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"On the Heterotreme-Thoracotreme Distinction in the Eubrachyura de Saint-Laurent, 1980"

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Notes on the position of the true freshwater crabs within the brachyrhynchan Eubrachyura (Crustacea: Decapoda: Brachyura)

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Abstract

Cladistic and phenetic relationships of 51 eubrachyuran crab genera, comprising 36 genera of marine crabs and 18 genera of true freshwater crabs from 7 families, were investigated using 121 parsimony-informative adult morphological characters. The data matrix was subjected to four different treatments: (1) a cladistic analysis with a combination of unordered and ordered characters, (2) a cladistic analysis with all characters unordered, (3) neighbour-joining, and (4) UPGMA phenetic analyses. The parsimony analysis conducted with a combination of ordered and unordered characters produced a set of hypotheses which supported monophyly of a Pseudothelphusidae+Potamoidea clade. Furthermore, exemplar genera of the Bythograeidae and Pinnotheridae formed an unresolved polytomy with the Pseudothelphusidae+Potamoidea group, the Thoracotremata. The trichodactylid freshwater crabs were positioned as the sister taxon of the basal portunoid *Carcinus*, but were unresolved relative to other portunoids and geryonids. Second, the parsimony analysis conducted with all characters unordered resulted in a [bythograeid, pseudothelphusid+potamoid, pinnotherid, thoracotreme] group with no hierarchical resolution, which in turn formed a polytomy with a goneplacid+portunoid clade and a polyphyletic Xanthoidea. And third, phenetic groupings of the eubrachyuran genera invariably placed the pseudothelphusids with the potamoids, and this clustered with a group containing the thoracotremes (either in whole or part). Support was thus found for morphological connections among the nontrichodactylid freshwater crabs, thoracotremes, bythograeids, and pinnotherids, and for the placement of the trichodactylids within the Portunoidea. These two latter findings (that used a range of genera from each family) are broadly congruent with a previous cladistic analysis of selected eubrachyuran familial groundpatterns that used a basal exemplar of each marine and freshwater crab family (Sternberg et al., 1999). However, it is clear that the large scale homoplasy identified here may nullify any reliable hypothesis of brachyrhynchan groupings at this stage.

Introduction

Freshwater crabs have historically received relatively less attention than their marine relatives, and until recently there have been few serious attempts to identify the relationships between the freshwater crabs to other brachyurans found in marine environments. This situation has gradually improved over the past 30 years and there is currently a wave if interest in freshwater crab biology. This has taken the form of an explosion of alpha-taxonomy and an increase in the number of described species from 600 to more than

950 (e.g. Bott, 1955, 1970; Rodríguez, 1982, 1992; Ng & Naiyanetr, 1993; Cumberlidge, 1999; Cumberlidge & Sternberg, unpublished), and an increase in the number of families from three (Bott, 1955) to 12 (Bott, 1970; Cumberlidge 1999). At present, most authors (Ng, 1988; Cumberlidge, 1999) recognise seven or eight families (Trichodactylidae, Deckeniidae, Gecarcinucidae, Parathelphusidae, Potamidae, Potamonautidae, Pseudothelphusidae, and Platythelphusidae). The recent literature on freshwater crabs includes a number of important monographic revisions of the faunas of the Neotropics, Africa and Asia (Rodríguez,

1982, 1992; Ng, 1988; Ng & Naiyanetr, 1993; Magalhães & Türkay, 1996a,b,c; Cumberlidge, 1999). This dramatically improved database, together with the availability of techniques such as cladistics, have laid the foundations for much-needed phylogenetic and biogeographic analyses of the group. The worldwide distribution of freshwater crabs throughout the inland waters of the continents and islands of the tropics and subtropics means that these decapods hold great potential as indicators of past geological events. However, in order for this potential to be realized, it must first be determined whether the freshwater crabs are a monophyletic group, and whether they originated relatively recently, or whether they are of more ancient origin.

A key attribute of all true freshwater crabs is direct development whereby larval stages are lacking and the eggs produce young crabs. The broad, shallow female sternoabdominal cavity and the equally-broad abdomen together form a brood pouch for the relatively small number (∼25–200) of large eggs and the hatchling crabs. The biogeographic importance of the freshwater crabs arises from their restriction to inland fresh water habitats of the continents, and their relatively poor powers of dispersal. This is because freshwater crabs lack the dispersive planktonic larval stage seen in most marine crabs. This means the geographic range of freshwater crab species is in part limited by their low dispersal capabilities, their low fecundity, their restriction to ecosystem microhabitats, their intolerance to desiccation, and to saline habitats (Rodríguez, 1986). As a consequence, freshwater crabs become isolated relatively easily and they tend to exhibit high rates of endemism. It is common for a relatively small geographic area to support a high species diversity of freshwater crabs (e.g. Ng, 1988; Ng & Naiyanetr, 1993; Cumberlidge, 1999).

Freshwater crabs are distributed pantropically along the lowland watersheds of South America, the Andean and Central American cloud forests, and some islands in the Caribbean; throughout sub-Saharan Africa; in southern Europe and parts of the Middle and Near East; Madagascar; the Seychelles; India and Southeast Asia; China, the Philippines, Indonesia, New Guinea, and Australia (Bott, 1970; Rodriquez, 1982, 1992; Ng, 1988; Ng & Naiyanetr, 1993; Magalhães & Türkay, 1996a,b,c; Cumberlidge, 1999). If the group should prove to be monophyletic, and if the group can be demonstrated to have an ancient origin, then this circumtropical distribution pattern could be interpreted in terms of plate tectonic movements and continental fragment migration; if not, then other explanations must be sought. However, the age and origin of the freshwater crabs is far from certain, and this is due in part to a poor fossil record for the group, with the oldest fossils dating back to the Miocene, 25–30 million years ago (Bott, 1955; Glaessner, 1969). On the other hand, all freshwater crabs are highly derived heterotremes, and this latter group has a more complete fossil record. It is likely that the heterotremes underwent a post-Cretaceous radiation (Glaessner, 1969) and it is, therefore, reasonable to assume that the freshwater crabs may have first appeared at some time in the early to mid-Cenozoic era (65–30 mya). Other attempts to establish the time of origin of the freshwater crabs include evidence from dated tectonic movements. For example, if the South American, African, Madagascan, and Indian freshwater crabs constitute a monophyletic group, then the stem group must have been present in or near the inland waters of the ancient southern continent of Gondwana. Because the breakup of Gondwana is believed to have taken place around 120–100 mya, authors have postulated an origin of freshwater crabs in excess of 120 mya (Ng & Rodríguez, 1995; Ng, Stevcic & Pretzmann, 1995). However, this reasoning has been questioned (Sternberg et al., 1999) because such an early origin would require (1) that the freshwater crabs significantly predate the eubrachyuran radiation, and (2) that the Brachyura as a whole is a great deal older than current data allow. On the other hand, if the freshwater crabs are an unnatural (polyphyletic) group, their distribution would reveal little about past geological events and if each of the freshwater crab families on different continents had a separate marine crab ancestry and a more recent (post-Cretaceous) origin (Pretzmann, 1973; Rodríguez, 1986; Ng & Rodríguez, 1995; Guinot et al., 1997).

The aim of the present study is to test the monophyly of the freshwater crabs, and to identify a possible marine sister group (or groups) of the Old World and New World freshwater crab families. Testing the monophyly of the freshwater crabs is intertwined with the identification of the marine sister taxon (or taxa) of the freshwater crabs, because knowledge of this sister group is a necessary prerequisite for the correct polarization of characters for cladistic analysis. The problem is that the freshwater crabs (alone of all brachyurans found in freshwater habitats) have no easily identifiable extant marine crab relatives.

The cladistic analysis of selected eubrachyuran familial groundpatterns by Sternberg et al. (1999) found

that the freshwater crabs fell into two broad lineages: (1) a clade that included the Neotropical Trichodactylidae within the Portunoidea, and (2) a clade that included all of the remaining freshwater crab families (Deckeniidae, Gecarcinucidae, Parathelphusidae, Platythelphusidae, Potamidae, Potamonautidae and Pseudothelphusidae). In addition, parsimony analysis of the eubrachyuran familial groundpatterns (Sternberg et al., 1999) positioned the Thoracotremata (*sensu* Guinot, 1977, 1979; Guinot & Richer de Forges, 1997) as the sister group of the Neotropical Pseudothelphusidae+Palaeotropical freshwater crabs, and placed the Trichodactylidae within the Portunoidea. The latter finding supports the hypothesis first presented by Rodríguez (1992), and at the same time falsifies the monophyly of the freshwater crabs. These findings have weakend the previous hypotheses that the freshwater crabs are either strictly monophyletic (Rathbun, 1904), extremely polyphyletic (Bott, 1970; Pretzmann, 1973), or that they are positioned within or near the Xanthoidea (Pretzmann, 1973; Rodríguez, 1986; Guinot et al., 1997).

The need for the present study arises out of the fact that the monophyletic status of many of the eubrachyuran marine crab families is itself uncertain. This uncertainty raises questions about the wisdom of relying on published accounts of familial groundpatterns of groups of marine crabs that may eventually prove to be unnatural entities. In order to overcome this problem, the present test of freshwater crab monophyly and sister taxon (or taxa) identification compares character states among genera that each represent a particular family, rather than comparing a familial groundpattern that relied on the correct selection of a representative of a putative family. In the present, study we have restricted our analysis to the brachyrhynchan eubrachyurans, which is the group of heterotreme crabs that includes both the freshwater crabs and their likely marine sister taxon (or taxa). In order to compare the taxic relationships resulting from the different treatments of these data, we have subjected our extensive dataset of adult morphological characters to both cladistic and phenetic analyses. As far as we are aware, this study constitutes the largest selection of taxa and the largest number of characters of any published cladistic analysis of the Eubrachyura to date.

