The Trepobatinae (Gerridae) of New Guinea and surrounding regions, with a review of the world fauna. Part 6. Phylogeny, biogeography, world checklist, bibliography and final taxonomic addenda

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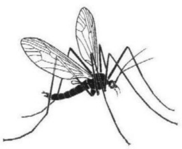

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The small waterstriders of the subfamily Trepobatinae have radiated extensively on New Guinea and surrounding archipelagos. The present contribution is the sixth in a series of reports dealing with this endemic fauna, and presents a cladistic analysis at the generic level for the subfamily, a biogeographic analysis, a world checklist, a complete bibliography, and final taxonomic addenda. The taxonomic appendix contains new distributional records for *Stygiobates mubi* Polhemus & Polhemus, and descriptions of the following new taxa: the new genus *Talaudia* to hold the previously described *Andersenella nilsi* Chen & Nieser from the Talaud Archipelago; *Metrobatoides bifurcatus* sp. n. from northern central Irian Jaya; and *Iobates ivimka* sp. n. from southern Papua New Guinea. The current cladistic analysis supports the previously proposed tribal classification, with the Metrobatini, Trepobatini, Naboandelini, and Stenobatini all resolved as discrete monophyletic groups. Our cladistic and biogeographic analyses also suggest that the current distribution of trepobatine genera in the New Guinea region has been strongly influenced by past tectonic events, most notably the accretion of island arc terranes derived from the Solomons and Halmahera arc systems. This has led to distinct areas of freshwater and marine endemism among the Metrobatini and Stenobatini in the areas surrounding Halmahera, the Vogelkop Peninsula, and northeastern New Guinea plus nearby islands. By contrast, the distribution of Naboandelini in the New Guinea region suggests a vicariance pattern with Australia across the Torres Strait.

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Introduction

This paper represents the sixth and final part of our monograph of the Trepobatinae of New Guinea and surrounding regions. In the previous five parts of this series (Polhemus & Polhemus 1993, 1994, 1995, 1996, 2000) we proposed four new tribes, providing taxonomic revisions for each, including descriptions of 10 new genera and 47 new species. In this final section we provide a phylogenetic analysis for the subfamily at the generic level, followed by a biogeographic discussion, a world bibliography, and a world checklist. We also attach an appendix dealing with a few small remaining taxonomic details, including one additional new genus and two additional new species.

Given the diversity of the Trepobatinae in the New Guinea region, we fully expect further new species and possibly even new genera to be discovered by future collecting, particularly on the more remote island groups to the east and west of New Guinea proper. Even so, any additions to the currently known biota can be treated in future supplements to the current monograph, which has reached a stage of completion sufficient for presentation of the synthetic phylogenetic and biogeographic analyses provided below.

Phylogeny

Character analysis. – Extensive character analyses of gerrid genera have been previously provided by Matsuda (1960) and Andersen (1982). Efforts to use these for the present study proved frustrating. Matsuda's work covers all gerrid genera known at that time, but for the purpose intended here is inadequate for several reasons: 1.) the amount of material available for certain key genera was inadequate, especially in Stenobatini and Naboandelini; 2.) almost half of the genera we have before us were unknown at that time; and 3.) the illustrations of the male aedeagus, provided for all genera for which males were available to him, are inaccurate, omitting important details of some sclerites while at the same time incorrectly depicting as sclerites darkened regions of the aedeagal cuticle and internal structures. Andersen's work covers the entirety of the Gerromorpha, with analyses and descriptions of all major features and aspects of these insects, and is thus extremely useful in understanding the homologies and variability of many structures and features. Conversely, because of the extremely broad coverage of this work, there is not enough included detail concerning the single subfamily Trepobatinae to establish a character set for genera. In addition, as with Matsuda's work, almost half of the genera treated here were unknown to Andersen. The character analysis that follows is therefore based primarily upon original investigations.

Characters have been analyzed with regard to developmental trends and stability. For some characters, the apomorphic state can be inferred by relatively simple tests or observations, i. e.: characters with exceptional occurrence (characters 8, 30, 35); characters that have arisen *de novo* (characters 25, 26, 31, 32); total or partial loss of a structure found in closely related groups or ancestors (character 10); characters that exhibit elaboration of structure (characters 3, 5, 6, 7, 9, 12, 16, 17, 20, 23, 29, 34). Conversely, the plesiomorphic character state can be inferred if a structure is homologous with that in more primitive taxa or ancestors (characters 14, 15).

Particularly important, controversial, or ambiguous character systems (ie., those for which polarity cannot be directly inferred *a priori*) are discussed in greater detail below.

1.) Predominant color (character 1). Unicolorous grey, without extensive additional markings, is considered to be plesiomorphic. Elaborations are considered to be apomorphic, but an apomorphic sequence of these is unclear.

2.) Body size (character 2). An essentially equal body size in males and females is considered to be plesiomorphic, while a great difference in body size between sexes is considered apomorphic.

3.) Head shape (character 4). The plesiomorphic head shape is considered to be that of *Rhagadotarsus*. Four other apomorphic morphologies provide unambiguous characters for the four tribes of Trepobatinae, however the anagenetic sequence of development is not clear.

4.) Omphalium position (character 11). The omphalium, or metasternal scent gland opening, occurs at the posterior edge of the metasternum, or is vestigial or absent, in all trepobatine genera except those now held in the tribe Stenobatini; in these latter five genera, the omphalium position is medial in three, and located near the anterior margin in the other two. The more anterior position is unusual, perhaps unique, in the Gerridae: Andersen (1982: 201) states that 'when present, the metasternal scent orifice (Omphalium) of the Gerridae is located in the posterior half of the segment,' but this clearly does not hold true for all Stenobatini.

5.) Wings (character 13). Wings, or vestiges thereof, are found in all genera of Gerridae except the truly marine genera. Thus the invariant lack of wings characterizes the tribe Stenobatini within the Trepobatinae. Other marine genera in the subfamily Halobatinae also are only known in the wingless form.

6.) Hind tarsal claws (character 18). The hind tarsal claws of trepobatine genera vary widely, from short or hair-like, to long slender and blade-like. The latter well developed claws are found in the marine tribe Stenobatini. The three genera of the tribe Naboandelini all have short or hair-like claws. The remaining genera, in the tribes Trepobatini and Metrobatini, have long slender claws reaching almost to the apex of the tarsi, except the genus *Metrobates* in which the claws are shorter, not nearly reaching the tarsal apex.

7.) Male anterior tibia, distal comb (character 19). The distal comb of the male fore tibia has different forms; the more elaborate are considered to be apomorphic, and help define clades, but the functional significance of the various forms is unclear.

8.) Posterior femur length (character 21). The Trepobatinae tend to have shorter middle and hind femora than gerrids in other subfamilies, with some genera in particular having very short middle femora. In most trepobatines the hind femur is shorter than or equal to the body length, but in a few genera it is longer than the body. While this character thus helps to define genera, it does not provide an unambiguous synapomorphy for the subfamily.

9.) Posterior tarsal segmentation (character 23). The posterior tarsi of Trepobatinae exhibit various tarsal length ratios, and may be completely fused in some genera. In the Trepobatini the two tarsal segments are either of about equal length, or segment I is the longest. In the Stenobatini segment I is about 1/2 to 2/3 the length of II, although in some species all are fused. The segmentation in the Naboandelini is similar to that of Stenobatini except for the genus *Calyptobates*, where the segments in all species are always fused. The segments are uniformly fused in the genera of Metrobatini, except in the genus *Metrobates* where segment I is about 1/4 the length of segment two. The functional significance of the segmentation is unclear, except to help define tribal clades.

10.) Sclerites of the vesica (chracter 26). The vesical sclerites and the plesiomorphic versus apomorphic states of various arrangements have been treated by Andersen (1982, 1991). Of particular interest is the proposal that the plesiomorphic state is represented by the four major medial sclerites [anterior (as), dorsal (ds), basal (bs), ventral (vs)] being separated and appearing as individual sclerites, whereas the continuously coiled vesica that continues anteriorly as seen in the genus *Rhagadotarsus* is considered to be apomorphic. This analysis, in our view, has the polarities reversed. A review of the vesical architecture of a wide range of Homoptera and Heteroptera argues that the continuous vesica is plesiomorphic. Furthermore, Andersen's cladistic analysis of the Gerridae places the Rhagadotarsinae as the basal subfamily, even though he holds that the male genitalia possess the most derived character state for the vesical sclerites, thus even a computer generated cladogram argues on the basis of parsimony that the continuous vesica is plesiomorphic.

We propose that the continuous uninterrupted vesical sclerites represent the plesiomorphic state (*Rhagadotarsus*), with the following trends increasingly apomorphic, although perhaps not exactly in the following sequence (abbreviations given are those used in figures published in previous parts of this monograph series): 1.) medial sclerites (as, ds, bs, vs) increasingly fragmented and/or reduced; 2.) lateral sclerites (ls) present, simple, rod-like; 3.) lateral sclerites modified distally, bifurcate, expanded, knob-like, etc.; 4.) lateral sclerites plate-like (e. g. *Metrobates*, many Trepobatini); 5.) appearance of the medial sclerite (ms) as a new structure (e. g. *Andersenella*); 6.) appearance of the apicolateral sclerite (als) as a new structure; 7.) base of anterior sclerite expanded, broadly bifurcate, even lyre-shaped (Stenobatini); 8.) loss of all median sclerites; usually accompanied by 9.) sclerotization of the distal portions of the phallotheca, as well as heavy basal, dorsal and ventral sclerotization (character 24).

11.) Male proctiger; ie., abdominal segment 10 (characters 27, 29). The proctiger is rather plastic, liable to modification, and its use as an indicator of phylogenetic relationships must be approached with caution. Various modifications and elaborations such as lobes, protuberances, tufts of spines, and lateral outgrowths in the form of digitate protuberances or spines are seen in various gerrid lineages e. g. Halobatinae (some *Halobates*), Ptilomerinae (some *Ptilomera*) and Trepobatinae (all Naboandelini, some Metrobatini, all Stenobatini). In some groups the lateral outgrowths are very large and accompanied by corresponding modifications to the pygophore and/or eighth segment. In these groups (e. g. Naboandelini, Stenobatini, some Metrobatini) the morphology seems considerably more stable than in those groups exhibiting modifications to the proctiger alone.

Lateral spines or protuberances that appear homologous in their form, function or origin may not be. The genus *Metrobatopsis* has lateral protuberances that appear to be analogous with those of the Naboandelini (*Naboandelus*, *Hynesionella* and *Calypobates*) and Stenobatini (*Rheumatometroides*, *Stenobates*, *Stenobatopsis*), however careful examination reveals that both the external and internal structure of the proctiger of *Metrobatopsis* (and genera closely related on other grounds) is quite different than any of the latter genera, suggesting that their origins and functions are different. Unfortunately, the small size of these water striders and the consequent difficulty in observing them in the field has limited our understanding of the function of these lateral spines. Involvement in copulation seems most likely, however.

12.) Male parameres, shape (character 28). Small simple parameres, or their absence, are most likely the plesiomorphic state in Gerridae. The larger or more complex shapes are considered to be apomorphic, and these may exhibit several forms whose significance is unclear, except that they help delineate the genus *Metrobates*, and the tribe Trepobatini wherein all genera possess large or complex parameres.

13.) Female ovipositor (character 29). In contrast to the poorly developed ovipositor of most gerrids, members of the subfamily Rhagadotarsinae possess a well developed, long ovipositor with distinct serrations on the first gonapophyses, thought to be assocated with embedding eggs in plant tissues. Andersen (1982: 224) believes that this is probably a secondary development. To our surprise, we discovered that an ovipositor with serrate second gonapophyses is also present in all genera of Stenobatini, suggesting egg deposition in a firm substrate, although the eggs are oval and show no modifications to indicate a particular oviposition site or substrate (Polhemus & Polhemus 1996: 287; Andersen & Weir 1998: 531, fig.38).

14.) Mesothorax shape (character 32). The mesothorax of Trepobatinae is usually tumid ventrally, however in two genera of Stenobatini the mesothorax is dorsoventrally flattened. The significance of this feature is unknown, but may aid in phoresy.

15.) Body shape (character 34). The usual body shape of trepobatine water striders is relatively narrow and not flattened. The genera *Metrobates* and *Metrobatoides* are unique in possessing a very broad, dorsoventrally flattened body, probably associated with their mode of living, which involves skating on the midstream sections of large streams and rivers.

Characters

Morphological data were analyzed to obtain a set of characters suitable for determining the phylogeny of trepobatine genera. In all, 39 characters were identified that offered useful phylogenetic information. These characters and their states are described below. The character states are coded using integers beginning with 0; many of these characters were coded as multistate, with the number of discrete states for a given character varying from 1-8 (see Tab. 1). The character numbering indicates no *a priori* assumptions as to character state polarity or weighting.

Descriptions of characters and character states for genera of Trepobatinae. – Characters followed by '(U)' had no hypothesis of polarity and were run unordered in all iterations of the phylogenetic analysis.

Body

1. Predominant color pattern (ground color mentioned first) (U)
   0 = grey*
   1 = black, grey or blackish grey with yellowish or leucine markings
   2 = black with light grey markings (except light spot on pronotum)
   3 = light brown, leucine, yellow or orange with dark markings
   4 = blackish brown with yellowish or leucine markings
   5 = black to blackish brown with light brown to red brown markings
2. Body size
   0 = essentially same in males and females
   1 = sexually dimorphic, males much smaller

Head

3. Antennae with stiff spine-like setae distally
   0 = absent, or scattered widely on segments I and II
   1 = present on distal 1/4 on at least segments I and II, few in number
   2 = present on distal extreme of at least segments I and II
4. Head shape (U)
   0 = Head long, extending anteriorly; gular region long; antennal socket removed from eye by width of socket; base of rostrum at mid eye level
   1 = Same as 0 except base of rostrum at ventral eye level
   2 = Head short, gular region short, usually tumid, extending below ventral eye level; antennal socket close to eye, not removed from eye by width of socket; base of rostrum enclosed in ventrally projecting differentiated rostral cavity, below ventral eye level, directed slightly posteriorly
   3 = Same as 2, except gular region not tumid; base of rostrum not enclosed, rostral cavity planar with gular region, usually at about ventral eye level
   4 = Same as 2, except gular region not tumid; base of rostrum arising anteriorly, not enclosed; rostral cavity at or above gular region, arising at about ventral eye level.
5. Male fourth antennal segment, cross section
   0 = round or oval
   1 = slightly widened and compressed
   2 = widened and strongly flattened
6. Rostrum shape, segment III
   0 = linear or tapering, posterior margin straight to slightly curved
   1 = posterior margin tumid, strongly curved
7. Length of rostral segment III
   0 = normal, length approximately 3x segment I
   1 = long, length 4x segment I or more
   2 = very long, length approximately 6x segment I

Thorax

8. Mesonotum with median membranous region in female
   0 = absent
   1 = present
9. Mesonotum with median suture or sulcus in female
   0 = absent
   1 = present
10. Metasternal scent gland opening (omphalium)
   0 = prominent in both sexes, large in males
   1 = reduced or vestigial
   2 = secondarily absent
11. Omphalium position (U)
   0 = located at posterior margin or absent
   1 = located medially
   2 = located near anterior margin
12. Mesothoracic spiracle region
   0 = undifferentiated
   1 = differentiated, cuticle surrounding spiracle definitely different than that of adjacent mesonotum
13. Wings
   0 = sometimes present
   1 = never present, always wingless

Abdomen

14. Male basal abdominal sternites
   0 = wide
   1 = narrow, ring-like
15. Female ventrite VII
   0 = posterior edge vertical or angled posteriorly; may or may not expose gonocoxae
   1 = posterior edge angled anteriorly or excavated; broadly exposing gonocoxae

Legs

16. Anterior tarsi, cross section
   0 = round, ovate, or flattened, narrow
   1 = blade-like, wide
17. Anterior tarsi, setiferation of first segment
   0 = without long setae
   1 = with long setae ventrally
18. Hind tarsal claws
   0 = short, often hair like
   1 = present, long slender, tapering, reaching almost to apex of tarsi
   2 = present, same as 1, but shorter, not nearly reaching apex of tarsi
   3 = present, long slender, blade-like
   4 = falcate
   5 = hairlike, extending far beyond tip of tarsus, or absent
19. Male anterior tibia, distal comb (U)
   0 = with normal brush of moderate length setae
   1 = with a well defined elongate brush of moderate length stout setae
   2 = with an elongate brush of short to moderate length setae mixed proximally with longer spines or spine-like setae
   3 = with differentiated pad of closely packed short or medium length setae
20. Anterior tibial distal spur, male
   0 = absent
   1 = present
21. Posterior femur length
   0 = shorter than or equal to body including head
   1 = longer than body including head
22. Middle tarsi, modifications for rowing
   0 = unmodified, without swiming plume

1 = with swimming plume of long silky setae present

23. Posterior tarsi, segmentation (U)
    0 = with two distinct segments of about equal length, or segment I longest
    1 = with two distinct segments, segment I about 1/2 to 2/3 the length of II, sometimes secondarily fused
    2 = with two distinct segments, segment I about 1/4 the length of II
    3 = segments always fused

Genitalia, terminalia

24. Phallotheca (U)
    0 = Normal, more or less cylindrical, open basally, membranous distally
    1 = Same as 0, except distally partly closed and sclerotized, forming a U-shaped wall [*Ciliometra*]
    2 = Sclerotized at least dorsally and distally, acuminate dorso-distally [*Metrobatopsis*, *Stygiobates*]
25. Male proctiger with broad internal phragma
    0 = absent
    1 = present, simple
26. Vesical sclerites (U)
    0 = all four major sclerites (as, ds, bs, vs) present, forming a ring; ls narrow, medial
    1 = as, ds, bs present; vs well formed; ls long, paired or bifurcate distally
    2 = same as 1 except: as large, broad, expanded between ls, lobe-like in lateral view
    3 = as, ds, bs present; ms long, large (may be poorly sclerotized); ls long, rod-like or slender
    4 = as, ds, bs present; ms short, narrow; ls large, plate-like; as basally large, expanded between ls
    5 = same as 4 except: ms absent; two (1+1) auxiliiary basal sclerites present.
    6 = as, ds, bs present, and sometimes vs; ms absent or poorly formed; ls narrow, basal, reaching only middle of phallotheca
    7 = as, ds, bs short or reduced, occupying lower distal part of phallotheca; ls long, slender; all other sclerites absent
    8 = all major medial sclerites lost (as, ds, bs, vs absent); ls commencing basally, long, lobed distally; als present
27. Male abdominal segment 10 (proctiger), with long lateral anteroventrally directed digitate or spine-like processes (U)
    0 = absent, or modified in different form
    1 = present
28. Male parameres, shape (U)

Table 1. Morphological character data for 25 genera of Trepobatinae and 4 outgroup taxa (*Aquarius*, *Charmatometra*, *Cylindrostethus* and *Rhagdotarsus*). For definitions of characters and character states see text.

