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On the marine sister groups of the freshwater crabs (Crustacea: Decapoda: Brachyura)

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Abstract

Freshwater crab sister group relationships with marine eubranchyuran families were investigated. A morphology-based cladistic analysis was conducted on representatives of the freshwater crab families Deckeniidae, Gecarcinucidae, Parathelphusidae, Potamidae, Potamonautidae, Pseudothelphusidae, and Trichodactylidae using a disparate assemblage of marine heterotreme and thoracotreme brachyurans as possible sister groups. The monophyly of the freshwater crabs *sensu lato* is falsified. The family Trichodactylidae and the marine portunid subfamily Carcininae form basal groups within the superfamily Portunoidea. The monophyly of the Pseudothelphusidae and the Paleotropical freshwater crab families is supported, and this clade is the sister group of the Thoracotremata (Gecarcinidae, Grapsidae s.l., and Ocypodoidea). The origin, groundplan, and diversification of freshwater crabs are discussed in the context of previously published scenarios of their evolution.

Key words: Eubranchyuran phylogeny – freshwater crabs – cladistic analysis

Introduction

Freshwater crabs are a diverse assemblage of eubranchyurans (Guinot 1977, 1978, 1979) distributed throughout the tropical and subtropical regions of Central and South America, Africa, Madagascar, southern Europe, India, Asia, and Australia. These decapods are characterized by direct development, maternal care of the young, low dispersal ability, restriction to a freshwater habitat, and the absence of close relatives in the marine environment. Freshwater crabs have colonized an array of habitats ranging from cold fast-flowing tributaries in the high Andean mountains, to warm tropical rivers and lakes, to marshes and rice paddies, to rain forest floors and dry savannas. Some species of freshwater crabs are completely aquatic, some are semi-terrestrial, and some are air-breathers that lead an arboreal existence (Rodríguez 1982; Ng 1988; Cumberlidge 1991; Cumberlidge and Sachs 1991; Rodríguez 1992). Despite more than one and a half centuries of collection activities, new species and new genera of freshwater crabs are still being discovered (e.g. Rodríguez 1992; Cumberlidge 1987, 1993, 1994, 1999; Cumberlidge and Clark 1992; Rodríguez and Pereira 1992; Ng and Naiyanetr 1993; Stewart et al. 1995; Ng et al. 1995; Magalhães and Türkay 1996a,b,c) and this group of brachyurans undoubtedly constitutes one of the most species-rich assemblages of decapods.

Although there is a large and increasing alpha-taxonomic literature on freshwater crabs, the higher-level systematics of this group is still very unstable. All freshwater crabs were originally placed into a single family, the Thelphusidae H. Milne Edwards 1837, the name of which was later revised to the Potamonidae Ortmann 1896 and, after emendation (Opinion 712, Bull. Zool. Nomenclature 1964), to the Potamidae. The late nineteenth and early twentieth century workers on 'telphusoid' systematics (Ortmann 1897; Rathbun 1904, 1905, 1906; Alcock 1910) considered all the world's freshwater crabs to comprise a single family with several distinct subfamilies; for example, Rathbun (1904, 1905, 1906) recognized three Paleotropical subfamilies, the Deckeniinae, Gecarcinucinae, and Potamoninae and two Neotropical subfamilies, the Pseudothelphusinae & Trichodactylinae. Bott (1955) greatly modified the taxonomy of freshwater crabs and placed all of the world's species in four families, the Paleotropical Deckeniidae, the Pale-

otropical Potamidae (as Potamonidae), the Neotropical Trichodactylidae, and the Neotropical Pseudothelphusidae. However, in his later works, Bott (1970a,b) recognized no less than 11 families of freshwater crabs separated into the Trichodactylidae plus three superfamilies: the Parathelphusoidea (later emended to the Gecarcinucoidea Rathbun 1904) for the Gecarcinucidae, Parathelphusidae, and Sundathelphusidae; the Potamoidea Ortmann 1896 for the Deckeniidae, Isolapotamidae, Potamidae, Potamonautidae, and Sinopotamidae; and the Pseudothelphusoidea Ortmann 1853 for the Potamocarcinidae and Pseudothelphusidae. The classification schemes of Bott (1955, 1970a,b) vaguely reflected the view that the freshwater crabs of the world constitute a polyphyletic assemblage with each family (and even groups within a family) having originated from distinct groups of marine crabs (envisioned as some sort of spiny mud crabs). Bott's (1970a,b) recognition of 11 distinct families of freshwater crabs influenced much of the later thinking on freshwater crab systematic and phylogenetic relationships, but investigations over the past two decades have revealed the artificiality of this arrangement. Serious doubts have been raised concerning the distinctions between the Paleotropical gecarcinucoid families Parathelphusidae and Sundathelphusidae (Ng 1988), and between the potamoid families Potamidae, Isolapotamidae, and Sinopotamidae (Ng 1988). It would thus appear that while the Paleotropical families Deckeniidae, Gecarcinucidae, Parathelphusidae, Potamonautidae, and Potamidae can be defined by various apomorphies, the same cannot be said about the other Paleotropical families (the Sundathelphusidae, Isolapotamidae, and Sinopotamidae). In addition, the referral of some genera and subfamilies to the latter three families is open to question because of vague taxonomic definitions by past workers. There is strong support for the idea that the Pseudothelphusidae and Trichodactylidae each form a natural group (Magalhães and Türkay 1996a,b,c; Rodríguez 1982, 1986, 1992; Sternberg 1997); but there is no support for the recognition of the Potamocarcinidae as a separate family, and this is now included in the Pseudothelphusidae (Rodríguez 1982). The familial groupings of the freshwater crabs are thus gradually becoming clarified in a piece-wise fashion, although no satisfactory progress concerning the higher systematics (interfamily relationships) of these crabs is

likely to be made until a rigorous search for synapomorphies has been undertaken.

