental microplates, or plate basement overthrust by the subsequent collisions. The evidence for these sequential microplate accretions has been to some degree obliterated by the subsequent Paleogene collision of the Indian subcontinent with southern Laurasia, but even so it is clear that at least three episodes of rifting and suturing occurred by which Gondwanan biotic elements could have been tectonically rafted to southern Laurasia in the Mesozoic.

Under the drifting Indochina hypothesis, then, the ancestors of the present Asian *Cylindrostethus* fauna could then have reached Southeast Asia via these rifted continental fragments any time between the middle Triassic and the early Cretaceous. The evolution of the two major Asian clades in the genus (the *costalis* and *scrutator* groups) from a basal stock similar to *C. sumatranus* would then be assumed to be an event which occurred in the Southeast Asian region, with a member of the *costalis* group subsequently invading India from the north and east via the Assam corridor following the subcontinent's Eocene suturing with Tibet, and dispersing as far southward as Ceylon. India's continued northward movement and the consequent rise of the Himalaya then resulted in the desertification of the northern portion of the subcontinent, causing elements of the tropical biota, including *Cylindrostethus*, to retreat southward to the mesic refugium afforded by Ceylon and splitting what was a previously continuous tropical Asian freshwater aquatic biota. The concurrent northward drift of Africa led to corresponding desertification and drying on that continent, forcing *Cylindrostethus* and other tropical insects into the rain forests of the west.

Support for the drifting Indochina hypothesis comes from present distribution of *Cylindrostethus* species in Asia. All three major Paleotropical clades, the *sumatranus*, *costalis* and *scrutator* groups, contain taxa which occur in Indochina, the Malay Peninsula, or Sumatra, while only one, the *costalis* group, has a representative in India. This is the type of distribution pattern one might expect if the common ancestors of all three Asian clades originally occurred in Indochina or on continental fragments that were subsequently incorporated into it.

The major argument against the drifting Indochina hypothesis is that it does not perfectly reflect the structure of area relationships derived from the species phylogeny for Paleotropical *Cylindrostethus* (fig. 14). If the mechanism of drifting Gondwanan continental fragments described above is adopted to explain the present Africa-Sumatra sister area relationships in the *sumatranus* group, then this basal lineage of Paleotropical *Cylindrostethus* must be assumed to be of great age, since all of the above blocks rifted from Gondwana between 200–130 Ma (Audley-Charles 1987; Mitchell 1989), well before the more extensive breakup of the remainder of east Gondwana which commenced at about 80–100 Ma. This should be reflected by the Asian taxa being sister to a clade containing the African and South American taxa, since available geological evidence indicates that all of the accreted Indochinese terranes derived from Gondwana had rifted away from that supercontinent prior to the separation of South America from Africa, which commenced in the early Cretaceous (Barron et al. 1981; Owen 1983; Pitman et al. 1993). Instead, the single African taxon is grouped in a clade with those from Asia. It is possible that vicariance events not related to rifting, such as arid barriers within an intact Gondwana supercontinent, could have isolated the Neotropical taxa on west Gondwana

long before South America actually rifted away, but as noted above this presupposes a great age for the *Cylindrostethus* lineage, since such vicariance would need to have occurred at least 160 Ma.

The drifting Indochina scenario presented above may be challenged by an alternative drifting India hypothesis, in which *Cylindrostethus* reached southern Eurasia much later in time by riding northward on the Indian subcontinent following its late Jurassic separation from eastern Gondwana. Rafting on India would appear to require the northern paleoposition for that subcontinent advocated by various authors (Smith and Hallam 1970; Hamilton 1979) in which its northwest flank was in contact with east Africa near present day Somalia. This configuration would put northwestern India, central Africa, and central South America approximately 15 to 20 degrees south of the equator in the Jurassic, thus allowing a band of tropical forest to have connected all three regions. India rifted away from Africa and Madagascar in the early Cretaceous and drifted northward across the equator as a tropical microcontinent. Following India's collision with southern Eurasia, which may have begun as early as the very late Cretaceous (Klootwijk et al. 1992) and was certainly complete by the Eocene (Searle 1991), *Cylindrostethus* (and many other tropical organisms) would have been able to disperse into Southeast Asia via Assam and Burma. Once again, as with the drifting Indochina hypothesis, the subsequent desertification of central and northern India would be considered a vicariance event producing the disjunction between the Southeast Asian and Ceylonese faunas seen at the present time.

A major argument against the drifting India hypothesis is the low diversity of *Cylindrostethus* currently seen on that subcontinent, with only a single species, *C. productus*, being present. The drifting India hypothesis also fails to explain the absence of *Cylindrostethus* or related genera in Madagascar, which remained attached to India after it rifted from Africa in the late Jurassic (Barron et al. 1981). One may note, however, that if Madagascar did indeed form the western portion of a Mesozoic India-Madagascar microcontinent lying in the southern hemisphere then it would have experienced a seasonally dry climate similar to that prevailing in the western two thirds of present day Madagascar. This could have represented an ecological barrier excluding many rainforest taxa that might still have occupied the eastern portion of the landmass, which later separated and drifted away as India.