Genus	Character			
	0000000001 1234567890	1111111112 1234567890	2222222223 1234567890	333333333 123456789
Aquarius	5002000001	0000100400	0000020000	000001100
Charmatometra	5002000001	0000100430	1000040000	010001000
Cylindrostethus	5001100001	0000100500	0000061000	000001100
Rhagadotarsus	0000000002	0000000000	1000000010	000000000
Pseudohalobates	4001010100	2110110310	0010021021	001110000
Rheumatometroides	4001010100	1110010310	0010021020	001110000
Stenobates	4001010100	2110010310	0010021020	001110000
Stenobatopsis	4001010100	1010010310	0010021021	001110000
Thetibates	4001010100	1110010311	0010021020	001110000
Calyptobates	1004100001	0001000000	0030011000	001110000
Hynesionella	1004000001	0001000000	0010011000	101110000
Naboandelus	1004000001	0001000000	0010011000	001110000
Metrobates	1023000012	0000101201	1020050100	011110000
Andersenella	3113010002	0001001131	0030060000	001110000
Ciliometra	2013000002	0001001131	1131060000	001110000
Iobates	1013000002	0001001131	0030180000	001110000
Metrobatoides	2013200002	0001001131	1130060000	011110000
Metrobatopsis	1013000002	0001001131	0032170000	001110000
Rheumatometra	3113000012	0001001131	0030060000	201110000
Stygiobates	1013000002	0001001131	1032170000	001110000
Cryptobates	3002002001	0001100120	0000030100	001110011
Cryptobatoides	3002000002	0000100120	0000040100	001110011
Gnomobates	3002002002	0000100100	0000030100	201110011
Halobatopsis	3002000002	0000100100	0000040100	201110011
Ovatometra	3002000002	0000100100	0000040100	001110011
Telmatometra	3002001002	0000100100	0000040100	001110011
Telmatometroides	3002001002	0010100100	0000040100	001110011
Trepobates	3002000002	0000100100	0000030100	001110011
Trepobatoides	3002000001	0000100100	0000040100	001110011

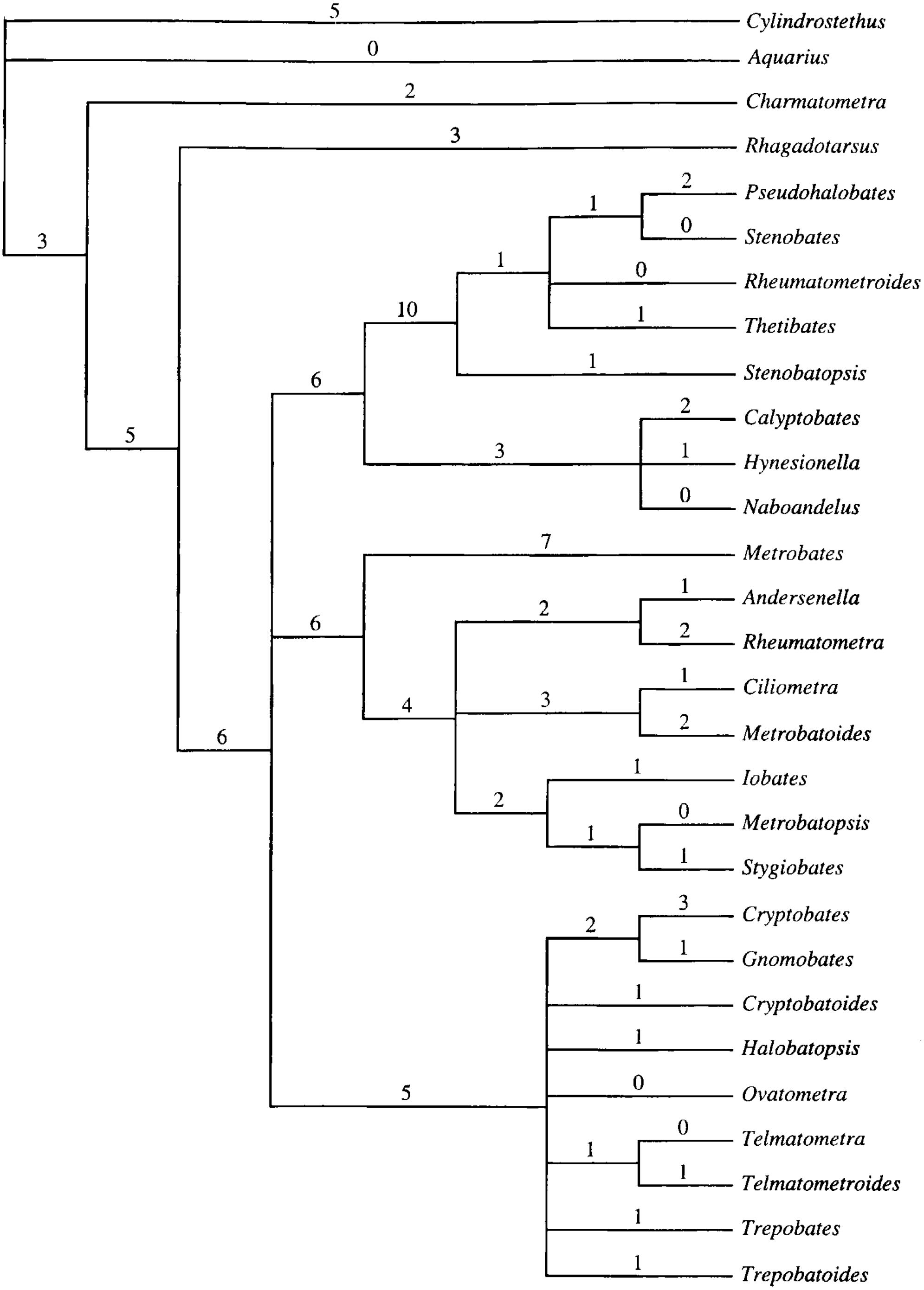

Figure 1. Strict consensus tree of 16 MPTs for genera of Trepobatinae based on 39 morphological characters with all characters run unordered (for discussion see text). Length = 102, CI = 0.676, RI = 0.851. Numbers above branches indicate branch lengths.

0 = small, simple, vestigial or absent
1 = long, blade-like, falcate or corkscrew shaped; complex

29. Female ovipositor
0 = plate-like, with out significant serrations or teeth
1 = first gonapophyses serrate
2 = second gonapophyses serrate

Additional characters

30. Mesothorax, shape (U)
0 = tumid ventrally
1 = dorsoventrally flattened, not tumid ventrally

31. Male fore femur, shape
0 = not strongly curved or modified
1 = strongly and smoothly curved, adapted for phoresy
2 = highly modified, thickened and sometimes bent, with basal or medial sculpturing and often large ventral protuberances

32. Body, shape
0 = relatively narrow, not flattened
1 = very broad, dorsoventrally flattened

33. Middle femur, length
0 = longer than middle tibia
1 = shorter than middle tibia

34. Fore wings, cells
0 = with more than two closed cells
1 = with two closed cells in basal half

35. Fore wings
0 = without transverse line of weakness
1 = with transverse line of weakness

36. Ocular setae
0 = longer than four eye facets
1 = shorter than four eye facets

37. Lateral intersegmental suture between meso- and metathorax
0 = distinct
1 = indistinct or absent

38. Base of rostrum
0 = not enclosed
1 = enclosed

39. Gular region
0 = not tumid
1 = tumid

Outgroups

Matsuda (1960) proposed that the Rhagadotarsinae and Trepobatinae are sister groups, a hypothesis rejected by Andersen (1982: 237), who instead hypothesized that the remaining seven gerrid subfamilies constitute the probable sister group of the Rhagadotarsinae, which his analysis placed as the basal gerrid clade. In Andersen's cladogram the Trepobatinae form a sister clade one position terminal to the Rhagadotarsinae near the base of the tree, a topology with which we agree. Given these considerations, the genus *Rhagadotarsus* Breddin (*R. kraepelini* Breddin coded), subfamily Rhagadotarsinae, was chosen as the outgroup for our initial phylogenetic analysis of trepobatine genera. Subsequently, the genera *Charmatometra* Kirkaldy [*C. bakeri* (Kirkaldy) coded], *Aquarius* Schellenberg [*A. remigis* (Say) coded], and *Cylindrostethus* Fieber [*C. erythropus* (Herrich-Schaeffer) coded] were also added in order to provide a broad representation of exemplar outgroup taxa from other gerrid subfamilies.

Parsimony analysis

The 39 characters described above were coded in a matrix and analyzed using the computer program PAUP 4.0b8 (Swofford 2001). Parsimony analyses were intially implemented using the heuristic search option with TBR branch swapping, and parsimony-uniformative characters excluded. The same data were then analyzed using a Heuristic search with 100 repetitions of random stepwise addition sequences, which discovers 'islands' of shortest trees that may not be detected by other addition sequences (Maddison 1991). All characters were run unordered, and no assumptions were made as to character weighting. These analyses both produced 16 most parsimonious trees (MPTs) of length 100, CI = 0.690, and RI = 0.860.

A strict consensus tree generated from this initial set of MPTs (Fig. 1) was examined with MacClade 3.01 (Maddison & Maddison 1992), to assess the distribution of individual character states on the tree. A second parsimony analysis was then run with all characters for which a reasonable hypothesis of polarity could be made on the basis of morphoclines or other evidence (see Character Analysis section above) run as ordered; this included all characters in the matrix except 1, 4, 11, 19, 23, 26, 27, 28, and 30. This analysis produced 18 trees of length 110, CI = 0.627, RI = 0.837. This same analysis was then run again using the more rigorous Branch and Bound algorithm, resulting in the same 18 MPTs. Although slightly longer than the trees generated from the unordered analysis (as is typical of ordered character sets), the ordered-character trees were significantly more resolved. A strict consensus tree generated from these latter trees (Fig. 2) contained well resolved clades representing the tribes Stenobatini, Naboandelini, Trepobatini, and Metrobatini, and improved internal resolution within the Metrobatini, a group of particular zoogeographic interest in relation to the current study.

Branch support for these clades was assessed by Bootstrap analysis under parsimony (Felsenstein

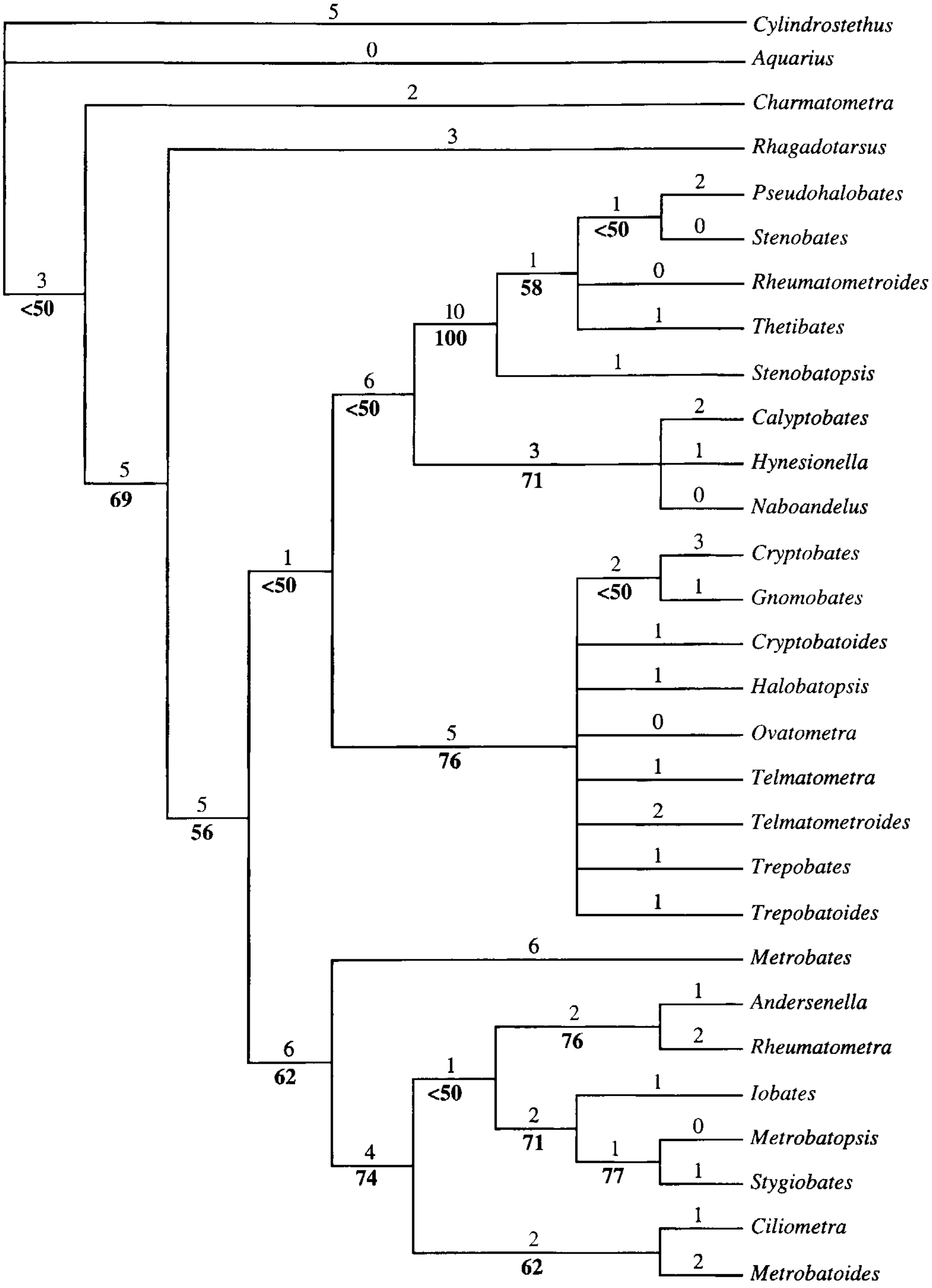

Figure 2. Strict consensus tree of 18 MPTs for genera of Trepobatinae based on 39 morphological characters with certain characters run as ordered (for discussion see text). Length = 102, CI = 0.676, RI = 0.851. Plain text numbers above branches indicate branch lengths, bold face numbers below branches indicate bootstrap support from 500 pseudoreplicates with 10 random-addition heuristic searches per pseudoreplicate in PAUP.