It is our opinion that investigating freshwater crab higher systematics from the phylogenetic (cladistic) standpoint can do much to remove the ambiguities in subfamilial, familial, and superfamilial relationships. To a large extent the taxonomic uncertainty created by previous classifications can only be resolved by a clear understanding of the sister group relationships of the entire assemblage of freshwater crabs at all levels which, in turn, is dependent upon the determination of synapomorphies (and all that that entails). In the present work, we have a more modest aim — to identify the likely marine sister groups of the freshwater crabs so as to lay the groundwork for more detailed investigations of the group as a whole.

Objectives

There are a number of major obstacles to overcome in attempting to reconstruct the phylogeny of the Neotropical and Paleotropical freshwater crabs. Outgroup comparison and character state ordering require the identification of appropriate marine taxa suitable for use as sister groups of the freshwater crabs. However, with the possible exception of the Portunidae as the sister group of the Trichodactylidae (Rodríguez 1992; Sternberg 1997), specialists cannot agree on the selection of marine crab taxa that represent the closest relatives of the freshwater crabs.

It has been argued (e.g. Guinot et al. 1997) that since all Neotropical and Paleotropical freshwater crabs appear to belong to the eubrachyuran section Heterotremata (Guinot 1977, 1978, 1979), the closest sister taxa (taxon) of the freshwater crabs most probably belongs to a marine heterotrematous group. For example, a number of authors (e.g. Alcock 1898, 1899; Ortmann 1902; Bott 1955; Pretzmann 1973; for review see Rodríguez 1986) hold the opinion that all freshwater crabs can be tied to some family or subfamily within the Xanthoidea MacLeay (1838). Alcock (1899: 3) was the most specific and suggested that ‘...from consideration both of structure and of habitat, [the freshwater crabs appear] to have branched off from the Oziine or Eriphiine stocks...’ within the Xanthoidea. Other proposals have tied the Potamidae and Potamonautidae with the Corystoidea Samouelle (1819) (Jamieson et al. 1997), the Pseudothelphusidae with the Panopeidae Ortmann (1893), and the Trichodactylidae with the Eriphiidae MacLeay (1838). However, such opinions are based on only vague phenetic similarities between freshwater crabs and marine heterotremes that may not be robust enough to withstand a rigorous comparative investigation. Nevertheless, these publications have had the effect of convincing many workers that freshwater crabs can be allied with the corystoids and xanthoids, the result being a perhaps too limited domain for comparative investigations.

In recent years, freshwater crab taxonomists have focused a great deal of attention on characters of the male first pleopod (first gonopod) and the mandible, with the effect that many phylogenetic reflections draw heavily on characters of these organs. Characters of the first gonopod are useful because of the presumably weak selection pressure acting on these protected intromittant organs (which remain sealed inside the sterno-abdominal cavity by the tightly fitting abdomen except during mating or molting). However, within clearly monophyletic groups the topology of the first gonopod can be enormously variant and it is clear that several different structural types can exist within a group of freshwater crabs. Examples are available for the Pseudothelphusidae (Rodríguez 1982), the Trichodactylidae (Rodríguez 1992; Magalhães and Türkay

1996a,b,c), the Potamidae, Gecarcinucidae, and Parathelphusidae (Ng 1988), and the Potamonautidae (Cumberland 1999). Similarly, characters of the mandible in the Potamonautidae can also be variable within a group, and may not be reliable indicators of higher level groups (Stewart 1997; Cumberland 1999).

However, past emphasis on gonopod and mandible structure has meant that many other characters of potential significance may have been overlooked, for it is very unlikely that all somatic characters are under such strong adaptive pressure that they can be discarded from consideration. For example, characters of the orbital region (Rodríguez 1992) and the sternal plastron (Rodríguez 1992; Magalhães and Türkay 1996a,b,c) have been used successfully in phylogenetic studies of Neotropical freshwater crabs. With this in mind, the present work includes a number of carefully selected conservative homologous characters of the carapace, mouthparts, orbital region, sternum, and abdomen of marine and freshwater crabs.

The problem of the search for likely marine sister groups of freshwater crabs is an integral component of freshwater crab cladistics. In this paper we approach this problem (1) by considering most eubrachyuran clades as possible sister taxa of the various freshwater crab families, and (2) by using both established and new morphological characters in the phylogenetic analysis. The first step in this process is aimed at identifying and eliminating all eubrachyuran clades that are not possible sister groups of the freshwater crabs. In this way, more energy and time can be focused on the search for synapomorphies between freshwater crab clades and their likely marine sister groups.

Materials and methods

Character comparisons

The extensive work of Guinot (1977, 1978, 1979) on eubrachyuran relationships (encompassing the sections Heterotremata and Thoracotremata) was used as the framework for identifying plesiomorphic and apomorphic character states. We followed the methodology of Christoffersen and Araújo-de-Almeida (1994) for analyses involving multiple outgroups as possible sister groups of the ingroup taxa. Inasmuch as any of the marine crab families studied herein could turn out to be a sister group of the freshwater crabs, no one marine family was used as the outgroup taxon. Instead, a hypothetical taxon termed the ‘outgroup’, with all character states plesiomorphic, was used for tree rooting in the cladistic analysis (‘Lundberg rooting’; Lundberg 1972).

Material examined

The species of freshwater crabs representing the seven families that were analysed to obtain family level morphological characters are listed in Appendix 1. The species of marine crabs representing 13 of the 14 families that were directly examined are listed in Appendix 2. The superfamily, family, and subfamily designations largely follow those of Bott (1970a) and Guinot (1978). Glaessner (1969) and Guinot (1968b, 1978) were consulted for the character states of the Carpiliidae and Guinot (1979) was used to identify the platyxanthid groundplan. Alcock (1898, 1899), Guinot (1978, 1979), and Rathbun (1930) were consulted for overviews of cancrid, xanthoid and portunoid character states. The aberrant ocypodoidid *Ucides* Rathbun 1897 and the ocypodoidid subfamilies Dotillinae Stimpson 1858, Heloeciinae H. Milne Edwards 1852, and Ocypodinae Dana 1851 are collectively referred to here as the Ocypodioidea. The Grapsidae s.s. refers to the Grapsinae Dana 1851 plus Sesarminae Dana 1852. Unless otherwise indicated, the taxonomy of the Paleotropical freshwater crab subfamilies follows Bott (1970a,b).