Recent Zoogeography

Whatever the mechanism by which *Cylindrostethus* reached tropical Asia, subsequent speciation within the major clades appears to have been the result of both vicariance and dispersal events. The present day areas of endemism defined by the ranges of *Cylindrostethus* species in Southeast Asia are shown in Figure 15, and illustrate how the core range of the genus in the region is centered on Indochina, the Malay Peninsula, and the Greater Sunda Islands, with the Philippines and Celebes as isolated outliers. Within the areas lying on the Asian continental shelf, the primary isolating mechanism appears to be altitudinal parapatry, with *C. scrutator* occupying rocky upland streams throughout the region while the members of the *costalis* group occur in disjunct pockets of lowland swamp forest. This pattern is markedly different from that seen in the sympatric gerriid genus *Metrocoris* or the veliid genus *Rhagovelis*, where the lowland species are widespread and the upland species locally endemic (Polhemus and Polhemus 1989; Polhemus 1990).

Of great interest is the presence of the plesiomorphic and apparently relictual *C. sumatranus* in south Sumatra, an area which is presently separated from the Malay Peninsula only by the narrow and shallow Straits of Malacca. The geological history of Sumatra is still incompletely understood, but as discussed previously the island appears to contain continental rocks of both Gondwanan and Laurasian origin. It thus seems likely that some type of barrier must have existed isolating *C. sumatranus* or its ancestral lineage in a section of Sumatra before the island attained its present configuration and close juxtaposition with continental Asia. Members of both the *scrutator* and *costalis* groups (*C. scrutator* and *C. malayensis* respectively) are now also present on Sumatra, but the dates of their arrivals cannot be ascertained. It is clear that the water barrier between the present northeastern coast of Sumatra and the Malay Peninsula has become progressively narrower throughout the Tertiary due to extensive sedimentation from the Barisan Mountains into the backarc basin adjoining the Straits of Malacca, and continues to become so, with the coast of Sumatra slowly advancing toward the Malay Peninsula. It is thus possible that the episodes of lowered sea level in the Quaternary may have represented the first instance of dry land connections between Sumatra and mainland Asia, and that as a result *C. scrutator* and *C. malayensis* may be comparatively recent arrivals to the island. For whatever reason, the plesiomorphic *sumatranus* stock has survived in south Sumatra, but is unknown elsewhere in tropical Asia.

At the present time the species of the *costalis* group are restricted to the southern portion of the Asian continent and to the adjacent Greater Sunda islands of Borneo and Sumatra that were connected to it during Pleistocene low sea level stands. All the *costalis* group species now recognized in Southeast Asia have non-overlapping distributions (fig. 9) and it appears that speciation within this species group has resulted primarily from the fragmentation of previously continuous ranges by rising post-Pleistocene sea levels. It is interesting to note that the narrow bottleneck at the Isthmus of Kra has also apparently functioned as an effective barrier to dispersal, allowing speciation on the lower portion of the Malay Peninsula to proceed as if it were an island in its own right, a pattern also noted for the narrow bottleneck at the base of the Minahasa Peninsula on Celebes (Polhemus and Polhemus 1990).

The members of the *scrutator* group are widely distributed across Indochina and throughout much of the Malay Archipelago (fig. 10). *C. scrutator*, the most widespread member of this clade, is known from Indochina, the Malay Peninsula, the Greater Sunda Islands, and from the Mentawai Archipelago; these latter islands must have been reached via overwater dispersal, since they represent the subaerial crest of the fore-arc ridge above the Sunda subduction zone and have never been closer to any other land mass than they are at the present time. The two other species in the *scrutator* group, *C. persephone* and *C. vittipes*, have distributions far more restricted than that of *scrutator*, occupying Celebes and the Philippines respectively. Based on the pattern of relationship among these species it appears that the Philippines were colonized first, probably via dispersal of a Bornean *scrutator* ancestor to Mindanao along the Sulu Archipelago. Whatever its initial route of entry into the Philippines, *C. vittipes* has now radiated throughout that entire archipelago, transgressing even the San Bernardino Strait that has proven a barrier to many other aquatic and terrestrial organisms. The isolation of *C. persephone* on Celebes appears to have occurred subsequently, probably after the opening of the Makassar Strait in the middle Tertiary. Although both *C. vittipes* and *C. scrutator* currently occupy highly frag-

mented ranges scattered across many islands there is no evidence of incipient speciation among the isolated populations of these species. This would indicate that either the rate of divergence among allopatric populations of the *scrutator* group is relatively slow, or that interisland dispersals have continued with sufficient regularity to mitigate genetic drift and preclude insular speciation.

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All types are deposited in the U. S. National Museum of Natural History, Washington, D. C. (USNM); paratypes are held in the J. T. Polhemus collection, Englewood, Colorado (JTPC), the Bishop Museum, Honolulu (BPBM), and the Museum Zoologicum Bogoriense, Bogor, Indonesia (MZB).

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LITERATURE CITED

- Andersen, N. M. 1982. The semiaquatic bugs (Hemiptera, Gerromorpha). Phylogeny, adaptations, biogeography and classification. *Entomonograph* 3. Scandinavian Science Press Ltd., Klampenborg. 455 p.