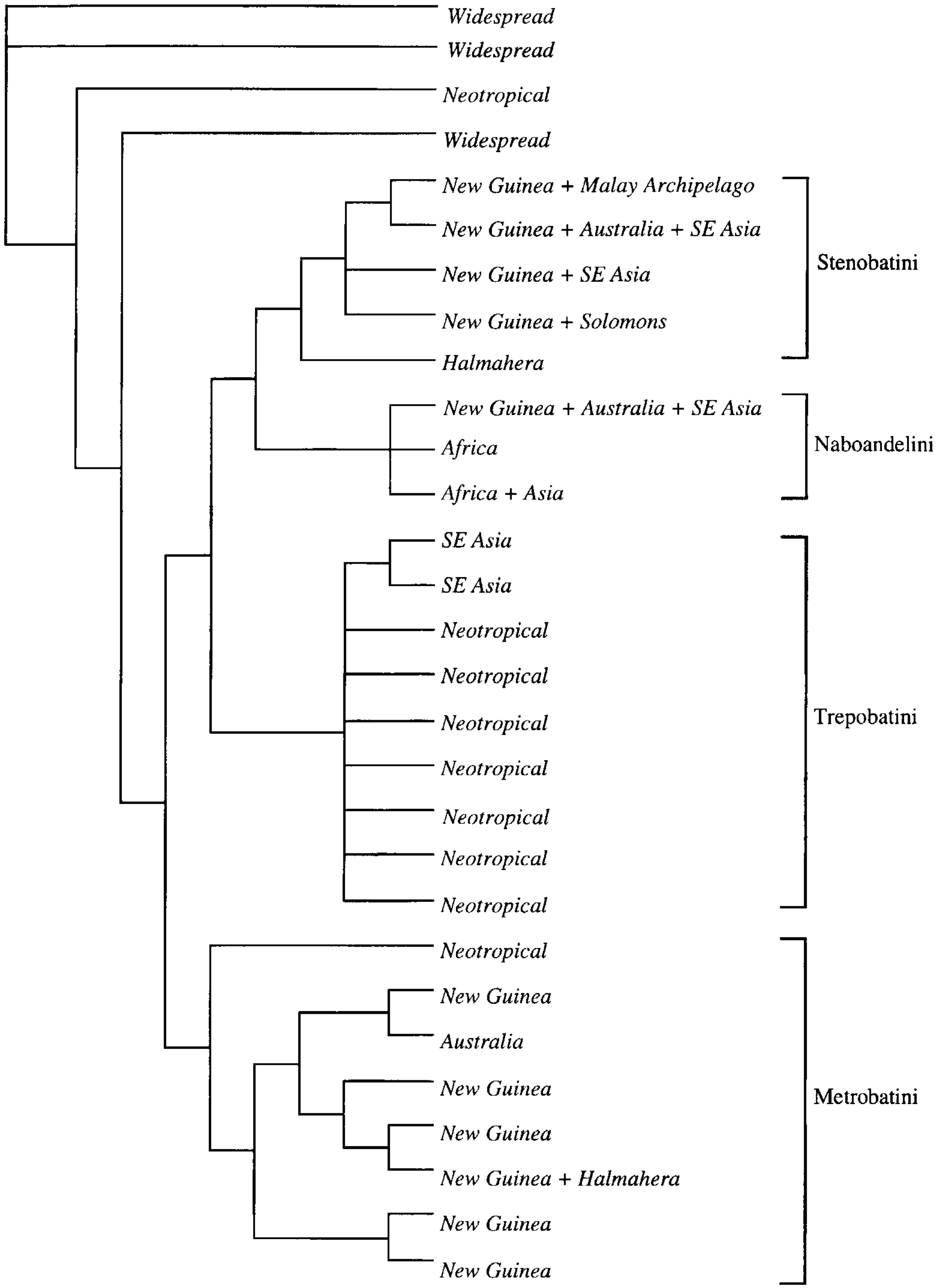

Figure 3. Taxon-area cladogram for genera of Trepobatinae, based on tree shown in Fig. 2.

1985) using 500 pseudoreplicates with 10 random-addition replicates per pseudoreplicate and parsimony-uninformative characters excluded; these Bootstrap values are shown in Fig. 2, and indicate strong branch support for all major clades. The tree thus generated forms the basis for the subsequent discussion of trepobatine biogeography in the New Guinea region.

Biogeography

The biogeographic history of New Guinea is closely interwoven with the complex tectonic history of the island's formation. As outlined by Polhemus (1996), and further discussed by Polhemus & Polhemus (1998), New Guinea consists of several layers of island arc terranes that were successively laminated onto the northern margin of the Australian craton between the Eocene and the Pliocene, with each episode of accretion producing a distinctive faunal signature. Pigram & Davies (1987) identified 32 separate terranes lying north of the former Australian cratonic margin, and these may be divided into two major groups, those resulting from an Eocene to Oligocene episode of arc collision, involving the Papuan Arc (terminology follows Polhemus & Polhemus 1998), and those deriving from a subsequent Miocene to Pliocene collison event, involving the Solomons Arc (Fig. 14-16). Polhemus & Polhemus (1998) provided evidence from aquatic Heteroptera indicating that the Eocene to Oligocene terranes harbored faunas whose affinities extended to the west, toward the Malay Archipelago, while the Miocene to Pliocene terranes had faunas with affinities extending to the east, toward the Solomons. Recently, researchers dealing with other groups of plants and animals have also begun to incorporate the terrane accretion hypthesis into their analyses of regional biogeography (Welzen 1997; Heads 1999).

In the context of the terrane accretion hypothesis, the distributions and relationships of Trepobatinae on New Guinea and surrounding archipelagos are instructive. A taxon-area cladogram for the genera of Trepobatinae was created by replacing the terminal taxa on our preferred tree with the geographic areas they occupy (Fig. 3). This taxon-area cladogram reveals some obvious patterns regarding the worldwide distribution of tribes:

1.) The Stenobatini are entirely confined to the eastern Indo-Pacific, with their greatest diversity in Melanesia and no representation in the Western Hemisphere.

2.) The Naboandelini are also an entirely Paleotropical group, with no Western Hemisphere representation. This tribe includes the only Trepobatinae known from Africa. It is represented in New Guinea by a single genus, *Calyptobates*, that also occurs in Australia and extends westward through Borneo and the Andamans to Ceylon.

3.) The Trepobatini are a predominantly Western Hemisphere group, with only two genera, *Cryptobates* and *Gnomobates*, present in the Eastern Hemisphere, where they are confined to Southeast Asia, from Borneo to India.

4.) The Metrobatini are primarily centered in New Guinea and surrounding islands, with a single large basal clade genus, *Metrobates*, in the Neotropical region and another genus, *Rheumatometra*, in Australia.

In regard to the fauna of New Guinea, which is the primary focus of this work, the island's assemblage of Trepobatinae was derived independently from three separate tribes, the Metrobatini, Naboandelini and Stenobatini, that are centered in different geographic regions and do not form a monophyletic cluster of sister groups on the cladogram. The island therefore has a multicentric biota, and will appear as a composite area on any summary area cladogram derived from this data using component analysis. In addition, these tribes have also had differing biogeographic histories in the region due to their divergent ecologies, with the Metrobatini and Naboandelini inhabiting freshwater, while the Stenobatini are marine. In light of these considerations, the biogeographic patterns of the three tribes are discussed separately in the following sections.

Metrobatini

The cladogram of Metrobatini shows a basal split in this tribe between the genus *Metrobates*, which occurs in the Neotropical region, and a clade containing the remaining genera, all of which are Paleotropical, occurring in Australia, New Guinea, and nearby archipelagos. This pattern is suggestive of an initial Gondwana distribution, which could have been fragmented by vicariance following the eventual separation of Australia from Antarctica, a process that was initiated near 95 Ma (Kroenke 1996). Australia contains only a single genus, *Rheumatometra*, with two species (Andersen & Weir 1998), while New Guinea and its associated archipelagos support a localized radiation of six genera, two of which, *Stygiobates*

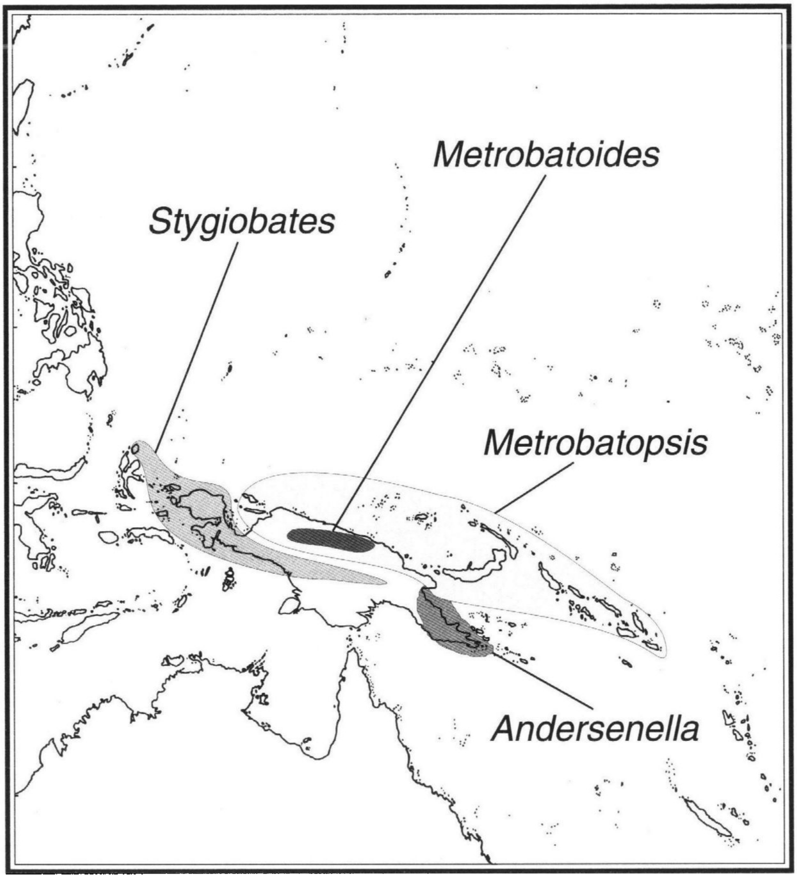

Figure 4. Distributions of four genera of Metrobatini in the New Guinea region.

and *Metrobatopsis*, extend westward to the northern Moluccas and eastward to the Solomons respectively (Fig. 4). Many of the taxa of Metrobatini occupying New Guinea have ranges that conform to the major geological provinces of the island as depicted in Polhemus & Polhemus (1998), or to individual terranes within these provinces as outlined by Pigram & Davies (1987) (Fig. 4-7).

Three genera of Metrobatini are confined to portions of New Guinea and adjacent islands that were derived from portions of the Miocene - Pliocene Solomons Arc as defined by Kroenke (1984, 1996):

1.) *Metrobatopsis* is distributed from the Solomons, through the Bismarcks, and along the northern coastal ranges of New Guinea, occupying islands and accreted terranes of Miocene to Pliocene age, but is not known from drainages on the Australian craton south of the island's central divide (Fig. 4, 5). Although the genus has many endemic species on the islands near New Guinea, only a single widely distributed species, *M. flavonotatus* Esaki, occurs within the northern zone of Miocene terranes on New Guinea proper (Fig. 5). This pattern strongly suggests that the overall distribution of the genus has been influenced by the tectonics of the Solomons Arc (compare Fig. 4, 16), and supports the concept advanced by Polhemus (1996) that species on arc terranes may retain their insular patterns of distribution even after such arc fragments are intergrated into a larger land mass.

2.) *Andersenella* is apparently confined to the

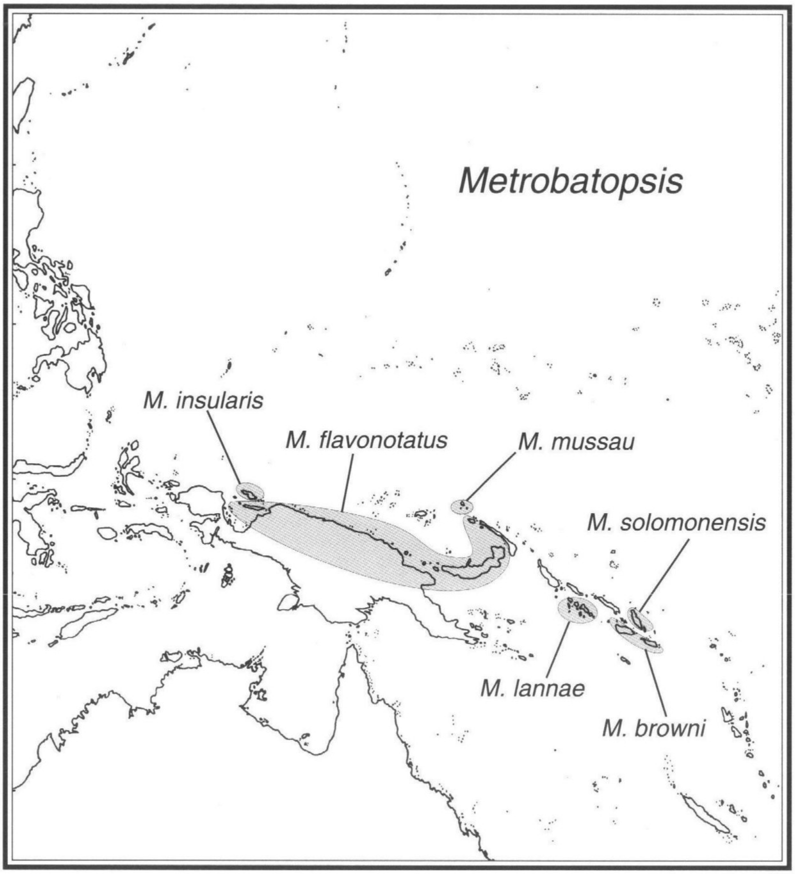

Figure 5. Distribution of *Metrobatopsis* species in the New Guinea region.

Papuan Peninsula (Fig. 4), a complex accreted terrane that was sutured to the remainder of New Guinea sometime between the Eocene and the Miocene. The exact tectonic history of the Papuan Peninsula is still a matter of debate; the circumscribed distribution of *Andersenella* in modern New Guinea supports the hypothesis that this land mass was separate from the remainder of the island until relatively recent geological time, thereby favoring the Miocene suturing hypothesis (see further discussion in Polhemus & Polhemus 1998).

3.) *Metrobatoides* is known from the Torricelli Mountains of northern coastal New Guinea, an area corresponding to the Torricelli terrane of Pigram & Davies (1987) which was accreted to the island in the Miocene, and from the northern face of the central ranges in the Mamberamo River basin (Fig. 4, 20). The terranes of the deeper mountains in the latter area are of Eocene age, but a sequence of Tertiary volcanics lying north of them may be of Miocene age and linked to a later episode of arc accretion (P.T. Freeport Indonesia field geologists, pers. comm.). In any case, the current distribution of the genus falls entirely within the zone of accreted terranes in the north of the island, and appears to have been tectonically mediated.

None of the above three genera are known from the portion of New Guinea formed from sections of the Australian continental craton, lying south of the island's central mountain chain. Instead, three other genera of Metrobatini have ranges extending into this region:

1.) *Stygiobates* occupies an elongate distribution extending from Morotai in the Northern

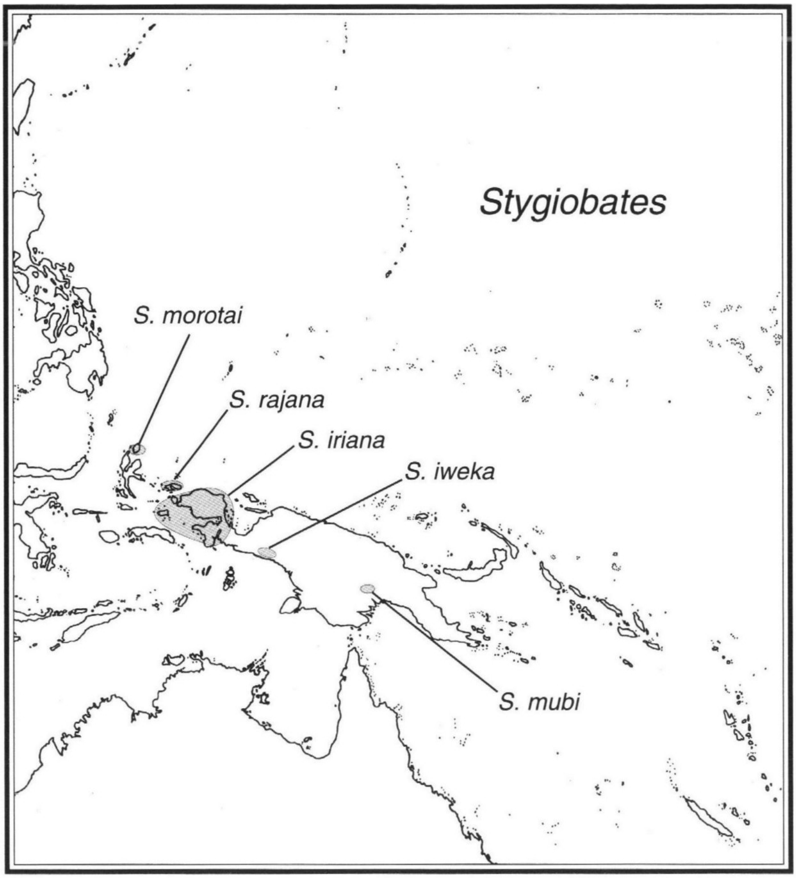

Figure 6. Distribution of *Stygiobates* species in the New Guinea region.

