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Phylogeny of the water strider genus *Rheumatobates* (Heteroptera: Gerridae)

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Abstract. The genus *Rheumatobates* comprises thirty-seven species and subspecies of New World water striders belonging to subfamily Rhagadotarsinae. Among species, males vary dramatically in the degree and nature of modifications of the antennae, three pairs of legs and abdominal and genital segments. Characters describing this modification have traditionally been used to differentiate and group species. The general assumption has been that modified species belong to one group and unmodified species to another. These two 'species groups' are subdivided into 'subgroups', but little effort has been made to resolve relationships among them. We conduct the first numerical cladistic analysis of *Rheumatobates* using a data set comprised of 102 characters, primarily describing modification of male external morphology. To address concerns about the inclusion of characters to be optimized on the phylogeny, characters describing modification of antennae and hind legs were included and then excluded in separate analyses. A preferred phylogeny was chosen from the four equally parsimonious cladograms found after successive reweighting of characters. There was good resolution at all levels of the phylogeny. Most of the major clades and terminal relationships were moderately to strongly supported, whereas the basal relationships were less well supported. The general assumption that unmodified and modified species form two monophyletic groups was not supported. However, traditionally recognized 'subgroups' within the modified species group were largely upheld. The analysis also suggested several major clades and relationships among these clades that were not previously recognized. The exclusion of characters describing modification of antennae and hind legs did not change the resolved major clades of the reconstructed phylogeny.

Introduction

Rheumatobates Bergroth is a New World genus of small water striders belonging to subfamily Rhagadotarsinae (Andersen, 1982). This genus represents one of the most striking cases of elaboration of male morphology. Comments on the unprecedented and truly impressive nature of male modification in this genus are numerous. For example, Schroeder (1931) described *Rheumatobates* as 'perhaps the most remarkable group of insects in the order Hemiptera'. Riley's (1891) drawing of a single apterous male of *Rheumatobates rileyi* Bergroth (on which the genus was established) has adorned the covers of the *Proceedings of the Entomological Society of Washington* since the beginning of volume 3 in 1893. Moreover, the remarkable interspecific variation in male modification observed in this peculiar group led to various species being recognized as five separate genera (Hungerford, 1954). Synonyms of *Rheumatobates* include: *Hymenobates* Uhler, *Halobatopsis* Ashmead (in part), *Telmatobates* Bergroth and *Hynesia* China. Among species, males vary dramatically in the degree and nature of modifications of the antennae, fore, mid and hind legs, and the abdominal and genital segments (see Figs 1, 2). Analogous traits in females are unmodified throughout the genus (see Fig. 3).

Hungerford (1954) provides a complete historical account of *Rheumatobates*. To summarize, Bergroth (1892) recog-

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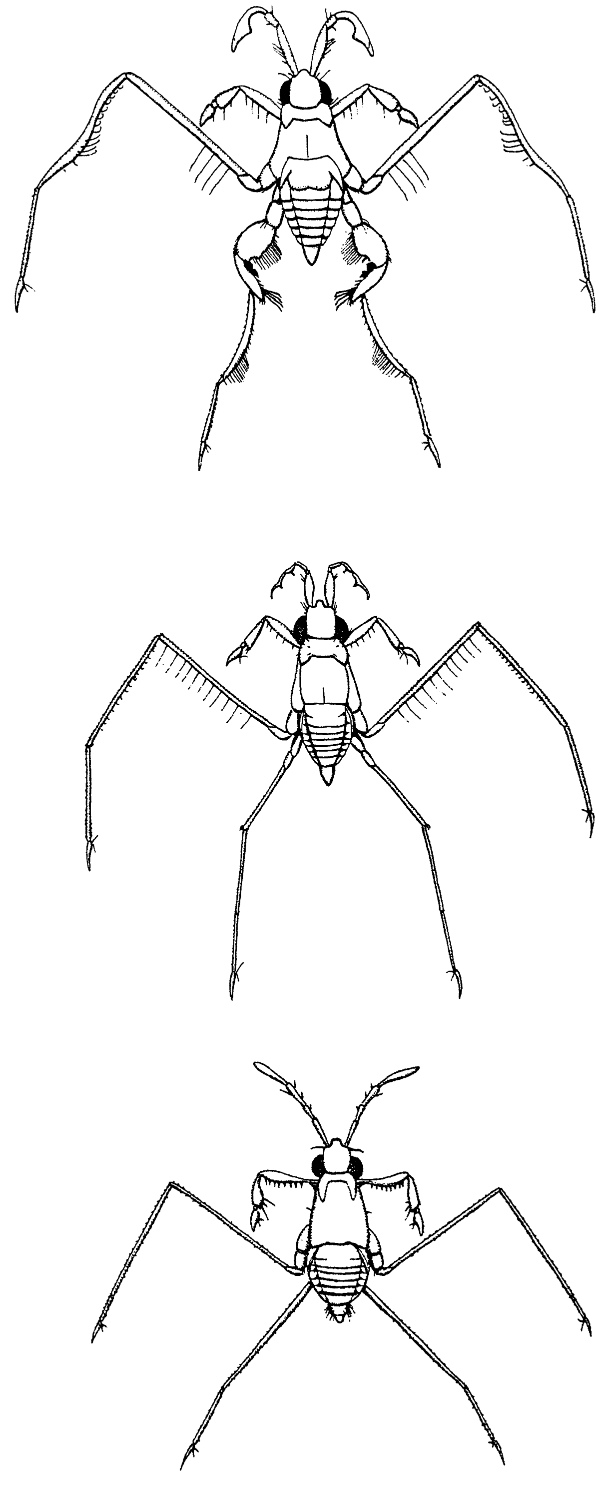

Fig. 1. A subset of species that highlight the dramatic interspecific variation in male modification observed in genus *Rheumatobates*. From top to bottom, *R. bergrothi*, *R. tenuipes* and *R. vegatus*.

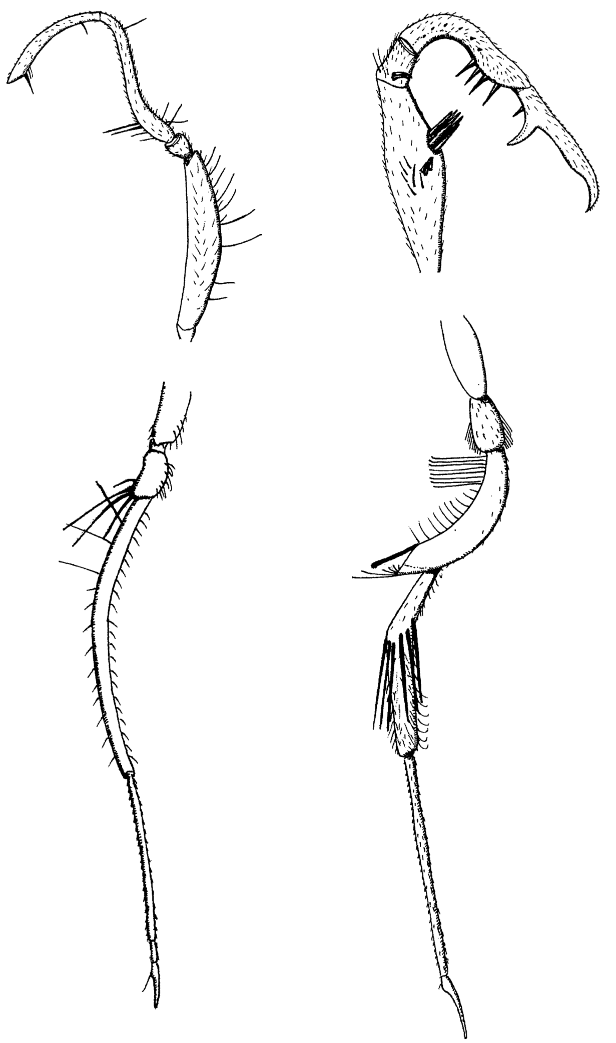

Fig. 2. A pair of antennae (top) and hind legs (bottom) that illustrate the extensive interspecific variation of modification within structures in genus *Rheumatobates*. Left, *R. carvalhoi*; right, *R. rileyi*.

nized the drawing published by Riley (1891) as an adult male and named it *Rheumatobates rileyi*, new genus and new species, stating that, '…the remarkable structure of the antennae and the hind femora are good generic characters of this insect.' Species with normal antennae and hind legs were since discovered and the strange and obvious characters that had led Bergroth to establish the genus were dropped.

The taxonomy of *Rheumatobate*s is well documented. Hungerford (1954) monographed the genus and provided descriptions and a key to the twenty-three known species (two new) and four subspecies (one new). Since then, Spangler *et al.* (1985) provided a checklist of the species (thirty) and subspecies (three) of *Rheumatobates*, Polhemus & Manzano (1992) provided keys for five new marine species and most recently Polhemus & Westlake (unpublished data) recognize thirty-seven taxa: thirty-two described species, three undescribed species and two subspecies.

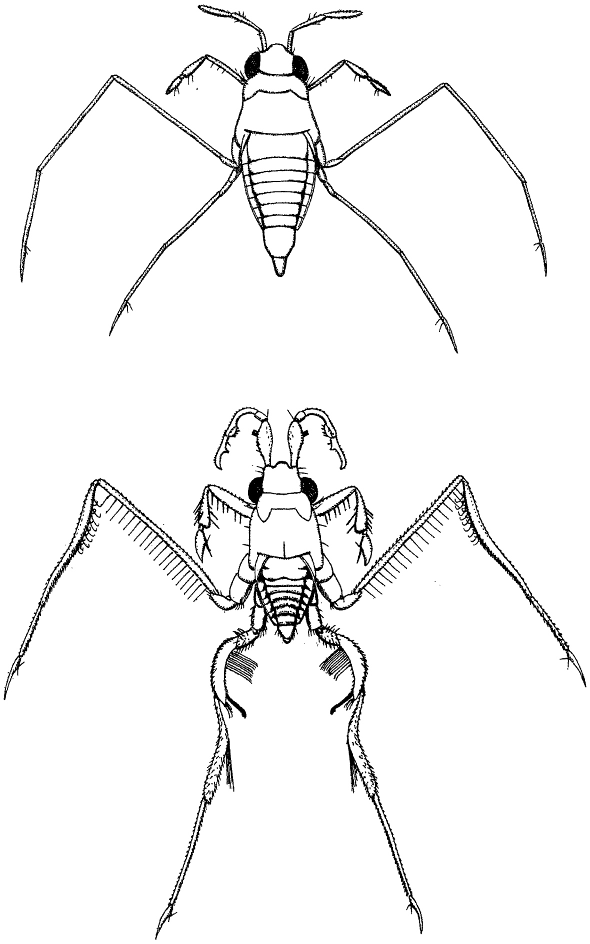

Fig. 3. Sexual dimorphism in *Rheumatobates rileyi*. Top, female; bottom, male.

Given the extensive interspecific variation in male modification, it is not surprising that taxonomists have traditionally relied on such variation to differentiate and group species of *Rheumatobates*. The general taxonomic assumption has been that modified species (defined by modified antennae and/or hind legs) belong to one major 'species group' and unmodified species to another. Hungerford (1954) divided the genus in this way and further divided the two major 'species groups' (primarily the modified species group) into various 'subgroups', but made little attempt to resolve the relationships among these. Most recently, Andersen (1997) tentatively recognized three 'species groups' based on the degree of modification of the male antennae and legs: group 'A' comprising species with relatively unmodified males, group 'B' comprising species where the middle and hind legs of males are modified and group 'C' containing species in which the legs as well as the antennae of males are modified.

In this contribution we reconstruct the first phylogeny of this genus and compare it with current taxonomic interpretations. A principal aim of the study was to determine whether modified and unmodified species indeed form two separate monophyletic groups, and to resolve phylogenetic relationships among current 'subgroups'. A future goal is to reconstruct the evolutionary history of male modification, specifically of the antennae and hind legs. In order to use the phylogeny in this way we need first to address concerns about the inclusion of characters to be optimized on the phylogeny (e.g. Coddington, 1988; Brooks & McLennan, 1991; Swofford & Maddison, 1992). To address these concerns, we reconstructed and compared phylogenies using two data sets, one that included characters describing modifications of the antennae and hind legs and one that excluded them.