- 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 Monographs in Biogeography No. 4, p. 5–25. Clarendon Press, Oxford.
- Barron, E. J., C. G. A. Harrison, J. L. Sloan, II, & W. W. Hay.** 1981. Paleogeography, 180 million years ago to the present. *Eclogae Geol. Helv.* **74**: 443–70.
- Bergroth, E.** 1916. New and little-known heteropterous Hemiptera in the United States National Museum. *Proc. U. S. Natl. Mus.* **51**: 215–39.
- Chen, P., & N. Nieser.** 1992. Gerridae, mainly from Sulawesi and Pulau Buton. Notes on Malesian aquatic and semiaquatic bugs (Heteroptera), III. *Tijd. Entomol.*, **135**: 145–162.
- Cheng, L., & C. H. Fernando.** 1969. A taxonomic study of the Malayan Gerridae (Hemiptera: Heteroptera) with notes on their biology and distribution. *Oriental Insects* **3**: 97–160.
- Distant, W. L.** 1903–1904. *The fauna of British India including Ceylon and Burma. Rhynchota. Vol. II (Heteroptera)*. Taylor and Francis, London. xvii + p. 1–242 (1903) and p. 243–503 (1904).
- Distant, W. L.** 1910. Some undescribed Gerrinae. *Ann. Mag. Nat. Hist.* (8) **5**(26): 140–53.
- Distant, W. L.** 1911. Rhynchota.-Vol. V. Heteroptera: Appendix. In: A. E. Shipley and G.A.K. Marshall, eds., *The Fauna of British India, including Ceylon and Burma*. xii + 362 p. Taylor and Francis, London.
- Erichson, W. F.** 1848. Die Insecten. In: Schomburgk, M. R., ed., *Versuch einer Fauna und Flora von Britisch Guiana* **18**, Band 3, p. 533–617.
- Fernando, C. H., & L. Cheng.** 1974. A preliminary study on the fauna and distribution of aquatic Hemiptera in Malaya and Singapore. *J. Fed. Malay Mus.* **29**: 21–44.
- Fieber, F. X.** 1860. *Die europäischen Hemiptera. Halbflüger (Rhynchota Heteroptera). Nach der analytischen methode bearbeitet*. Wien. P. 1–112 (1860), 113–444 and III–VI (1861).
- Hamilton, W.** 1979. Tectonics of the Indonesian region. *U. S. Geol. Surv. Prof. Paper* **1078**, 345 p.
- Hungerford, H. B., & R. Matsuda.** 1962. The genus *Cylindrostethus* Fieber from the Eastern Hemisphere. *Univ. Kan. Sci. Bull.* **63**: 83–111.
- Hutchinson, C. S.** 1989. The paleo-tethyan realm and Indosinian orogenic system of Southeast Asia. In: A. M. C. Sengör, ed., *Tectonic Evolution of the Tethyan Region*, p. 585–643. Kluwer Acad. Pub., Dordrecht.
- Kirkaldy, G. W.** 1899. Sur quelques hémiptères aquatiques nouveaux ou peu connus. *Rev. Entomol., Caen* **18**(5–6): 85–96.
- Kirkaldy, G. W.** 1909. Hemiptera, old and new. No. 2. *Can. Entomol.* **41**(11): 388–92.
- Klootwijk, C. T., J. S. Gee, J. W. Pierce, G. M. Smith & P. L. McFadden.** 1992. An early India-Asia contact: Paleomagnetic constraints from Ninetyeast Ridge, ODP Leg 121. *Geology* **20**: 395–98.
- Lundblad, O.** 1933. Zur Kenntnis der aquatilen und semiaquatilen Hemipteren von Sumatra, Java und Bali. *Arch. Hydrobiol.* 1933, Suppl. Bd. **12**, Tropische Binnen-gewasser **4**: 1–195, 263–489.

- Matsuda, R.** 1960. Morphology, evolution and a classification of the Gerridae (Hemiptera - Heteroptera). *Univ. Kansas Sci. Bull.* **41**: 25-632.
- Mayr, G. L.** 1865. Diagnosen neuer Hemipteren, II. *Verh. Zool.-Bot. Ges. Wien* **15**: 429-446.
- Mitchell, A. H. G.** 1981. Phanerozoic plate boundaries in mainland S.E. Asia, the Himalayas and Tibet. *J. Geol. Soc. London* **138**: 109-22.
- Mitchell, A. H. G.** 1989. The Shan Plateau and western Burma: Mesozoic-Cenozoic plate boundaries and correlations with Tibet. In: A. M. C. Sengör, ed., *Tectonic evolution of the Tethyan Region*, p. 567-83. Kluwer Acad. Publ., Dordrecht.
- Owen, H. G.** 1983. *Atlas of continental displacement. 200 million years to the present.* Cambridge Univ. Press, Cambridge. 159 p.
- Pitman, W. C., III, S. Cande, J. LaBrecque & J. Pindell.** 1993. Fragmentation of Gondwana: the separation of Africa from South America. In: P. Goldblatt, ed., *Biological relationships between Africa and South America*, p. 15-34. Yale University Press, New Haven.
- Polhemus, D. A.** 1990. A revision of the genus *Metrocoris* Mayr (Heteroptera: Gerridae) in the Malay Archipelago and the Philippines. *Entomol. Scand.* **21**: 1-28.
- Polhemus, J. T.** 1979. Results of the Austrian-Ceylonese Hydrobiological Mission 1970, of the Institute of Zoology of the University of Vienna (Austria) and the Department of Zoology of the University of Sri Lanka, Vidyalankara Campus, Kelaniya. Part XIX: Aquatic and semiaquatic Hemiptera of Sri Lanka from the Austrian Indo-Pacific Expedition, 1970-71. *Bull. Fisheries Res. Sta., Sri Lanka* **29**: 89-113.
- Polhemus, J. T. & D. A. Polhemus.** 1989. Zoogeography, ecology and systematics of the genus *Rhagovelia* Mayr (Heteroptera: Veliidae) in Borneo, Celebes and the Moluccas. *Insecta Mundi* **2**: 161-230.
- Polhemus, J. T. & D. A. Polhemus.** 1990. Zoogeography of the aquatic Heteroptera of Celebes: regional relationships versus insular endemism. In: W. J. Knight and J. D. Holloway, eds., *Insects and the rain forests of South East Asia (Wallacea)*, p. 73-86. Royal Entomological Society of London, London.
- Schmidt, E. T.** 1915. Das Genus *Cylindrostethus* Fieber. *Stett. Entomol. Ztg.* **76**: 361-64.
- Searle, M. P.** 1991. *Geology and tectonics of the Karakoram Mountains.* John Wiley and Sons, Chichester. 358 p.
- Smith, A. G. & A. Hallam.** 1970. The fit of the southern continents. *Nature* **225**: 139-44.
- Spinola, M.** 1840. *Essai sur les insectes hémiptères, rhyngotes ou hétéroptères.* J. B. Baillié, Paris. 383 p., 5 folding tables.
- Stål, C.** 1870. Hemiptera insularum Philippinarum. Bidrag till Philippinska öarnes Hemipter-fauna. *Ofv. Kongl. Svenska Vet.-Akad. Forh.* **27** (7): 607-776.
- Swofford, D. L.** 1990. PAUP: phylogenetic analysis using parsimony, version 3.0m. Computer program distributed by the Illinois Natural History Survey, Champaign, Illinois.
- Torre-Bueno, J. R. de la.** 1925. On some aquatic Hemiptera from Ceylon, with descriptions of new forms. *Spolia Zeylanica* **8** (2): 223-34.