Moluccas, south through Waigeo and the Vogelkop Peninsula, and then eastward along the southern New Guinea premontane foreland as far as the Lakekamu River basin of Papua New Guinea (Fig. 4, 6). This genus appears to be completely absent from the accreted terranes of Miocene age along New Guinea's northern coast, indicating that the Vogelkop and Raja Ampat areas were not influenced by the Miocene to Pliocene accretion of terranes belonging to the Solomons Arc, a notable conclusion, since the western terminus of this arc has not been well defined geologically.

The current distribution of *Stygiobates* suggests that it may have instead evolved on the Vogelkop microcontinent, which was fused to the main body of New Guinea in the Miocene or early Pliocene (Polhemus & Polhemus 1998 and references therein), followed by dispersal of the genus eastward through cratonic New Guinea south of the mountains following this fusion event. Conversely, it is possible that *Stygiobates* evolved on the Halmahera Arc, which lay north of New Guinea from the Oligocene through the Miocene (Fig. 14-16), since one species is endemic to Morotai, a current element in this arc (Baker & Malaihollo 1996), while another is endemic to the Waigeo/Gam island complex, which is also hypothesized to contain terranes derived from this arc (Charlton et al. 1991); following this hypothesis, the arrival of the genus on the Vogelkop terrane would be a more recent event. This latter scenario is also suggested by the fact that a clear morphocline exists in terms of male abdominal modifications, with the least complex morphologies occurring in species on Morotai and Waigeo, while

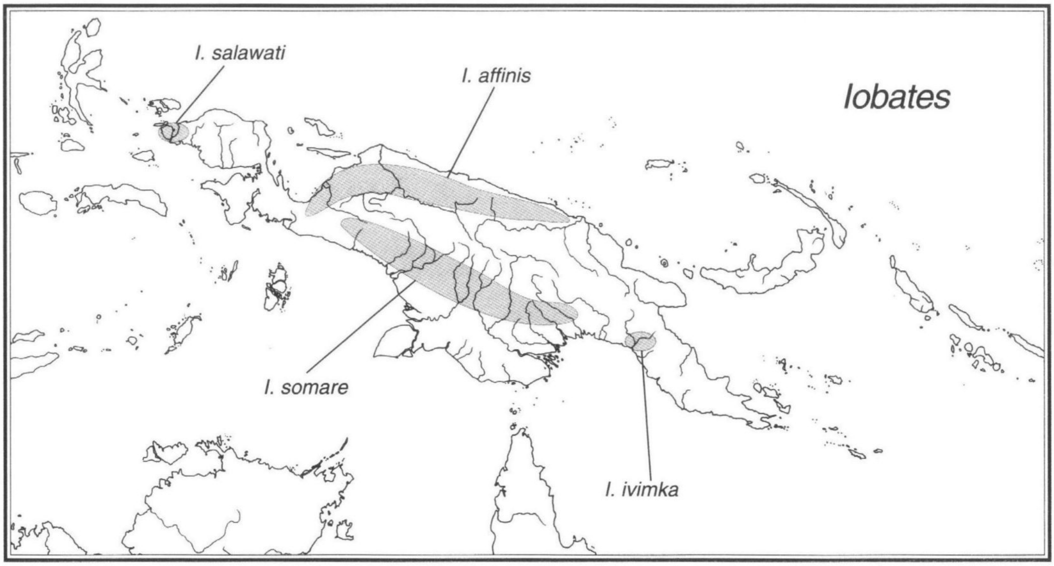

Figure 7. Distribution of *Iobates* species in New Guinea.

progressively more complex (and therefore presumably more recently derived) morphologies occur in species found in the Vogelkop Peninsula and southern New Guinea proper. It is also significant that *Stygiobates* and its sister genus on the cladogram, *Metrobatopsis*, occupy mutually exclusive ranges in the northern coastal terranes of New Guinea (Fig. 4), indicating that they may have occupied allopatric distributions within adjacent arc systems that formed along the southern boundaries of the Caroline and Philippine Sea plates (Fig. 14-16).

2.) *Iobates* displays a quadripartite distribution, with one species, *I. affinis*, confined to the northern coastal ranges of New Guinea, another, *I. salawati*, in the Vogelkop area, a third, *I. somare*, widespread through the southern premontane foreland of New Guinea as far east as the Kikori River basin, and a fourth, *I. ivimka*, in the southern Papuan Peninsula east of the Aure Scarp (Fig. 7). The segregation of this genus into separate species in the northern, southern, and Vogelkop and Papuan Peninsula sections of the island is a typical pattern seen in many other groups of aquatic organisms, including fishes (Allen 1991), and conveys limited information about the role of tectonics, if any, in structuring the distribution of this genus. However the position of *Iobates* in the cladogram as the sister group to the clade containing *Metrobatopsis* and *Stygiobates* (Fig. 2), both of which show strongly arc-linked distributions, does suggest that it may also have evolved on arc systems north of New Guinea and then been subsequently integrated into the biota of the modern island.

3.) *Ciliometra* occurs throughout New Guinea, occupying lowland river basins both north and south of the New Guinea central drainage divide, and is also present on the island of Waigeo to the northwest of the Vogelkop Peninsula. Unlike *Stygiobates* and *Iobates*, this genus also occurs on the Papuan Peninsula, with different endemic species occurring on the north and south sides. Although some endemic *Ciliometra* species do show congruence with arc terranes on Waigeo and in the Papuan Peninsula, the generally broad distribution of species in this genus on lowland rivers in mainland New Guinea, which flow through basins lying between mountain ranges formed by accreted terranes, makes it difficult to determine how tectonic events may have influenced their distributional history. In the phylogenetic analysis (Fig. 2) this genus is consistently sister to *Metrobatoides*, which is confined entirely to the northern zone of accreted terranes, and this coupled with localized speciation of *Ciliometra* in the Papuan Peninsula suggests that the latter genus may have had an arc-mediated distribution as well.

It is notable that two of the three genera of Metrobatini occurring south of the central ranges, *Iobates* and *Ciliometra*, are also present in the northern section of New Guinea, while none of the remaining genera found in the north of the island are also present in the south. In addition, the one genus that occurs in southern New Guinea but is not found in the north, *Stygiobates*, has representatives in the Vogelkop Peninsula, the Raja Ampat Islands, and the Northern Moluccas. This strongly suggests that the major diversification of Metrobatini occurred on arc systems that formed along the southern margins of the Caroline and Philippine Sea plates and eventually collided with northern New Guinea (Fig. 14-16), followed by subsequent dispersal of certain genera into the southern section of the island after the episodes of arc terrane accretion. This is view is further supported by the fact that the only Australian representative of the Metrobatini, *Rheumatometra*, is not a basal clade sister group to the South American *Metrobates*, but is instead in a more terminal subclade (Fig. 2), indicating that it was derived from ancestors on New Guinea or antecedent land masses. This weakens the case for an initial vicariance of Gondwana metrobatine lineages in the Mesozoic, and suggests the possibility of sweepstakes dispersal, since a tectonic mechanism by which metrobatines could have colonized the arcs that formed along the southern margins of the Caroline and Pacific plates in the early Tertiary while bypassing Australia is not immediately evident.

A summary of the area relationships discussed above is provided in Fig. 8, which represents a taxon-area cladogram derived from the subtree for the Metrobatini, in which the tectonic units discussed herein have been substituted for terminal generic level taxa. This analysis illustrates once again that only a single taxon deep in the tree is distributed exclusively on the Australian craton, while all remaining taxa have distributions either confined to arc systems and their accreted remnants, or to such systems plus the New Guinea portion of the Australian craton, exclusive of Australia proper. Although this pattern of area relationships does not preclude the possibility that basal lineages of Paleotropical Metrobatini were present on the extreme northern margin of the Australian craton which later became New Guinea and dispersed subsequently onto the arcs lying to the north and northeast, we feel it is more suggestive of an intial arc-based pattern with subsequent dispersal southward onto the Australian craton by several genera following arc collision.

In summary, the current distributional and phylogenetic evidence is compatable with the hypothesis (Fig. 8) that the Metrobatini diversified into a complex of local genera on one or more early Tertiary arc systems lying north of New Guinea, and that these genera were later incorporated into the biota of New Guinea following a series of tectonic collisions that occurred between the Eocene and the Pliocene.

Naboandelini

Only a single genus of Naboandelini, *Calyptobates*, occurs on New Guinea. This genus is also known to occur on Australia, the Moluccas, Borneo, the Andaman Islands, and Sri Lanka, but has so far not been collected in any of the island arcs lying east or southeast of New Guinea. Although it is likely that the distribution of this genus is still incompletely documented, due to the small size of its constituent species which are easily overlooked by most collectors, it is still clear that its range extends primarily south and westward from New Guinea, in contrast to the Metrobatini, which occur from New Guinea primarily north and eastward. In addition, all three species of *Calyptobates* so far known from New Guinea occur south of the central mountains, on the cratonic portions of the island. These lines of evidence all suggest that *Calyptobates* is a Gondwanan genus that reached New Guinea from Australia, and that it was not present on the arcs north of New Guinea that later contributed accreted terranes to the island.

Stenobatini

The Stenobatini are a predominantly Melanesian group. Four of the five known genera in this tribe are present along the coasts of New Guinea, and the remaining genus occurs in nearby Halmahera, with diversity dropping rapidly as one moves away from Melanesia in any direction. The constituent genera show widely varying patterns in their overall distributions:

1.) *Thetibates* is found only in the Solomons, the Bismarcks, and along the coast of the Adelbert-Finisterre terrane in northeastern New Guinea (Fig. 9). Polhemus & Polhemus (1998)

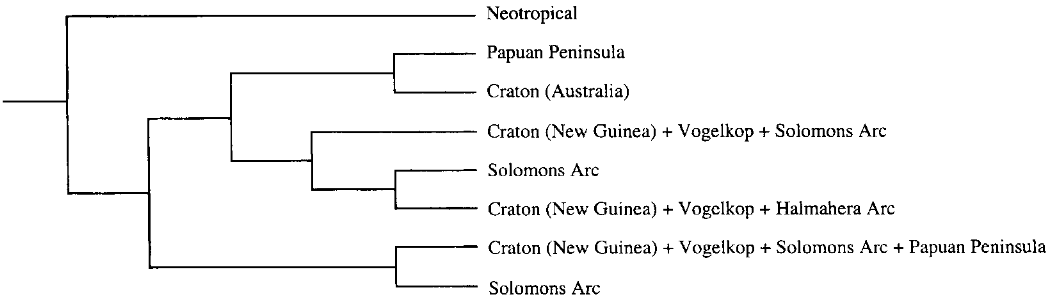

Figure 8. Taxon-area subtree for Metrobatini derived from the larger taxon-area cladogram shown in Fig. 3. Areas represent tectonic units in the New Guinea region as defined by Polhemus & Polhemus (1998) and herein (see Fig. 14-16). The notation 'Craton (Australia)' indicates the Australian continental craton exclusive of the portion comprising southern New Guinea; the notation 'Craton (New Guinea)' indicates the portion of southern New Guinea derived from the Australian continental craton but exclusive of the current Australian continent south of the Torres Strait.

noted that the distribution pattern of *Thetibates* is congruent with geological terranes recently derived from the Miocene Solomons Arc (Kroenke 1984), and suggested that the genus might have evolved in isolation on this arc system prior to accretion of the arc's western sector into the modern island of New Guinea.

2.) *Pseudohalobates* occupies a roughly rectangular range bounded by Mindanao on the north, the Minahasa Peninsula of Celebes on the west, and the Vogelkop Peninsula of New Guinea on the east (Fig. 9). Since it occurs on many different island arc systems of differing ages and trajectories, any linkage between its distribution and geological events is difficult to assess, and suggests that this genus may have relatively high dispersal abilities.

3.) *Rheumatometroides* occupies an elongate, east-west distribution through the center of the Malay Archipelago and into Melanesia. It is recorded from Singapore and adjacent southern peninsular Malaysia, Borneo, Celebes, New Guinea and the Raja Ampat Islands, the Bismarcks, the Solomons, and northern Australia (Fig. 10). It is unknown from Sumatra, Java, the Lesser Sunda Islands, the Moluccas or the Philippines. Species diversity is much higher along the coasts of New Guinea than in any other area, a pattern of distribution suggesting that the genus may have evolved in the New Guinea region and later spread westward into the central Malay Archipelago, a hypothesis reinforced by the apparent absence of this species on any islands of the Sunda Arc east of Sumatra.

4.) *Stenobates* is widespread, being recorded from Singapore, Celebes, the southern Philippines (Palawan, Mindanao), the northern Moluccas, New Guinea and the Raja Ampat Islands, and northern Australia (Fig. 11). It is unknown from the Greater Sunda Islands, the Lesser Sunda Islands, the northeastern coast of New Guinea beyond Cenderawasih Bay, the Bismarcks, or the Solomons. This distribution indicates that the genus never occupied the Miocene Solomons Arc, since its current distribution is completely allopatric with that of *Thetibates*, which occupies terranes derived from that arc system (compare Fig. 9, 11 and 16). *Stenobates* instead shows its highest species diversity in the Vogelkop region (Fig. 12), suggesting that it evolved on the Vogelkop microcontinent or on arc systems such as the Halmahera Arc lying immediately to the north and west. The absence of *Stenobates* on Borneo is odd given that its distribution surrounds this island, and we predict that future collecting will prove it to be present there. Like *Rheumatometroides*, this genus is also unknown to date from the islands of the Sunda Arc.

5.) *Stenobatopsis* is confined to the northern Moluccas, being known from Bacan and Halmahera (Fig. 9). Both are parts of a Miocene arc that formed at the southeastern corner of the Philippine Sea Plate, although Bacan also appears to contain a small continental fragment (Mt. Sabela) derived from the Vogelkop microcontinent via westward translation along the Sorong Fault (Malaihollo & Hall, 1996). The position of *Stenobatopsis* as the most basal member of the Steno-

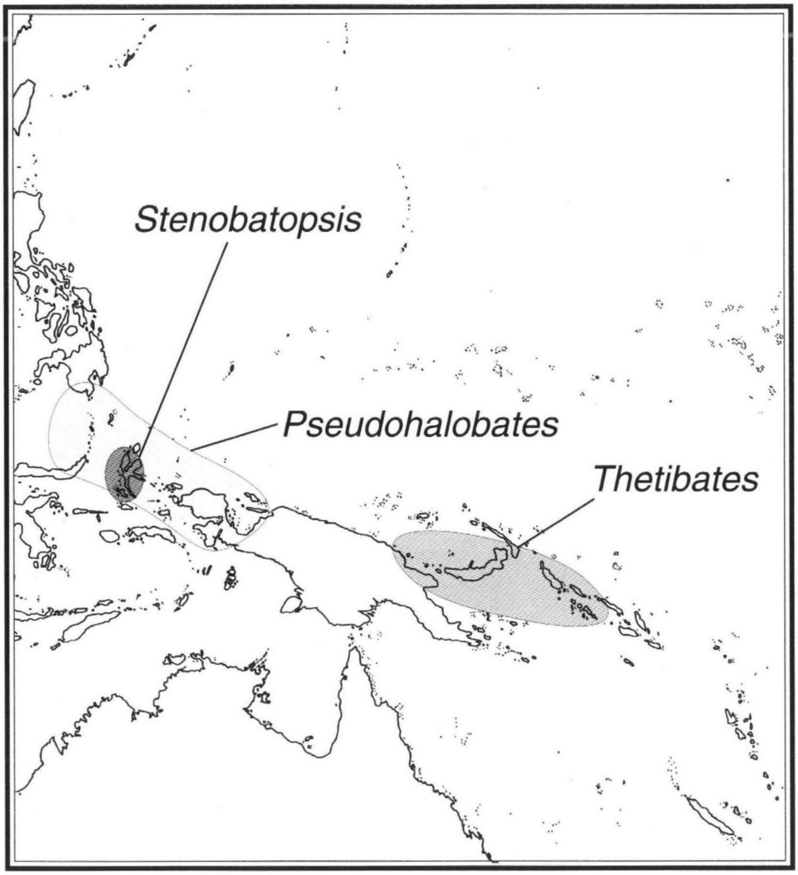

Figure 9. Distributions of three genera of Stenobatini in the New Guinea region.

batini (Fig. 2) further supports the hypotheses that it and the remaining members of the tribe evolved on arc systems that formed along the southern margins of the Caroline and Philippine Sea plates, remants of which are now incorporated into the Moluccas and New Guinea. Following such a hypothesis, the broader distributions now displayed by certain genera within the tribe are the result of subsequent dispersal to the south and west following tectonic convergence of formerly isolated arc systems.