Bott (1970) recognised eight Palaeotropical freshwater crab families and placed these in two superfamilies: the Gecarcinucoidea (for the Parathelphusidae, Gecarcinucidae and Sundathelphusidae) and the Potamoidea (for the Potamidae, Potamonautidae, Deckeniidae, Isolapotamidae and Sinopotamidae), presumably to reflect two distinct evolutionary lineages. Bott (1970) recognised a third superfamily (the Pseudothelphusoidea, for the Pseudothelphusidae and Potamocarcinidae) and placed the Neotropical Trichodactylidae in a separate family. However, there is no cladistic support for such an elaborate polyphyletic ancestry for the freshwater crab families (Sternberg & Cumberlidge, 1999; Sternberg et al., 1999).

Furthermore, the morphological characters traditionally used to separate the members of Bott's (1970) two Old World superfamilies (i.e. gecarcinucoids and potamoids) are of dubious significance (Cumberlidge, 1999). Available cladistic studies of freshwater crab relationships (Sternberg & Cumberlidge, 1999; Sternberg et al., 1999) support the grouping of all the Palaeotropical freshwater crab families into a single superfamily, the Potamoidea. For this reason, the term 'potamoid' in the present context refers to the clade comprised of all the Old World families.

Methods

A data matrix of fifty-one taxa (Appendix 1) and 121 characters (Table 2) was compiled using MacClade 3.06 (Maddison & Maddison, 1996). The taxonomic authorities for all of the taxa are given in full in Appendix 1, and the details of the characters used are given in Table 1. All the characters in Table 1 pertain to aspects of adult morphology. We have included genera from 22 families of marine eubrachyurans, but we have not included genera from highly derived families such as the Mictyridae and Palicidae, because such forms can bias investigations of taxic relationships (Danser, 1950).

Two different cladistic analyses (one using all unordered characters, the other using a combination of unordered and ordered characters) and two different phenetic analyses ['neighbor joining' (NJ) and UPGMA] were performed using PAUP 4.0 (Swofford, 2000, unpublished). In view of the complexity of the database, the two cladistic analyses were carried out using the 'general heuristic search' option for 100 bootstrap replicates. No outgroup was specified during the searches for the shortest trees. Phenetic relationships among the brachyrhynchan genera were determined in order to compare the resulting phenograms in which taxic groupings are based on total character state distances, with the consensus cladograms (batches 1 and 2) based on shared derived charac-

Table 1. Adult morphological character states used in the cladistic and phenetic analyses of brachyrhynchan relationships

1. Carapace frontal margin: with median incision (0); entire, without notch (1).
2. Degree of carapace frontal margin downward deflexion: none (0); moderate (1): vertical (2); 'pseudothelphusid' (3).
3. Carapace front: distinct and moderately broad (0); narrow, subtriangular to spatulate (1).
4. Carapace frontal margin: cut into distinct teeth or lobes (0); low, blunt lobes present (1); straight, no trace of lobes (2).
5. Lateral margin of carapace front: separated from medial-inferior orbital angle (0); associated with medial-inferior orbital angle (1).
6. Carapace frontal margin: singular (0); horizontally split into inferior and superior margins (1).
7. Supraorbital margin: distinct or faint notch(es) present (0); complete (1).
8. Supraorbital margin shape: semi-circular (0); sigmoidal and elongate (1).
9. Eyestalks and eyes: well-formed and functional (0); vestigial (1).
10. Number of supraorbital notches, if present: one (0); two (1).
11. Medial-inferior occlusive orbital tooth (see Rodríguez, 1992): absent (0); present (1).
12. Medial-inferior infra-orbital ridge: absent (0); present (1).
13. Epigastric crest: absent (0); present (1).
14. Position of the epigastric crest: posterior to the imaginary line linking the supraorbital margins (0); anterior to the imaginary line linking the supraorbital margins (1); located at point of frontal margin downward deflexion (2).
15. Epigastric lobes: well-formed (0); reduced to scars (1); barely discernable to absent (2).
16. Postorbital crest: absent (0); present (1).
17. Branchial groove: weak to absent (0); marginally developed (1); distinct (2).
18. Epibranchial crest: absent (0); present and tuberculated (1).
19. Crest associated with posterior-most carapace lateral tooth: absent (0); present (1).
20. Posterior-most carapace lateral tooth prominent: absent (0); present (1).
21. Carapace lateral margin (separating surface from the sidewall): weakly defined (0); defined by a '"cancroid' ridge (1).
22. Anterior half of carapace lateral margin: not distinctly convex (0); distinctly convex and delimited by a low line of tubercles (1); distinctly convex and delimited by a raised lateral margin (2).
23. Carapace lateral margin: indistinct (0); distinct for the entire length and sharply projecting (1).
24. Carapace posterolateral region: smooth or weakly tuberculated (0); with posterolateral carinae and/or rugosities (1).
25. 'Potamoid' posterolateral carapace carina: absent (0); present (1).
26. Carapace posterior border: defined by distinct but low carina (0); defined by sharp, high carina (1).
27. Carina defining posterior extremity of carapace: distinct but low (0); reduced in length and height (1); very reduced to absent (2).
28. Longitudinal orientation of epimeral sulcus: merging with carapace lateral margin approximately halfway along length (0); remaining subparallel to carapace lateral margin throughout length (1).
29. Carapace sidewall vertical groove: absent (0); vaguely defined (1); distinct (2).
30. Outline of carapace sidewall vertical groove: straight (0); semi-circular in outline (1).
31. Carapace sidewall vertical sulcus: distant from lateral-inferior orbital margin (0); flanking lateral-inferior orbital margin (1).
32. Carapace sidewall: smooth or weakly tuberculate (0); with carinae or rugosities (1).
33. Pterygostomial region: not projecting relative to suborbital region (0); dorsal region produced and shelf-like relative to suborbital region (1).
34. Antennular septum: distinct (0); very reduced in width, forming a thin bridge (1).
35. Basal antennal article: having a (sub)rectangular outline in frontal view (0); distinct distolateral tooth present (1).
36. Buccal frame vertical margins: parallel (0); detectable to moderate ventral widening (1); pronounced ventral widening (2).
37. Buccal frame vertical margins: parallel (0); detectable to moderate dorsal widening (1); pronounced dorsal widening (2).
38. Vertical margin of buccal frame: visible (0); covered by 3rd maxilliped exopods and/or ischia (1).
39. Carapace weak, flexible, bulbous in conformation: absent (0); present (1).
40. Carapace outline pseudothelphusid-like in dorsal view: absent (0); present (1).
41. Lateral regions of the epistome posterior margin everted to form roofs of efferent 'tubes': absent (0); moderately developed (1); very pronounced (2).
42. 'Deckeniid' conformation of the epistome: absent (0); present (1).

Table 1. Continued

43. Median projection on epistomial posterior margin (projecting into space between the 3rd maxilliped palps): slight to absent (0); moderately developed (1); pronounced, tongue-like (2); block-like (3).

44. Median projection on epistomial posterior margin: projecting ventrally (0); projecting outward (1).

45. Median projection on epistomial posterior margin flanked laterally by longitudinal incisions: absent (0); present (1).

46. Epistome with longitudinal notches present near the lateral regions, lateral to the endostomial ridges if present: absent (0); present (1).

47. Orientation of the epistome: facing ventrally (0); facing anteriorly (i.e. vertical when crab is upright) (1); posterior margin visible from the dorsal perspective (2).

48. Endostomial gutter: distinct (0); reduced to highly reduced (1); absent (2).

49. Endostomial gutter deep, defined by sharp margins: absent (0); present (1).

50. Endostomial ridges (defining median sides of the efferent channels): distinct (0); reduced (1); absent (2).

51. Posterior margin of the epistome with three low, ventral projections, one median and two near the lateral margins: absent (0); present (1).

52. Mandibular palp: 3-segmented (0); proximal and penultimate segments intermediately fused (1); 2-segmented (2).

53. Mandibular palp terminal segment: 'simple' (0); small anterior lobe present (1); large anterior lobe present (2).

54. Mandibular palp terminal segment: flat and laminar (0); somewhat enrolled (1).

55. Endopod of first maxilliped: flat and laminar (0); rolled, tube-like (1).

56. Length of first maxilliped endopod: not reaching anterior margin of the endostome (0); reaching the anterior margin of the endostome (1).

57. 'Portunoid-lobe' on first maxilliped endopod: absent (0); slightly developed (1); distinct (2).

58. Exopod of third maxilliped: robust, almost 0.5–0.3X the width of the ischium (0); moderately thin, equal to or slightly less than 0.25X the width of the ischium (1); thin, less than 0.1X the width of the ischium.

59. Exopod of third maxilliped: medial part of the base curving under the ischium (0); medial part of the base only slightly curving under the ischium (1); base not curving under the ischium (2).

60. Ischia, meri and palps of third maxillipeds: leaving a medial space (0); completely enclosing the buccal cavity (1).

61. Articulation junction of the third maxilliped ischia-meri: not constricted (0); constricted (1).

62. Teeth located along medial margin of third maxilliped ischium: distinct (0); reduced to absent (1).

63. Anterolateral border of third maxilliped merus: rounded (0); flared, moderately projecting (1); distinctly flared (2).

64. Anterior margin of third maxilliped merus adjacent to proximal segment of the palp: not projecting (0); forming a distinct lobe or spine-like (1).