Cladistic analysis

The data matrix is presented in Table 1 and the characters and states analysed are presented in Appendix 3. The characters chosen for

Table 1. Data matrix of characters and character states (see Appendix 3)

Outgroup	000000000	000000000	000000000	000000000	000000000	000000000	0
Cancridae	000000000	0001000010	100000000	110000000	000000000	000000000p	0
Carpiliidae	000000000	1000000010	0000p00p0	110000000	000000000	000000101	0
Eriphiidae	000100000	1000000010	000000000	000000011	000000000	000000101	0
Panopeidae	000000000	1000000000	000000000	1100000111	000000000	000000001	0
Platyanthidae	000000000	1000000010	000000000	000000011	000000000	000000001	0
Pilumnidae	000100000	1000000010	000000000	000000111	000000000	000000001	0
Trapeziidae	000001000	2000000010	000000000	000000011	000000000	000000001	0
Xanthidae	000000000	1000000000	000000000	1100000111	000000000	000000001	0
Bythograeidae	0001001000	2000001010	1000000010	0000000011	1000p0000	1p00000001	0
Geryonidae	000000000	0001000010	?00000020	111000011	100000000	000000000	0
Carcininae	000000000	0001000010	1000000020	1110000011	100000000	0000111000	0
Trichodactylidae	0000000100	0000001011	1000000020	1110000011	110000000	0000111000	0
Portuninae	000000000	0001100010	1000000020	1110000011	210000000	0000212010	0
Podophthalminae	000000000	000?100010	1000000020	1110000011	210000000	0000212010	0
<i>Eriocheir</i>	0020010010	1011010011	0000001211	0001011011	2101011101	1111111000	1
<i>Varuna</i>	0020000110	2010010010	0000000211	0001011011	2101010101	1111111000	1
<i>Euchirograpsus</i>	0000000?0	2000010011	0000000210	0001011011	2100011111	1110000000	1
<i>Hemigrapsus</i>	p020000100	2000010011	0000000211	0001011011	2100011111	0100000000	1
Grapsidae s.s.	1112011101	2000010011	0000p01p1p	0001011011	2101111111	1110000000	1
Gecarcinidae	1102011101	2000010011	0000p01211	0001011011	2101111111	1110000000	1
<i>Ucides</i>	0002101101	1000011011	0000100201	0001011011	2112111101	1110000000	1
Ocypodidae	00p2101100	2000011011	0000100201	0001011011	2112111101	1110000000	1
Deckenidae	1100001120	2010011111	0110110110	0000100011	0000011111	0110000000	1
Gecarcinucidae	110p001120	2110011111	0111p0111p	0000100011	Pp01011111	011000000p	p
Parathelphusidae	110p001120	2110011111	0111p01111	0000100011	Pp01011111	011000000p	p
<i>Platythelphusa</i>	1100001120	2110011111	0100010110	0000100011	0000011111	0110000000	1
Potamidae	1101001120	2110011111	0100010110	0000100011	pp00011111	111000000p	p
Potamonautidae	1101001120	2110011111	011p010110	0000100011	0000011111	111000000p	p
Pseudothelphusidae	0002001121	2000011111	0111110110	0001000011	2p00011111	1100000001	0

p, polymorphic 0 and 1; p, polymorphic 1 and 2; P, polymorphic 0 and 1 and 2;?, uncertainty.

inclusion in the analysis were those found to have qualitative states which are generally invariant within a family. States for some otherwise 'good' characters (e.g. carapace frontal deflexion) were found to vary between groups within a family; inasmuch as it is difficult to unambiguously identify groundplan states in such cases prior to cladistic analysis, the taxa were scored as being 'polymorphic' for such characters. Characters 60 and 61 were excluded from the parsimony analysis because of their plasticity within groups (see p. 11). The cladograms were established using the 'Heuristic, Branch Swapping, Nearest Neighbor Interchanges' search option of PAUP 3.1 (Swofford 1993) and all characters were treated as equally weighted, unordered transformation series. MacClade 3.06 (Maddison and Maddison 1996) was used to study character state distributions and character argumentation (Waggle 1994) was used to optimize nodal character states.

Results

Possible freshwater crab sister groups

All the freshwater crabs studied herein have a habitus which restricts possible marine sister groups to subgroups of the Heterotremata and Thoracotremata. Freshwater crabs and the following families have a shared groundplan (dorsal and frontal views of a generalized Paleotropical freshwater crab are shown in Fig. 1a,b, respectively): Bythograeidae Williams 1980, Cancridae (in part) Latreille 1803, Carpiliidae Ortmann 1893; Eriphiidae MacLeay 1838, Geryonidae Colosi 1923, Goneplacidae s.l. MacLeay 1838, Hexapodidae Miers 1886, Panopeidae Ortmann 1893; Pilumnidae Samouelle 1819, Pinnotheridae de Haan 1833, Platyanthidae Guinot 1977; Portunoidea Rafinesque 1815, Trapeziidae Miers 1886, and Xanthidae MacLeay 1838 in the Heterotremata; and Gecarcinidae MacLeay 1838, Grapsidae s.l. MacLeay 1838, and Ocypodoidea Rafinesque 1815 in the Thoracotremata. The syn-

apomorphic groundplan of all these families can be summarized under the concept of the 'cyclometopan' or 'brachyrhynchan facies' (e.g. Alcock 1898, 1899); that is, all of these families have the following derived characters:

- the carapace is broader than long,
- the anterolateral margin of the carapace is distinct,
- the carapace front is broad and does not form a 'rostrum',
- the antennules fold transversely,
- the orbits are present and well-defined, and the buccal frame is rectangular to square in general outline.