Within the regional context of New Guinea, the distributions of individual species in the Stenobatini are indicative of several general areas of marine endemism (Fig. 13):

1.) Vogelkop Peninsula and associated islands - this area is broadly defined by the distribution of *Pseudohalobates inobonto*. It appears to contain two distinctive subareas:

1a.) Bomberai Peninsula and Raja Ampat Islands, which contain the endemic species *Rheumatometroides sele* and *Stenobates fakfak*.

1b.) Vogelkop Peninsula and the Cenderwasih Bay islands of Biak and Yapen, which contain the endemic species *Rheumatometroides wabon* and *Stenobates kamojo*.

Within this area of endemism, the distributions of Stenobatini are particularly complex near the western tip of the Vogelkop Peninsula (Fig. 12), indicating that this has been a zone of secondary contact for a number of previously separate regional stenobatine faunas. Salawati, for example, supports the endemic *Stenobates kasim*, has another *Stenobates* species, *S. kamojo*, shared with

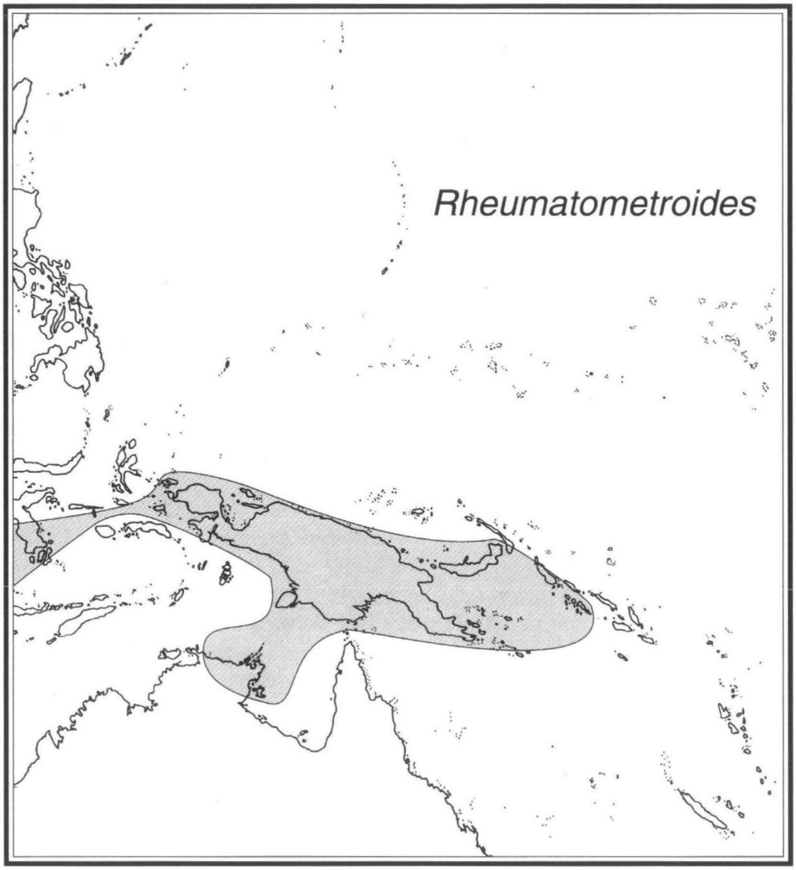

Figure 10. Distribution of *Rheumatometroides* in the New Guinea region. The larger distribution of this genus extends westward off the map to include Celebes, Borneo, peninsular Malaysia and Singapore.

the Vogelkop Peninsula, Biak and Yapen, and shares *Rheumatometroides sele* with the Vogelkop Peninsula, the Bomberai Peninsula, Misool, Waigeo, Gam and Batanta. Misool, by contrast, is part of the same distribution of *Rheumatometroides sele* noted above, but shares its single *Stenobates* species, *S. australicus*, with southern New Guinea and northeastern Australia.

2.) Torres Strait – this area is defined by *Rheumatometroides kikori*, *Rheumatometroides carpentaria* and *Stenobates australicus*. It basically corresponds to the warm, shallow epicontinental seas of the Australian craton, including the coasts of southern New Guinea and northern Australia (Fig. 13). One member of the species assemblage typical of this area, *S. australicus*, ranges eastward into the Coral Sea, and westward as far as Misool Island.

3.) Northeastern New Guinea, Bismarcks, and Solomons – this area is defined by the distributions of *Rheumatometroides browni*, *Thetibates serena*, and *Thetibates matawa*. It corresponds to the remnants of the Miocene Solomons Arc system as defined by Kroenke (1984), including the Adelbert-Finisterre terrane of northeastern New Guinea. Taxa typical of this area's assemblage are not known from northern New Guinea west of the mouth of the Sepik River.

Summary

To summarize the above discussion, we hypothe-

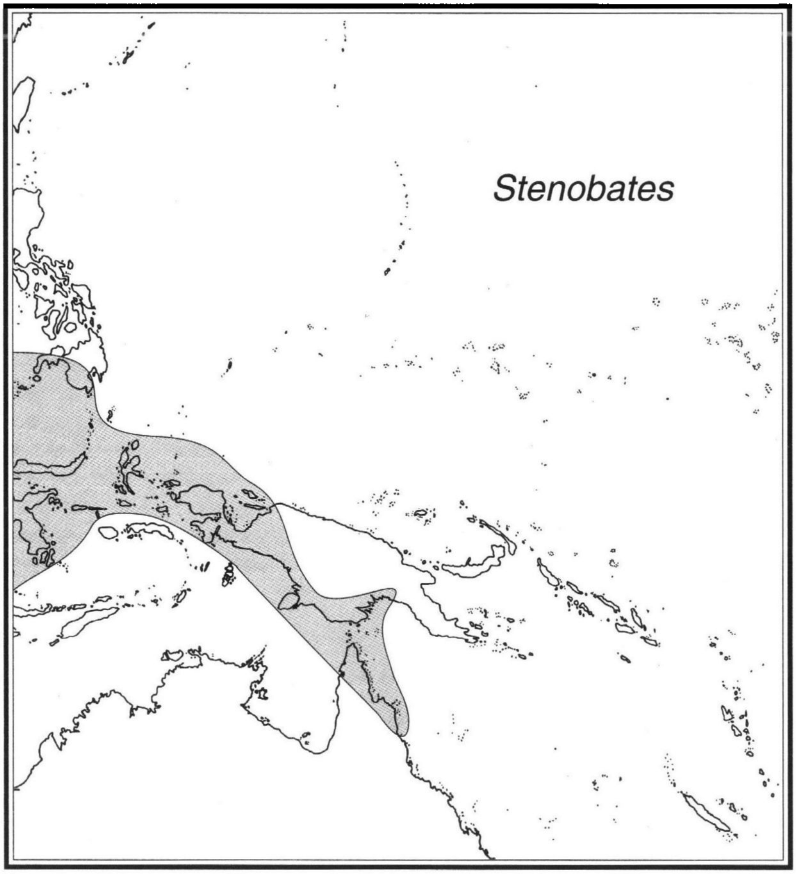

Figure 11. Distribution of *Stenobates* in the New Guinea region. The larger distribution of this genus extends westward off the map to Singapore.

size the following histories for the three tribes of Trepobatinae present in the New Guinea region:

1.) The Metrobatini have one component of genera (*Metrobatopsis*, *Metrobatoides*, *Andersenella*) that on the basis of cladistic and biogeographic evidence clearly appear to have evolved on terranes north and east of New Guinea, particularly those linked to the Solomons Arc. Another genus (*Stygiobates*) appears to have evolved on terranes north and west of New Guinea linked to either the current Halmahera Arc or the Vogelkop microcontinent. Several other genera (*Ciliometra*, *Iobates*) are widespread in the island and, though possessing regionally endemic species, are not unequivocally informative concerning tectonic controls on past distributions.

2.) The Naboandelini are represented in New Guinea by a single genus, *Calyptobates*, confined to the cratonic portion of the island south of the central mountains. This genus is shared with Australia, suggesting a vicariance pattern across the Torres Strait.

3.) The Stenobatini are similar to the Metrobatini in exhibiting one genus (*Thetibates*) whose distribution mirrors that of the Solomons Arc terranes, another (*Stenobatopsis*) confined to the Halmahera Arc, and three more widespread genera (*Pseudohalobates*, *Stenobates*, *Rheumatometroides*) with numerous locally endemic species that provide intriguing regional patterns but no clear indication of overriding tectonic control in their distributions.

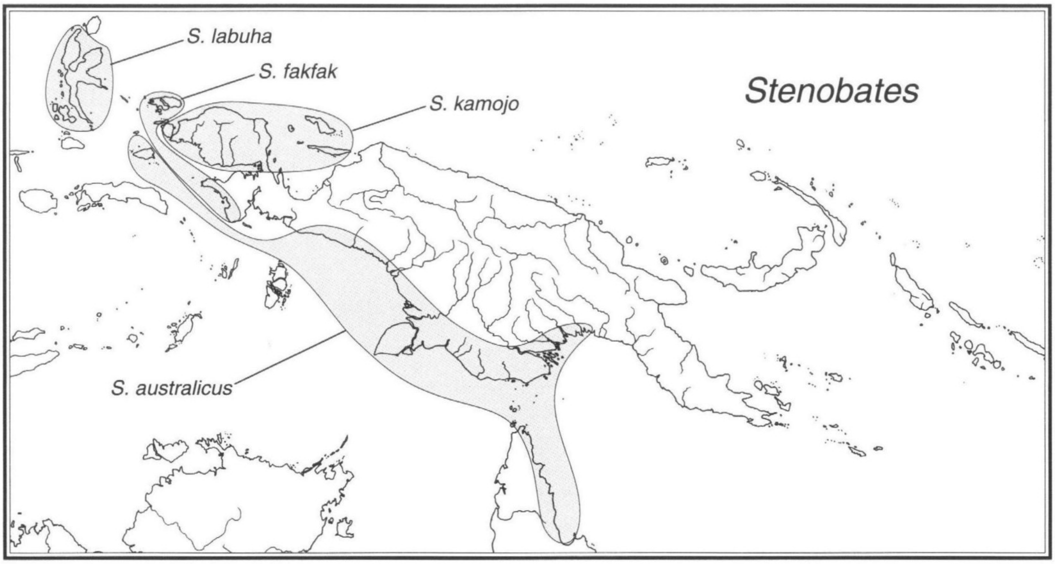

Figure 12. Distributions of *Stenobates* species on New Guinea and nearby islands. Note the complex juxtaposition of species ranges in the area surrounding the Vogelkop Peninsula.

World checklist of Trepobatinae

Subfamily TREPOBATINAE Matsuda, 1960: 330. Type-genus *Trepobates* Uhler.

Tribe METROBATINI J. & D. Polhemus, 1993: 244. Type-genus *Metrobates* Uhler.
Andersenella J. & D. Polhemus, 1993: 247. Type-species *Andersenella binotata* J. & D. Polhemus, 1993.
binotata J. & D. Polhemus, 1993: 248. Papua New Guinea

Ciliometra J. & D. Polhemus, 1993: 249. Type-species *Ciliometra kiunga* J. & D. Polhemus, 1993.
femorata J. & D. Polhemus, 1993: 252. Papua New Guinea
hirsuta Lansbury, 1996: 59. Papua New Guinea
kiunga J. & D. Polhemus, 1993: 251. Papua New Guinea
minajerwi J. & D. Polhemus, 2000: 296. Indonesia (Irian Jaya)
priori Lansbury, 1996: 55. Papua New Guinea
sepik J. & D. Polhemus, 1993: 252. Papua New Guinea
setosa J. & D. Polhemus, 2000: 292. Papua New Guinea
waigeo J. & D. Polhemus, 2000: 295. Indonesia (Irian Jaya)

Iobates J. & D. Polhemus, 1993: 253. Type-species *Metrobatopsis affinis* Esaki, 1926.
affinis (Esaki), 1926: 146. [*Metrobatopsis*]. Indonesia (Irian Jaya), Northern Papua New Guinea.
ivimka J. & D. Polhemus, 2002: 287. South Central Papua New Guinea
salawati J. & D. Polhemus, 1993: 255. Indonesia (Irian Jaya, Salawati Isl.)
somare J. & D. Polhemus, 1993: 256. Indonesia (Irian Jaya), Papua New Guinea

Metrobates Uhler, 1871: 108. Type-species, *Metrobates hesperius* Uhler, 1871.
= *Trepobatopsis* Champion, 1898: 157. Type-species, *Trepobatopsis denticornis* Champion, 1898. Syn. by Anderson, 1932b: 300.
† *aeternalis* Scudder, 1890: 353. Oligocene fossil, Florissant Beds, Colorado
alacris Drake, 1955: 130. U. S. (La., Tx.)
amblydonti Nieser, 1993: 23. Trinidad
anomalus anomalus Hussey, 1948: 123. U. S. (Fl.)
anomalus comatipes Hussey & Herring, 1949: 169. U. S. (Fl.)
artus Anderson, 1932a: 56. Mexico, U. S. (N. M., Tx.)
curracis Drake & Roze, 1954: 228. Venezuela
denticornis (Champion), 1898: 158. [*Trepobatopsis*]. Mesoamerica, Mexico, U. S. (Az., N. M., Tx.)
fugientis Drake & Harris, 1945: 180. Bolivia, Peru
hesperius hesperius Uhler, 1871: 108. U. S. (east)
= *beginii* (Ashmead), 1897: 56. [Halobatopsis]. Syn. by Torre-Bueno, 1911b: 243.
hesperius depilatus Hussey & Herring, 1949: 168. U.S. (Fl.)
hesperius ocalensis Hussey & Herring, 1949: 167. U. S. (Fl.)
laetus Drake, 1954: 50. Brazil
laudatus Drake & Harris, 1937: 357. Costa Rica, Panama, Puerto Rico
plaumanni plaumanni Hungerford, 1951: 72. Argentina (north), Brazil
plaumanni genikos Nieser, 1993: 23. Brazil (Minas Gerais)
porcus Anderson, 1932a: 59. Belize, Honduras, Mexico,

Nicaragua
= *spissus* Drake & Harris, 1932b: 88. Syn. by Drake & Harris, 1937: 357.
tumidus Anderson, 1932a: 57. Cuba, Haiti, Jamaica
= *cubanus* Drake & Harris, 1932b: 86. Syn. by Drake & Harris, 1937: 358.
trux trux (Torre Bueno), 1921: 274. [Trepobatopsis]. U. S. (west)
trux infuscatus Usinger, 1953: 179. U. S. (Ca., Or.)
vigilis Drake, 1958: 100. Argentina (north), Brazil (Minas Gerais, Santa Catarina)

Metrobatoides J. & D. Polhemus, 1993: 259. Type-species *Metrobatoides genitalis* J. & D. Polhemus, 1993.
bifurcatus J. & D. Polhemus, 2002: 284. Indonesia (Irian Jaya)
genitalis J. & D. Polhemus, 1993: 261. Papua New Guinea

Metrobatopsis Esaki, 1926: 144. Type-species, *Metrobatopsis flavonotatus* Esaki, 1926.
browni J. & D. Polhemus, 1993: 266. Solomon Islands
flavonotatus Esaki, 1926: 146. Indonesia (Irian Jaya), Papua New Guinea
insularis J. & D. Polhemus, 1993: 266. Indonesia (Irian Jaya; Biak Isl.)
lannae J. & D. Polhemus, 1993: 269. Solomon Islands
mussau J. & D. Polhemus, 1993: 269. Bismarck Archipelago (Mussau Isl.)
solomonensis Hungerford & Matsuda, 1959b: 35. Solomon Islands

Rheumatometra Kirkaldy, 1902: 280. Type-species, *Rheumatometra philarete* Kirkaldy, 1902, monobasic.
dimorpha Andersen & Weir, 1998: 519. Eastern Australia
philarete Kirkaldy, 1902: 280. Eastern Australia.