APPENDIX: Coding of characters for phylogenetic analysisCharacter Matrix for Paleotropical *Cylindrostethus* species

South American species	110000000000
<i>quadrivittatus</i>	002111000001
<i>sumatranus</i>	001111000001
<i>productus</i>	0013011120020
<i>costalis</i>	0012011110020
<i>malayensis</i>	0013011110020
<i>samarinda</i>	0013011110020
<i>scrutator</i>	0011001001110
<i>persephone</i>	0010001001100
<i>vittipes</i>	0011001001000

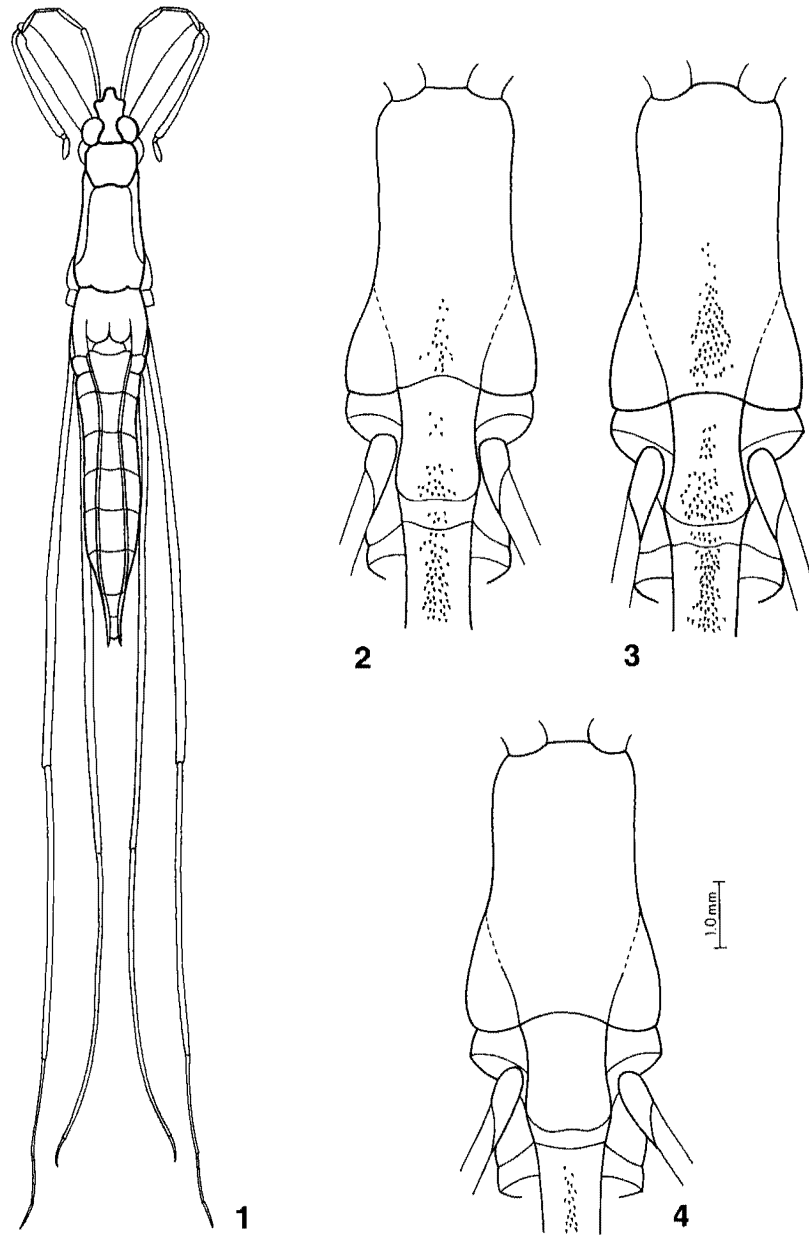
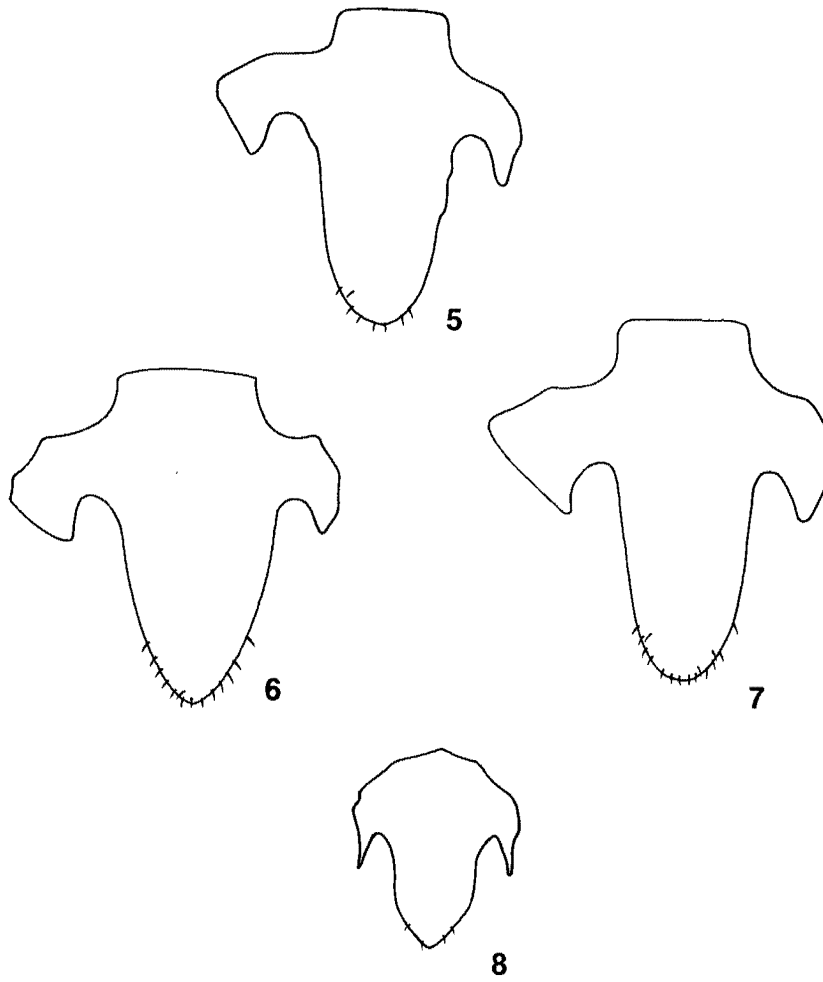