This excludes the Atelecyclidae Ortmann 1893, Belliidae (in part) Dana 1852, Calappoidea (in part) de Haan 1833, Corystidae Samouelle 1819, Dorippidae de Haan 1833, Haplocarcinidae Calman 1900, Leucosioidea Samouelle 1819, Majoidea Samouelle 1819, Palicidae Bouvier 1897, Parthenopoidea MacLeay 1838, Pirimelidae Alcock 1899, Retroplumidae Gill 1894, and Thiidae Dana 1852 from consideration as plausible sister groups of the freshwater crabs. The morphotype of the freshwater crabs can not be derived from that of very specialized eubrachyuran lineages such as the Hexapodidae, Pinnotheridae & Mictyridae Dana 1852 and thus these (super)families were excluded from consideration. In addition, many members of the Xanthoidea (e.g. Panopeidae and Xanthidae) have specialized carapace (e.g. areolations of the carapace surface) and gonopod morphologies which argue against a sister group relationship between any freshwater crab clade and these derived xanthoids. Representatives of derived xanthoid families were nonetheless included in the present study because of the above-mentioned citations positing a sister group relationship between the freshwater crabs and one or more

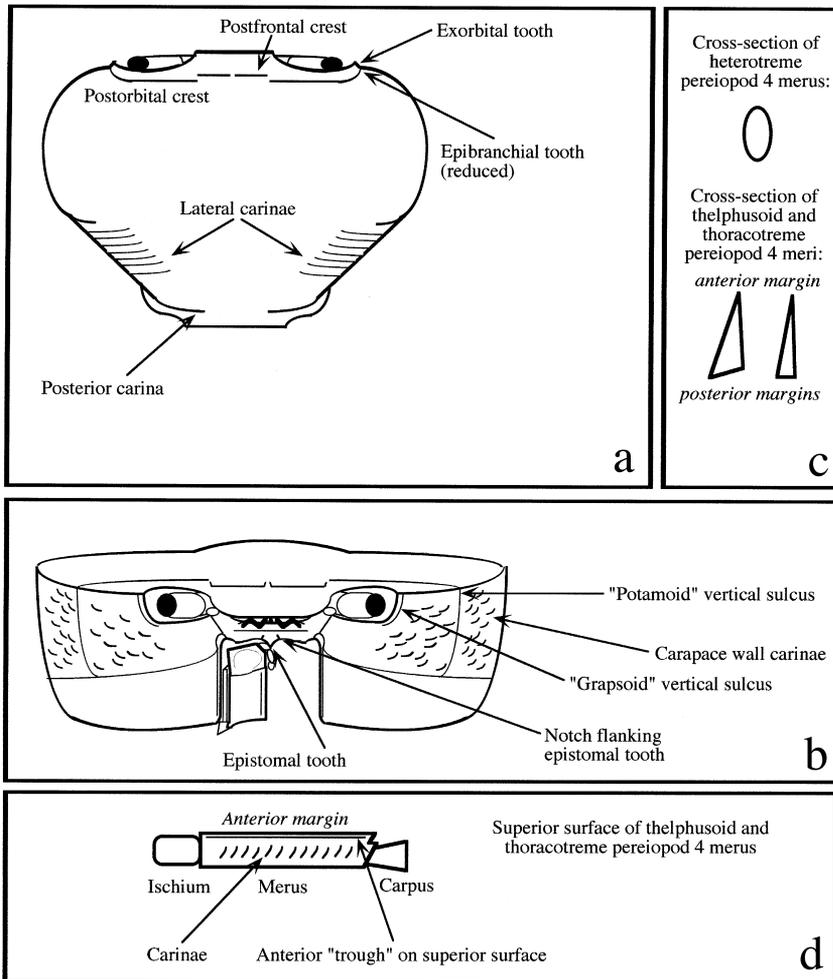


Fig. 1. Schematic outline of telphusoid and thoracotreme synapomorphies and homoplasies (refer to the text for discussion)

xanthoid lineages. The same could be said for the 'higher' portunoids except that basal portunoids do share apomorphies with the Trichodactylidae and thus the position of this freshwater crab family *vis-à-vis* the basal and derived portunoids is an open question. The goneplacids are a polyphyletic assemblage of heterotremes (Guinot 1969a,b,c) and many are highly specialized. Several of the goneplacid subfamilies are derived side-branches of the Panopeidae, Pilumnidae, and Xanthidae and reveal no apomorphic character states in common with the freshwater crabs studied; thus, these 'goneplacid grade' xanthoids are not considered further.

Since almost all of the marine families listed above as possible sister groups are species-rich and morphologically disparate, type genera and/or taxa with a morphologically generalized habitus were used to score character states for analysis (e.g. *Varuna* H. Milne Edwards 1830 for the Varuninae Alcock 1900). Uninformative (autapomorphic) character states were not considered and relevant literature (see below) was consulted to insure that the morphological characters chosen for analysis were indeed informative at the family level. Characters 60 and 61 ('oziine' and 'grapsoid' carapace outlines, respectively) were excluded from the cladistic analysis because of the extreme variability in carapace morphology observed within the eubranchyuran families studied.

Eighty-one equally parsimonious trees were obtained with a length of 152 steps, consistency index = 0.618, and a retention

index = 0.855. All trees placed the Trichodactylidae within the Portunoidea, and indicated a sister group relationship for a lineage consisting of the Pseudotelphusidae/Paleotropical freshwater crabs and the Thoracotremata. The 50% majority-rule consensus tree of the 81 trees is presented in Fig. 2. The Eubranchyura reveal a number of distinct trends for many major morphological characters (Guinot 1977, 1978, 1979) and this aids in the determination of plesiomorphic from apomorphic states. We agree with Wägele (1994, 1996) that cladistic hypotheses are only as good as the underlying hypotheses of synapomorphic groundplans for taxa and transformation series of each character. Thus, explicit hypotheses of morphological transformation are presented for the characters used in this analysis. Figures 3 and 4 present hypotheses of character state transitions within the framework of the consensus tree (Fig. 2). However, the reader should note that the consensus tree presented in Fig. 2 has been modified in Figs 3 and 4: first, the Carpiliidae and Panopeidae + Xanthidae form an unresolved polytomy with the branch encompassing the remainder of the Xanthoidea, the Bythograeidae, telphusoids, and Thoracotremata (Fig. 3); second, the grapsoid subfamily Varuninae is presented as monophyletic on the basis of sharing a character state reversal [7(0)] (Fig. 4); and third, the Potamonautidae, Potamidae, and the [Deckeniidae, *Platythelphusa* [Gecarcinucidae, Parathelphusidae]] clade are presented as forming an unresolved polytomy (Fig. 4) due to the absence of unam-