Materials and methods

Taxa

Rheumatobates presently consists of thirty-seven taxa, all of which were included in the cladistic analysis. In their revision of *Rheumatobates*, Polhemus & Westlake (unpublished) describe three new species, and in this paper they are designated provisionally as species A, B and C. The three nominal subspecies of *R. crassifemur crassifemur* Esaki, *R. crassifemur schroederi* Hungerford and *R. crassifemur esakii* Schroeder (Hungerford, 1954) are retained in this analysis, but *R. curracis* Drake & Carvalho and *R. minutus flavidus* Drake & Harris are recognized as synonyms (Polhemus & Westlake, unpublished). One outgroup taxon was included, the sister genus of *Rheumatobates*, *Rhagadotarsus*. Together these two genera comprise subfamily Rhagadotarsinae (Andersen, 1982). This subfamily is defined as a monophyletic group by four autapomorphies: egg shell differentiated anteriorly; metathoracic scent apparatus absent, distinct first laterotergites and sternum of abdomen; serrate female ovipositor (Andersen, 1982: Table 11). Rhagadotarsinae are more plesiomorphic than other gerrids in three characters: ventral lobes of head large, anteriorly produced; second gonocoxae present; second gonapophyses largely sclerotized; fecundation canal short, without fecundation pump (Andersen, 1982). Rhagadotarsinae is therefore placed as the sister group of the remaining seven subfamilies of Gerridae (Andersen, 1982: Fig. 480). We examined three of the five species that comprise the sister genus *Rhagadotarsus*: *R. kraepelini*, *R. hutchinsoni* and *R. anomalus,* and chose the latter species as the outgroup. These three species differ in their states for only one of the 102 characters used in the analysis.

Specimens examined in this study were borrowed from the following institutions: AMNH, American Museum of Natural History; FSCA, Florida State Collection of Arthropods; JTPC, J. T. Polhemus Collection; TAMU, Texas A & M University; USNM, National Museum of Natural History; SEMC, Snow Entomological Museum.

Characters

The data set consists primarily of male external morphological characters. Figure 4 illustrates the basic body plan of

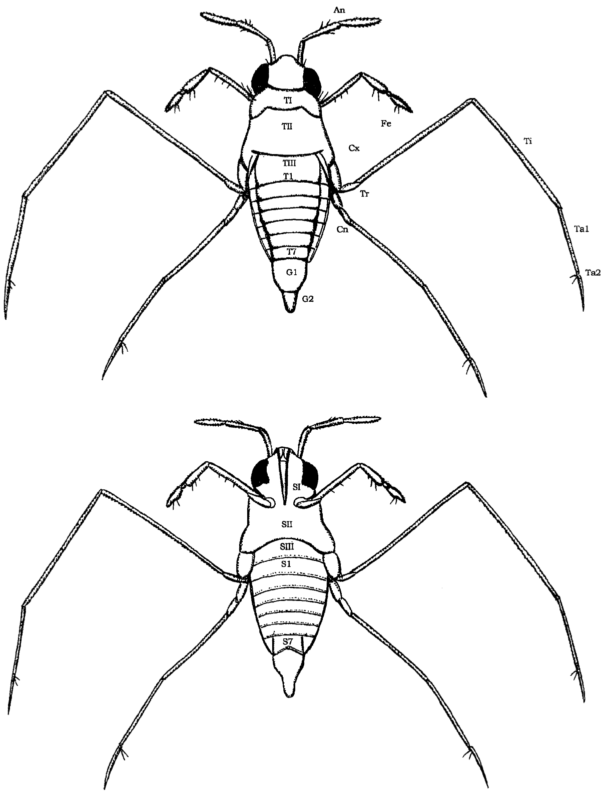

Fig. 4. The basic body plan of *Rheumatobates* as represented by the female of *R. rileyi*. Dorsal (top) and ventral (bottom) views, with selected structures labelled according to Andersen's (1982) terminology. An = antennae; Cn = connexivum or abdominal laterotergites; Cx = coxa; Fe = femur; G1 = genital segment 1; G2 = genital segment 2; SI, SII, SII = pro-, meso- and metasterno-pleura; S2, S7 = abdominal sterna; TI, TII, TII = pro-, meso- and metanota; T1, T7 = abdominal terga; Ta = tarsus; Ti = tibia; Tr = trochanter.

Rheumatobates as exemplified by the female of *R. rileyi*. Both dorsal and ventral views are illustrated, with selected structures labelled according to the terminology of Andersen (1982). Aspect is defined with the insect in its natural state. There are ninety male characters that primarily describe modification of the antennae, three pairs of legs and the abdominal and genital segments. There are ten female characters that describe colour, colour patterns and setal variation of the head, thorax, fore legs and the abdominal and genital segments. We searched intensively for interspecifically variable female characters, however few were found. Variable female characters were often non-discrete (e.g. body shape, relative sizes of structures), requiring further work to quantify accurately. One ecological character describing habitat and one life history character describing wing development are also included in the data set, for a total of 102 characters. Characters and character states are listed below with the corresponding data matrix in Appendix 1.

Characters were chosen and scored primarily through examination of alcohol-preserved specimens, as well as a small number of pinned specimens. Most characters were scored on three specimens per sex except in the few cases where multiple specimens were not available. We did not have males of *R. praeposterus* Bergroth and females of *R. creaseri* Hungerford, hence characters were scored from the literature (e.g. Bergroth, 1908; Hungerford, 1936). For one species, *R. creaseri*, where data for female characters such as coloration was unavailable, such characters were scored using males.

Male characters

Antenna

1. *Ventrolateral margin of segment 1*: (0) without a group of elongate setae; (1) with a group of elongate setae (Fig. 5A,B).
2. *Group of elongate setae on ventrolateral margin of segment 1*: (0) inapplicable; (1) few in number, hair-like, loosely grouped (Fig. 5A); (2) numerous, thicker, closely grouped (giving the appearance of a spine) (Fig. 5B).
3. *Ventromedial margin of segment 1*: (0) without a group of setae; (1) with a group of setae (Fig. 5 A,B).
4. *Group of setae on ventromedial margin of segment 1*: (0) inapplicable; (1) hair- or bristle-like setae only (Fig. 5A); (2) bristle-like and/or spine-like setae (Fig. 5B).
5. *Lateral margin of segment 1*: (0) without 2 stout spines; (1) with 2 stout spines (Fig. 5C).
6. *Base of segment 2*: (0) not distinctly expanded ventrally or constricted relative to apex; (1) with a distinct expansion ventrally (Fig. 5D); (2) distinctly constricted relative to apex (Fig. 5E,F).
7. *Ventral base of segment 2*: (0) without one or a group of hair- or bristle-like setae; (1) with one or a group of hair- or bristle-like setae (Fig. 5A,B).
8. *One or a group of setae on ventral base of segment 2*: (0) inapplicable; (1) short (Fig. 5B); (2) long (Fig. 5D).
9. *Lateral margin of segment 2*: (0) without at least one stout spine; (1) with at least one stout spine (Fig. 5C).
10. *Ventrolateral margin of segment 2*: (0) without one or 2 fine, long setae; (1) with one or 2 fine, long setae (Fig. 5G).
11. *Apicoventral margin of segment 3*: (0) without fossa; (1) with fossa (Fig. 5A,B).
12. *Fossa on apicoventral margin of segment 3*: (0) inapplicable; (1) basally pronounced (Fig. 5A); (2) medially pronounced (Fig. 5B).
13. *Segment 3 with apicoventral fossa*: (0) inapplicable; (1) somewhat basally pronounced (Fig. 5A); (2) significantly basally pronounced (Fig. 5D); (3) somewhat medially pronounced (Fig. 5B); (4) significantly medially pronounced.

14 *Length from base of segment 3 to apicoventral fossa*: (0) inapplicable; (1) short (Fig. 5D); (2) long (Fig. 5B).

15. *Dorsal margin of segment 3*: (0) not markedly concave or convex; (1) markedly concave (Fig. 5A); (2) markedly convex (Fig. 5F).

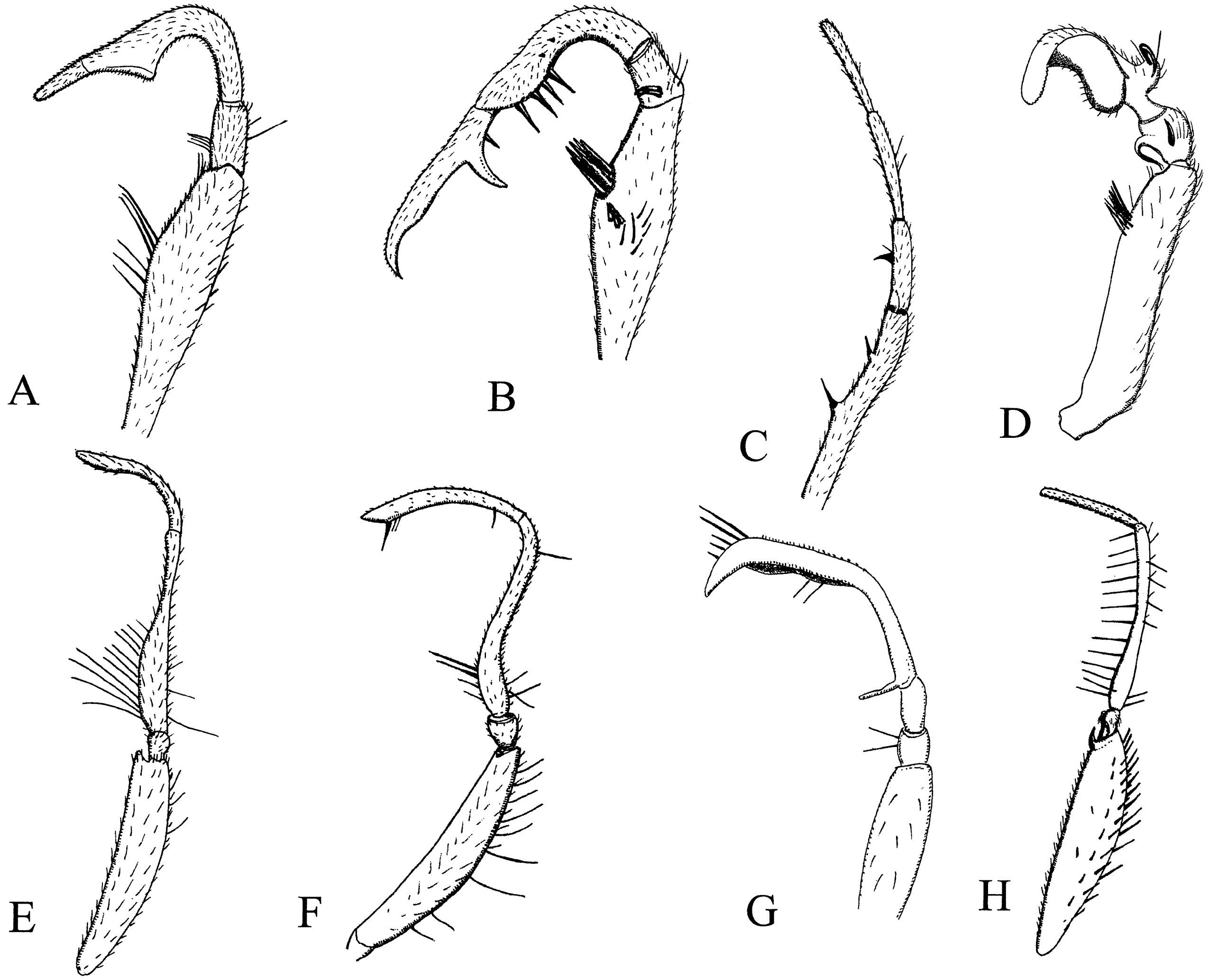

Fig. 5. Antennae (male). A, *Rheumatobates bergrothi* (lateral view); B, *R. rileyi* (ventromedial view, right antenna); C, *R. mangrovensis* (dorsal view, left antenna); D, *R. citatus* (ventromedial view, right antenna); E, *R. ornatus* (lateral view); F, *R. carvalhoi* (lateral view); G, *R. crassifemur crassifemur* (dorsal view, left antenna); H, *R. aestuarius* (lateral view).