Fig. 1. *Cylindrostethus samarinda*, n.sp. Female, dorsal habitus. Figs. 2-4. Ventral view of mesosternum, metasternum, and basal abdominal ventrites of *Cylindrostethus* species, illustrating variation in numbers and placement of spinules. 2, *C. malayensis* n.sp. 3, *C. samarinda* n.sp. 4, *C. costalis* Schmidt.



Figs 5-8. Male proctigers of *Cylindrostethus* species. 5, *C. costalis* Schmidt. 6, *C. malayensis* n.sp. 7, *C. samarinda* n.sp. 8, *C. scrutator* (Kirkaldy).

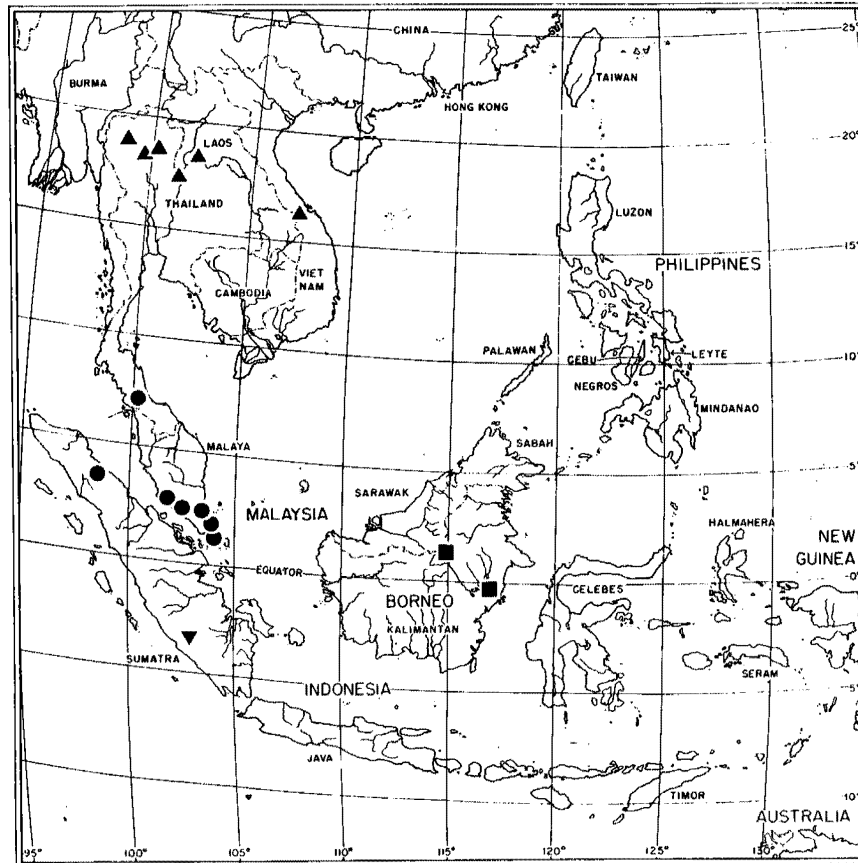


Fig. 9. Distribution of species of the *costalis* and *sumatranus* groups in Southeast Asia. Circles = *C. malayensis* n.sp. Triangles = *C. costalis* Schmidt. Squares = *C. samarinda* n.sp. Inverted Triangle = *C. sumatranus* Lundblad.