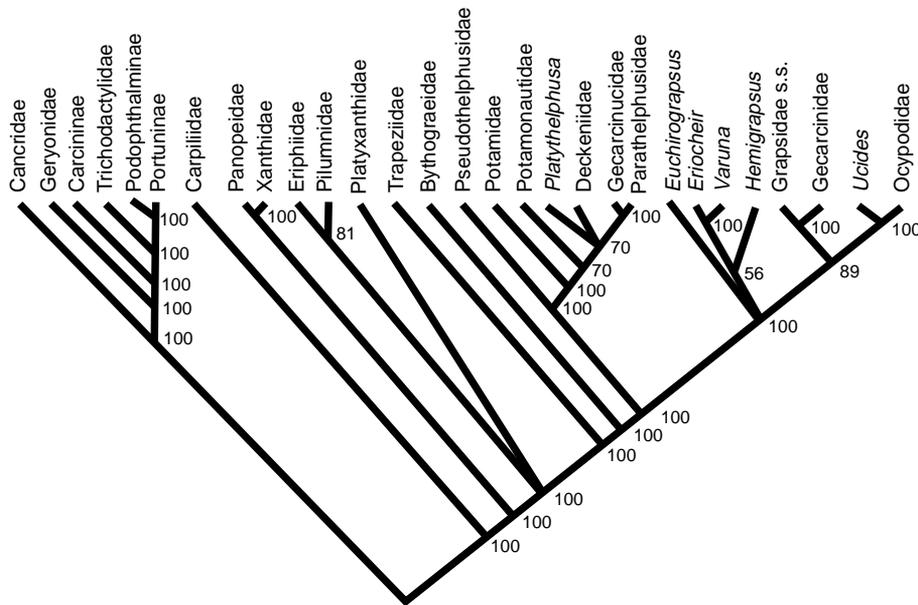


Fig. 2. Fifty per cent majority-rule consensus tree of 81 equally parsimonious trees. The numbers adjacent to nodes indicate the frequency of particular groupings. The placement of the thelphusoid clade next to the thoracotremes was invariant for all trees

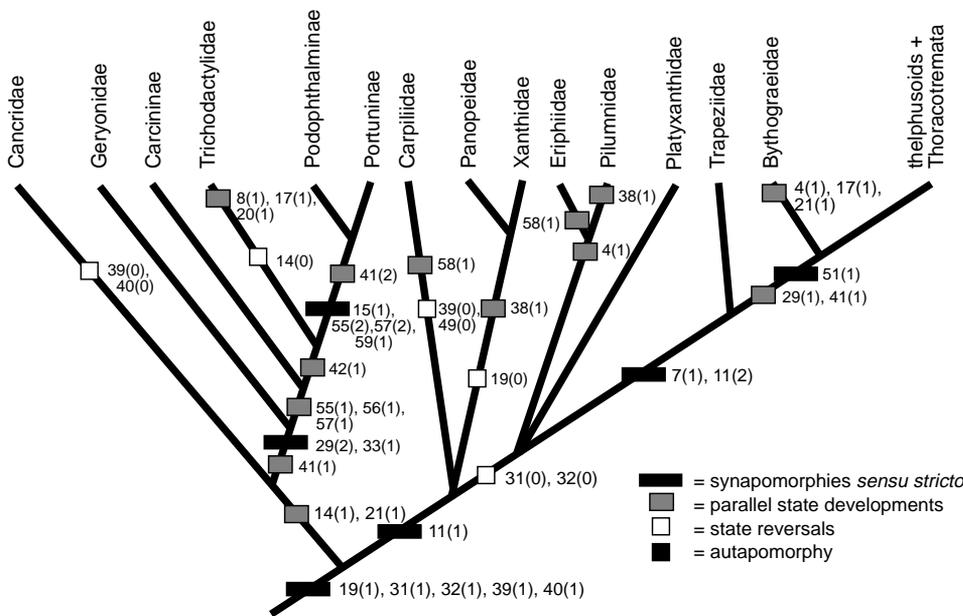


Fig. 3. Character states mapped onto the modified consensus tree (Fig. 2) of eubrachyuran relationships. See text for details concerning character argumentation

biguous synapomorphies allowing for the identification of potamid sister groups.

Carapace

Distinct plesiomorphic and apomorphic conditions were identified for a number of carapace characters. Within the section Heterotremata the plesiomorphic carapace states include: a carapace lacking lateral carinae or striae 1(0), no carinae on the carapace sidewall (subbranchial, subhepatic, and pterygostomial regions) 2(0), a frontal margin that projects horizontally and which is not deflexed 4(0), a distinct notch (or several) on the supraorbital margin 7(0), a frontal margin with a distinct medial cleft (unless the cleft is obscured by teeth on the frontal margin) 8(0), a carapace sidewall that lacks a ‘potamid’ vertical sulcus extending from the epibranchial tooth to the epi-

meral sulcus (see below) 9(0), a carapace sidewall that lacks a ‘grapsoid’ vertical sulcus close to the outer orbital margin 10(0), and a sharp, high carina on the posterior margin of the carapace 11(0). The Cancridae, Geryonidae, Portunoidea, and Trichodactylidae have states 1(0), 2(0), 4(0), 7(0), 8(0), 9(0), 10(0), and 11(0). The xanthoid families Carpliidae, Eriphiidae, Panopeidae, Pilumnidae, Platyxanthidae, and Xanthidae also exhibit these synplesiomorphies [the Eriphiidae and Pilumnidae have state 4(1)] except that these families have a somewhat reduced posterior carapace carina 11(1); that is, the posterior carina is distinct although not as sharp and high as the carina seen in the cancrids, geryonids, and portunoids. State 11(1) is postulated here to be the morphological precursor of the very narrow and reduced posterior carina 11(2) synapomorphic for the Trapeziidae, Bythograeidae, nontrichodactylid freshwater