16. *Segment 3 basally*: (0) not thickened dorsoventrally; (1) markedly wider than apex dorsoventrally (Fig. 5E,H).
17. *Apicomedial margin of segment 3*: (0) without a row of elongate setae; (1) with a row of elongate setae (Fig. 5B).
18. *Row of elongate setae on apicomedial margin of segment 3*: (0) inapplicable; (1) hair-like setae; (2) spine-like setae (Fig. 5B).
19. *Basoventral margin of segment 3*: (0) without long setae; (1) with long setae (Fig. 5E,F,H).
20. *Long setae on basoventral margin of segment 3*: (0) inapplicable; (1) not fused into a spine-like process; (2) fused into a spine-like process (Fig. 5F).
21. *Basomedial margin of segment 3*: (0) without a spine-like process; (1) with a spine-like process (formed by fused setae) (Fig. 5D).
22. *Lateral margin of segment 4*: (0) without subapical fold; (1) with subapical fold (Fig. 5G).
23. *Length between base of segment 4 and subapical fold*: (0) inapplicable; (1) short; (2) long (Fig. 5G).
24. *Curvature of segment 4*: (0) not curved ventrolaterally; (1) curved ventrolaterally (Fig. 5G).
25. *Base of segment 4*: (0) without an elongate lateral projection; (1) with an elongate lateral projection (Fig. 5G).
26. *Medial or ventral margin of segment 4*: (0) not denticulate; (1) denticulate (Fig. 5B,D).
27. *Denticulation on medial or ventral margin of segment 4*: (0) inapplicable; (1) basal or apical on segment (Fig. 5D); (2) on subapical hook (Fig. 5B).
28. *Apicodorsal margin of segment 4*: (0) without a row of setae; (1) with a row of stout setae (Fig. 5G).
29. *Basomedial margin of segment 4*: (0) without a single setae; (1) with a single hair-like or spine-like setae (Fig. 5B).

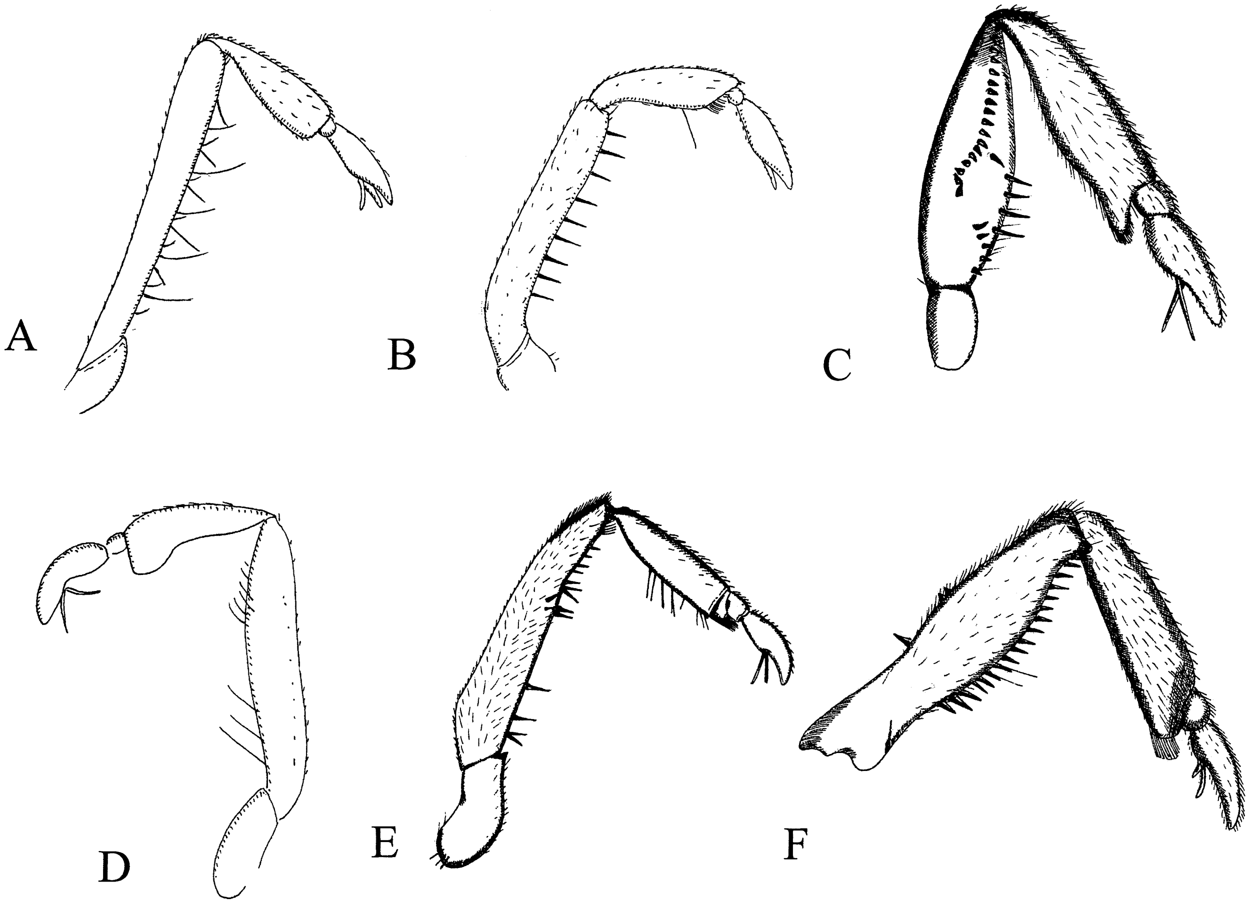

Fig. 6. Fore legs (male). A, *Rhagadotarsus anomalus* (medial view); B, *R. rileyi* (lateral view); C, *R. mangrovensis* (ventrolateral view); D, *R. crassifemur crassifemur* (medial view); E, *R. probolicornis* (lateral view); F, *R. mangrovensis* (lateral view).

30. *Apicoventral margin of segment 4*: (0) without a single stout setae; (1) with a single stout setae directed anteroventrally (Fig. 5F).

Fore leg

31. *Basoventral margin of trochanter*: (0) without a prominent rounded lobe; (1) with a prominent rounded lobe.
32. *Dorsobasal margin of femur*: (0) without a prominent tubercle; (1) with a prominent tubercle (see Polhemus & Cheng, 1976: Fig. 1c).
33. *Basoventral margin of femur*: (0) without a groove; (1) with a groove.
34. *Ventral margin of femur*: (0) with several irregular rows of hair-like setae (Fig. 6A); (1) with one row of evenly spaced setae (Fig. 6B); (2) with a relatively scattered pattern of variously lengthened bristle-like setae (see Polhemus & Cheng, 1976: Fig. 1c); (3) one or 2 rows of spines (Fig. 6C); (4) with 3 or 4 long hair-like setae basally (Fig. 6D); (5) with a markedly irregular pattern of variously sized and shaped setae (Fig. 6E); (6) with only one elongate apically directed setae; (7) with irregularly set spines and bristles (see Polhemus & Spangler, 1989: Fig. 5).
35. *Rows of spines on ventral margin of femur*: (0) inapplicable; (1) one row; (2) 2 rows (Fig. 6C).
36. *Scattered pattern of variously lengthened bristle-like setae on ventral margin of femur*: (0) inapplicable; (1) few in number; (2) numerous.
37. *Armature on dorsomedial margin of femur*: (0) without a tuft of bristle-like setae on basal half; (1) with a tuft of close-set partly fused bristle-like setae on basal half (Fig. 6F).
38. *Ventromedial margin of femur*: (0) without a group of closely set bristle-like setae; (1) with a group of closely set bristle-like setae (Fig. 6D).

Mid leg

39. *Femur*: (0) not significantly thickened apically; (1) significantly thickened on apical two-thirds (Fig. 7A); (2) significantly thickened on apical one-fifth (Fig. 7B).

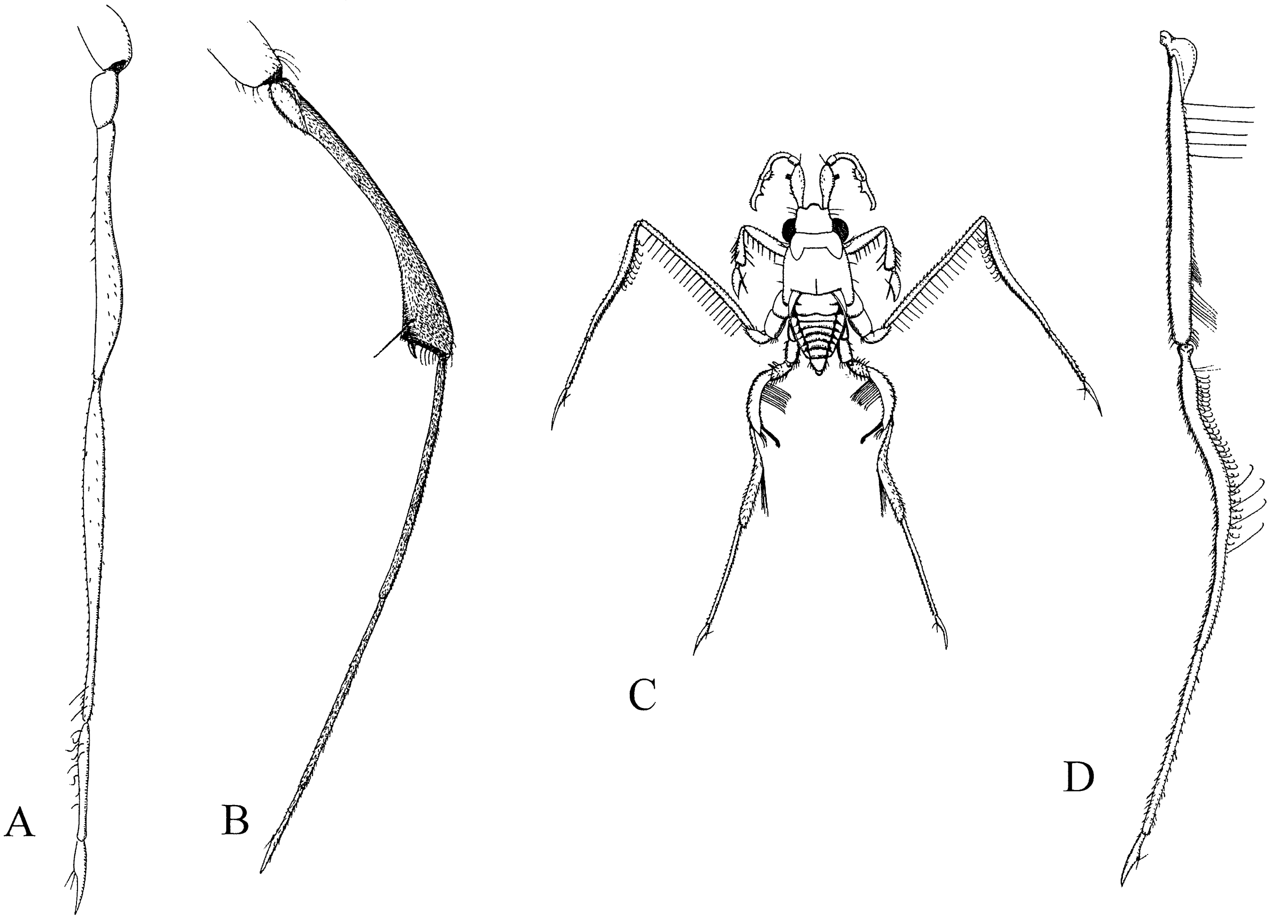

Fig. 7. Mid legs (male). A, *Rheumatobates crassifemur esakii* (dorsal view, right leg); B, *R. citatus* (dorsolateral view, right leg); C, *R. rileyi* (dorsal view); D, *R. bergrothi* (dorsal view, left leg).

40. *Thickening of apical two-thirds of femur*: (0) inapplicable; (1) significant; (2) very significant (Fig. 7A).
41. *Medial margin of femur*: (0) without long hair-like setae; (1) with long hair-like setae throughout its length (Fig. 7C); (2) with long hair-like setae only along basal one-fifth (Fig. 7D).
42. *Apex of femur*: (0) without a hook; (1) with a broadly flattened curved hook (Fig. 7B).
43. *Medial margin of tibia*: (0) without curled hair-like setae; (1) with dense, curled hair-like setae (Fig. 7C).
44. *Basomedial margin of mid tarsus 1*: (0) without a row of dense long hair-like setae; (1) with a row of dense long hair-like setae (Fig. 7A).