65. Anterior margin of third maxilliped merus: slanted, nearly straight (0); with medial depression (1).

66. Outline of third maxilliped merus *Nectocarcinus*-like: absent (0); present (1).

67. Palp of third maxilliped: articulating at disto-medial angle (0); articulating at disto-lateral angle (1).

68. Terminus of third maxilliped palp distal segment: extending to ischium (0); extending to ischium-merus junction (1).

69. Male abdomen outline narrowly triangular: absent (0); intermediate (1); distinct (2).

70. Male abdomen an equilateral triangle in outline: absent (0); intermediate (1); distinct (2).

71. Male abdominal segments a3–a4: freely articulating (0); fused (1).

72. Suture between male abdominal segments a3–a4: visible (0); erased (1).

73. Male abdominal segments a4–a5: freely articulating (0); fused (1).

74. Suture between male abdominal segments a4–a5: visible (0); erased (1).

75. Male abdominal locking facets on a6: distinct (0); absent (1).

76. Male abdominal segment 6 widened along the posterior region: absent (0); present (1).

77. Male telson tongue-shaped: absent (0); intermediate (1); distinct (2).

78. Male telson triangular: absent (0); intermediate (1); distinct (2).

79. Male abdominal segments a5 and a6 laterally constricted: absent (0); present (1).

80. Male abdominal segments a2–a3 dorsoventrally curved: absent (0); present (1).

Table 1. Continued

81.	Outline of female abdomen: thinly oval (0); oval, longer than broad (1); round (2); broadly oval (3).
82.	Female abdomen: all segments free (0); segments a3–a5 ankylosed (1); segments a3–a6 ankylosed (2).
83.	Female abdominal segment 1 covered by carapace: absent (0); present (1).
84.	Female telson: subtriangular in outline (0); semi-circular in outline (1).
85.	Female telson: subtriangular in outline (0); tongue-shaped in outline (1).
86.	Female pleopodal exopods: long, narrow and pediform (0); slightly broad and flattened (1); very broad and flattened (2).
87.	Female pleopodal endopods: long, narrow, and pediform (0); distal end slightly paddle-like (1); distal end paddle-like (2).
88.	Female pleopodal endopods lacking hinge: absent (0); present (1).
89.	*Sella turcica* reduced to rim-like structure: absent (0); present (1).
90.	Endosternites 3–4: incomplete and sheet-like (0); reduced to apophyse (1).
91.	Endophragmal apophyse 3–4: ends juxtaposed (0); ends well separated (1).
92.	Endosternites 4–5, 5–6: medially confluent (0); medially interrupted (1).
93.	Endosternites 6–7: medially confluent (0); medially interrupted (1).
94.	Anterior terminus of male sternal cavity: middle of sternite 4 (0); at, or anterior, to s3–4 boundary (1).
95.	Longitudinal, median line on sternite 4: absent (0); present (1).
96.	Posterior margin of sternite 3: merges smoothly with sternite 4 (0); laterally expanded relative to sternite 4 (1).
97.	Female sternum distinctly excavated to form a bowl-like egg-chamber: absent (0); present (1).
98.	Position of male penial openings: pereiopod 5 coxae (0); via paired apertures on sternite 8 or near the s7–8 border (1).
99.	Male first pleopod (gonopod) with terminal article: absent (0); present (1).
100.	Articulating joint of first gonopod terminal article: poorly developed (0); prominent (1).
101.	'Panopeid' ornamentation on first gonopod distal end: absent (0); present (1).
102.	First gonopod 6-shaped or geryonid-like in outline: absent (0); present (1).
103.	First gonopod stout with apical spine field (pseudothelphusid-like): absent (0); present (1).
104.	First gonopod subtriangular in cross-section, grapsid-like: absent (0); present (1).
105.	First gonopod thin, xanthid-like: absent (0); present (1).
106.	Second gonopod terminal segment and flagellum: at least equal in length to first gonopod (0); length approximately half that of first gonopod (1): short (2).
107.	Second gonopod flagellum with a whip-like end: absent (0); intermediate (1): present (2).
108.	Second gonopod terminal segment-flagellum articulation point: distinct (0); lacking (1).
109.	Second gonopod apex: styliform (0); spoon-shaped (1).
110.	Pereiopod 2–5 meri: margins rounded in outline (0); subtriangular in outline (1); sharply triangular in outline (2).
111.	Dorsal surface of pereiopod 2–5 meri: smooth or weakly tuberculate (0); rugose or with carinae (1).
112.	Pereiopod 2–5 dactyl spines: absent (0); present (1).
113.	Pereiopod 2–5 dactyl articulation knob: absent (0); present (1).
114.	Pereiopod 5 dactylus: styliform (0); spatulate (1).
115.	Pereiopod 5 dactylus-propodus lined with silk-like setae: absent (0); present (1).
116.	Ventral margin of the pereiopod 1 merus: rounded (0); sharp and demarcated with tubercles (1).
117.	Dorso-interior margin of the pereiopod 1 merus: straight (0); lined with low, irregular tubercles (1); lined with sharp, irregular teeth (2); line with a few sharp, curved teeth (3).
118.	Dorso-external surface of the pereiopod 1 merus: smooth (0); rugose or with carinae (1).
119.	Pereiopod 1 merus short, slightly longer than the carpus and squat: absent (0); present (1).
120.	Dorsal margin of the pereiopod 1 merus: inconspicuous or well-defined (0); with a curved, sharp tooth (1).
121.	Outer surface of pereiopod 1 propodus: smooth or weakly tuberculate (0); with one or more distinct longitudinal ridges (1).

Table 2. Data matrix of the 121 adult morphological characters used in the cladistic and phenetic analyses. Character state codes are: 0 = plesiomorphies; 1, 2, & 3 = apomorphies; p = 0 & 1; q = 1 & 2; r = 0 & 1 & 2; s = 2 & 3; and ? = undetermined

Combined Outgroup:						
0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	
0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0
Carpilius:						
0q01001000	0000200010	000000000?	?000000000	000?010001	0000001000	
0110000000	1100010000	0000000000	0000110000	0000002000	0010000010	0
Platyxanthus:						
0001000001	0000000110	000000000?	?000000000	000?010001	0000000000	
0010000000	0000000000	0001000001	0100110000	0000000000	0000000010	0
Eriphia:						
0102100001	0000000100	0000000021	0000000000	000?011000	1000000000	
0010000000	0000010000	0001000001	0100110000	0000001000	0010000010	0
Ozius:						
0101000001	0000000010	000000000?	?000001000	000?011000	1100000000	
0010100000	0000010000	0001000001	0100110000	0000002000	0010000010	0
Menippe:						
010p000001	0000000010	000000000?	?000p01000	000?010000	0100000000	
0010100000	0000000000	0001000001	0100110000	0000002000	0010000010	0
Panopeus:						
0002000001	0000000110	000000001?	?000101000	000?011001	0000000000	
0020100000	1111000000	0001000001	0100110000	1000120000	0000000010	0
Rhithropanopeus:						
0002000001	0000000110	000000000?	?000101000	000?011001	0000000000	
0020100000	1111000000	0001000001	0100110000	1000120000	0000000010	0
Beuroisia:						
0002010101	0010011000	000000000?	?000000000	000?010000	0000000q00	
0010000020	0000000000	1001000001	0110000000	0000000001	0110000000	0
Pilumnus:						
0102000001	0000000000	000000000?	?000001000	000?011000	0000000000	
0010100010	0000000000	0001000001	0100100000	0000120000	0010000010	0
Leptodius:						
0002000001	0000000010	000000000?	?000001000	000?010002	0000000000	
0020100000	1111000000	0001000001	0100100000	0000120000	0010000010	0
Actaea:						
0002000001	0000000010	000000000?	?000001000	000?010002	0000000000	
0010100000	1111000000	0001000001	0100100000	0000120000	0010000010	0

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Table 2. Continued

Trapezia:						
0000101100	000?200010	000000200?	?000?01000	001p011100	0100010010	
0110000020	1111000000	0001000001	0000100000	0000120000	0020002010	0
Geryon:						
0000000101	0000000101	100001010?	?000101000	000?010000	0000001000	
0110010001	1010000201	1001000001	1110000000	0100000000	0000000001	1
Carcinus:						
0000000101	1000000100	100001010?	?000000000	0010011002	0100000000	
0021010001	1111000201	2100000001	1110000000	0100010000	0011100010	1
Nectocarcinus:						
000r000101	0000000110	100001000?	?000101000	000?010000	0000000000	
0001010020	1010000201	1000000001	1100000000	0000001001	0001101001	1
Benthochascon:						
0000000101	1000000101	100001010?	?000101000	000?011002	0100000000	
0020000010	0000000201	1000000001	1110000000	0100000000	0011100001	1
Bathynectes:						
0000000101	1000000101	100001010?	?000101000	000?011000	0100002000	
0020000010	0101000201	1000000001	1110000000	0100000000	0011103001	1
Trichodactylus:						
1102000100	1000200000	100000210?	?000100000	0030001012	0000012200	
0101010001	1p1p000200	2011010011	1110000000	0100001000	0000000000	0
Valdivia:						
1102000100	1000000000	100001010?	?000100000	0030002012	0000002210	
0101010001	1111000201	2110020111	1110000000	010000q000	0001103001	0
Sylviocarcinus:						
1002000100	1000000000	100001010?	?000100000	0030002012	0100002210	
0101010001	1111000201	2110020111	1110000000	0100002000	0001103001	0
Goneplax:						
1002011100	0000000000	000000000?	?010001000	000?011000	0000000000	
0020100020	0000000201	3001000001	1110000000	0000000000	0001100001	0
Carcinoplax:						
1002011100	1000200000	000000000?	?010101000	000?011000	0000000000	
0020p00020	0000000201	10p0000001	1110000000	0000000000	0001100001	p
Coenophthalmus:						
0000100101	0000000100	000001000?	?000001000	000?011000	0200001000	
01101p0011	0000002000	2000000001	1111000000	0000000000	0101103001	1
Cyanograea:						
1202001?10	0010000000	010000200?	?001?00101	0010001002	0000000100	
0100000020	0000000200	1001000001	1110000000	0000001001	1000001010	0