Stygiobates J. & D. Polhemus, 1993: 272. Type-species *Stygiobates iriana* J. & D. Polhemus, 1993.
iriana J. & D. Polhemus, 1993: 273. Indonesia (Irian Jaya)
iweka J. & D. Polhemus, 2000: 297. Indonesia (Irian Jaya)
moratai J. & D. Polhemus, 1993: 275. Indonesia (Moratai, Moluccas)
mubi J. & D. Polhemus, 2000: 300. Papua New Guinea
rajana J. & D. Polhemus, 2000: 301. Indonesia (Irian Jaya)

Talaudia J. & D. Polhemus, 2002: 289. Type-species *Andersenella nilsi* Chen & Nieser, 2000.
nilsi (Chen & Nieser), 2000:70. [*Andersenella*] Indonesia (Talaud Archipelago)

Tribe NABOANDELINI J. & D. Polhemus, 1993: 244. Type-genus *Naboandelus* Distant.

Calyptobates J. & D. Polhemus, 1994: 334. Type-species *Calyptobates jourama* J. & D. Polhemus, 1994.
amboina J. & D. Polhemus, 1994: 337. Indonesia (Ambon)
andaman J. & D. Polhemus, 1994: 338. Andaman Islands
jourama J. & D. Polhemus, 1994: 339. Australia (north Queensland)
kamoro J. & D. Polhemus, 2000: 308. Indonesia (Irian Jaya)
kopi J. & D. Polhemus, 2000: 306. Indonesia (Irian Jaya)
minimus J. & D. Polhemus, 1994: 340. Australia (Northern Territory)
rubidus J. & D. Polhemus, 1994: 342. Australia (north Queensland)
samarinda J. & D. Polhemus, 1994: 344. Indonesia (Borneo; East Kalimantan, Sumba)
simplex J. & D. Polhemus, 1994: 345. Papua New Guinea

Hynesionella Poisson, 1949: 83. Type-species *Hynesionella aethiopica* Poisson, 1949.
aethiopica Poisson, 1949: 83. Ethiopia
capensis (Poisson), 1955: 130. [*Naboandelus*]. South Africa
= *omercooperi* Hungerford & Matsuda, 1959a: 37. Syn. by J. & D. Polhemus, 1994: 357.
cobbeni Linnavuori, 1975: 46. Central African Republic
karatara J. Polhemus, 1998: 191. South Africa
schuhi J. Polhemus, 1998: 192. South Africa
Naboandelus Distant, 1910a: 151. Type-species *Naboandelus signatus* Distant, 1910.
africanus Hoberlandt, 1950: 14. Angola
bandama Linnavuori, 1981: 18. Ivory Coast
bergevini bergevini Bergroth, 1911: 256. Egypt, Iraq, Israel (Palestine, Sinai), Lybia, Palestine, Sudan, Syria, Zaire
bergevini boukeanus Linnavuori, 1975: 45. Ivory Coast, west and central Africa
bergevini orientalis Zettel, 1996: 250. Iraq
bergevini popovi Brown, 1951: 227. Israel, Jordan, Saudi Arabia, Yemen
bergevini pygmaea Linnavuori, 1971: 360. Sudan
borneensis J. & D. Polhemus, 1994: 350. Indonesia (Borneo; East Kalimantan)
dentipes Linnavuori, 1981: 21. Ivory Coast
hynesi Poisson, 1949: 83. Ethiopia, Somalia
johorensis J. & D. Polhemus, 1994: 351. West Malaysia
madacascariensis Poisson, 1952: 31. Madagascar
monodi Poisson, 1928: 73. Cameroon, Ghana, Nigeria
patrizii patrizii Mancini, 1939: 311. Ethiopia, Somalia, Sudan
patrizii danae Linnavuori, 1981: 20. Ivory Coast
patrizii migrans Linnavuori, 1971: 361. Sudan
signatus Distant, 1910a: 152. India, Myanmar, Nepal, Sri Lanka, Thailand, Vietnam
taprobanicus J. & D. Polhemus, 1994: 351. Sri Lanka
umuahia Linnavuori, 1981: 20. Nigeria
wittei Poisson, 1950: 72. Zaire

Tribe STENOBATINI J. & D. Polhemus, 1993: 245. Type-genus, *Stenobates* Esaki.

Pseudohalobates J. & D. Polhemus, 1996: 292. Type-species, *Pseudohalobates inobonto* J. & D. Polhemus, 1996.
inobonto J. & D. Polhemus, 1996: 294. Indonesia (Celebes, Moluccas, Irian Jaya: Biak, Kri Misool, Yapen, Vogelkop), Philippines (Mindanao)

Rheumatometroides Hungerford & Matsuda, 1958a: 203. Type-species *Rheumatometroides browni* Hungerford & Matsuda, 1958.

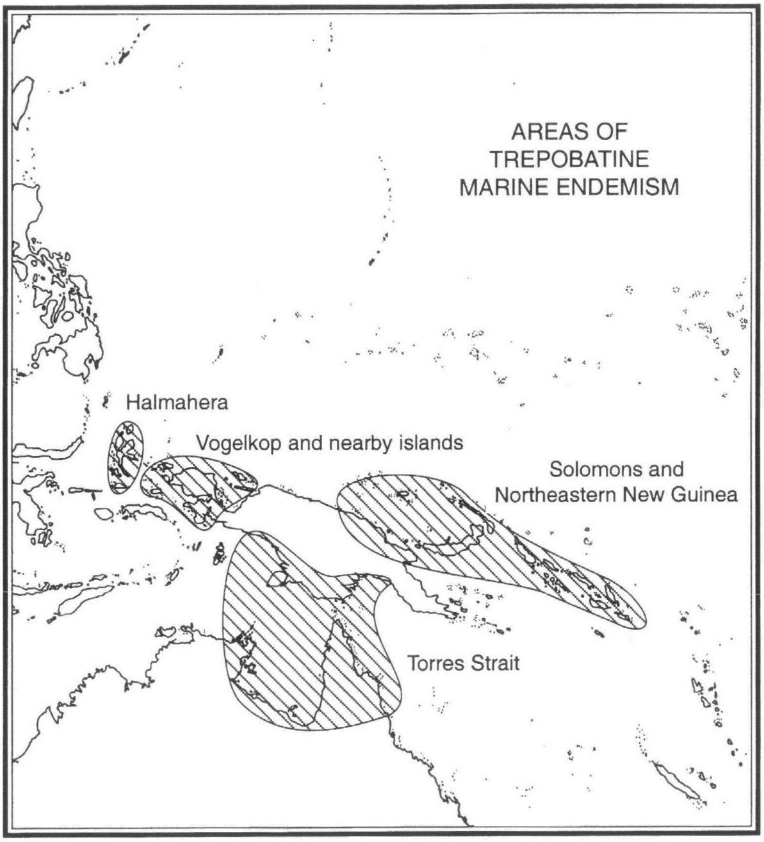

Figure 13. Areas of marine endemism in the New Guinea region as defined by the distributions of Stenobatini species (for further discussion see text).

browni Hungerford & Matsuda, 1958a: 204. Solomon Islands, PNG
carpentaria (J. & D. Polhemus), 1991: 5. [Stenobates]. N. Australia
drepanephoros Chen & Nieser, 1992: 160. Celebes
insularis insularis (Polhemus & Cheng), 1982: 225. [Stenobates]. Singapore, W. Malaysia
insularis papar J. & D. Polhemus, 1996: 303. Sabah
kikori J. & D. Polhemus, 1996: 305. Papua New Guinea
sele J. & D. Polhemus, 1996: 307. Indonesia (Irian Jaya; Batanta, Bomberai Peninsula, Gam, Misool, Salawati, Waigeo)
wabon J. & D. Polhemus, 1996: 311. Indonesia (Biak)

Stenobates Esaki, 1927: 184. Type-species, *Stenometra biroi* Esaki, 1926, monobasic; nom. n. for *Stenometra* Esaki, 1926.
= *Stenometra* Esaki, 1926: 118. Type-species *Stenometra biroi* Esaki, 1926, monobasic. Preocc. by *Stenometra* Clark, 1909, in Echinodermata.
australicus J. & D. Polhemus, 1991: 3. Australia (north Queensland), Indonesia (Irian Jaya; south central, Misool), Papua New Guinea
biroi (Esaki), 1926: 119. [*Stenometra*]. Singapore
fakfak J. & D. Polhemus, 1996: 317. Indonesia (Irian Jaya; southwest, Batanta, Waigeo)
kamajo J. & D. Polhemus, 1996: 319. Indonesia (Irian Jaya; Biak, Salawati and nearby,Yapen)
kasim J. & D. Polhemus, 1996: 320. Indonesia (Irian Jaya)
labuha J. & D. Polhemus, 1996: 324. Indonesia (Bacan, Halmahera)
langoban J. & D. Polhemus, 1996: 326. Philippines (Palawan)
makraitos (Chen & Nieser), 1992: 159. [*Rheumatometroides*]. Indonesia (Celebes)
sangihe J. & D. Polhemus, 1996: 333. Indonesia (Sangihe Archipelago)
zamboanga J. & D. Polhemus, 1996: 335. Philippines (Mindanao)

Stenobatopsis J. & D. Polhemus, 1996: 338. Type-species, *Stenobatopsis stygius* J. & D. Polhemus, 1996.
stygius J. & D. Polhemus, 1996: 340. Indonesia (Halmahera, Mamboa Isl.)

Thetibates J. & D. Polhemus, 1996: 341. Type-species, *Rheumatometroides serena* Lansbury, 1992.
matawa (Lansbury), 1989: 67. [*Rheumatometroides*]. Solomon Islands
= *aqaaqa* Lansbury, 1989: 65. Syn. by J. & D. Polhemus, 1996: 343.
serena (Lansbury), 1992: 1. [*Rheumatometroides*]. Papua New Guinea

Tribe TREPOBATINI Matsuda, 1960: 330. Type-genus *Trepobates* Uhler.

Cryptobates Esaki, 1929a: 412. Type-species, *Gerris raja* Distant,1910.
johorensis J. & D. Polhemus, 1995: 102. West Malaysia, Thailand
obscurus Miyamoto, 1967: 253. Brunei, Malaysia (Sabah)
raja (Distant), 1910a: 142. [*Gerris*]. India (Kerala), Sri Lanka
rufus J. & D. Polhemus, 1995: 105. West Malaysia, Singapore

Cryptobatoides J. Polhemus, 1991: 82. Type-species, *Cryptobatoides brunneus* J. Polhemus, 1991.
brunneus J. Polhemus, 1991: 84. Brazil

Gnomobates J. & D. Polhemus, 1995: 107. Type-species *Cryptobates kuiterti* Hungerford & Matsuda, 1958.
kuiterti (Hungerford & Matsuda), 1958c: 246. [*Cryptobates*]. India, Myanmar [Burma], Thailand

Halobatopsis Bianchi, 1896: 70. Type-species, *Halobates platensis* Berg,1879.
chrysocastanis Nieser & Lane de Melo,1999: 98. Brazil
delectus Drake & Harris,1941: 237. Brazil
platensis (Berg), 1879: 24. [*Halobates*]. Argentina, Brazil
spiniventris Drake & Harris, 1936: 107. Argentina, Brazil

Ovatametra Kenaga, 1942: 136. Type-species, *Halobatopsis parvulus* Drake & Harris,1935.
amnica Drake, 1957: 112. Panama
bella Drake, 1957: 111. Bolivia
fusca Kenaga, 1942: 139. Brazil, Guyana
gualeguay Bachmann, 1966a: 87. Argentina, Brazil
minima Kenaga, 1942: 137. Brazil
obesa Kenaga, 1942: 138. Brazil
parvula (Drake & Harris), 1935: 3. [*Halobatopsis*]. Brazil
thaumana Drake, 1959: 107. Brazil

Telmatometra Bergroth, 1908: 374. Type-species, *Telmatometra whitei* Bergroth, 1908.
fusca Kenaga, 1941: 178. Brazil
indentata Kenaga, 1941: 176. Peru
panamensis Drake & Harris, 1941: 239. Panama, Peru
= *acuta* Kenaga, 1941: 176. Syn. by J. Polhemus, 1992: 439.
parva Kenaga, 1941: 180. Brazil
ujhelyi Esaki, 1926: 133. Mesoamerica
whitei Bergroth, 1908: 376. Mesoamerica

Telmatometroides J. Polhemus, 1991: 78. Type-species, *Telmatometra rozeboomi* Drake & Harris, 1937.
rozeboomi (Drake & Harris), 1937: 358. [*Telmatometra*]. Colombia, Costa Rica,Ecuador, Panama

Trepobates Uhler, 1894: 213. Type-species, *Halobates pictus* Herrich-Schaeffer, 1847; nom. n. for *Stephania* B. White, 1883.
= *Stephania* B. White, 1883: 79. Type-species, *Halobates pictus* Herrich-Schaeffer, 1847. Preoccupied by *Stephania* Leseur, 1813, in Coelenterata.
becki Drake & Harris, 1932c: 120. Mexico, U. S. (Az., Ca., N. M.)
carri Kittle, 1982: 157. Belize, Cuba, Guatemala, Honduras, Jamaica, Mexico, U. S. (Tx.)
floridensis Drake & Harris, 1928c: 273. U. S. (Al., Ga., Fl., Ms.)
inermis Esaki, 1926: 140. Canada (southeast), U. S. (east)
knighti Drake & Harris, 1928a: 28. U. S. (central)
panamensis Drake & Hottes, 1952: 35. Mesoamerica, Colombia, Ecuador,Venezuela
pictus (Herrich-Schaeffer), 1847: 111 [*Halobates*]. Canada (southeast, U. S. (east)
polhemi Kittle, 1982: 161. Mexico (central, western)
subnitidus Esaki, 1926: 141. Canada (southeast), U. S. (central, east, N. M., Tx.)
= *citatus* Drake & Chapman, 1953: 111. Syn. by Kittle, 1991: 945.
taylori (Kirkaldy), 1899: 28 [*Kallistometra*]. Mesoamerica, South America,U. S. (Tx.), West Indies
= *comitialis* Drake & Harris, 1928b: 7. Syn. by Drake & Harris, 1932a: 112.
trepidus Drake & Harris, 1928a: 27. U. S. (Az.), Mesoamerica, Colombia,Ecuador, Venezuela
vasquezae Drake & Hottes, 1951: 141. Mexico (southwest)

Trepobatoides Hungerford & Matsuda, 1958b: 125. Type-species *Trepobatoides boliviensis* Hungerford & Matsuda, 1958.
boliviensis Hungerford & Matsuda, 1958b: 125. Bolivia, Peru

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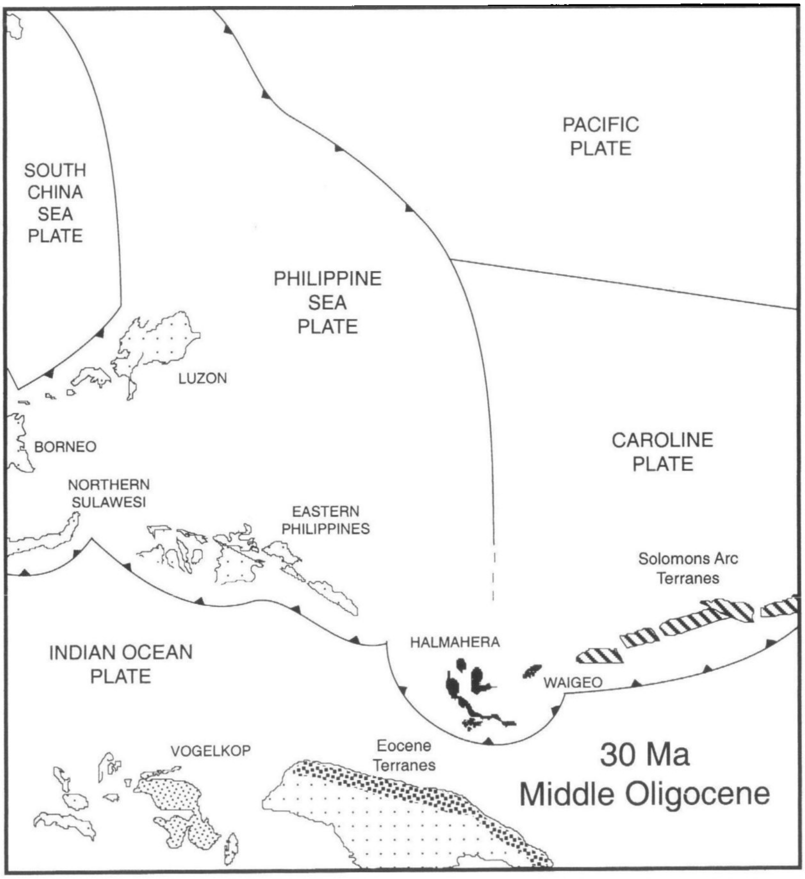

Figure 14. Paleopositions of tectonic units in the New Guinea region at 30 Ma (middle Oligocene) after Hall (1998). Note the position of the Solomons Arc terranes, Halmahera and Waigeo to the north of proto-New Guinea along the southern margins of the Caroline and Philippine Sea plates, and the existence of Vogelkop as a separate microcontinent to the west. By this time the Eocene to early Oligocene island arc terranes that form the northern portion of the New Guinea central ranges had already been emplaced.