Hind leg

45. *Trochanter shape*: (0) not markedly thickened medially at base relative to apex; (1) markedly thickened medially at base relative to apex (Fig. 8A).
46. *Trochanter rotation*: (0) not rotated; (1) rotated such that lateral margin is positioned dorsally.
47. *Dorsomedial margin of trochanter*: (0) without a broad-edged projection; (1) with a broad-edged projection (Fig. 8B).
48. *Broad-edged projection on dorsomedial margin of trochanter*: (0) inapplicable; (1) small; (2) large (Fig. 8B).
49. *Medial margin of trochanter*: (0) without a row or tuft of hair-like setae; (1) with a row of long hair-like setae (Fig. 8C); (2) with a tuft of hair-like setae basally (Fig. 8A).
50. *Tuft of hair-like setae on basomedial margin of trochanter*: (0) inapplicable; (1) few in number, short; (2) many in number, long (Fig. 8A).
51. *Medial margin of trochanter*: (0) without a pronounced projection; (1) with a pronounced projection.
52. *Articulation between trochanter and femur*: (0) apex of trochanter joined to base of femur; (1) apex of trochanter joined to lateral base of femur (Fig. 8A).
53. *Curvature of femur*: (0) not bowed laterally; (1) bowed laterally (Fig. 8C,D).

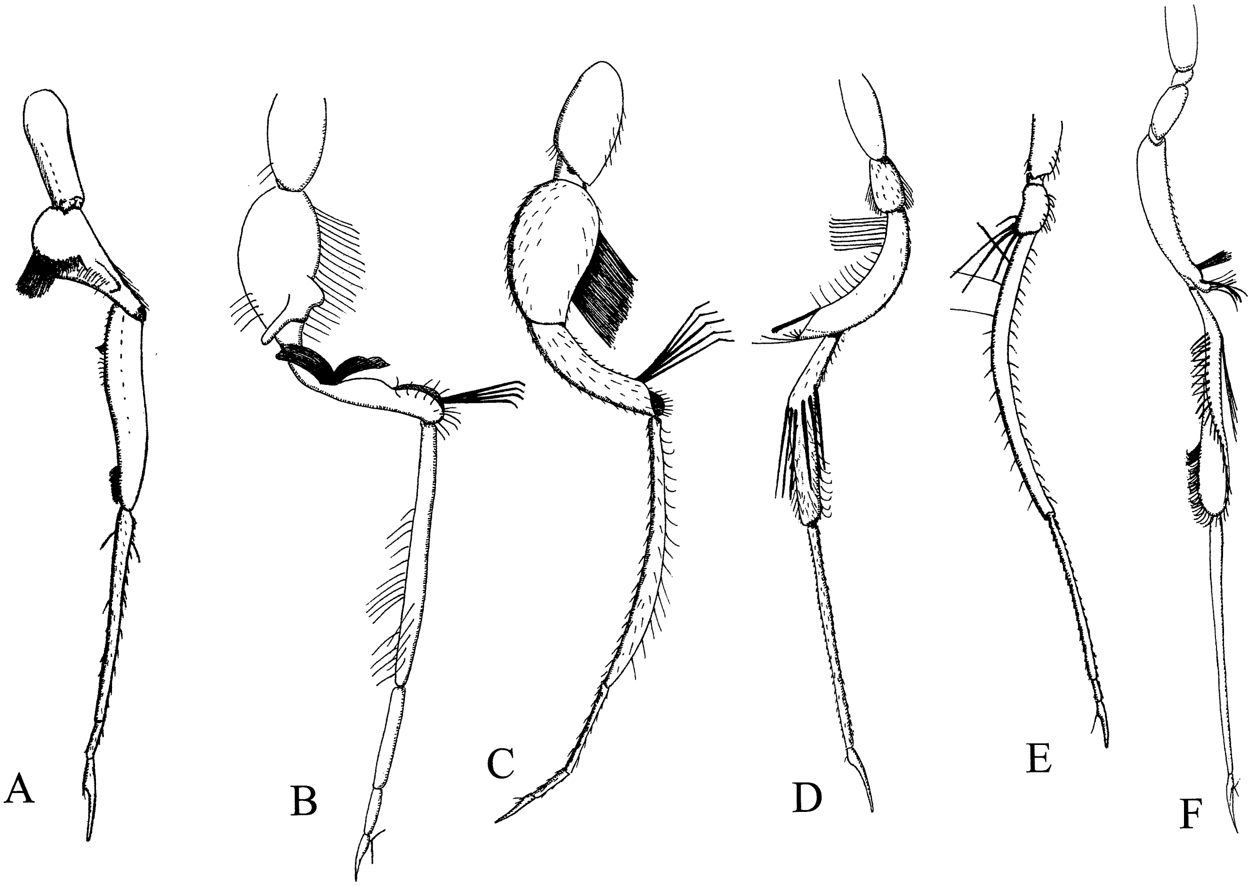

Fig. 8. Hind legs (male). A, *Rheumatobates crassifemur crassifemur* (dorsal view, right leg); B, *R. bergrothi* (dorsal view, left leg); C, *R. bergrothi* (ventral view, right leg); D, *R. rileyi* (dorsal view, right leg); E, *R. carvalhoi* (dorsal view, right leg); F, *R. trulliger* (dorsal view, left leg).

54. *Medial margin of femur*: (0) without a row or fringe of long hair-like setae along entire length or basal third; (1) with a row of widely spaced long hair-like setae along entire length (Fig. 8E); (2) with a fringe of long hair-like setae only on basal third (Fig. 8D).
55. *Ventromedial margin of femur*: (0) without a brush of stout setae within basal third; (1) with a brush of stout setae within basal third (Fig. 8A).
56. *Apicomedial margin of femur*: (0) without a projection comprised of stiff setae; (1) with a medially directed projection comprised of stiff setae (Fig. 8C,D).
57. *Projection comprised of stiff setae on apicomedial margin of femur*: (0) inapplicable; (1) short (Fig. 8D); (2) long (Fig. 8C).
58. *Apex of femur*: (0) without fan-like array of setae; (1) with fan-like array of setae (Fig. 8C,D).
59. *Fan-like array of setae at apex of femur*: (0) inapplicable; (1) short (Fig. 8C); (2) long (Fig. 8D).
60. *Dorsomedial margin of femur*: (0) without a flattened T-shaped structure; (1) with a flattened T-shaped structure (see Hungerford, 1954: Fig. 30, Pl. 15).
61. *Size of flattened T-shaped structure on dorsomedial margin of femur*: (0) inapplicable; (1) small; (2) large.
62. *Dorsomedial base of femur*: (0) without a row of stiff setae; (1) with a row of stiff setae (Fig. 8B).
63. *Dorsomedial apex of femur*: (0) without a fringe of setae; (1) with a fringe of setae (Fig. 8A).
64. *Articulation between femur and tibia*: (0) base of tibia joined to apex of femur; (1) base of tibia joined to femur subapically (Fig. 8C,D).
65. *Base of tibia joined to femur subapically*: (0) inapplicable; (1) somewhat subapically (Fig. 8C); (2) significantly subapically (Fig. 8D).
66. *Tibia shape*: (0) without a distinct bend in basal one-third; (1) with a distinct medial bend in basal one-third (Fig. 8D).
67. *Tibia*: (0) without a longitudinal concavity; (1) with a longitudinal concavity (Fig. 8F).
68. *Size of longitudinal concavity of tibia*: (0) inapplicable; (1) small; (2) large (Fig. 8F).
69. *Aspect of longitudinal concavity of tibia*: (0) inapplicable; (1) along dorsomedial margin; (2) along dorsolateral margin (Fig. 8F).

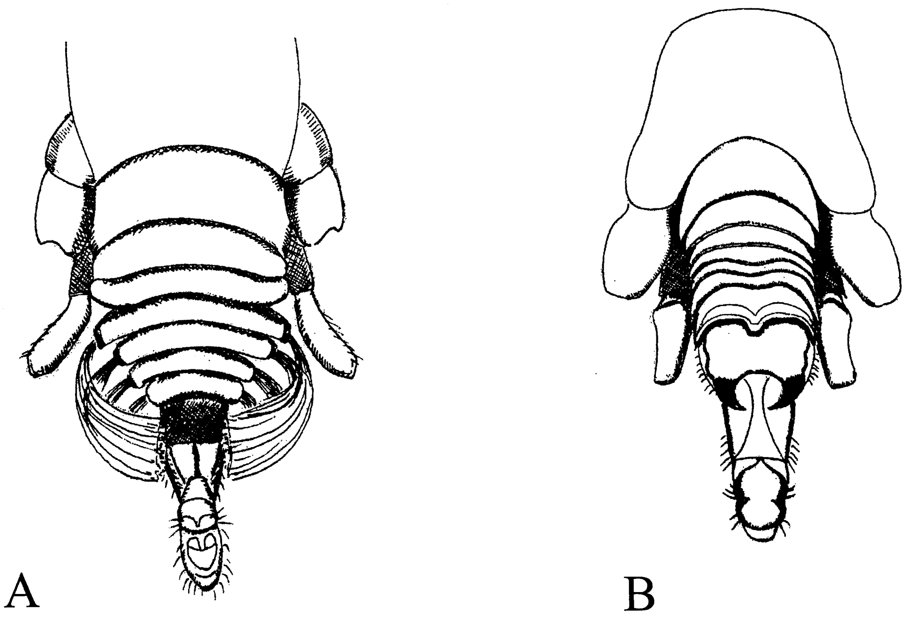

Fig. 9. Abdominal and genital segments (male). A, *Rheumatobates carvalhoi* (ventral view); B, *R. ornatus* (ventral view).

70. *Curled setae on ventromedial or ventrolateral margin of tibia*: (0) absent; (1) present (Fig. 8F).
71. *Fringe of setae on dorsomedial or dorsolateral margin of tibia*: (0) absent; (1) present (Fig. 8F).
72. *Base of tibia*: (0) without markedly elongate, closely approximated setae; (1) with markedly elongate, closely approximated, posteriorly directed setae (Fig. 8D,F).
73. *Medial margin of tibia*: (0) without long setae; (1) with several long, widely spaced, bristle-like setae (Fig. 8A).
74. *Ratio of tibia to tarsus 1*: (0) much less than 0.75 (Fig. 8C,E); (1) no less than 0.75 to slightly greater than 1.0 (Fig. 8D).

Thorax, abdomen and genitalia

75. *Metasternum*: (0) not concave; (1) concave.
76. *Abdominal sterna*: (0) not concave; (1) concave (Fig. 9A).
77. *Concavity of abdominal sternites 5–7*: (0) inapplicable; (1) shallow (Fig. 9A); (2) deep.
78. *Lateral margins of at least one of the abdominal sternites*: (0) not produced; (1) produced (Fig. 9A).
79. *Lateral margins of abdominal sternites*: (0) without one or several tufts of extremely long stout setae; (1) with one or several tufts of extremely long stout setae that arch under abdominal venter (Fig. 9A; and see Polhemus & Manzano, 1992: Fig. 20.56).
80. *One or several tufts of extremely long stout setae on lateral margins of abdominal sternites*: (0) inapplicable; (1) loosely clumped (Fig. 9A); (2) tightly clumped (see Polhemus & Manzano, 1992: Fig. 20.56).
81. *Position of dominant loosely clumped setal tufts on lateral margin of abdominal sternites*: (0) inapplicable; (1) on sternites 6 and 7; (2) on sternites 5 and 6 (Fig. 9A).
82. *Anterior margin of abdominal sternite 1*: (0) nearly straight; (1) bowed medially (see Polhemus, 1975: Fig. 1A).
83. *Abdominal sternite 4*: (0) without a distinct protuberance; (1) with a distinct protuberance (see Polhemus, 1975: Fig. 1A).
84. *Anterior margin of abdominal sternites 2–6*: (0) not markedly overlapped by posterior margin of preceding sternite; (1) markedly overlapped by posterior margin of preceding sternite (Fig. 9B).
85. *Abdominal sternites 6 and 7*: (0) longitudinally furrowed (see Polhemus & Karunaratne, 1993: Fig. 2); (1) not longitudinally furrowed.
86. *Vestiture of abdominal sternum 7*: (0) without longitudinal rows of hair-like setae; (1) with several longitudinal rows of hair-like setae (see Cheng & Lewin, 1971: Fig. 5).
87. *Connexival segments*: (0) evident dorsally on segments 1–7; (1) not evident dorsally posteriorly (see Polhemus & Manzano, 1992: Fig. 20.56).
88. *Genital segments*: (0) not arched ventrally; (1) arched ventrally (see Polhemus & Manzano, 1992: Fig. 20.56).
89. *Venter of genital segment 1*: (0) with a deep longitudinal furrow (see Polhemus & Karunaratne, 1993: Fig. 2); (1) with a shallow, broad furrow (Fig. 9A,B); (2) entire segment deeply excavated, appearing cup-like (see Polhemus & Spangler, 1989: Fig. 4); (3) not significantly modified.
90. *Lateral margins of venter, of genital segment 1*: (0) not raised; (1) raised (Fig. 9A).