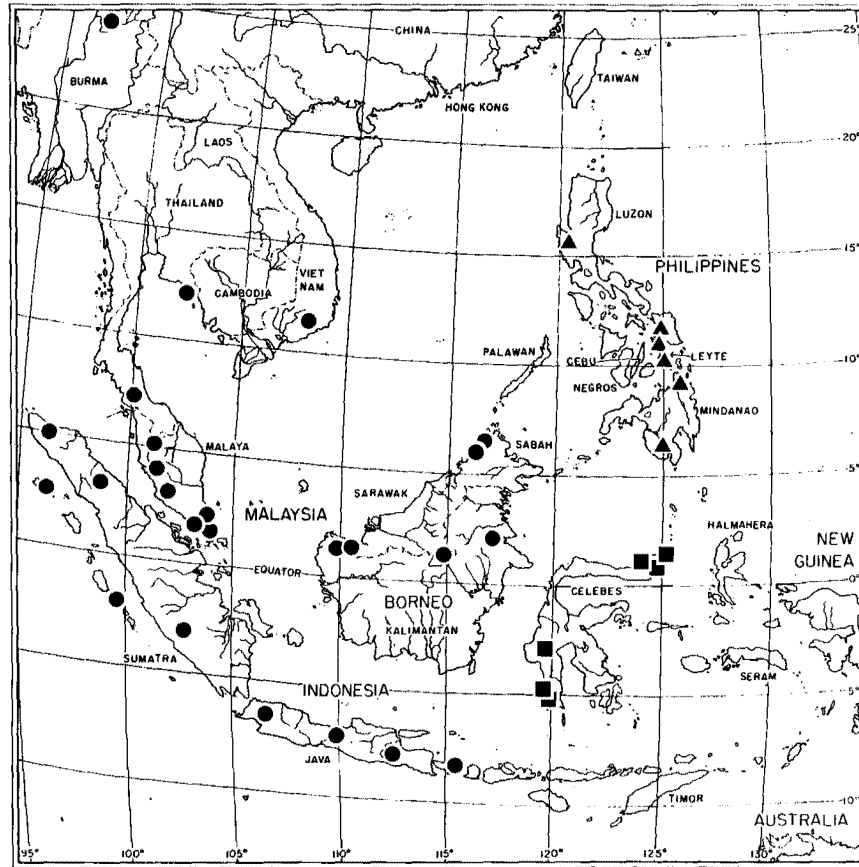


Fig. 10. Distribution of species of the *scrutator* group in Southeast Asia. Circles = *C. scrutator* (Kirkaldy). Triangles = *C. vitipes* Stål. Squares = *C. persephone* Kirkaldy.

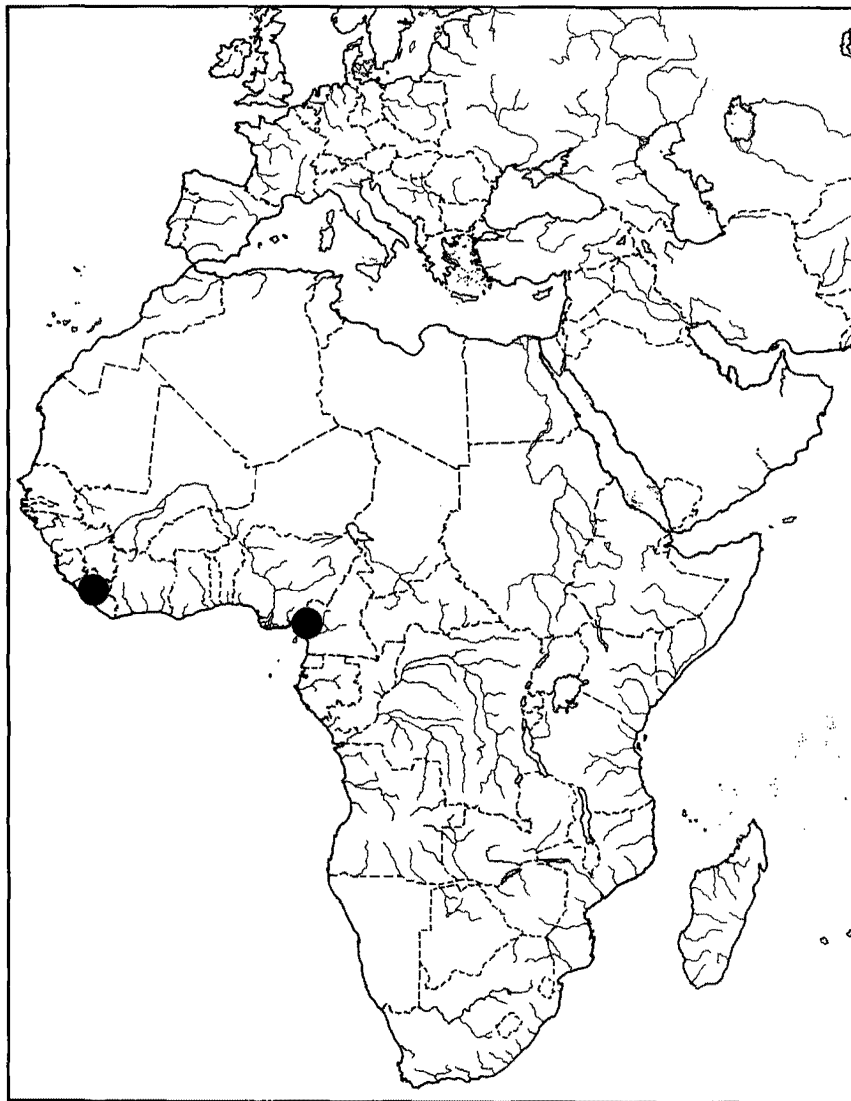


Fig. 11. Distribution of *C. quadrivittatus* Bergroth in Africa.