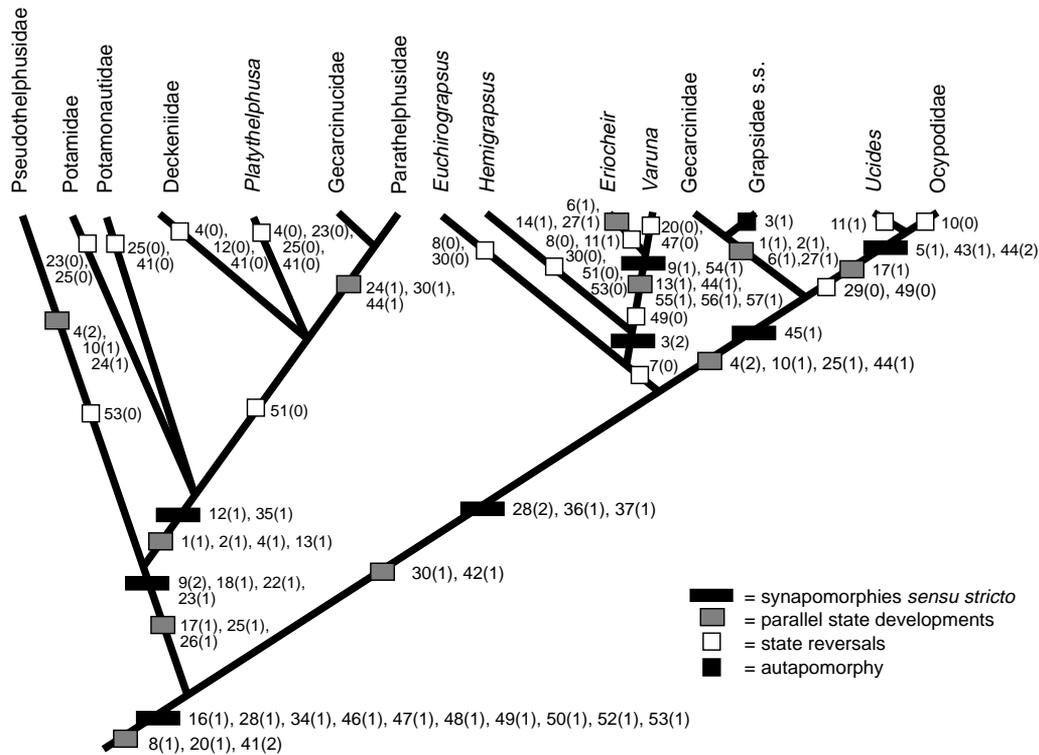


Fig. 4. Character states mapped onto the modified consensus tree (Fig. 2) of thelphusoid and thoracotreme relationships. See text for details concerning character argumentation

crabs, and thoracotremes. Adults of the Bythograeidae and Trapeziidae have the apomorphic state for character 7, positioning them basal to the nontrichodactylid freshwater crabs and thoracotremes.

Regarding characters 7 and 11, some state variability exists within the xanthoid groups examined. This variability is a matter of degree, however, inasmuch as virtually all xanthoid taxa studied possess supraorbital notches and have a distinct posterior margin carina, although the number of supraorbital notches (usually one or two), the development of the supraorbital notches, and the height of the posterior margin carina can differ among taxa. For example, *Carpilius* Leach (in Desmarest 1825) has state 11(1) although the large, high carina, distinct on the lateral margins, has been secondarily 'smoothed' medially. Furthermore, supraorbital notches are absent in *Carpilius* although distinct in other carpiliids (Guinot 1968b). A review of fossil corystoids, portunoids, and xanthoids (Glaessner 1969) strongly supports the position that states 7(0) and 11(1) are consistent attributes of the xanthoid groundplan. The presence of state 7(0) within certain grapsoid lineages [varunines; also state 11(1) within some varunines and *Ucides*] and thelphusoid (parathelphusid) lineages are cases of state reversals having independently occurred (see below).

The Pseudothelphusidae and the Paleotropical freshwater crab families Deckeniidae, Gecarcinucidae, Parathelphusidae, Potamidae, Potamonautidae, and *Platythelphusa* form a monophyletic group (Fig. 4) henceforth referred to collectively as the 'thelphusoids'. (The taxic designation 'thelphusoid' is used for convenience only and is not intended to supersede the currently recognized superfamilies.) All thelphusoids have a vertical sulcus on the carapace subhepatic region extending from the epibranchial tooth (or very near this tooth) to the epimeral sulcus

9(2), and this sulcus is very distinct in all potamoids and many gecarcinucoids (Fig. 1b). In these families this sulcus is usually lined with a row of tubercles on the posterior side. Many pseudothelphusids have a faint 'potamoid' vertical sulcus on the carapace sidewall although this sulcus is distinct in the most primitive members of the family (subfamily Epilobocerinae). To our knowledge, no Paleotropical thelphusoid completely lacks this character and state 9(2) is considered a robust synapomorphy for the Pseudothelphusidae + Paleotropical freshwater crabs. Some varunines (*Eriochelir* de Haan, 1835, and *Varuna*) have a weak vertical sulcus with a topological position identical to that seen in the thelphusoids 9(1).

All of the Paleotropical thelphusoid families (except the Deckeniidae) possess a distinct postorbital crest 12(1) (Fig. 1a) indicating the monophyly of a clade comprising the Gecarcinucidae, *Platythelphusa*, Parathelphusidae, Potamidae, Potamonautidae; the absence of a postorbital crest in the Deckeniidae is interpreted as a character state reversal [12(1) → 12(0)] because other characters (see below) support the inclusion of this family in a Paleotropical thelphusoid clade. Carapace character states 1(1) and 2(1) (homoplastically developed in the Grapsidae s.s. and Gecarcinidae; see below) support the monophyly of all the Paleotropical thelphusoids as does another character, namely a distinct posterior carina that is parallel to the posterolateral margin of the carapace and anterior to the space for the pereopod 5 coxa 13(1) (Fig. 1a), which is homoplastically present in the varunines *Eriochelir* and *Varuna*.