Female characters

Colour and coloration

91. *Marking on the posterior margin of head*: (0) chevron shaped (see Esaki, 1926: Fig. 9a); (1) U-shaped; (2) broad longitudinal band on either side of midline, with apex curved laterally (see Drake & Harris, 1942: Fig. 1a); (3) crescent-shaped (see China, 1943: Fig. 3); (4) concolorous with rest of head.
92. *Coloration on lateral margin of pronotum*: (0) entirely dark; (1) entirely light; (2) contrasting light stripe on dark background (see China, 1943: Fig. 2a).
93. *Colour of mesosternum*: (0) dark; (1) light.
94. *Coloration above mesocoxae*: (0) entirely dark; (1) lightly pigmented area forming part of longitudinal stripe on mesopleurae (see Cheng & Lewin, 1971: Fig. 2); (2) entirely light; (3) with light spot (see China, 1943: Fig. 2a).

Setation

95. *Apex of antennal segment 4*: (0) without a bristle-like setae; (1) with a bristle-like setae.
96. *Fore femur with thickened hair-like setae*: (0) absent; (1) present.
97. *Setae on mesopleurae*: (0) with fine hair-like setae or setae absent; (1) with several or many thicker hair-like setae.
98. *Posterior margin of mesonotum*: (0) without a patch of setae medially; (1) with a patch of hair-like setae medially.
99. *Vestiture of connexival segments*: (0) inconspicuous; (1) with several to many thickened hair-like setae.
100. *Dorsum of genital segment 1*: (0) with only a few bristle-like setae, or setae absent; (1) with thicker, longer and more numerous setae on lateral and posterior margin; (2) with thicker, longer and more numerous setae on anterior margin.

Ecological character

101. *Habitat*: (0) strictly freshwater or primarily found in freshwater and only secondarily found in marine habitats; (1) strictly marine.

Life history character

102. *Wing morph*: (0) both macropterous and apterous morphs known; (1) only apterous morphs known, macropterous unknown.

Character coding

Unknown states for characters were coded as missing using the symbol '?'; inapplicable character states (e.g. states that are impossible to assign to a taxon) were scored as another state, 'inapplicable', as recommended by Maddison (1993). This is one of many ways to deal with inapplicable character states. To examine the underlying influence of inapplicable state characters scored in this fashion, we subsequently re-analysed the data set excluding them.

A similar issue concerns the subdivision of interspecific variation in modification of the antenna; specifically the recognition of many separate antennal characters. The reasoning behind using this approach was the presence of so much interspecific variation within each segment of the antennae, even among otherwise very similar species. We consolidate characters into a single, unordered, multistate character only if their states were mutually exclusive. For example, in character 15, dorsal margin of antennal segment 3, the states markedly concave or convex are mutually exclusive, and thus they were included in one character. Furthermore, characters and character states are treated equally in cladistic analysis, therefore our method of coding characters should not affect the results.

Cladistic analysis

Phylogenetic reconstruction was performed using the method of maximum parsimony with the general heuristic search procedure in PAUP 3.1.1 (Swofford, 1993). All characters were first considered unordered and unweighted. Successive approximations by reweighting characters according to their maximum rescaled consistency index (base value = 1000) was used to reduce the number of equally parsimonious cladograms (EPCs). A strict consensus cladogram was used to summarize concordance among multiple equally parsimonious cladograms (MEPCs). The ACCTRAN option in PAUP 3.1.1 was used to optimize characters on the phylogeny to investigate support for nodes. MacClade 3.0 (Maddison & Maddison, 1992) was used to examine and choose amongst MEPCs. Character polarities were determined with reference to the outgroup *Rhagadotarsus*.

Three separate phylogenetic analyses were performed. First, we ran an analysis including all characters. Second, in order to examine the effect of coding inapplicable character states as described above, we re-analysed the data set excluding them. When inapplicable state characters were excluded, seventy-nine of 102 characters remained. Second, in order to address the concern over the use of characters to be optimized on the phylogeny, those describing modification of the antennae and hind legs, we re-analysed the data set excluding them. When characters describing modification of the antennae and hind legs were excluded (chs 1–30; 45–74), forty-three characters remained.

Results

All characters included

The complete data set produced 13 550 EPCs of length 200 steps (CI = 0.74, RI = 0.91, RC = 0.67). A strict

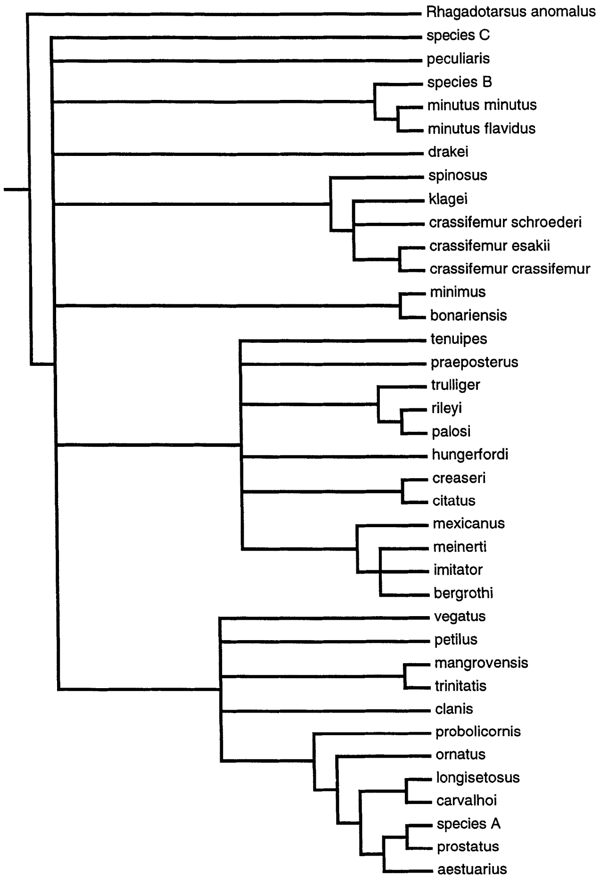

Fig. 10. A strict consensus cladogram of the 13 550 EPCs found for the complete data set, including *R. peculiaris*. Length = 230 steps, CI = 0.64, RI = 0.85 and RC = 0.55.

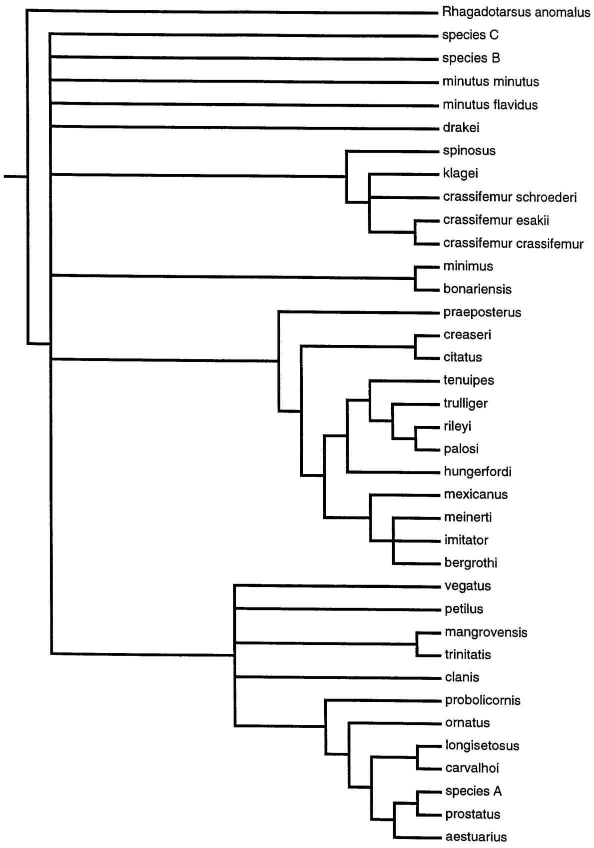

Fig. 11. A strict consensus cladogram of the fifty-six EPCs found for the complete data set, excluding *R. peculiaris*. Length = 215 steps, CI = 0.68, RI = 0.87 and RC = 0.59.

consensus cladogram was used to summarize information among rival cladograms (length = 230 steps, CI = 0.64, RI = 0.85, RC = 0.55; Fig. 10). After examining some of the 13 550 EPCs it was noted that *R. peculiaris* Polhemus & Spangler was a particularly problematical taxon in that it was placed variously throughout the phylogeny. This taxon is indeed peculiar; it is primarily defined by autapomorphies, sharing almost no characteristics with other taxa in the genus. Excluding this taxon from the analysis reduced the number of EPCs from 13 550 to fifty-six (length = 196 steps, CI = 0.75, RI = 0.91, RC = 0.68). Given the major effect *R. peculiaris* has on the number of EPCs, it was excluded from this and all subsequent analyses. A strict consensus cladogram was used to summarize information common to the fifty-six EPTs (Fig. 11). The consensus cladogram length was 215 steps (CI = 0.68, RI = 0.87, RC = 0.59). Successive approximations reduced the number of EPCs to four. The strict consensus cladogram of these four EPCs was 196 steps in length (CI = 0.75, RI = 0.91, RC = 0.68; Fig. 12). There was good resolution at all levels with only two unresolved areas; however, we chose one of the four EPCs to facilitate further discussion (Fig. 13). We chose the cladogram in which the relationships among the *trinitatis-clanis* and *probolicornis-aestuarius* clades and *R. petilus* Drake & Hottes remained unresolved, *R. crassifemur schroederi* was resolved the sister species of the *crassifemur esakii-crassifemur crassifemur* clade and *R. klagei* Schroeder was resolved as the sister species of the latter. There was no support for the resolution of the relationships among the first group. In the second group, we chose the resolved over the unresolved arrangement because two characters supported this choice. The thickening of the apical two-thirds of the mid femur is much less significant in *R. klagei* than in the three *R. crassifemur* subspecies (ch. 40), and the basal tuft of setae on the medial margin of the hind trochanter is smaller and shorter in *R. klagei* than in the three *R. crassifemur* subspecies (ch. 51).

Each node on the phylogeny in Fig. 13 is numbered, and numbers at the internodes indicate the number of synapomorphies supporting each node. Numbers in parentheses indicate the number of synapomorphies that are uniquely derived. Character state changes at each node are summarized in Appendix 2, with homoplasious changes indicated.