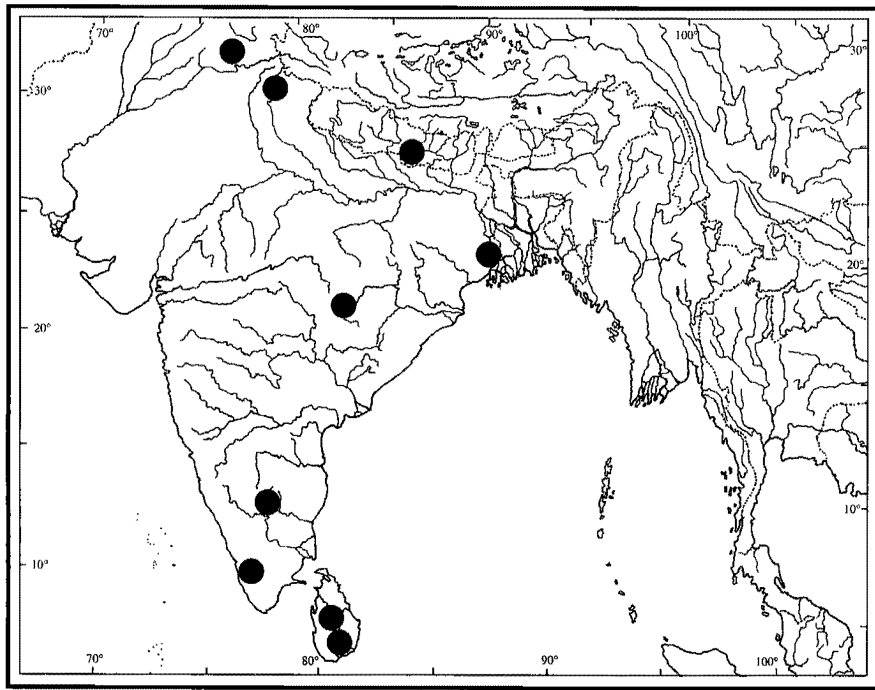


Fig. 12. Distribution of *C. productus* Spinola in Asia.

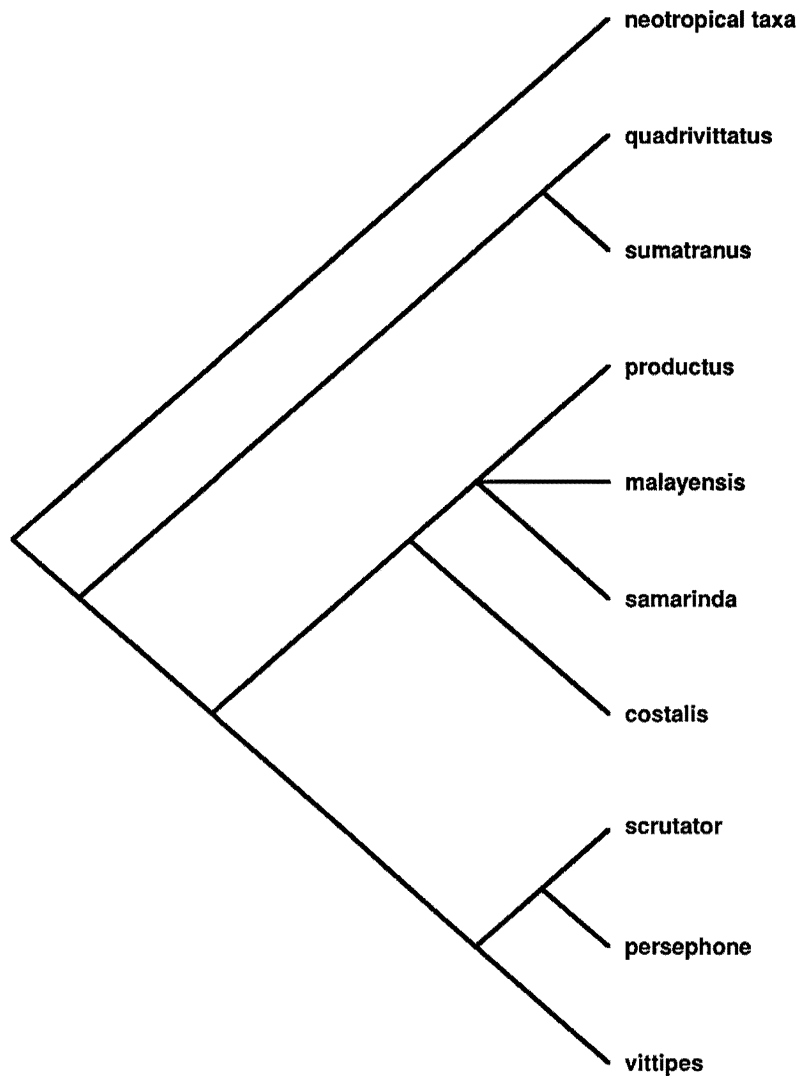


Fig. 13. Phylogenetic diagram of relationships among Paleotropical *Cylindrostethus* species. All South American species are treated as a single group.