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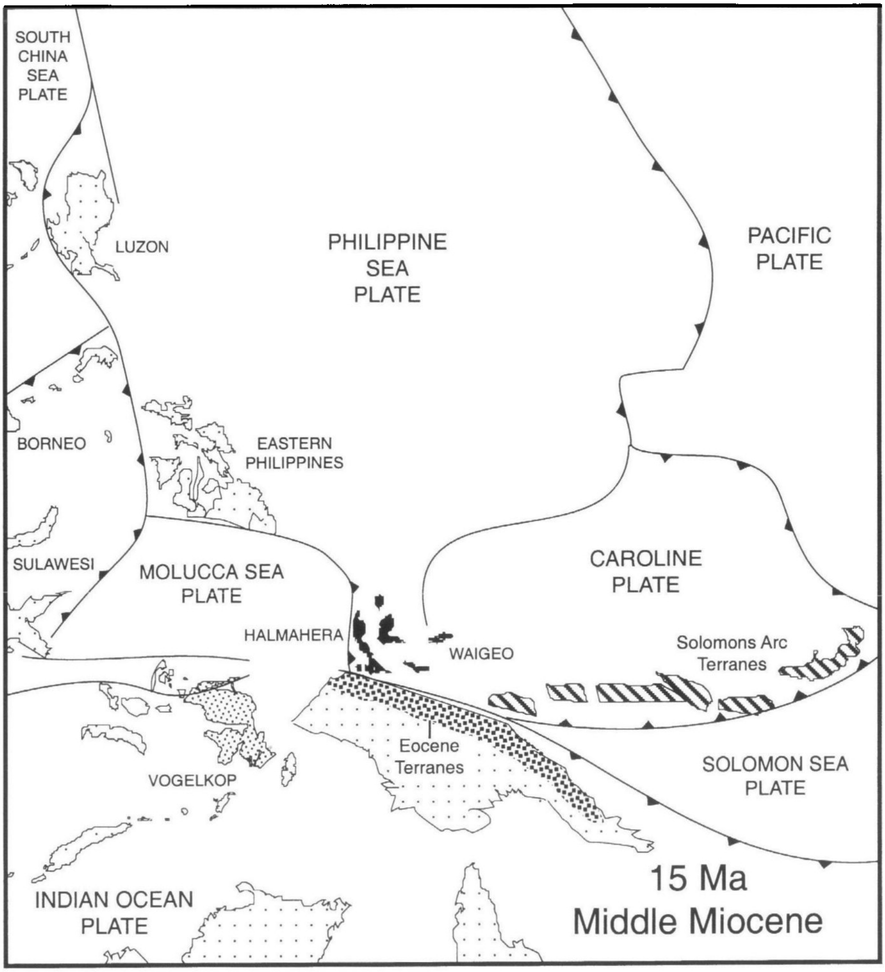

Figure 15. Paleopositions of tectonic units in the New Guinea region at 15 Ma (middle Miocene) after Hall (1998). Note the close proximity of proto-Halmahera to the northern margin of proto-New Guinea, and the continued closure of the Solomons Arc terranes with northeastern proto-New Guinea.

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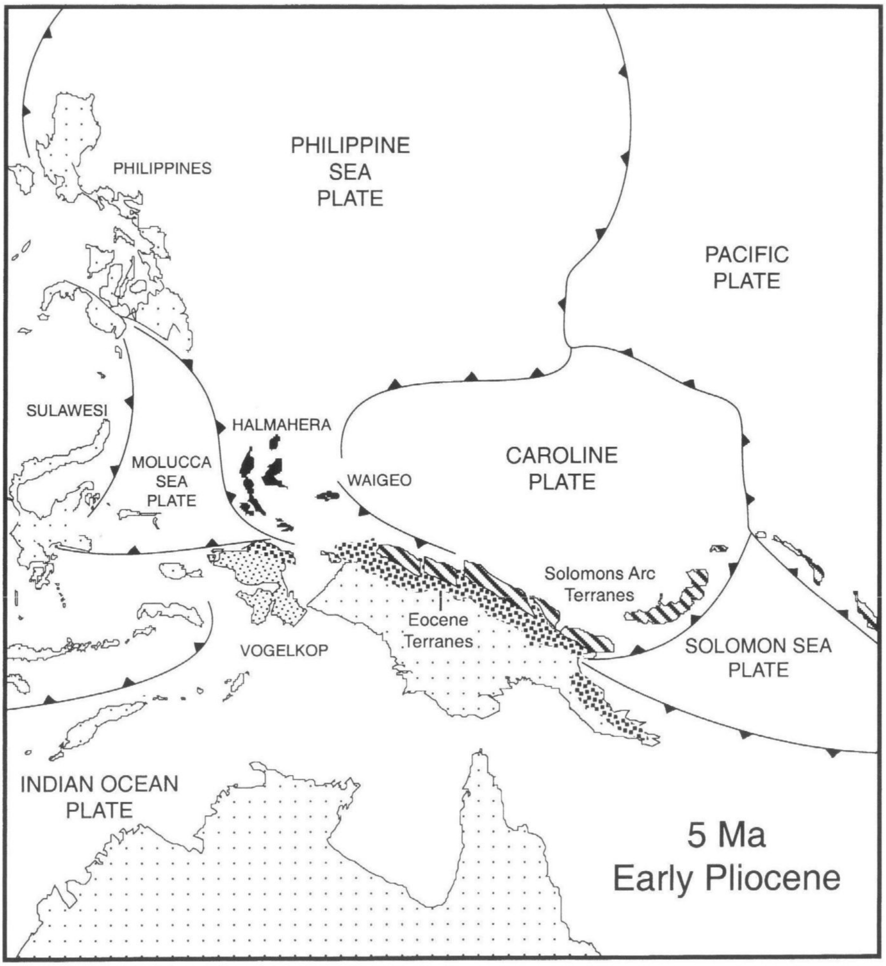

Figure 16. Paleopositions of tectonic units in the New Guinea region at 5 Ma (early Pliocene) after Hall (1998). Note the emplacement of the Solomons Arc terranes along the northern margin of New Guinea, which has at this point attained a semblance of its current configuration. Note also the close juxtaposition of proto-Halmahera and the Vogelkop microcontinent; the latter was sutured to the western tip of mainland New Guinea at about this same period.

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APPENDIX 1: Taxonomic addenda

Several important taxonomic additions to the trepobatine fauna of the New Guinea region were discovered after the text of this final section of the monograph was substantially complete. Although we include these taxa here in order to provide a more complete picture of the New Guinea regional biota, the new genus *Talaudia* (see below) was brought to our attention too late to be included in the foregoing phylogenetic and biogeographic analyses.

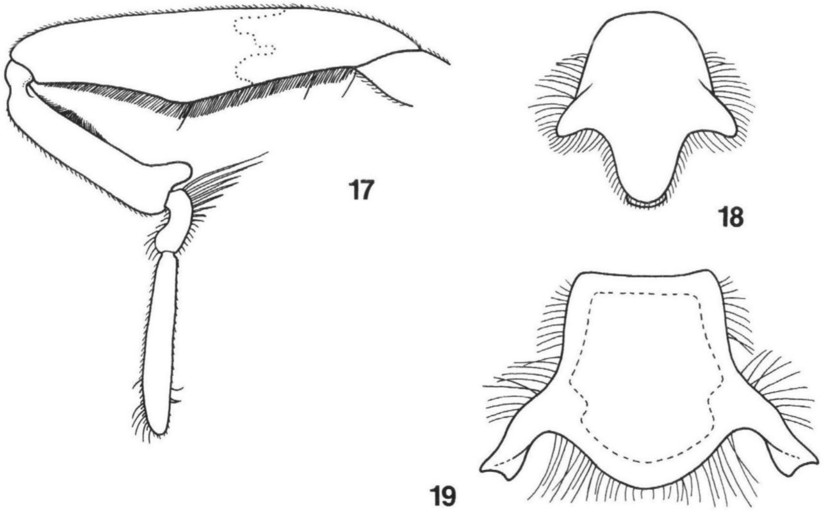
Tribe METROBATINI

Metrobatoides bifurcatus sp. n.

(Fig. 17-20)

Type area. – North Central New Guinea.

Type material examined. – INDONESIA. Holotype, apterous male: Irian Jaya Prov., New Guinea, Tiri River, 4.5 km. SW of Dabra, 60 m., 3°17'30"S, 138°34'53"E, water temp. 25.0 °C, 9-13 September 2000, CL 7140, D. A. Polhemus (LIPI). Paratypes (all apterous): 7 males, 23 females, same data as holotype (USNM, LIPI, JTPC); 5 males, 15 females, 10 nymphs (nymphs not paratypes), lower Doorman River above confluence with Idenburg River, 50 m., 3°14'40"S, 138°35'29'E, water temp. 26.5 °C, 6 September 2000, CL 7139, D. A. Polhemus (USNM, JTPC, LIPI).



Figures 17-19. *Metrobatoides birfurcatus* sp. n., structural details: (17) Male foreleg. (18) Male proctiger. 19. Male pygophore.

Description.–Size. Apterous male, length 3.59 mm. (mean, N = 10; min. 3.35, max. 3.71), maximum width 1.84 mm. (mean, N = 10; min. 1.69, max. 1.94). Apterous female, length 4.27 mm. (mean, N = 10; min. 4.03, max. 4.50), maximum width 2.05 mm. (mean, N = 10; min. 1.84, max. 2.20).

Color. Ground color black with leucine markings and extensive gray pruinose areas. Head dull black, with brownish markings narrowly on posterior margin; pronotum with a single median leucine region overlain with a slightly broader pruinose gray region, both widening posteriorly; mesonotum of both sexes with broad median area pruinose gray, not reaching anterior margin, not sharply demarcated laterally, laterally black. Metanotum, abdominal tergite I medially gray pruinose, black laterally; all other abdominal tergites mostly gray pruinose. Pleural regions tinged with gray pruinose. Thoracic venter dull gray, mesosternum posteriorly thickly set with long golden setae medially in males; anterior acetabulae yellowish, mid and posterior acetabulae dark blackish brown. Abdominal ventrites gray in females, marked with brown medially, all ventrites brown in males. Legs and antennae mostly blackish brown, fore femora basally, coxae beneath, trochanters, sbrown to leucine.

Structural characters. Head short, length 0.47, width 1.30, truncate anteriorly, ventrally flattened, with a longitudinal sulcus widening posteriorly; sides subparallel (excluding eyes), posteriorly widened; anteclypeus not prominent; eye width (0.36), more than half of interocular space (0.56); eyes moderately exserted, extending posteriorly halfway along pronotum in males, almost to mesonotum in females; rostrum large, almost straight, with 4 very prominent segments, second very short and ring-like, third longest, one and four subequal. Male antennae moderately long, relatively stout, segment I weakly incrassate with small inner basal knob, segment IV flattened, length of antennal segments I-IV: 0.72; 0.62; 0.29; 0.40; female antennae longer, slender, without modifications, length of antennal segments I-IV: 0.54; 0.56; 0.36; 0.47.

Pronotum short, margins concave anteriorly, almost staight posteriorly, length on midline less than half that of mesonotum, length 0.43, width 1.15, width less than head through eyes. Mesonotum long, broad, length 0.90, width 1.71, sides weakly convex in males, subparallel in females, slightly wider posteriorly, anterolateral angles rounded, much wider than head. Metanotum indicated by a suture laterally, evanescent medially, fused with abdominal tergites I and II, combined length 0.54. Abdominal tergites III-VI subequal in length (0.08-0.11), VII much longer (0.43), bent ventrad.

Male anterior femur abruptly thickened at distal two thirds, forming an oblique triangle (Fig. 17)

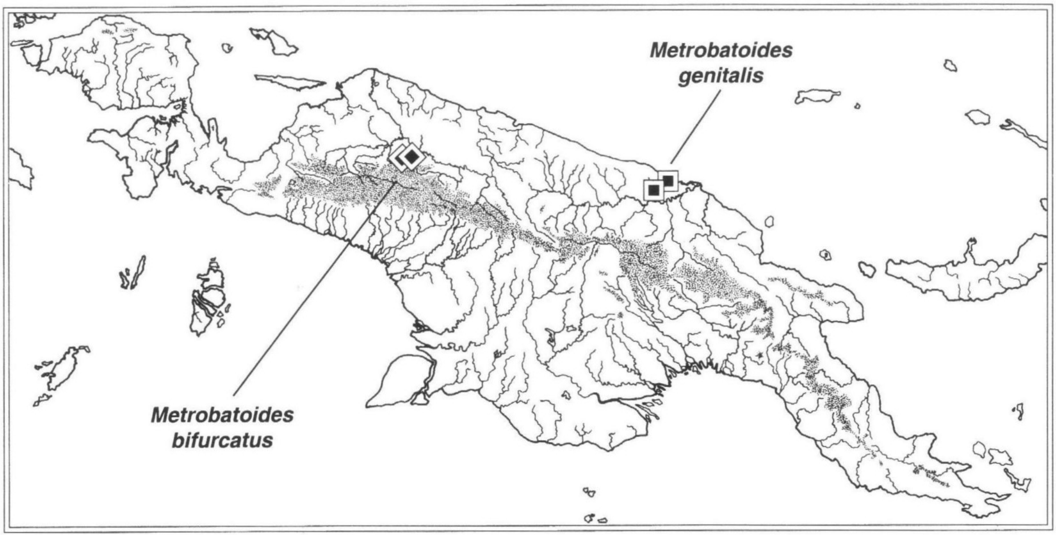


Figure 20. Distribution of *Metrobatoides* species in New Guinea.

inner face clothed with short stiff setae; tibia almost straight, flattened, with a semi-circular tuft of stiff setae on inner side near base, somewhat broadened distally, with large blunt apical process; anterior tarsal segment 1 cylindrical, about one third as long as 2, basally with several very long erect setae followed by several shorter stiff setae; segment 2 increasingly flattened distally, tarsi longer than tibia. Middle femur long, slender, much stouter and much shorter than hind femur; mid tibia long, about 1/5 longer than mid femur; tarsi very long, first segment almost 4 times as long as second, thickly set over basal 7/8 with long soft setae (swimming plume). Hind femur long, slender, about 2-1/2 times as long as hind tibia; tarsi short, with a single segment. Claws of fore leg small, short, slender, blade-like, curved distally, situated beyond distal 2/3 of second tarsal segment, downcurving arolium flattened, almost as long as claws, dorsal arolium not evident; claws of middle leg tiny, preapical, arolia not evident; claws of hind leg long, slender, blade-like, slightly widened and curved distally, arising from beyond middle of the single tarsal segment, reaching almost to apex of tarsus; single hair-like arolium visible. Measurements of male legs as follows: femur, tibia, tarsal 1, tarsal 2 of fore leg, 1.37, 0.65, 0.14, 0.58; of middle leg, 3.16, 4.18, 2.12, 0.65; of hind-leg (tarsal 1 and 2 fused), 3.78, 1.54, 0.47. Female fore legs of similar proportions, but fore femur and tibia cylindrical, not flattened ventrally, with apical process; fore tarsi subequal in length to fore tibia.

Male basal abdominal ventrites extremely short, compressed, appearing as ridges, the length of all taken together less than that of ventrite VII, which is short; ventrite VIII much longer, broad; genital segments modified, pygophore and proctiger large, both with lateral wings (Fig. 18, 19); phallotheca short, deep; most primary vesical sclerites present, connected, continuous, ventral sclerite not evident; vesica with short lateral sclerites in basal half, expanded distally, the same as in *M. genitalis* (see J. Polhemus & D. Polhemus, 1993: 277, Fig. 50-51). Female subgenital plate (ventrite VIII) triangular, sculptured, longitudinally carinate medially; tergite VIII short, convex distally; proctiger cylindrical, projecting directly posteriorly.

Macropterous forms unknown.

Etymology. – The name 'bifurcatus' refers to the bifurcate processes on the male pygophore.

Comparative notes. – Easily separated from the only previously described species in the genus, *M. genitalis* Polhemus & Polhemus, by the structure of the male foreleg (Fig. 17), the relatively short lateral processes of the male proctiger (Fig. 18), and the bifurcate lateral processes on the male pygophore (Fig. 19). Both sexes have less extensive grey pruinose regions on the metasternum and tergite I, and the female lacks the distict medial quadrate depression on the mesonotum, plus the female anal cone projects directly posteriorly rather than curving upward.