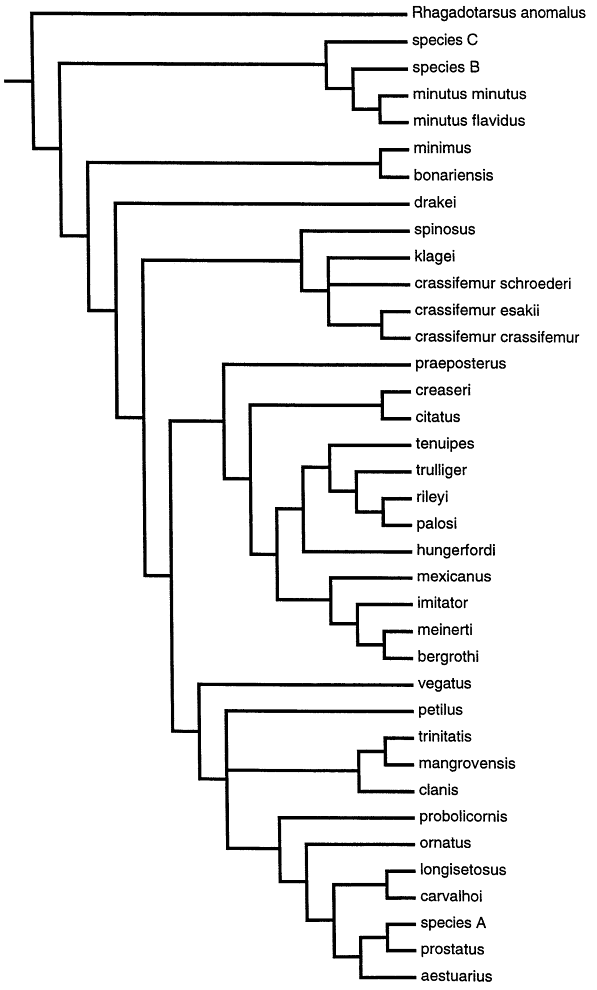

Fig. 12. A strict consensus cladogram of the four EPCs found for the complete data set, excluding *R. peculiaris,* after successive reweighting of the characters. Length = 196 steps, CI = 0.75, RI = 0.91 and RC = 0.68.

Inapplicable state characters excluded

This data set produced 1464 equally parsimonious cladograms of length 143 steps (CI = 0.69, RI = 0.90, RC = 0.62). A strict consensus cladogram was used to summarize information common to the MEPCs (Fig. 14). The consensus cladogram was 177 steps (CI = 0.56, RI = 0.82, RC = 0.46). When inapplicable state characters were excluded from the analysis, the resulting consensus cladogram was similar to the consensus cladogram when they were included, in that all the resolved major clades were the same. Differences of minor significance include much less resolution of the *tenuipes-bergrothi* clade, slightly less resolution of the species A-*aestuarius* clade, and slightly more resolution of *R. vegatus* Drake & Harris, *R. clanis* Drake & Harris, *R. petilus* and the *trinitatis-mangrovensis* clade (cf. Figs 14 and 11). Note also that the statistics for both of these cladograms are similar, with only a slightly lower CI, RI and RC in the partial data set.

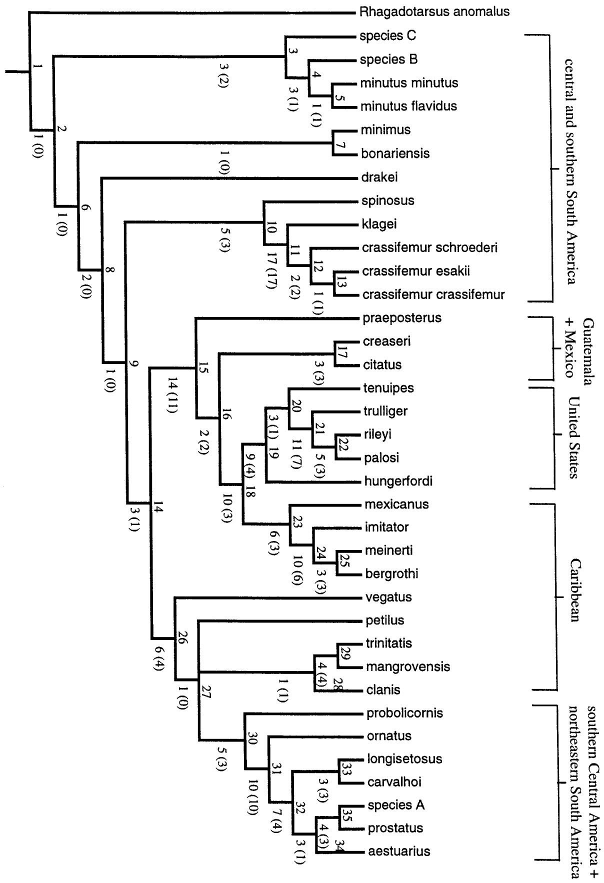

Fig. 13. The preferred phylogeny of the four EPCs found for the complete data set, excluding *R. peculiaris*, after successive reweighting of the characters. Length = 196 steps, CI = 0.75, RI = 0.91 and RC = 0.68. Nodes are indicated by numbers for reference to the text and Appendix 2. Numbers to the right of the internodes indicate the number of synapomorphies supporting each node and the numbers in parentheses indicate the number of synapomorphies that are uniquely derived. Additional support for the preferred phylogeny includes biogeographical evidence.

Male antennal and hind leg characters excluded

This data set produced 390 EPCs of length 86 steps (CI = 0.72, RI = 0.90, RC = 0.65). The strict consensus cladogram (Fig. 15) was 107 steps (CI = 0.58, RI = 0.81, RC = 0.47). When characters describing modification of the antennae and hind legs were excluded from the analysis, the resulting consensus cladogram was similar to that when they were both included, in that all of the resolved major clades were the same, except for the *trulliger-bergrothi* clade, which no longer includes *R. praeposterus*. Differences of minor significance include the resolution of the clade including species C, species B, *R. minutus minutus* Hungerford and *R. minutus flavidus* (relationships among these taxa were unresolved when these characters were included), resolution of the *spinosus-crassifemur crassifemur* clade as basal to the rest of taxa (all basal

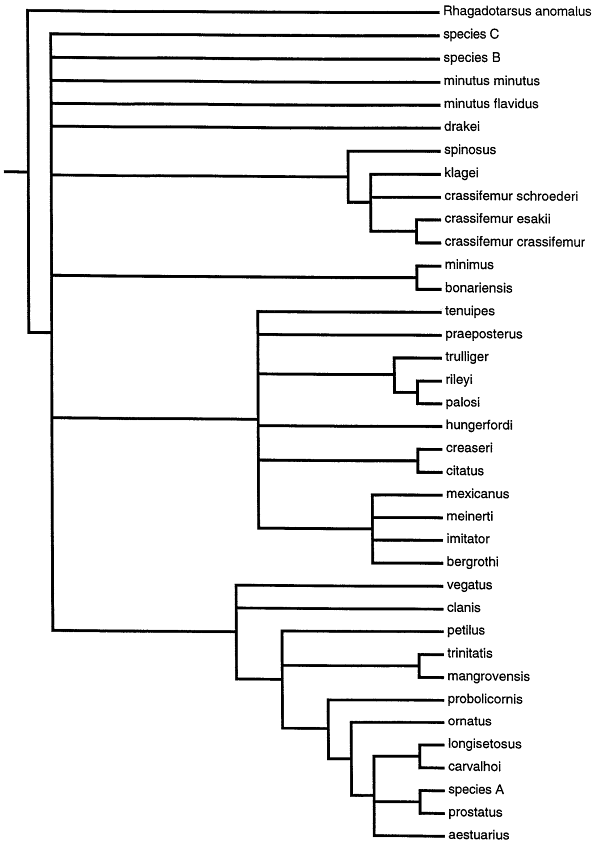

Fig. 14. A strict consensus cladogram of the 1464 EPCs found for the complete data set, excluding inapplicable state characters and *R. peculiaris*. Length = 177 steps, CI = 0.56, RI = 0.82 and RC = 0.46.

relationships were unresolved when these characters were included), slightly less resolution of the aforementioned clade and much less resolution of the *tenuipes-bergrothi* clade, when these characters were excluded (cf. Figs 11 and 15). Note also that the statistics for both of these cladograms are similar, with only a slightly lower CI, RI and RC in the partial data set.

Discussion

The preferred phylogeny of genus *Rheumatobates* is 196 steps in length (CI = 0.75, RI = 0.91, RC = 0.68). This phylogeny was chosen from the four EPCs found after successive reweighting of the characters. There was good resolution at all levels of the phylogeny. When characters describing modification of antennae and hind legs were excluded in a separate analysis, the resultant consensus the cladogram was similar to the consensus cladogram when they were both included.

Support for the preferred phylogeny

Cladogram statistics. The preferred phylogeny was 196 steps in length (CI = 0.75, RI = 0.91, RC = 0.68). The CI and RC are reasonably high, indicating that the majority of characters used to reconstruct this cladogram are not homoplasious.

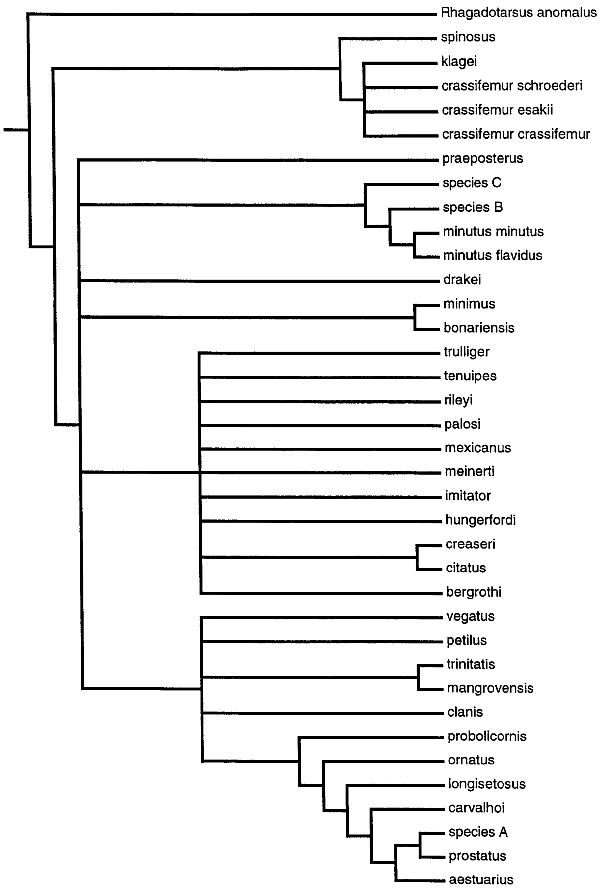

Fig. 15. A strict consensus cladogram of the 390 EPCs found for the complete data set, excluding male antennal and hind legs characters and *R. peculiaris*. Length = 107 steps, CI = 0.58, RI = 0.81 and RC = 0.47.

Number of synapomorphies. The nodal support for most of the major clades was high (see Fig. 13; Appendix 2); the number of synapomorphies ranged from one to fourteen among these clades, but the majority were supported by at least six synapomorphies. In contrast, basal relationships were weakly supported, with only one to three synapomorphies at each basal node. Furthermore, cladogram length was only increased from one to four steps when the major clades involved in these weakly supported basal relationships (e.g. the species C-*minutus flavidus*, *minimus-bonariensis, spinosus-crassifemur crassifemur*, *praeposterus-bergrothi* and *vegatus-aestuarius* clades, and *R. drakei*), were moved from their current position in the phylogeny to the following positions: (node 1–2), (node 2–6), (node 6–8), (node 8–9) and (node 9–14). Moreover, cladogram length was not increased when the relationships among these major clades were collapsed together. Finally, most of the relationships within the major clades (e.g. terminal relationships) were moderately to strongly supported.

Phylogenetic reliability and information content of different kinds of characters. Most of the major clades were supported by multiple uniquely derived synapomorphies. Moreover, they are defined primarily by characters describing the presence/absence of a structure, which are likely to be more phylogenetically reliable than those than describing only variation within a pre-existing structure (e.g. inapplicable state characters). The exceptions are the *minimus-bonariensis* and *petilus-aestuarius* clades, which are each supported by only one synapomorphy, neither of which are uniquely derived.

The major clade *vegatus-aestuarius* is defined by characters describing habitat (ch. 101) and wing morph (ch. 102); members of this clade (node 14–26) live in a marine habitat and consist only of the apterous form, whereas all species below this node occur in freshwater habitats and are found in both macropterous and apterous forms. These characters are likely to be particularly phylogenetically reliable because changes from one state to another, i.e. a shift from a freshwater to marine habitat and from being both macropterous and apterous to only apterous, suggest fundamental changes in the organism. In contrast to this view, Andersen (1982) suggested that the transition from freshwater habitats to estuarine or intertidal habitats has probably occurred several times in genus *Rheumatobates*, both along the Californian Gulf and Pacific Coast of Central America, and in the Caribbean Sea. However, when we ran the analysis again excluding these two characters, the resulting strict consensus cladogram did not differ from the consensus cladogram when they were included. Thus, the *vegatus-aestuarius* clade is supported even in the absence of these characters. Four other synapomorphies that support this clade (34(3), 91(3), 92(2), 100 (1)), which describe ventral armature of the male fore femur, and shape of markings on the posterior margin of the head, coloration on the lateral margins of the pronotum and setation on the first genital segment in females, seem unlikely to be correlated with habitat or wing morph. Therefore, the transition to marine habitat appears much more conservative than suggested by Andersen (1982).