Table 2. Continued

Austinograea:						
1102001?10	0000000000	010000200?	?001001101	0021002202	0000001110	
0100000020	0000000200	1001000001	1110000000	0000000001	0000002000	0
Bythograea:						
1102011?10	0010010000	010000200?	?001001101	0021012102	0000002110	
0100000020	0000000200	1001000001	1110000000	0000000002	1000002100	0
Cancer:						
0000000001	0000000000	100001010?	?000000000	000?010001	0000001000	
0010000000	1111000000	1000000000	0000000000	0000000000	000000000	0p
Pinnixia:						
1202001000	000?000000	000000200?	?000020010	0010011202	0000000?20	
0100001?00	0000002000	3001000001	1111001000	0000020001	1000000000	0
Pinnotheres:						
1102001000	000?000000	000000200?	?000020010	0010011202	0000000?20	
0100001?00	0000002000	3001000001	1111001000	0000020000	0000000000	0
Epilobocera:						
1302001100	0100100000	0100002020	0000010101	0011101200	1220010111	
0?p0100120	0000000200	1001022101	1110000000	0010000101	1100012100	0
Fredius:						
1302001100	0100100000	0100002000	0000010101	0011101200	1220010?21	
0?00000120	0000000200	1001022101	1110000000	0010000111	1100012100	0
Kingsleya:						
1302001100	0100100000	0100002000	0000010101	0011101200	1220010?21	
0?00000120	0000000200	1001022101	1110000000	0010000111	1100012100	0
Potamon:						
1202001100	0110010000	0201102021	01000p0000	001p101200	1000010211	
0110100120	0000000200	q001021001	1110000011	0000000002	1100012100	0
Potamonautes:						
1102001100	0110012000	0201102021	0100010000	0011101200	0200010211	
0110100120	0000000200	1001021001	1110000011	0000000002	1100012100	0
Sudanonautes:						
1102001100	0110012000	0201102021	0100010000	0011101200	02p0010211	
0110100120	0000000200	1001021001	1110000011	0000000002	1100012100	0
Platythelphusa:						
1002001100	0110011000	0001102011	0100000000	0011101200	p000000211	
0110100020	0000000200	2001021001	1110000011	0000000002	1100012100	0
Globonautes:						
1102001100	0110011000	0101102021	0100020000	0021101200	1220010221	
01p0000120	0000000200	1001021001	1110000011	0000000002	1100012100	0

Table 2. Continued

Socotra:						
1202001100	0110010000	0101101021	00000q0000	1021101200	0000110111	
0110000120	0000000200	q001021001	1111000011	0000000002	1100012100	0
Hydrothelphusa:						
1002001100	0110011000	0201102021	0100000000	0021101200	0210010221	
01p0100120	0000000200	q001021001	1110000011	0000000002	1100012100	0
Deckenia:						
1q02001100	0100000000	0201102021	0100020000	2121101200	0200210221	
0100000120	0000000200	2001021001	1110000011	0000000002	1100012100	0
Gecarcinucus:						
1202001100	0110010000	0100101011	0000000000	1021101200	0220210221	
0110100120	0000002000	0001011001	11?1000000	0000000002	1100011100	0
Holthuisana:						
1002001100	0110010000	0101102021	01000p0000	1010101201	0220110221	
0110000120	0000001010	1001021001	1111000010	0000000002	1100011100	0
Sayamia:						
1002001100	0110010000	0201102021	0100000000	101p101201	0220110221	
0110p00120	0000002010	q001021001	1111000000	0000000002	1100011100	0
Seychellum:						
1202001100	0110011000	0201100021	0100020000	2121101201	0220210221	
0100000120	0000000000	2001021001	1111000011	0000000002	110001?100	0
Cardisoma:						
1202001100	0101200000	0201101010	1100020000	000?001202	0001000220	
1100001120	0000102000	s0 00100001	1111000100	0001020002	1100012100	0
Grapsus:						
1202001100	0102000000	0011102020	11000q0000	000?001200	0000000220	
1100001120	0000001100	s0 00000001	1111000100	0001020002	1100012100	0
Euchirograpsus:						
0002000100	0100000000	001000202?	?000001000	000?001200	0000000220	
j 0110000020	0000000200	2000000001	1110000100	0001020002	0110012100	0
Varuna:						
0002000100	0100000000	001010000?	?0000p0000	000?000200	0000000010	
0120001120	0000102000	3000100001	1111000100	0001020002	1001112100	0
Sesarma:						
1202001100	0102000000	0011102000	0000000000	000?001200	0000000220	
1100001120	0000102000	3000100001	1111000100	0001020002	1100011100	0
Uca:						
1212001100	0101200000	0011?0000?	?000020000	000?001200	0000000220	
0100001110	0000102000	3000100001	1111000100	0001020002	1000012100	0
Ucides:						
1212001100	0101200000	0000?00010	1000020000	002000120?	0001000220	
0100001110	0000102000	s000100001	1111000100	0001020002	?0000111000	

ters. This approach identifies significant tree topology discrepancies when taxa are grouped based on their overall similarities, rather than grouped according to synapomorphies.

Results

Parsimony analysis with a combination of unordered and ordered characters (batch-1)

Figure 1 shows the 50% majority-rule consensus tree of the 100 bootstrap replicates (batch-1) that was obtained when characters **1**, **3**, **7**, **9**, **11–14**, **16**, **18–19**, **21**, **23–26**, **28–35**, **39**, **41–42**, **45–46**, **48–49**, **53**, **55–57**, **62**, **67**, **71–75**, **77–79**, **84–89**, **97–101**, **103–105**, **109–110**, **112–116**, and **119–121** were coded as ordered transformation series. Almost none of the apomorphies included in the analysis can be viewed as being uniquely derived. Instead, the majority of derived states have incongruent distributions when mapped onto the consensus tree (or any shortest length tree). No attempt was made to identify synapomorphies for each node, because of the general absence of hierarchical groupings (Fig. 1).

Batch-1 trees support a clade consisting of the Pseudothelphusidae and the potamoids, with the Thoracotremata, Bythograeidae and Pinnotheridae placed as the (unresolved) sister groups of the pseudothelphusid+potamoid clade (Fig. 1). These findings are partially consistent with the cladistic study of brachyrhynchan groundpatterns conducted by Sternberg et al. (1999) and Sternberg & Cumberlidge (1999). Also consistent with the groundpattern groupings obtained in Sternberg et al. (1999) is that *Carcinus* was placed as the sister taxon of the Trichodactylidae (see Rodríguez, 1992), with this clade forming a polytomy with the remaining portunoids and the Geryonidae. A weakly supported group consisting of the portunoids (inclusive of the geryonids and trichodactylids) and Goneplacidae s.s. (i.e. subfamilies Carcinoplacinae and Goneplacinae), and the *incertae sedis* genus *Beuroisia*, formed a trichotomy with the [bythograeid, pinnotherid, pseudothelphusid+potamoid clade, Thoracotremata] set. Interestingly, both the hypothesis presented in Sternberg et al. (1999) and the cladistic analysis presented here revealed no evidence for a monophyletic Xanthoidea.

Among the batch-1 trees (Fig. 1), the African potamonautids were found to have a polytomous arrangement relative to *Potamon*, *Platythelphusa*, *Globonautes*, [*Deckenia+ Seychellum*], *Hydrothelphusa*,

and a [*Gecarcinucus* [*Holthuisana+Sayamia*]] group. A new freshwater crab genus from Socotra (*Socotra* Cumberlidge & Wranik, 2000) was likewise grouped in the above-mentioned polytomy (Fig. 1).

Parsimony analysis with all characters unordered (batch-2)

General heuristic search analyses of 100 bootstrap replicates were performed with all characters coded as unordered transformation series (batch-2). The 50% majority-rule consensus tree of the batch-2 hypotheses (Fig. 2) generated a pattern largely congruent with the batch-1 hypothesis (Fig. 1). The only trenchant difference between the two hypotheses is that the Portunoidea+Goneplacidae s.s. clade formed a polytomy with the [bythograeid, pinnotherid, pseudothelphusid+potamoid clade, Thoracotremata] set, Cancridae, Platyxanthidae, Carpiliidae, two eriphiid groups, a [[Panopeidae+Xanthidae] Pilumnidae] line, and the *incertae sedis* genus *Beuroisia*.

Phenetic analyses

Both the neighbour-joining (NJ) and UPGMA analyses of morphological distances generated a pattern of groupings somewhat consistent with the parsimony-generated results: the pseudothelphusids and potamoids exhibit a greater amount of overall morphological similarity with the thoracotremes than with any other heterotreme group (Figs 3 and 4). The pseudothelphusids as a group are placed next to the potamoids in both phenograms (Figs 3 and 4) indicating that they are sister taxa, regardless of the criteria used for grouping. The position of the trichodactylids, on the other hand, differs greatly according to the algorithm used. In the UPGMA analysis, the trichodactylids are shown to be part of the goneplacid, portunoid, and xanthoid cluster, although somewhat distant from each of these. Largely consistent with the batch-1 and batch-2 hypotheses, a UPGMA-based {{Pseudothelphusidae+Potamoidea} + {Thoracotremata {Bythograeidae +Pinnotheridae}}} grouping was apparent (Fig. 3). Also congruent with the parsimony-based results is the juxtapositioning of the goneplacids (+ *Beuroisia*) and portunoids by UPGMA. The xanthoids form a cluster with the Cancridae and hypothetical outgroup on the grounds of total morphological distance.