All most parsimonious hypotheses of relationships place a clade consisting of the [varunines [[Gecarcinidae + Grapsidae s.s.] Ocypodoidea]] (i.e. Thoracotremata) as the marine sister group of the thelphusoid clade (Figs 2 and 4). Only one carapace condition supports this arrangement: the frontal median cleft

8(1) is absent, that is, the carapace frontal margin is straight (reversed in *Eriocheir* and in *Euchirograpsus* H. Milne Edwards 1853; homoplastically developed in the Trichodactylidae).

Several apomorphies are homoplastically shared among thelphusoids and thoracotreme subclades. One most noticeable homoplasy is the presence of distinct carapace lateral carinae or striae 1(1) in the Paletropical thelphusoids, Gecarcinidae + Grapsidae s.s. clade, and some species of *Hemigrapsus* Dana 1851. In all these taxa the presence of carapace lateral carinae is independent of carapace shape and degree of 'inflation' of the carapace and it is not correlated with habitat. The Paletropical thelphusoids and the Gecarcinidae + Grapsidae s.s. clade also have distinct carinae on the carapace sidewall 2(1). A front that is elongated and vertically deflexed 4(2) is synapomorphic for the [[Gecarcinidae + Grapsidae s.s.] Ocypodoidea] clade and is a homoplastic development in the Pseudothelphusidae. The Paletropical thelphusoids have a moderately deflexed front 4(1) that covers most of the antennular fossae (a condition also seen in the Eriphiidae, Pilumnidae, and Bythograeidae) but it should be noted that various degrees of character state reversal are also seen in subclades (e.g. *Platythelphusa*). In addition, the Gecarcinidae, Grapsidae s.s. (except some sesarmines), *Ucides*, and basal members of the Pseudothelphusidae have a 'grapsoid' vertical sulcus on the carapace subhepatic region which flanks the outer orbital margin 10(1) (reversed in the Ocypodidae; Fig. 1b). This 'grapsoid' vertical sulcus is not topologically homologous with character 9; the epilobocerine pseudothelphusids have both characters.

The ocypodoids have one carapace synapomorphy: the deflexed region of the carapace front has a narrowly trapezoid-to-spatulate conformation 5(1). In the Gecarcinidae and Grapsidae s.s. the epigastric lobes are considerably anterior to the line of the supraorbital margins 6(1), an attribute of this clade which has also been independently developed in *Eriocheir*. The varunines *Eriocheir*, *Hemigrapsus*, and *Varuna* have in common a distinct oblique margin running divergently subparallel to the posterior half of the carapace margin; this margin begins to diverge from a region posterior to the middle point of the carapace margin 3(2) and forms a triangular facet on the postero-lateral region of the carapace. A less distinct oblique margin 3(1) is characteristic of the Grapsidae s.s., and is found in some ocypodoids.

Given the large number of genera and species found in the thelphusoid families, some variation is to be expected in character state expression. Such is the case with characters 1 and 4 where, even within a genus, variation exists in the development of the lateral carinae and in the degree of frontal margin deflexion. The Potamonautidae, for example, show a range in the development of the lateral carinae from distinct (*Sudanonautes africanus* A. Milne-Edwards 1869, *Liberonautes chapleri* A. Milne-Edwards 1887, and *Potamonautes ecorseii* Marchand 1902) to secondarily faint or absent (*S. monodi* Balss 1929, *L. paludicolis* Cumberlidge & Sachs 1989, and *P. senegalensis* Bott 1970). Similarly, in some Australasian freshwater crab genera (e.g. *Holthuisana* Bott 1969) the lateral carinae are very pronounced in some species and very weak in others (Bishop 1963). The Pseudothelphusidae entirely lack lateral carapace carinae. *Platythelphusa armata* A. Milne-Edwards 1887 has a front that projects straight out and shows no deflexion 4(0), while different species in the Parathelphusidae exhibit variable degrees of deflexion of the front 4(0,1). [The 'frontal median triangle' of Bott 1970b (see also Ng 1988) seen in the Parathelphusidae may be a special case of carapace front vertical

deflexion in some taxa.] It is highly unlikely that lateral carinae and frontal deflexion have developed *de novo* within the hundreds of species of freshwater crabs: it is far more likely that these two carapace characters are an ontogenetic attribute of these thelphusoids and are treated as such in Fig. 4 (i.e. as synapomorphies for the Paletropical thelphusoids with reversals having occurred in subclades). Indeed, a preliminary morphological analysis of hatchlings of *Sudanonautes africanus* A. Milne-Edwards 1869 revealed lateral carinae on the carapace and a pronounced frontal deflexion.

Traces of orbital notches can be detected in a few Asiatic freshwater crabs of the family Parathelphusidae. These orbital notches are entirely fused in species of *Sommaniathelphusa* Bott 1968 from Thailand, but slight depressions can be found in the region topologically equivalent to where such notches occur. Incompletely fused orbital notches are present in *Ceylonthelphusa rugosa* Kingsley 1880 indicating that a parathelphusid-specific morphocline exists for these structures, a morphocline which is a reversal of the general eubranchyuran morphocline: complete absence of supraorbital notches → fused supraorbital notches with slight sutures (remnants) present → incompletely fused orbital notches (supraorbital notches are not completely redeveloped in parathelphusids). In other words, whereas the putative ancestral group of the Trapeziidae, Bythograeidae, thelphusoids, and thoracotremes acquired fused supraorbital notches, a few parathelphusid taxa (not the majority of the reviewed family members) have redeveloped the plesiomorphic condition. All varunines examined exhibit very distinct orbital notches and this state reversal is interpreted as supporting the monophyly of the varunine clade.

The Trichodactylidae, in contrast to the thelphusoids, have plesiomorphic states for all carapace characters studied except 8 (the frontal margin cleft). The frontal margin cleft is highly reduced 8(1) in the trichodactylids although the front is bilobed. The placement of the Trichodactylidae within the Portunoidea (Rodríguez 1992) is supported in the present study by several synapomorphies (see below) although none of the carapace characters used here supports a sister group relationship between the Trichodactylidae and any portunoid family. The Cancridae, Geryonidae, and Portunidae have a frontal carapace margin that has large, blunt teeth 14(1) (also seen in *Eriocheir*; absent in Trichodactylidae) although the Podophthalminae are ambiguous for this character because of the highly reduced carapace front. The portunoid subfamilies Podophthalminae and Portuninae have a distinct transverse epibranchial carina 15(1) (in addition to having an oval carapace outline), and the absence of the epibranchial carina in the Carcininae and Trichodactylidae is evidence that these clades occupy basal positions within the Portunoidea.