Unlike the major clades, the basal dichotomies were each defined by only one to three homoplasious characters. The dearth of characters resolving basal relationships can be attributed to the fact that male external morphology has evolved so rapidly that the early phylogenetic signal has been obscured. At the other extreme, female external morphology has evolved so conservatively that the phylogenetic signal was very weak.

Terminal relationships were partially resolved by characters describing variation within a pre-existing structure, e.g. inapplicable state characters, which are likely to be less phylogenetically reliable than those describing the presence/absence of a structure. However, these characters proved to be phylogenetically reliable and informative; only five of the twenty-three inapplicable state characters were homoplasious. Furthermore, when these inapplicable state characters were excluded from the analysis, the resulting consensus cladogram did not differ substantially, in that all the resolved major clades were the same.

Additional support for the phylogeny

Additional support for the phylogeny includes biogeographical evidence (Fig. 13): the *probolicornis-aestuarius* clade is found in southern Central America and north-eastern South America (except for *R. aestuarius* Polhemus, which has been collected only in Mexico) and is restricted to the Pacific Ocean; *R. vegatus, R. petilus* and the *trinitatis-clanis* clade are found in the Caribbean (except for *R. petilus*, which has been collected only in Mexico); the *mexicanus-bergrothi* clade is also found in the Caribbean (except for *R. mexicanus* Drake & Hottes, which has been collected only in Honduras and Mexico); the *tenuipes-hungerfordi* clade are located primarily in the United States; *R. praeposterus* and the *creaseri-citatus* clade are found in Guatemala and Mexico; the *spinosus-crassifemur crassifemur,* species C-*minutus flavidus* and *minimus-bonariensis* clades, and *R. drakei* are all found in central and southern South America (note that *R. minutus minutus* has been collected in Peru but occurs predominantly in Central America) (Polhemus & Westlake, unpublished).

Other promising characters

The preferred phylogeny is preliminary but will serve as a working hypothesis of the evolutionary relationships within *Rheumatobates*. More work is required to find additional characters that address, in particular, the weakly resolved basal relationships. An area, formally unexplored in this study, that promises to yield such additional characters is a detailed internal examination of the female and male genitalic structures, specifically the gonapophyses and gynatrial complex of females and the shafts and plates of the endosoma of males (Schroeder, 1931; Matsuda, 1960; Andersen, 1982).

There is evidence of promising characters in the gynatrial complexes of Rhagadotarsinae. The gynatrial structures appear to be completely different in the two genera of this subfamily, *Rheumatobates* and *Rhagadotarsus*, and appear to be apomorphic among Gerridae (Andersen, 1982). Sperm cells are received and stored by the female in this specialized part of its genital tract (Andersen, 1982). *Rheumatobates* has a small gynatrial sac which ends in an extremely long spermathecal tube (Andersen, 1982: Fig. 471). A long spermathecal tube suggests high last male sperm precedence (e.g. Spence & Andersen, 1994), and thus some potential for female control over paternity. It would be worthwhile examining whether the length of this spermathecal tube varies interspecifically. This tube is terminated by a distinct bulb-like structure (Andersen, 1982). Andersen (1982) suggests that the development of a spermathecal bulb in *Rheumatobates* is probably secondary in Gerridae. Andersen (1982) examined only three species (*R. bergrothi* Meinert, *R. clanis* and *R. rileyi*) of genus *Rheumatobates* in his determination of the presence of this ‘spermathecal bulb’, and it would be worthwhile examining whether the presence/absence of this structure varies interspecifically. These characters may prove useful in independently testing relationships suggested primarily by male modification.

The vesical sclerites of the male genitalia, which are located in the distal part of the inflated phallus, appear to be of phylogenetic importance in *Rheumatobates*. Schroeder (1931) dissected the genitalia of four *Rheumatobates* species and found that in *R. trulliger* Bergroth, *R. hungerfordi* Wiley and *R. palosi* Blatchley the ventral shaft terminates in a long slender coiled thread, whereas in *R. klagei* it does not. The ventral shaft also terminates in a long slender coiled thread in *R. mangrovensis* China and *R. trinitatis* China (China, 1943), *R. vegatus* (Herring, 1949) and *R. rileyi* (Westlake, personal observation), while it does not in *R. crassifemur crassifemur* and the outgroup *Rhagadotarsus kraepelini* (Hungerford & Matsuda, 1960). Furthermore, Herring (1949) noted that the dorsal and ventral shafts exist as two separate pieces in *R. vegatus*, whereas in Schroeder's (1931) work the shafts are completely fused so that no joint is perceptible in the species studied. Finally, China (1943) erected the new genus, *Hynesia*, for the two species now known as *R. mangrovensis* and *R. trinitatis*, based on the presence of a distinct bridge-like structure surrounding the dorsal shaft of the vesica, which he proposed was absent in *Rheumatobates* species which had otherwise similar genitalia. But Hungerford (1954) synonymized this genus with *Rheumatobates* when he discovered that nine species with unmodified hind legs and seven species with unmodified antennae in *Rheumatobates* have this structure present. Unfortunately, he did not state which species, but this could be determined by the process of elimination and examination of some specimens. Interestingly, these internal sclerites probably play an important role during the insertion of the male organ into the female genital tract (Andersen, 1982).

Taxonomic verses phylogenetic relationships

The taxonomically recognized 'unmodified species group' was defined by the absence of modification of the antennae and hind legs in males (e.g. Herring, 1949; Drake & Hottes, 1951). In Hungerford (1954), this 'unmodified species group' included *R. minutus minutus, R. minutus flavidus, R. minimus* Drake, *R. bonariensis* Bergroth, *R. drakei* Hungerford, *R. clanis, R. vegatus* and *R. petilus.*

Most notably, our phylogenetic analysis split the 'unmodified species group' of taxonomists into four major clades (Fig. 13). *Rheumatobates minutus flavidus*, *R. minutus minutus*, species B and species C (these two species are both unmodified) are grouped together; *R. minimus* and *R. bonariensis* are grouped together; *R. drakei* is grouped with the *spinosus-aestuarius* clade; *R. vegatus*, *R. petilus* and *R. clanis* are grouped with the *probolicornis-aestuarius* clade. A monophyletic 'unmodified species group' is not supported in the phylogenetic analysis because it was defined by the absence of modifications in the antennae and hind legs in males, both of which represent the plesiomorphic state. Female characters describing colour and colouration (chs 91–94) and setation (chs 96, 97, 99–100), male characters describing modification of the abdominal and genital segments (chs 85, 89) and fore femur (ch. 34) and the two characters describing habitat and wing morph (chs 101, 102) are particularly useful in disbanding this 'unmodified species group'. Imposing monophyly on the 'unmodified species group' was not parsimonious because this arrangement increased the cladogram length by almost 6% (from 196 to 207 steps). Thus, the general taxonomic assumption that unmodified and modified species form two monophyletic groups is not supported by the present study.

However, traditionally recognized 'subgroups' within the modified species were largely upheld in the phylogenetic analysis, as discussed briefly below (Fig. 13). Polhemus & Manzano (1992) assigned four species (*R. aestuarius, R. carvalhoi* Drake & Harris, *R. longisetosus* Polhemus & Manzano and *R. prostatus* Polhemus) to the *aestuarius* group. They also noted that *R. carvalhoi* has been found together with *R. probolicornis* Polhemus & Manzano and that the habitat and behaviour of *R. ornatus* Polhemus & Cheng was similar to that of *R. aestuarius*. Similarly, these four species and species A were grouped together. *Rheumatobates probolicornis* and *R. ornatus* were grouped with this clade as previously implied. *Rheumatobates imitator* Uhler, *R. bergrothi, R. mexicanus* and *R. meinerti* Schroeder have been closely allied taxonomically (Meinert, 1895; Schroeder, 1931; Hungerford, 1954; Spangler *et al*., 1985). Similarly, these four species were grouped as a clade. *Rheumatobates tenuipes* Meinert, *R. rileyi*, *R. palosi*, *R. hungerfordi* and *R. trulliger* have been closely allied taxonomically (Riley, 1893; Wiley, 1923; Blatchley, 1926; Schroeder, 1931; Hungerford, 1954). Similarly, these five species were grouped as a clade. *Rheumatobates praeposterus*, *R. creaseri* and *R. citatus* Drake & Hottes were described as showing close taxonomic relationships (Schroeder, 1931; Hungerford, 1936; Drake & Hottes, 1951; Hungerford, 1954). Similarly, *Rheumatobates creaseri* and *R. citatus* were grouped as sister species and these two species and *R. praeposterus* were grouped with the *tenuipes-bergrothi* clade. Hungerford (1954) stated that the three *crassifemur* subspecies and *R. klagei* formed a distinct group in the genus. He also compared *R. spinosus* Hungerford with this group. Similarly, the three *R. crassifemur* subspecies and *R. klagei* were grouped as a clade and *R. spinosus* was grouped with this clade.

Although traditionally recognized modified species 'subgroups' were largely upheld in the phylogenetic analysis, there was little previous attempt to resolve relationships among the 'subgroups'. The phylogenetic analysis suggested the following groupings not previously recognized by taxonomists (Fig. 13): (1) *R. vegatus, R. petilus* and the *trinitatis-clanis* clade were grouped with the *probolicornis-aestuarius* clade; (2) the *tenuipes-palosi* clade was grouped with the *mexicanus-bergrothi* clade; (3) *R. praeposterus* and the *creaseri-citatus* clade were grouped with the *tenuipes-bergrothi* clade; (4) the *praeposterus-bergrothi* clade was grouped with the *vegatus-aestuarius* clade; (5) the *spinosus-crassifemur crassifemur* clade was grouped with the *praeposterus-aestuarius* clade; (6) *R. drakei* was grouped with the *spinosus-aestuarius* clade; (7) the *minimus-bonariensis* clade was grouped with the *drakei-aestuarius* clade; and finally, (8) the species C-*minutus flavidus* clade was grouped with the *minimus-aestuarius* clade. Thus, the phylogenetic analysis suggests several major clades and relationships among these clades, that were not previously recognized by taxonomists.

A species that was excluded from the analysis but warrants brief discussion is *R. peculiaris*. This species was excluded because of its effect on the number of EPCs. Its removal decreased the number of EPCs from 13 550 to fifty-six. In the strict consensus of the original 13 550 EPCs (Fig. 10), the relationship of *R. peculiaris* with the other species is unresolved. Polhemus & Spangler (1989) suggest that this species vaguely resembles *R. klagei*, but also note that most of its characteristics are unique and diagnostic, as we have concluded.

Combined data set excluding antennal and hind leg characters

The acceptability of using the same set of characters to both estimate a phylogeny and to map on the phylogeny for the purpose of examining evolutionary hypotheses remains a contentious issue (Swofford & Maddison, 1992). Many have vigorously argued that this is tautological, e.g. Coddington (1988) and Brooks & McLennan (1991). Coddington (1988) stated ‘to avoid circularity, that [cladistic] structure should not be inferred from the characters involved in the hypothesis of adaptation’. Swofford & Maddison (1992) suggest that such concerns are overemphasized and stress that what is important is that the phylogeny be estimated as accurately as possible. They propose that if these characters can make a useful contribution toward estimating the phylogeny then they should be included. Steps can then be taken to investigate the extent of any biases introduced (Swofford & Maddison, 1992). A similar proscription has subsequently been given by Brooks & McLennan (1994).

We have used characters describing modification of the antennae and hind legs in males in reconstructing the phylogeny, and wish to use this phylogeny to study the evolution of these characters. To test the phylogenetic reliability and information content of these characters and their effect on the reconstructed phylogeny (and ultimately their optimization), we performed a separate analysis excluding them as recommended by Swofford & Maddison (1992). When these characters are excluded from the analysis, the resulting consensus cladogram was similar to the consensus cladogram when they were both included, in that all but one of the resolved major clades were the same. Thus, the exclusion of characters describing modification of the antennae and hind legs did not substantially change the resolved topology of the reconstructed phylogeny. These characters appear to be phylogenetically informative and reliable. Furthermore, characters such as habitat, wing morph and some of the female colour, coloration and setation characters did not conflict with clades defined by these characters, but did contribute to the resolution of clades that these characters had difficulty with. Finally, biogeography generally corroborates the relationships defined by male characters.