Biological notes. – The Tiri River at the type locality was a small, shallow river in a sand and cobble bed, bordered by primary lowland rain forest. The type series of *M. bifurcata* was taken on broad, smoothly flowing pools approximately 0.5 m in depth. On the Doorman River near its mouth this species was taken on a sheltered, unshaded eddy on the outside of a river bend, and other scattered individuals were observed on open midstream waters up to 10 m from shore. A large school of immatures and teneral adults was also found at this latter locality on a cut off side pool, where they aggregated in the shade of overhanging trees.

The discovery of *M. bifurcatus* extends the range of *Metrobatoides* significantly to the west, from the Prince Alexander Mountains of Papua New Guinea into the basin of the Mamberamo River in northern Irian Jaya. It seems likely that the genus will eventually be shown to occur in the Sepik River basin as well.

Distribution. – New Guinea (Fig. 20). Known to date only from the Mamberamo River basin.

Iobates ivimka sp. n.

(Fig. 21-22)

Type area. – Southern Papua New Guinea.

Type material examined. – PAPUA NEW GUINEA. Holotype, apterous male: Gulf Prov., Ivimka Creek along Kakoro Track, SE of Ivimka Research Station, 30 m., 07°44'20"S, 146°30'06"E, water temp. 25° C., 17 January 2001, 07:30-13:00 hrs., CL 7149, D. A. Polhemus (BPBM).

Paratypes (all apterous): 29 males, 26 females, same data as holotype (USNM, BPBM, JTPC).

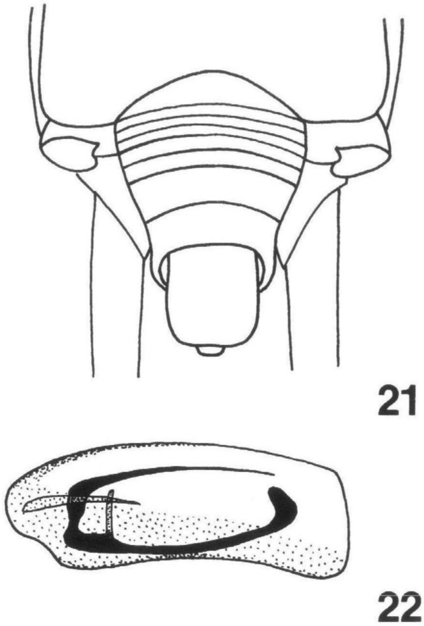
Description. – Size. Apterous male, length 2.66 mm. (mean, N = 10; min. 2.59, max. 2.77), maximum width 1.17 mm. (mean, N = 10; min. 1.12, max. 1.26). Apterous female, length 3.25 mm. (mean, N = 10; min. 3.13, max. 3.42), maximum width 1.67 mm. (mean, N = 10; min. 1.58, max. 1.73).

Color. Ground color black with leucine markings and extensive gray pruinose areas. Head dull black, with leucine markings narrowly on posterior margin; pronotum mostly leucine, with an irregular blackish brown region on each side, narrower in females; mesonotum of both sexes with broad pruinose gray areas on each side of midline, broadly black medially. Metanotum, abdominal tergite I medially dark, gray pruinose laterally; all other abdominal tergites mostly gray pruinose. Pleural regions tinged with gray pruinose, more pronounced toward venter. Thoracic venter gray pruinose, females with a few leucine markings. Anterior acetabulae leucine, males with brown spots; mid and posterior acetabulae dark blackish brown. Abdominal ventrites leucine in females, marked with brown medially, all ventrites mostly brown in males. Legs and antennae mostly blackish brown; fore femora basally, all trochanters leucine; coxae brown to leucine.

Structural characters. Head short, length 0.27, width 0.83, truncate anteriorly; sides subparallel (excluding eyes), posteriorly widened; anteclypeus not prominent; eye width (0.22), less than interocular space (0.33); eyes exserted, extending onto mesonotum in both sexes; rostrum large, almost straight, with 4 very prominent segments, second very short and ring-like, third longest, one half the length of four. Male antennae long, slender, unmodified, segment I with 3 stout setae distally, segment IV flattened, length of antennal segments I-IV: 0.61; 0.50; 0.39; 0.33; female antennae with similar proportions, segment IV fusiform.

Pronotum short, almost lenticular, posterior margin convex, length on midline less than one-third that of mesonotum, length 0.22, width 0.67, width much less than head through eyes. Mesonotum long, broad, length 0.72, width 1.11, sides weakly convex in males, subparallel in females, slightly wider posteriorly, anterolateral angles rounded, much wider than head. Metanotum indicated by a suture laterally, evanescent medially, fused with abdominal tergites I and II, combined length 0.44. Abdominal tergite III short (0.05), tergites IV-VII increasing in length (0.10-0.17).

Male, female anterior femora unmodified, stouter in male; tibia straight, cylindrical, with a small apical tuft of setae in both sexes; anterior tarsal segment 1 cylindrical, about one fifth as long as 2, basally with several very long erect setae followed by several shorter stiff setae; segment 2 increasingly flattened distally, tarsi shorter than tibia. Middle femur long, slender, stouter and shorter than hind femur; mid tibia long, slightly longer than mid femur; tarsi very long, first segment almost 3 times as long as second. Hind femur long, slender, about 2-1/2 times as long as hind tibia; tarsi short, with a single segment. Claws of fore leg blade-like, curved, situated at about middle of second tarsal segment, downcurving aroli-



Figures 21, 22. *Iobates ivimka* sp. n., structural details: (21) Male ventral abdomen. (22) Male endosoma, lateral view.

um flattened, almost as long as claws, dorsal arolium slender; claws of middle leg slender, hair-like, preapical, arolia not evident; claws of hind leg long, slender, preapical, reaching apex. Measurements of male legs as follows: femur, tibia, tarsal 1, tarsal 2 of fore leg, 0.89, 0.66, 0.05, 0.26; of middle leg, 1.63, 1.81, 1.00, 0.37; of hind-leg (tarsal 1 and 2 fused), 1.91, 0.72, 0.37. Female fore legs of similar proportions.

Male basal abdominal ventrites extremely short, compressed, ring-like, the length of all taken together about that of ventrite VII, which is short; ventrite VIII about twice as long as VII; genital segments unmodified (Fig. 21); phallotheca long, slender; most primary vesical sclerites present, dorsal, basal and ventral connected, continuous (Fig. 22); vesica with narrow lateral sclerites in basal half; slender median sclerite present (for explanation of sclerites, see Polhemus & Polhemus 1993: 277, fig. 52-56). Female subgenital plate (ventrite VIII) not modified, posterior margin straight; tergite VIII short, sinuate distally; proctiger cylindrical, projecting slightly postero-dorsally.

Macropterous forms unknown.

Etymology. – The name 'ivimka' is a noun in apposition and refers to the type locality, Ivimka Creek.

Comparative notes. – *Iobates ivimka* may be easily separated from the other described species of the genus by the lack of modifications in either male or female. This species clearly keys to the genus *Iobates* on the basis of all characters except the complement of endosomal sclerites, which is much more complete than in other *Iobates* species. The endosomal sclerites of *I. somare* Polhemus & Polhemus, which have never been illustrated, are very similar to those of *I. affinis* (Esaki) (see Polhemus & Polhemus 1993: 277, fig. 72-73).

Biological notes. – Ivimka Creek at the type locality was a heavily shaded, sandy-bottomed stream with vertical, muddy banks, flowing slowly through primary lowland rain forest. The type series of *I. ivimka* was taken from smoothly flowing pools along the main channel, in areas of dappled sunlight.

The discovery of *I. ivimka* extends the range of *Iobates* significantly eastward, from the Kikori River basin of Papua New Guinea into the southern section of the Papuan Peninsula (Fig. 7).

Distribution. – Southern Papua New Guinea (Fig. 7). Known to date only from the Lakekamu River basin, but likely to be broadly distributed on lowland forest streams of the southern Papuan Peninsula east of the Aure Scarp.

Revised key to species of *Iobates*

1. Male fore femur with acuminate denticle on inner face at basal two-fifths; sternite VIII with two (1+1) posteriorly directed processes on either side of midline. Female with posterior margin of mesonotum straight, not sinuate; middle and hind femora with numerous erect setae .... *affinis* (Esaki)

– Male fore femur without denticle on inner face; sternite VIII without posteriorly directed lateral processes. Female mesonotum may or may not be sinuate; middle and hind femora without numerous erect setae 2

2. Male with posterior margin of sternite VIII weakly V-shaped, set with small fringes of dark setae. Female with posterior margin of mesonotum strongly sinuate, medially curving posteriorly; without a fringe of erect setae on the metacetabulae .. *salawati* Polhemus & Polhemus

– Male with posterior margin of sternite VIII not V-shaped, but either straight or with a posteriorly directed protuberance medially. Female with posterior margin of mesonotum straight to very weakly sinuate; with or without a fringe of erect setae on the metacetabula 3

3. Male with posterior margin of sternite VIII straight. Female with posterior margin of mesonotum weakly sinuate; without a fringe of erect setae on the metacetabulae.......... *ivimka* sp. n.
– Male sternite VIII with an acuminate posteriorly directed protuberance medially on the posterior margin. Female with posterior margin of mesonotum straight, not sinuate, not medially curving posteriorly; with a fringe of erect setae on the metacetabulae .... *somare* Polhemus & Polhemus

Stygiobates mubi Polhemus & Polhemus

Stygiobates mubi Polhemus & Polhemus 2000: 300.

Additional material examined. – PAPUA NEW GUINEA: 13 apterous males, 6 apterous females, Gulf Prov., Ivimka Creek along Kakoro Track, SE of Ivimka Research Station, 30 m., 07°44'20"S, 146°30'06"E, water temp. 25° C., 17 January 2001, 07:30-13:00 hrs., CL 7149, D. A. Polhemus (USNM).

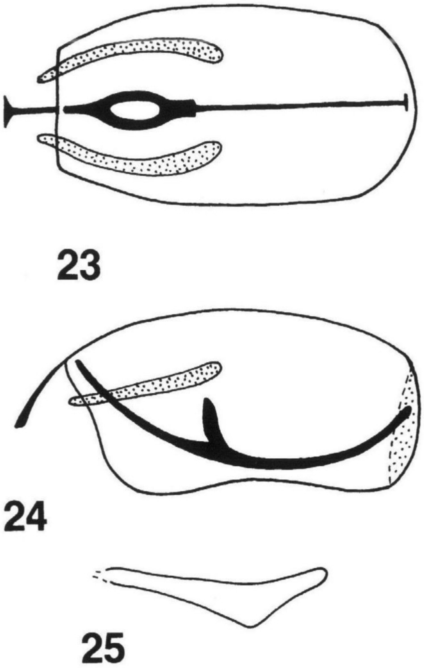
Distribution. – Although originally described from the Kikori River basin, new captures from a tributary to the Lakekamu River have extended the range of this species significantly to the east, indicating that it occurs widely in southern Papua New Guinea. Given the current records, *S. mubi* will undoubtedly be found to occur in the intervening Purari River catchment as well.

Talaudia **gen. n.**

(Fig. 23-25)

Description. – Size. Apterous form, body strongly sexually dimorphic, length of body in males 1.26-1.33 mm., in females 2.77-3.13 mm.

Color. Ground color black with sparse leucine to fuscous markings, entire dorsum, grey pruinose, in females continuing onto pleura and venter. Head with small weakly developed transverse fuscous band on posterior margin, continuing forward along inner eye margins to form a U, broader and strongly developed between eyes and antennal sockets; pronotum with a single median quadrate sordid leucine region, small in males, larger in females and continuing as a narrow band along posterior margin; mesonotum without light markings; metanotum and first two abdominal segments of females with irregular longitudinal leucine to fuscous band; connexiva of females tinged with leucine. Thoracic venter entirely dark, luteous on anterior acetabulae. Legs, antennae mostly blackish brown, first antennal segments basally (basal fourth in males, basal half in females), fore femora basally, fore coxae, trochanters at least ventrally, yellowish to fuscous, darker in males.



Figures 23-25. *Talaudia nilsi*, gen. n., comb. n., structural details: (23) Male endosoma, dorsal view. (24) Male endosoma, lateral view. (25) Male paramere.

Structural characters. Head short, rounded anteriorly, ventrally flattened, depressed anteriorly; sides subparallel (excluding eyes), anteclypeus not prominent; interocular space about 2.0 times eye width in males, about 1.7 times in females; eyes moderately exserted, extending posteriorly almost to mesonotum in males, touching in females; rostrum large, slightly curved anteriorly, with 4 very prominent segments, second shortest, third longest, one and four subequal. Antennae short stout in males, first segment fusiform and longest, two and four subequal but three sightly shorter; antennae much longer and more slender in females, first segment longest, three shortest, two slightly longer than four. Pronotum short, very slightly concave anteriorly, slightly convex posteriorly, in male almost lenticular, essentially without lateral margins, in females more quadrate with lateral margins widening posteriorly, length on midline about 0.5 times that of mesonotum in males, 0.45 in females, width less than head through eyes in males, much less in females.

Mesonotum long, sides convex, anterolateral angles rounded, much wider than head, thickly set with stiff black semi-decumbent setae except in broad median depression of females. Metanotum indicated by a weak suture laterally, evanescent medially, fused with abdominal tergites I and II. Abdominal tergites III-VII subequal in length. In females the median part of mesonotum, metanotum, abdominal tergites I and II depressed, forming a 'cradle' for the male in phoresy.

Male anterior femur thickened, arched slightly and flattened, slightly scuptured at distal 2/3, entire inner face clothed with short stiff setae; tibia slightly broadened distally, with well developed apical spur, inner face flattened and slightly excavated beneath, clothed with short stiff setae; female fore femur and tibia long, slender, unmodified; anterior tarsal segment I short and cylindrical, set with long setae basally in female (not evident in male), segment II very slightly flattened, oval and about 3 times longer than I in males, long, slender, about 4 times I in females. Middle femur slender, stouter and much shorter than tibia or hind femur in females, much shorter than tibia and slightly shorter than hind femur in males; tarsi long, first segment about 1.5 times as long as second in males, 2.5 times in females. Hind femur long, slender, about twice as long as hind tibia in males, 3 times as long in females and flattened laterally plus slightly widened distally; tarsi short, segments fused. Claws of fore leg short, slender, blade-like, curved distally, situated beyond middle of second tarsal segment, downcurving arolium flattened (not evident in males), as long as claws, dorsal arolium not evident; claws of middle leg long, very slender, arising near tip of second tarsal segment, arolia not evident; claws of hind leg long, very slender, preapical.

Male pregenital abdomen and genital segments without modifications; small parameres present (Fig. 25), not protruding from the genital capsule; phallotheca short, rotund; primary vesical sclerites (except ventral sclerite) present, connected, continuous (Fig. 23, 24); vesica with oval aperture basally in dorsal sclerite, short lateral sclerites in basal half, a short stout median sclerite; no other sclerites evident. Female gonapophysis partially sclerotized, not serrate, membranous distally.

Type species. – *Andersenella nilsi* Chen & Nieser, 2000.

Comparative notes. – *Talaudia* gen. n. is most closely related to the genus *Rheumatometra* Kirkaldy. It is similar to this genus in ground color, the reduced setae of the male first anterior tarsal segment, the prominent male fore tibial process, the phoretic male which is much smaller than the female, the arched male fore tibia, the female head greatly widened between the eyes posteriorly, the vesica with an oval aperture basally in the dorsal sclerite, and the small and simple male genital segments; all of these are characteristics similar to *Rheumatometra*.

Talaudia differs from *Rheumatometra* in the following ways: in *Talaudia*, the complement of male vesical sclerites is different (see discussion above, Fig. 23, 24 in this work, and fig. 57-58 in Polhemus & Polhemus 1993: 277) with a longer basal sclerite, a shorter dorsal sclerite, and the apicolateral scerites absent; distinct parameres are present; the eyes cover most (female) or all (male) of the lateral pronotal margin (vs. about 1/2 in *Rheumatometra*); the mesonotum lacks a median sulcus; and the male/female antennae much more sexually dimorphic.

The type species of *Talaudia* was placed by Chen & Nieser (2000) in the genus *Andersenella*, however all of the similarities to the genus *Rheumatometra* listed above are differences from *Andersenella*, and serve to separate *Talaudia* from the latter.

Etymology. – The generic name is derived from the place of origin of the only known specimens, the Talaud Archipelago. Feminine.

Distribution. – Talaud Archipelago, lying between the Minahasa Peninsula of northern Sulawesi and the southern tip of Mindanao.

Talaudia nilsi (Chen & Nieser), **comb. n.**

(Fig. 23-25)

Andersenella nilsi Chen & Nieser 2000: 70.

Comparative notes. – This is the only species so far assigned to the new genus *Talaudia*. The characters given in the foregoing generic discussion will be sufficient to separate it from any other currently known species of Trepobatinae in the Indo-Australian region. Excellent figures of the dorsal habitus for both the male and female were provided by Chen & Nieser (2000)