The results of the NJ analysis (Fig. 4) positioned the trichodactylids within a portunoid set, and the Goneplacidae s.s. is again placed as the nearest
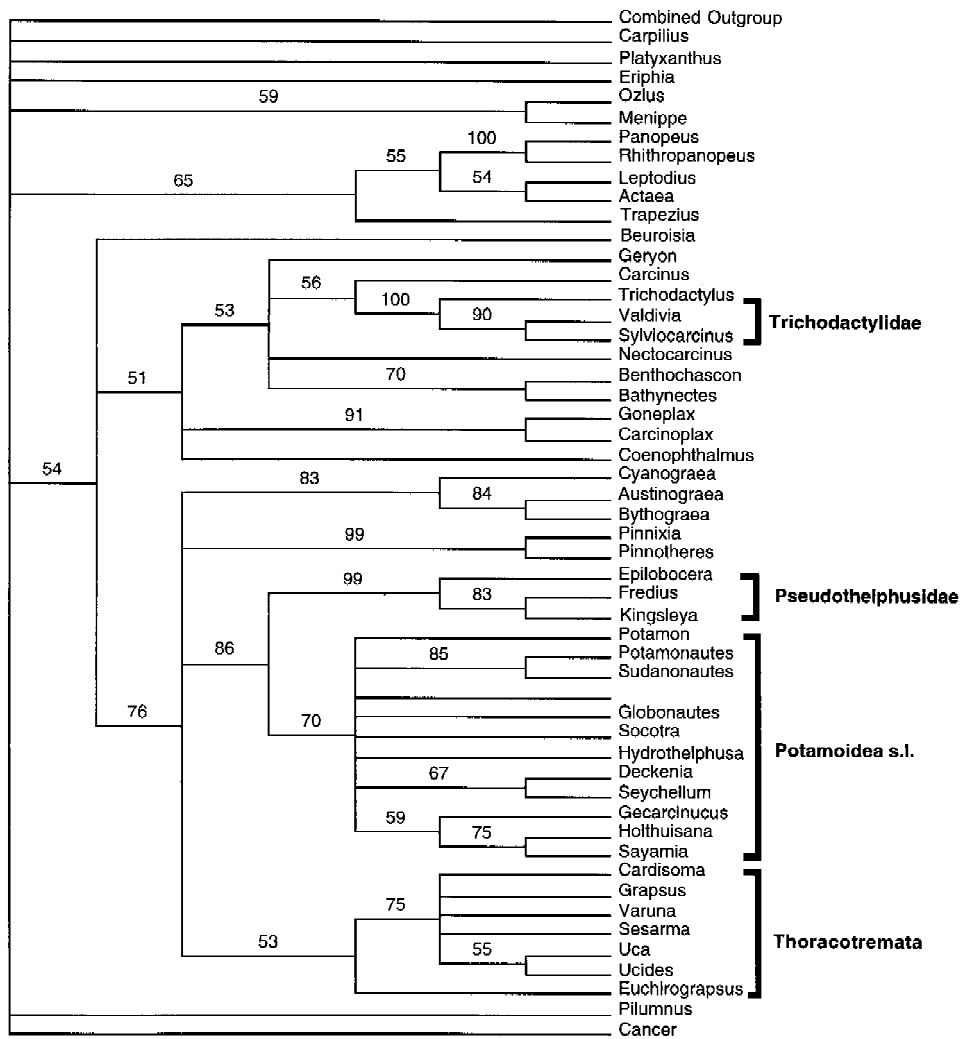
32

Figure 1. Bootstrap 50% majority rule consensus tree of Eubrachyuran relationships supported by bootstrapped parsimony using a combination of ordered and unordered characters. Numbers indicate bootstrap proportions >50 obtained from a heuristic search of 100 bootstrap replicates of 121 parsimony-informative characters for 51 ingroup taxa and a combined outgroup (Table 2), using the heuristic search option of PAUP 4.0 (Swofford, 2000).

morphological relation of the Portunoidea. In addition, the portunoid+goneplacid NJ 'line' is placed basal to a {pinnotherid {bythograeid {Thoracotremata {pseudothelphusid+potamoid}}}} pattern as is seen in the batch-1 hypothesis (Fig. 1). And the xanthoids form a cohesive set in the NJ tree (Fig. 4).

It should also be noted that the UPGMA and NJ calculated relationships among the potamoid genera are (at least in part) consistent with some recent taxonomic arrangements (e.g., Cumberlidge, 1999).

Conclusion

Parsimony searches for nested hierarchical relation-

ships among 51 representative brachyrhynchan genera, using 121 morphological characters, resulted in a small set of hypotheses concerning the position of the freshwater crab families in the Eubrachyura (Figs. 1 and 2). The majority of the bootstrap replicate clado-grams support a sister group relationship between the Neotropical Pseudothelphusidae and a Palaeotropical potamoid clade. This finding supports the results of the groundpattern analysis of Sternberg et al. (1999) and Sternberg & Cumberlidge (1999). Four almost invariant apomorphies are found among the pseudothel-phusids and Old World freshwater crabs. These are: (i) a distinct semicircular vertical groove on the carapace sidewall, extending from the epibranchial tooth to the
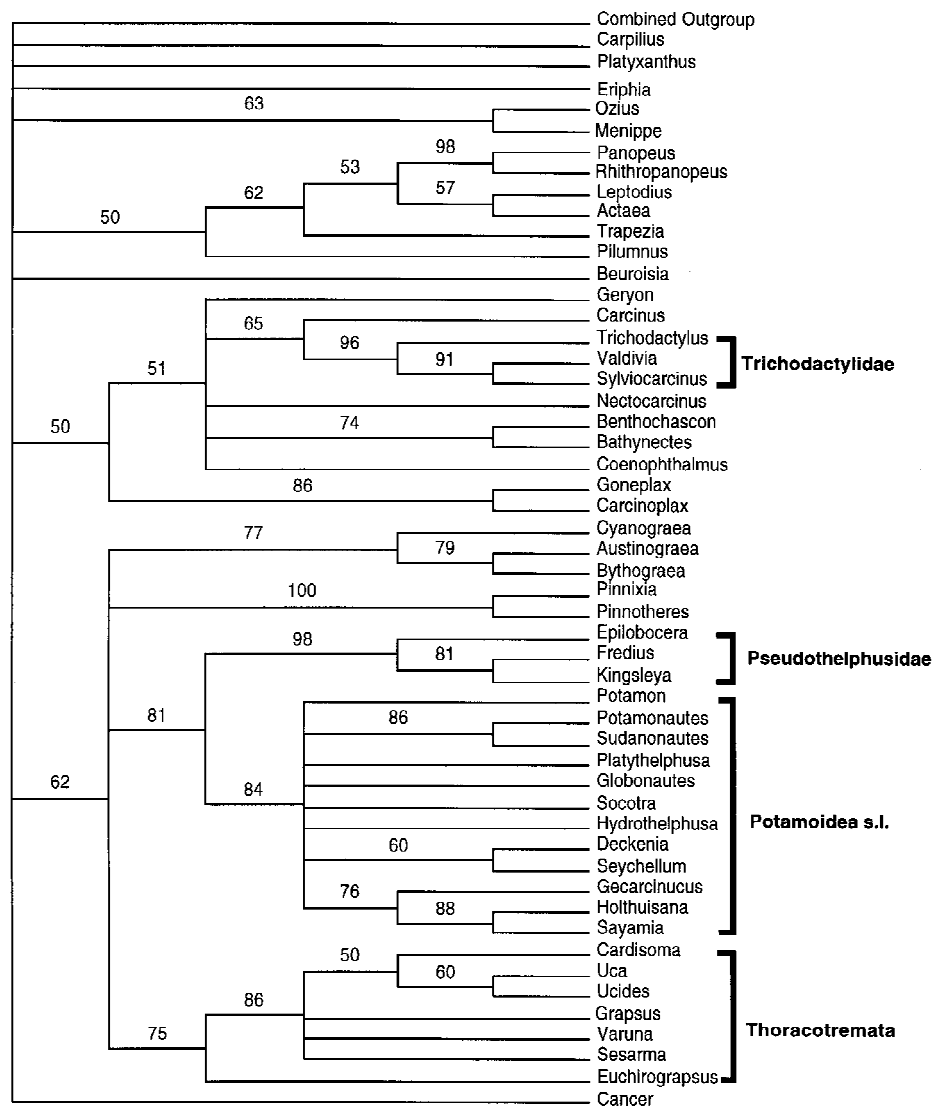
Figure 2. Bootstrap 50% majority rule consensus tree of Eubrachyuran relationships supported by bootstrapped parsimony using all un-ordered characters. Numbers indicate bootstrap proportions >50 obtained from a heuristic search of 100 bootstrap replicates of 121 parsimony-informative characters for 51 ingroup taxa and a combined outgroup (Table 2), using the heuristic search option of PAUP 4.0 (Swofford, 2000).

epimeral sulcus (**29-1**); (ii) a sharp and prominent median projection on the epistome (**43-1**), which is (iii) flanked by distinct incisions (**45-1**); and (iv) third maxillipeds which completely enclose the buccal chamber (**60-1**). These four apomorphies support a node linking the pseudothelphusids and Potamoidea. Given that no evidence has been found to discount a [Pseudothelphusidae+Potamoidea] clade, such a relationship is considered here to be a good working hypothesis (see also Sternberg et al., 1999).