Excluding male characters describing modification of the antennae and hind legs from the analysis (thereby examining their effect on the phylogeny) was a compromise between excluding all characters describing modification in males, thereby leaving twelve other characters to resolve thirty-seven taxa (approach of Coddington, 1988), and including all of them, thereby ignoring their effect on the phylogeny (the ‘total evidence’ approach). When sensitivity analyses (approach of Swofford & Maddison, 1992) are conducted, they typically involve excluding and examining the effect on the phylogeny of one character of interest at a time (e.g. only those describing modification of the antennae). However, to be even more conservative we excluded characters describing modification of the antennae and hind legs simultaneously. These characters comprise almost 60% of the data set and thus their exclusion makes the sensitivity analysis quite rigorous.

Male characters describing modification of various traits appear to be reasonably independent. One might argue that all male characters are under analogous selection pressure (sexual selection), and therefore are expected to have correlated evolutionary trajectories. However, in most of these male characters, the presence or absence of one character state is not perfectly correlated with the presence or absence of another. For example, the *praeposterus-bergrothi* clade have a ventrolateral spine on antennal segment 1 (ch. 1), but only some of these species have a basomedial spine-like process on antennal segment 3 (ch. 21) and the hind femur roughly bowed laterally (ch. 53). Therefore, the correlation within and between these structures is not perfect and can be considered reasonably independent.

In summary, the results of this analysis provides strong support for most of the major clades in *Rheumatobates*. The basal relationships remain weakly defined. The topology of the preferred phylogeny is consistent with biogeographical data. In contrast to the general taxonomic assumption, unmodified and modified species do not form two separate clades. As such, the preferred phylogeny provides an initial basis upon which to test hypotheses for the evolutionary elaboration of males in this genus. Tests of hypotheses requiring definition of the basal relationships are not yet possible. More informative characters are required to define these basal relationships. We suggest that female genitalic characters or molecular characters will be most informative.

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Appendix 1. Data matrix of 102 characters for thirty-seven ingroup taxa of *Rheumatobates* and one outgroup taxon, *Rhagadotarsus anomalus.* Missing data scored as '?'.

	Character
	1111111111222222222233333333334444
Taxon	1234567890123456789012345678901234567890123
aestuarius	0000020000000001001100000000000102010000000
bergrothi	1111011200111210120010000110101001000000201
bonariensis	0000000000000000000000000000000001000000000
carvalhoi	0000020000000021001200000000010102020000000
citatus	1211011200112100110010000110001001000020010
clanis	0000000000000000000000000000000003100000000
crassifemur crassifemur	0000000001000000000001231001000004000112000
crassifemur esakii	0000000001000000000001231001000004000112000
crassifemur schroederi	0000000001000000000001231000000004000112000
creaseri	1211001200112100110000000110101000000020010
drakei	0000000000000000000000000000000001000000000
hungerfordi	1211000000124210120000000120101001000000101
imitator	1111011200111210120010000110101001000000201
klagei	0000000001000000000001231000000004000?11000
longisetosus	0000020000000021001200000000010102020000000
mangrovensis	0000100010000000000000000000000013101000000
meinerti	1111011200111210120010000110101001000000000
mexicanus	1211011200111210120010000110101001000000000
minimus	0000000000000000000000000000000001000000000
minutus flavidus	0000000000000000000000000000000000000000000
minutus minutus	0000000000000000000000000000000000000000000
ornatus	0000020000000001001100000000000102020000000
palosi	1212011100123210120000000120101001000000101
peculiaris	0000000001000000000000000000000007000000000
petilus	0000000000000000000000000000000003000000000
praeposterus	1?1?0?1?001??1001?0000000000?0?001000000000
probolicornis	0000020000000000000000000000000005000000000
prostatus	0000020000000001001100000000000102010000000
rileyi	1212011100123210120000000120101001000000101
spinosus	0000000001000000000001100000000000000000000
tenuipes	1212000000124210120000000120101001000000101
trinitatis	0000100010000000000000000000000013101000000
trulliger	1212000000124210120000000120101001000000000
vegatus	0000000000000000000000000000000003000000000
species A	0000020000000001001100000000000102010000000
species B	0000000000000000000000000000000000000000000
species C	000000000000000000000000000000?006000000000
Rhagadotarsus anomalus	0000000000000000000000000000000000000000000

Appendix 1. Continued.

	Character
	4444445555555555666666666677777777778888888
Taxon	4567890123456789012345678901234567890123456
aestuarius	0000000000100000000000000000000111111100011
bergrothi	0001220003001211121011011101000000000000010
bonariensis	0000000000000000000000000000000000000000000
carvalhoi	0000000000100000000000000000000111111200011
citatus	0000000000000000000000000000000000000000010
clanis	0000000000000000000000000000000000000000010
crassifemur crassifemur	1100012110010000000010000000001000000000001
crassifemur esakii	1100012110010000000100000000010000000000010
crassifemur schroederi	1100012110010000000100000000010000000000010
creaseri	0000000000000000000000000000000000000000010
drakei	0000000000000000000000000000000000000000010
hungerfordi	0000000003000011000011000000001000000000010
imitator	0001100003001211120011011201000000000000010
klagei	1100011110010000000?00000000010000000000010
longisetosus	0000000000100000000000000000000111112000110
mangrovensis	0000000000000000000000000000000000000000010
meinerti	0001220003001211121011011101000000000000010
mexicanus	0000000003001211110011000000000000000000010
minimus	0000000000000000000000000000000000000000000
minutus flavidus	0000000000000000000000000000000000000000010
minutus minutus	0000000000000000000000000000000000000000010
ornatus	0010000000000000000000000000000111000000110
palosi	0000000003201112000012112221101000000000010
peculiaris	0000000000000000000000000000000?00000000010
petilus	0000000000000000000000000000000000000000010
praeposterus	0000000000000000000000000000000000000000010
probolicornis	0010000000000000000000000000001000000000010
prostatus	0000000000000000000000000000000112111211010
rileyi	0000000003201112000012112221101000000000010
spinosus	0000000000000000000000000000000000000000010
tenuipes	0000000000000000000000000000001000000000010
trinitatis	0000000000000000000000000000000000000000010
trulliger	0000000003001112000012112221101000000000010
vegatus	0000000000000000000000000000000000000000010
species A	0000000000000000000000000000000112111211010
species B	0000000000000000000000000000000000000000010
species C	0000000000000000000000000000000000000000000
Rhagadotarsus anomalus	0000000000000000000000000000000000000000000

Appendix 1. Continued.

	Character
	0000000000000111
	8889999999999000
Taxon	7890123456789012
aestuarius	1111221100101011
bergrothi	0030101301101000
bonariensis	0000100000100000
carvalhoi	1111221300101111
citatus	0030001301101000
clanis	0030321300100111
crassifemur crassifemur	0003000001100000
crassifemur esakii	0030000011000000
crassifemur schroederi	0030000011000000
creaseri	0030???30?1??000
drakei	0030000000100000
hungerfordi	0030101300100000
imitator	0030001300101000
klagei	0030000011000000
longisetosus	1111221300101111
mangrovensis	0030321300101111
meinerti	0030001301101000
mexicanus	0030101301101000
minimus	0000100001100000
minutus flavidus	0030011200110200
minutus minutus	0030021200110200
ornatus	1110221300101111
palosi	0030101300100000
peculiaris	0020001300100000
petilus	0030321100101111
praeposterus	0030?0030??0??00
probolicornis	0030221300101111
prostatus	1111221100101011
rileyi	0030101300100000
spinosus	0030000001000000
tenuipes	0030101300000000
trinitatis	0030321300101011
trulliger	0030101300100000
vegatus	0030321301100111
species A	1111221100101111
species B	0030111200110000
species C	0000411200100000
Rhagadotarsus anomalus	0000000000000000

Appendix 2. Character state changes for the preferred phylogeny. Homoplasious character state changes are indicated with an asterisk.

Node 1–2: 97 (0–1)*
Node 2–6: 34 (0–1)*
Node 6–8: 85 (0–1)*, 89 (0–3)*
Node 8–9: 96 (0–1)*
Node 9–14: 93 (0–1)*, 94 (0–3), 99 (0–1)*
Node 14–26: 34 (1–3), 91 (0–3), 92 (0–2)*, 100 (0–1)*, 101 (0–1), 102 (0–1)
Node 26–27: 96 (1–0)*
Node 27–30: 6 (0–2)*, 34 (3–2), 46 (0–1)*, 75 (0–1), 91 (3–2)
Node 30–31: 16 (0–1), 19 (0–1), 20 (0–1), 32 (0–1), 36 (0–2), 76 (0–1), 77 (0–1), 87 (0–1), 88 (0–1), 89 (3–1)
Node 31–32: 46 (1–0)*, 54 (0–1)*, 78 (0–1), 79 (0–1), 80 (0–1), 81 (0–2)*, 90 (0–1)
Node 32–34: 36 (2–1), 94 (3–1)*, 100 (1–0)*
Node 34–35: 54 (1–0)*, 77 (1–2), 82 (0–1), 83 (0–1)
Node 32–33: 15 (0–2), 20 (1–2), 30 (0–1)
Node 27–28: 35 (0–1)
Node 28–29: 5 (0–1), 9 (0–1), 33 (0–1), 37 (0–1)
Node 14–15: 1 (0–1), 2 (0–2), 3 (0–1), 4 (0–1), 7 (0–1)*, 8 (0–2)*, 11 (0–1), 12 (0–1), 13 (0–1), 14 (0–1), 17 (0–1), 18 (0–1), 29 (0–1)*, 31 (0–1)
Node 15–16: 26 (0–1), 27 (0–1)
Node 16–18: 14 (1–2), 15 (0–1), 18 (1–2), 43 (0–1)*, 53 (0–3)*, 58 (0–1)*, 59 (0–1)*, 64 (0–1)*, 65 (0–1)*, 91 (0–1)*
Node 18–23: 6 (0–1)*, 21 (0–1)*, 56 (0–1)*, 57 (0–2), 60 (0–1), 61 (0–1)
Node 23–24: 2 (2–1), 41 (0–2)*, 47 (0–1), 48 (0–1), 67 (0–1)*, 68 (0–1), 69 (0–1), 61 (1–2), 71 (0–1)*, 91 (1–0)*
Node 24–25: 48 (1–2), 49 (0–2), 62 (0–1)
Node 18–19: 7 (1–0)*, 8 (2–0)*, 12 (1–2), 13 (1–4), 27 (1–2), 41 (0–1)*, 74 (0–1), 96 (1–0)*, 99 (1–0)*
Node 19–20: 4 (1–2), 59 (1–0)*, 65 (1–0)*
Node 20–21: 56 (0–1)*, 57 (0–1), 59 (0–2), 65 (0–2), 66 (0–1), 67 (0–1)*, 68 (0–2), 69 (0–2)*, 70 (0–2), 71 (0–1)*, 72 (0–1)
Node 21–22: 6 (0–1)*, 7 (0–1)*, 8 (0–1), 13 (4–3), 54 (0–2)
Node 16–17: 13 (1–2), 39 (0–2), 42 (0–1)
Node 9–10: 10 (0–1), 22 (0–1), 23 (0–1), 34 (1–0)*, 97 (1–0)*
Node 10–11: 23 (1–2), 24 (0–3), 25 (0–1), 34 (0–4), 38 (0–1), 39 (0–1), 40 (0–1), 44 (0–1), 45 (0–1), 49 (0–1), 50 (0–1), 51 (0–1), 52 (0–1), 55 (0–1), 63 (0–1), 73 (0–1), 95 (0–1)
Node 11–12: 40 (1–2), 50 (1–2)
Node 12–13: 28 (0–1)
Node 6–7: 91 (0–1)*
Node 2–3: 92 (0–1), 93 (0–1)*, 94 (0–2)
Node 3–4: 85 (0–1)*, 89 (0–3)*, 98 (0–1)
Node 4–5: 100 (0–2)