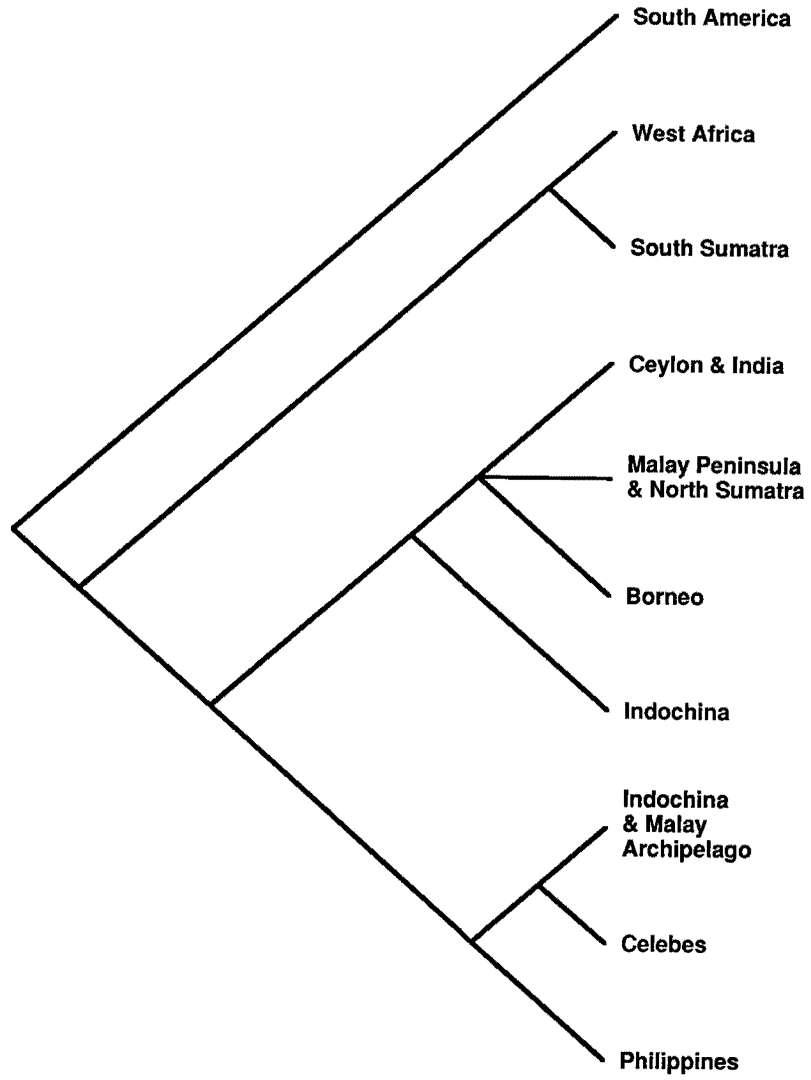


Fig. 14. Area cladogram for Paleotropical *Cylindrostethus* species.

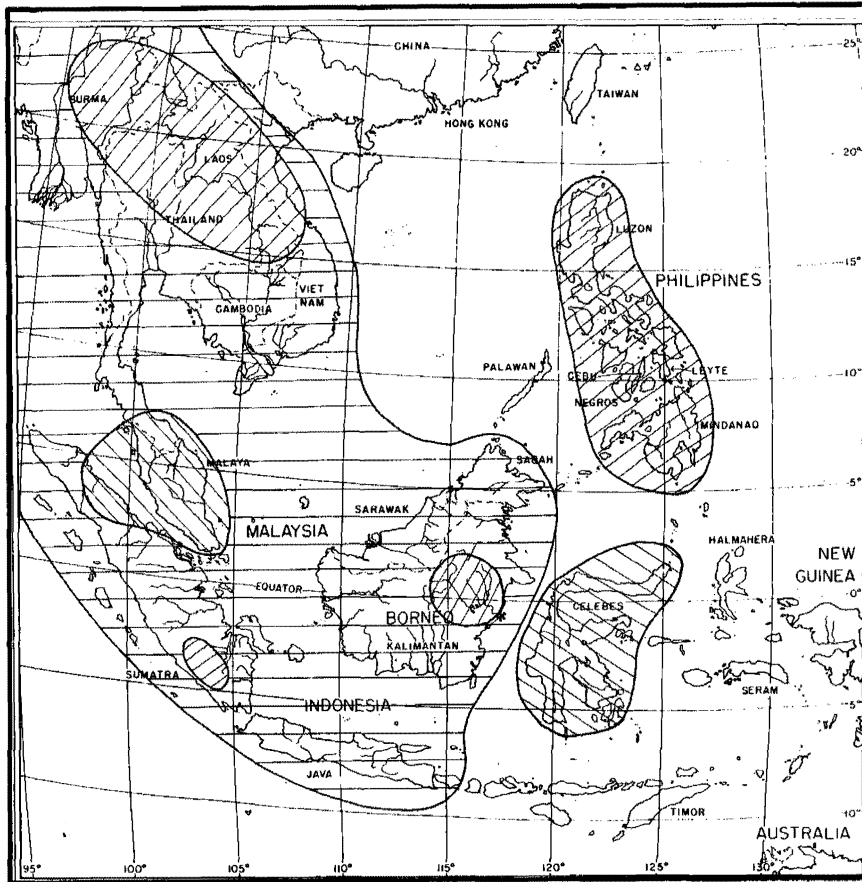


Fig. 15. Areas of endemism in Southeast Asia as defined by the ranges of *Cylindrostethus* species.