The objective of this study was to clarify the position of the freshwater crab families within the Eubrachyura, as opposed to resolving relationships within any one freshwater crab group. The general absence of hierarchical freshwater crab generic relationships observed for the batch-1 and batch-2 consensus trees, are undoubtedly due to the high degree of incongruence seen for almost all character states that have been examined (excepting for the four just mentioned above). Numerous other mosaic character state combinations are also found distributed among the
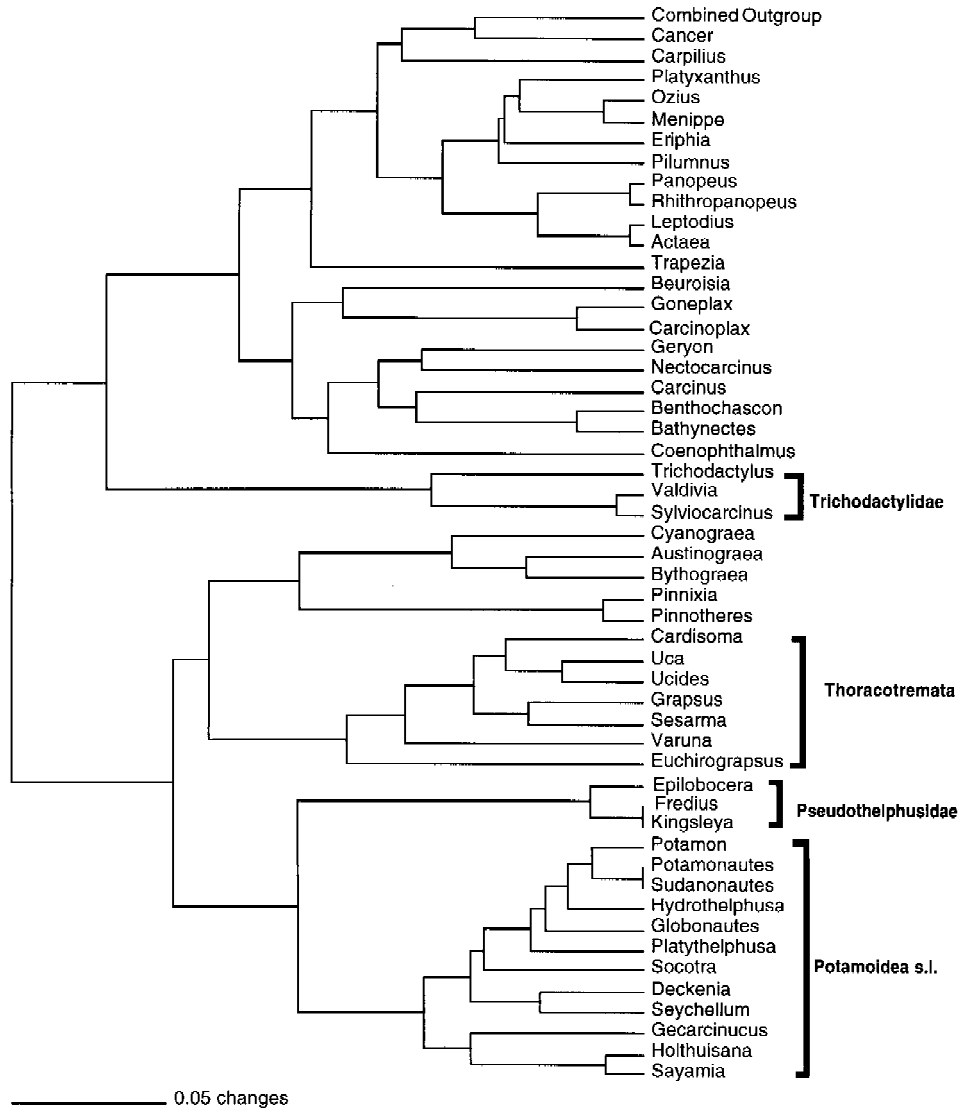
Figure 3. Phylogram derived by UPGMA cluster analysis of Eubrachyuran relationships for 51 ingroup taxa and a combined outgroup (Table 2). Phylogram based on 121 characters generated by PAUP 4.0 (Swofford, 2000). Branch lengths are drawn to scale.

pseudothelphusids and various subclades of potamoids in combinations that support conflicting hypotheses of relationships. For example, pseudothelphusids and the African potamoids have the following characters in common: (a) a horizontally-oriented median projection on the epistome (**44-1**); (b) a male telson which tends to be triangular in outline (**78-1**); (c) a specific conformation of the anterior region of the plastron (sternites 1–5) (see Rodriguez, 1992; Cumberlidge, 1999); and (d) similarities in the subbranchial, suborbital, and pterygostomial regions of the carapace, and in the outline of the buccal frame. Many of these

characters need to be investigated further and so have not been included in the present work.

On the other hand, pseudolungs are found in the Pseudothelphusidae (Rodriguez, 1986), the African globonautines (Cumberlidge, 1991), the African deckeniids (unpublished data), *Madagopotamon* (unpublished data), *Seychellum* (unpublished data), and some Australian parathelphusids (Taylor & Greenaway, 1979). Pseudolungs are notably absent from most African and Australasian potamoids, and so this character state distribution would conflict with
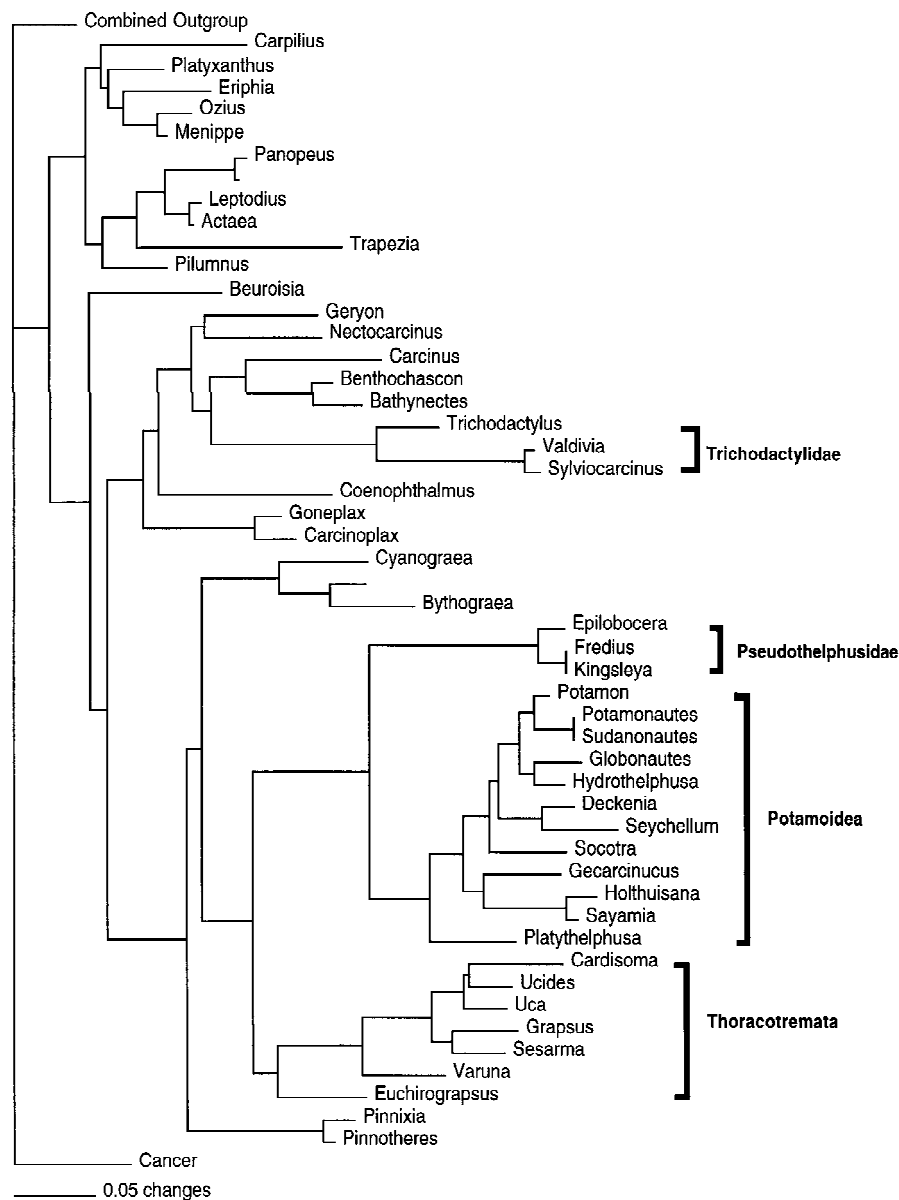
Figure 4. Neighbor-joining phylogeny of Eubrachyuran relationships for 51 ingroup taxa and a combined outgroup (Table 2). Phylogram based on 121 characters generated by PAUP 3.1.1 (Swofford, 1993). Branch lengths are drawn to scale.

a [pseudothelphusid+African potamoid] sister group relationship.

A mandibular palp with a bilobed terminal segment is shared by the Asian and Australian gecarcinucids and parathelphusids, African globonautines, and pseudothelphusids (see Bott, 1970; Rodríguez, 1986; Ng, 1988; Cumberlidge, 1999), and has been considered to be a synapomorphy for a [Pseudothelphusidae [Gecarcinucidae+Parathelphusidae]] lineage

(Rodríguez, 1986; Ng et al., 1995). However, the presence of various intermediate conditions of the terminal segment of the mandibular palp such as those found among the African and Madagascan potamonautids undermines confidence in such intercontinental relationships. Moreover, a close relationship between the Pseudothelphusidae, Gecarcinucidae, and Parathelphusidae is contradicted by a number of characters found in the latter two Old World families that are

not found in the pseudothelphusids. These characters include: epigastric crests (**13-1**), postorbital crests (**16-1**), posterolateral carapace carinae (**24-1**), a distinct lateral carina on the extreme posterior margin of the carapace (**25-1**), carapace sidewall carinae (**32-1**), and a first gonopod with a significantly developed terminal article (**99-1**, **100-1**). These features are also shared by a number of other Old World potamoids (e.g. deckeniids, potamids and most potamonautids) with a mandibular palp with a 'simple' (i.e. single) terminal segment. It is clear that relationships among the Old World potamoids must first be resolved before additional character states can be added to the node linking the pseudothelphusids and the Old World potamoids. Whatever the final hypothesis of relationships within and among the various nontrichodactylid freshwater crab groups, homoplasy on a massive scale will have to be accommodated.

A comment must also be made about the taxonomic distribution of the two-segmented mandibular palp in brachyuran crabs. A two-segmented mandibular palp was previously hypothesized to be a synapomorphy linking the pseudothelphusids and potamoids (Sternberg & Cumberlidge, 1999; Sternberg et al., 1999). Insofar as nearly all basal members of the various eubrachyuran families and superfamilies have a three-segmented mandibular palp (a plesiomorphy), it was correct to code the groundpattern of groups such as the eriphiids or xanthids as having the plesiomorphic state. However, it is now apparent that marine crab genera from a diverse range of families have either a two-segmented mandibular palp or a 3-segmented palp that shows incomplete fusion of the proximal and penultimate segments. A two-segmented mandibular palp is by no means an exclusively freshwater crab characteristic, and it is found in many marine crab groups including most portunoids, some corystoids, some trichodactylids, various xanthoids and possibly all majoids (unpublished results). Because parsimony analysis does not support a singular derivation of a two-segmented mandibular palp, it is a strong possibility that this apomorphy is a rampant homoplasy among eubrachyurans. For example, the Portunoidea includes families with a 3-segmented mandibular palp (e.g. the Geryonidae), families with a 3-segmented palp with intermediately fused proximal-penultimate segments (e.g. *Scylla*), and families with a 2-segmented palp. This means that either the apomorphic 2-segmented mandibular palp has repeatedly arisen in the portunoids, or that recurrent reversals to the 3-segmented condition are common.

The strict consensus of the shortest trees in our parsimony searches (Figs 1 and 2) both position the [pseudothelphusid+potamoid] clade in a polytomy with the Thoracotremata, a result that robustly supports the conclusions of Sternberg & Cumberlidge (1999) and Sternberg et al. (1999). However, many of the apomorphies previously thought to be unique to the [Thoracotremata [Pseudothelphusidae+Potamoidea]] lineage have since been identified in members of the Pinnotheridae. For example, pinnotherids lack an endostomial gutter (**48-2**) and some taxa also have pereiopod 2–5 meri which are subtriangular in cross-section (**110-1**), with rugosities on the surface (**111-1**). The presence of states **48-2**, **110-1**, and **111-1** in pinnotherids suggests that this family might either occupy a position basal to the Thoracotremata, with the pseudothelphusids and potamoids as the sister taxon of a pinnotherid+thoracotreme clade, or as the group basal to the [Thoracotremata [Pseudothelphusidae+Potamoidea]] lineage. Guinot (1977, 1979) previously placed the Pinnotheridae in the Thoracotremata although Guinot & Richer De Forges (1997) moved the family to the Heterotremata on the basis that this taxon lacks truly sternal male gonopore openings. It is clear that additional pinnotherid genera must be examined before any firm conclusions regarding sister group relationships of the pinnotherids *vis-à-vis* the thoracotremes and nontrichodactylid freshwater crabs can be reached. This is especially important insofar as some pinnotherid genera (e.g. *Pinnotherelia* and *Tritodynamia*) have a distinctly thoracotreme-like habitus and thus may hold a basal station within the group.

The same applies to the bythograeids which were found to form a polytomy with the pinnotherids, thoracotremes and nontrichodactylid freshwater crabs. The bythograeid groundpattern is remarkably like that of pseudothelphusids, and it seems unlikely that a family associated with deep-sea hydrothermal vents (bythograeids) on the one hand, and a family associated with semiterrestrial habitats and cloud-forest environments (Pseudothelphusidae) on the other, could have attained strikingly similar habitus by 'convergence.' However, more detailed morphological comparisons (and molecular analyses) must be conducted before a definite conclusion can be reached about the placement of the Bythograeidae in the Eubrachyura.

Jamieson et al. (1995) tested the position of the African potamonautid *Potamonautes* within the context of the Brachura through a cladistic study of mainly

spermatozoal characters. *Potamonautes* was placed basal to the xanthid *Pilodius* and the trapeziid *Calocarcinus* in a 50% majority rule consensus tree of 959 shortest cladograms obtained from a parsimony analysis using only spermatozoal characters (Fig. 1a of Jamieson et al., 1995). However, when the 27 spermatozoal characters were combined with 7 non-spermatozoal morphological characters in a heuristic search, the resulting strict consensus tree positioned *Potamonautes* as part of a polytomy with the majids, thoracotremes, *Portunus*, and the xanthoids (Fig. 1a of Jamieson et al., 1995). Since the spermatozoal characters used by Jamieson et al. (1995) cannot resolve relationships within the Heterotremata s.l., that study should not be viewed as incongruent with the results obtained here or elsewhere (Sternberg et al., 1999).

It must be reiterated that a disconcertingly high incidence of character state incongruence was found with the adult eubrachyuran morphological characters used in the present study. Aside from universal support for a Pseudothelphusidae+Potamoidea sister group hypothesis, hierarchical relationships are obscured within the Eubrachyura in general and freshwater crabs in particular. Our preliminary studies (unpublished) indicate that the degree of confidence in any hypothesis of taxic relationships of freshwater crabs decreases dramatically as the number of characters and taxa is increased. This appears to be the result of a 'theme/variation' model of diversification within the Eubrachyura, as opposed to an inappropriate choice of characters or inappropriate character coding. The theme/variation model (Thomson, 1988) posits that whereas a hierarchy of morphotypes or 'morphological themes' can be discerned, the considerable taxic variation observed within a morphotype hinders precise determination of sister group relationships. In other words, it is easier to determine relationships among morphotypes (groundpatterns) than among taxa that share the same morphotype. Presumably this is because the morphotype reflects a preferred domain in morphospace, wherein considerable character state recombination can occur (Thomson, 1988). The fact that very few apomorphies appear to be unique to any one eubrachyuran group suggests that the various crab lineages have differentially parcelled morphological conditions derived from a basic set of shared, potential morphological conditions. Cladistic analyses of eubrachyuran familial relationships using a set of genera from each family (as performed here) would thus be expected to generate much weaker hypotheses compared to those using groundpatterns,

because of the 'conflicting' character recombinants found among genera and species within a family or superfamily. A test of the theme/variation model of eubrachyuran morphological relationships hinges upon comparing the parsimony results obtained from using a larger set of characters from a larger and more representative set of marine and freshwater crab genera, selected on the basis of rigorously inferred familial groundpatterns.

Appendix 1

Listing and current systematic placement of Eubrachyuran taxa used in the cladistic and phenetic studies. Institution acronyms are: FM = Field Museum, Chicago; MNHN = Paris Museum; MT = R.G. Mus. Afr. Centr.; NMU = Northern Michigan Univ. Biol. Dept. Collection; SM = Senckenberg Museum, Frankfurt; UMML = University of Miami Marine Laboratory Invertebrate Museum; and USNM = Smithsonian Institution.

Heterotremata Guinot, 1977
    Bythograeoidea Williams, 1980
    Bythograeidae Williams, 1980
    Austinograea alayseae Guinot, 1989; exMNHN 24055 (NMU uncatalogued)
    Bythograea thermydron Williams, 1980; FM 5591
    Cyanograea praedator de Saint Laurent, 1984; USNM 239196
Corystoidea Samouelle, 1819
    Cancridae Latreille, 1803
    Cancer (*Metacarcinus*) *borealis* Stimpson, 1859; UMML 32.2431
Xanthoidea Macleay, 1838
    Carpiliidae Ortmann, 1893
    Carpilius corallinus (Herbst, 1783); UMML 32.839

Eriphiidae MacLeay, 1838

Eriphia gonagra (Fabricius, 1781); UMML 32.1132

Menippe mercenaria (Say, 1818); UMML 32.8217

Ozius reticulatus (Desbonne & Schramm, 1867); NMU uncatalogued

Panopeidae Ortmann, 1893

Panopeus purpureus (Lockington, 1877); NMU uncatalogued

Rhithropanopeus harrisii (Gould, 1841); UMML 32.3160

Pilumnidae Samouelle, 1819

Pilumnus dasypodus Kingsley, 1879; uncatalogued

Pilumnus sayi Rathbun, 1897; uncatalogued

Platyxanthidae Guinot, 1977

Platyxanthus crenulatus A. Milne Edwards, 1879; UMML 32. 7651

Trapeziidae Miers, 1886

Trapezia cymodoce (Herbst, 1801); USNM 286050

Xanthidae Macleay, 1838

Actaea acantha (H. Milne Edwards, 1834); UMML 32.529

Leptodius agassizii A. Milne Edwards, 1880; UMML 32.7286

Portunoidea Rafinesque, 1815

Geryonidae Colosi, 1923

Chaceon quinquedens (Smith, 1879); UMML 32.3950

Portunidae Rafinesque, 1815

Bathynectes superba (Costa, 1853); UMML 32.2450

Benthochascon schmitti Rathbun, 1931; UMML 32.2434

Carcinus maenas (Linnaeus, 1758); NMU uncatalogued

Coenophthalmus tridentatus A. Milne Edwards, 1879; USNM 65037

Nectocarcinus tuberculosus A. Milne Edwards, 1860; USNM 64716

Superfamily Uncertain

Goneplacidae MacLeay, 1838

Beuroisia Guinot & Richer de Forges, 1981 sp.; USNM 371429

Carcinoplax longimanus (de Haan, 1833); USNM 265063

Goneplax sigsbei A. Milne Edwards, 1880; UMML 32.7236, 32.7269

Pinnotheridae de Haan, 1833

Pinnixia cristata Rathbun, 1900; UMML 32.1967

Pinnotheres maculatus Say, 1818; UMML 32.7661

Potamoidea Ortmann, 1896

Deckeniidae Ortmann, 1897

Deckenia mitis Hilgendorf, 1869; NMU III.1990

Gecarcinucidae Rathbun, 1904

Gecarcinucus jacquemonti (H. Milne Edwards, 1844); SM 1763

Globonautes macropus (Rathbun, 1898); NMU 18.VIII.1988

Seychellum alluaudi (A. Milne Edwards & Bouvier, 1893); MT 56.895

Parathelphusidae Colosi, 1920

Holthuisana (Austrothelphusa) transversa (Martens, 1868); SM 5156

Holthuisana festiva (Roux, 1911); SM 7369

Sayamia sexpunctata (Lanchester, 1906); NMU uncatalogued

Potamidae Ortmann, 1896

Potamon edule (Latreille, 1818); NMU 17.1996

Potamonautidae Bott, 1970

Erimetopus brazzae (A. Milne Edwards, 1886); MNHN BP 71

Hydrothelphusa bombetokensis (Rathbun, 1904); MNHN BP 63

Potamonautes aloysiisabaudiae (Nobili, 1906); NMU VII.1993

Platythelphusa armata A. Milne Edwards, 1887; uncatalogued

Sudanonautes africanus (A. Milne Edwards, 1869); NMU 9.IV.1983B(#37)

Superfamily Unknown

Pseudothelphusidae Rathbun, 1893

Epilobocera sinuatifrons (A. Milne Edwards, 1866); NMU uncatalogued

Fredius reflexifrons (Ortmann, 1897); NMU uncatalogued

Kingsleya latifrons (Randall, 1840); NMU 13.IX.1994

Superfamily Unknown

Trichodactylidae H. Milne Edwards, 1853

Sylviocarcinus pictus Pretzmann, 1968; NMU uncatalogued

Trichodactylus fluviatilis Latreille, 1828; NMU 29.V.1999

Valdivia serrata White, 1847; NMU 30.VI.1983

Thoracotremata Guinot, 1977

Gecarcinoidea Dana, 1851

Gecarcinidae Dana, 1851

Cardisoma guanhumi Latreille, 1825; UMML 32.7414

Grapsoidea Dana, 1851

    Grapsidae Dana, 1851

    Grapsinae Dana, 1851

    Goniopsis pulchra Lockington, 1877; NMU 6.XI.1996

    Sesarminae Dana, 1852

    Sesarma curacaoense de Man, 1892; UMML 32.1333

    Sesarma reticulatum (Say, 1817); UMML 32.1337

    Varuninae Alcock, 1900

    Euchirograpsus americanus A. Milne Edwards, 1880; uncatalogued

    Varuna litterata (Fabricius, 1798); MNHN B 25736

Ocypodoidea Fabricius, 1798

Ocypodidae Fabricius, 1798

    Heloeciinae H. Milne Edwards, 1852

    Ucides occidentalis (Ortmann, 1898); UMML 32.929, 32.7400

    Ocypodinae Fabricius, 1798

    Uca pugilator (Bosc, 1802); UMML 32.859

    Uca vocator vocator (Herbst, 1804); UMML 32.8680

References

Bott, R., 1955. Die Süsswasserkrabben von Africa (Crust., Decap.) und ihre Stammesgeschichte. Ann. Mus. R. Congo Belge C (3,3) 1: 213–349.

Bott, R., 1970. Die Süsswasserkrabben von Europa, Asien, Australien und ihre Stammesgeschichte. Abh. Senckenberg naturf. Ges. 526: 1–338.

Cumberlidge, N., 1991. The respiratory system of *Globonautes macropus* (Rathbun, 1898), a terrestrial freshwater crab from Liberia (Gecarcinucoidea, Gecarcinucidae). Crustaceana 61 (1): 69–80.

Cumberlidge, N., 1999. The freshwater crabs of West Africa. Faune et flore tropicales 35: 1–382 (IRD, Paris).

Danser, B. H., 1950. A Theory of Systematics. Bibliotheca Biotheoretica series D, IV, pars 3. E.J. Brill, Leiden: 117–180.

Glaessner, M. F., 1969. Decapoda. In: Moore, R. C. (eds), Treatise on Invertebrate Paleontology. Part R. Arthropoda 4. Geological Soc. of America 2: R399–533.

Guinot, D., 1977: Donnés nouvelles sur la morphologie, la phylogenèse et la taxonomie des Crustacés Décapodes Brachyures: Thèse de Doctorat d'État es Sciences, Université Pierre-et-Marie-Curie; 2 vols.: i–xv, pp. 1–486, cvi-ssiv; 56 feuilles n.n., 78 figs., 31 pls., 14 tabs.

Guinot, D., 1979: Donnés nouvelles sur la morphologie, la phylogenèse et la taxonomie des Crustacés Décapodes Brachyoures. Mém. Mus. natn. Hist. nat., Paris (A Zool.) 112: 1–354, pls. 1–27.

Guinot, D., B. G. M. Jamieson & C. C. Tudge, 1997. Ultrastructure and relationships of spermatozoa of the freshwater crabs *Potamon fluviatile* and *Potamon ibericum* (Crustacea, Decapoda, Potamidae). J. Zool., Lond. 241: 229–244.

Guinot, D. & B. Richer De Forges, 1997. Affinités entre les Hymenosomatidae MacLeay, 1838 et les Inachoididae Dana, 1851 (Crustacea, Decapoda, Brachyura). Zoosystema 19: 453–502.

Maddison, W. P. & D. R. Maddison, 1996. MacClade. Ver. 3.06. Analysis of Phylogeny and Character Evolution. Sinauer Associates, Sunderland, Massachusetts.

Magalhães, C. & M. Türkay, 1996a. Taxonomy of the Neotropical freshwater crab family Trichodactylidae. I. The generic system with description of some new genera (Crustacea: Decapoda: Brachyura). Senckenbergiana Biol. 75: 63–95.

Magalhães, C. & M. Türkay, 1996b. Taxonomy of the Neotropical freshwater crab family Trichodactylidae. II. The genera *Forsteria*, *Melocarcinus*, *Sylviocarcinus* and *Zilchiopsis* (Crustacea: Decapoda: Brachyura). Sencken. Biol. 75: 97–130.

Magalhães, C. & M. Türkay, 1996c. Taxonomy of the Neotropical freshwater crab family Trichodactylidae. III. The genera *Fredilocarcinus* and *Goyazana* (Crustacea: Decapoda: Brachyura). Sencken. Biol. 75: 131–142.

Ng, P. K. L., 1988. The Freshwater Crabs of Peninsular Malaysia and Singapore. Department of Zoology, National University of Singapore, Shinglee Press. pp. I–viii, 1–156, 4 color plates.

Ng, P. K. L. & P. Naiyanetr, 1993. New and recently described freshwater crabs (Crustacea: Decapoda: Brachyura: Potamidae, Gecarcinucidae and Parathelphusidae) from Thailand. Zool. Verhandel. 284: 1–117.

Ng, P. K. L. & G. Rodríguez, 1995. Freshwater crabs as poor zoogeographical indicators: a critique of Banarescu (1990). Crustaceana 68 (5): 636–645.

Ng, P. K. L., Z. Stevcic & G. Pretzmann, 1995. A revision of the family Deckeniidae Ortmann, 1897 (Crustacea: Decapoda: Brachyura: Potamoidea), with description of a new genus (Gecarcinucoidea: Gecarcinucidae) from the Seychelles, Indian Ocean. J. nat. Hist., Lond. 29: 581–600.

Pretzmann, G., 1973. Grundlagen und Ergebnisse der Systematik der Pseudothelphusidae. Z. zool. Syst. Evol. Forsch. 11: 196–218.

Rodríguez, G., 1982. Les crabes d'eau douce d'Amerique. Familie des Pseudothelphusidae. Faune Tropicale 22: 1–223 (ORSTOM, Paris).

Rodríguez, G., 1986. Centers of radiation of freshwater crabs in the Neotropics. Crust. Issues 4: 51–67.

Rodríguez, G., 1992. The freshwater crabs of America. Family Trichodactylidae and a supplement to the family Pseudothelphusidae. Faune Tropicale 31: 1–189. (ORSTOM, Paris).

Swofford, D. L., 2000. PAUP-Phylogenetic Analysis Using Parsimony. Ver. 4.0 Sinauer Associates, Sunderland, Massachusetts.

Taylor, H. H. & P. Greenaway, 1979. The structure of the gills and lungs of the arid-zone crab, *Holthuisana* (*Austrothelphusa*) *transversa* (Martens) (Sundathelphusidae: Brachyura) including observations on arterial vessels within the gills. J. Zool. 189: 359–384.

Thomson, K. S., 1988. Morphogenesis and Evolution. Oxford University Press, New York.

Sternberg, R. von, N. Cumberlidge & G. Rodríguez, 1999. On the marine sister groups of the freshwater crabs (Crustacea: Decapoda). J. Zool. Syst. Evol. Res. 37: 19–38.

Sternberg, R. Von & N. Cumberlidge, 1999. A cladistic analysis of the genus *Platythelphusa* A. Milne-Edwards, 1887 from Lake Tanganyika, East Africa (Decapoda: Potamoidea: Platythelphusidae) with comments on the phylogenetic position of the group. J. nat. Hist. 33: 493–511.