Epistome and mouthparts

Symplesiomorphic character states in the Brachyura (including the Podotremata) include: a bilobed median subepistomal projection 16(0) (referred to as an 'epistomal gutter'; Rodríguez 1992; Guinot 1976: Fig. 8); the median projection on the posterior epistomal margin is low 17(0); and notches flanking the projection are lacking 18(0); endostomial ridges demarcating the efferent channels are absent 19(0) (see Ng 1983); the third maxilliped exopod is approximately 0.5–0.35X the width of the ischium 20(0); the first maxilliped endopod lacks a 'portunoid lobe' 21(0); the first maxilliped endopod is not medially expanded beyond the endostomial ridges 22(0); the mandibular palp is three-segmented 23(0) and has a simple terminal segment

24(0); the buccal frame has a square to rectangular outline 25(0); and the medial margins of the third maxilliped ischia and meri do not meet, that is, they do not completely enclose the buccal cavity 26(0). Ng (1983) presented evidence to suggest that endostomial ridges 19(1) are an apomorphy within the Eubrachyura. The distribution of this character state is congruent with Ng's hypothesis because state 19(1) is a synapomorphy for all the families included in this study, and reversals to the plesiomorphic state are characteristic of the Panopeidae, Xanthidae, and of some taxa in the Eriphiidae, Pilumnidae, and Trapeziidae.

The thelphusoids + Thoracotremata lack an epistomal gutter 16(1) and this is a strong synapomorphy for this clade. However, some Parathelphusidae (*Oziothelphusa senex* Fabricius 1798, *Archipelothelphusa grapsoides* H. Milne Edwards 1853, *Travancoriana schirnerae* Bott 1969; and *Mainitia mainitensis* Balss 1937) have remnants of an epistomal gutter. Another synapomorphy for the thelphusoids + Thoracotremata is a slender third maxilliped exopod 20(1), where the width of the exopod is less than 0.35X the width of the ischium. State 20(1) was homoplastically developed in the Trichodactylidae. *Varuna* exhibits the plesiomorphic condition for character 20.

As pointed out by Rodríguez (1992), the presence of a portunoid lobe on the endopod of the 1st maxilliped 21(1) is a robust synapomorphy for a clade consisting of the Cancridae, Geryonidae, Trichodactylidae, and the Portunidae. A portunoid lobe is homoplastically present in the Bythograeidae. The presence of state 21(1) in the trichodactylids constitutes a strong argument that this family is not allied with any of the Paleotropical thelphusoids, all of which lack a portunoid lobe.

The Gecarcinidae + Grapsidae s.s. have a third maxilliped with an ischium and merus are sharply constricted at the point of their articulation 27(1), and a similar condition is seen in *Eriocheir*. In all thelphusoids the ischia and meri of the third maxillipeds are medially expanded so that they completely fill the buccal frame 26(1). In contrast, the ischia and meri of the third maxillipeds of the trichodactylids are slim and do not enclose the buccal frame 26(0). The traditional interpretation of the broadening of the ischium and merus of the third maxilliped is that this is an adaptation to semiterrestrial life. However, slim third maxillipeds that leave a conspicuous gap along their medial margins when closed are found in semiterrestrial grapsids and in the terrestrial land crabs (Gecarcinidae), while completely aquatic thelphusoids (such as *Platythelphusa* and all members of the Potamonautidae) uniformly possess broad, medially expanded third maxillipeds that completely fill the buccal frame. The expanded third maxillipeds of the thelphusoids are therefore decoupled from semiterrestriality and thus cannot be dismissed as convergent adaptations. It should also be noted that some carpiliids have state 26(1) as do some bellioids (e.g. *Bellia* H. Milne Edwards 1848), calappoids, hymenosomatids, and majoids, and this is undoubtedly homoplastic with the condition seen in the thelphusoids.

The thelphusoids can be distinguished by the following set of apomorphies: the median projection on the posterior epistomal margin forms a strong triangular tooth (the epistomal tooth) that juts outward and/or downward 17(1) (Fig. 1b); a notch is present on either side of the epistomal tooth on the posterior epistomal margin 18(1) (Fig. 1b; this notch is reduced but present in some pseudothelphusids); the endopod of the first maxilliped is medially expanded, extending considerably beyond the endostomial ridges 22(1); and the synapomorphic groundplan

of the thelphusoids includes a two-segmented mandibular palp 23(1). State 17(1) is also seen in the Bythograeidae, Trichodactylidae, and ocypodoids; although homoplastically developed in other eubrachyuran families, the epistomal tooth is a consistent feature of the thelphusoids and thus is considered an aspect of the thelphusoid synapomorphic groundplan. The notches flanking the epistomal tooth 18(1) must likewise be considered an attribute of the ur-thelphusoids as it is distinct in primitive pseudothelphusids (Epilobocerinae) and all Paleotropical thelphusoids examined. All thelphusoid families except the Potamidae and *Platythelphusa* have a two-segmented mandibular palp (Bott 1970a; Rodríguez 1986; Ng 1988; Ng et al. 1995; Ng and Rodríguez 1995; Cumberlidge 1999). It has been stated that the three-segmented mandibular palp seen in the potamids and platythelphusids represents the ancestral condition and thus the Deckeniidae, Gecarcinucoidea, Potamonautidae, and Pseudothelphusidae form a clade by reason of having a two-segmented palp. The cladistic evidence suggests, however, that the two-segmented palp is a synapomorphy for the Pseudothelphusidae and Paleotropical clades (Fig. 4), with independent reversals [23(1) → 23(0)] in the Potamidae and *Platythelphusa*. However, a mandibular palp with a bilobed terminal segment 24(1), characteristic of the Gecarcinucoidea and the Pseudothelphusidae, appears to have arisen independently in these two clades (Fig. 4). States 18(1), 22(1), and 23(1) appear to be unique within the Eubrachyura; in addition, no marine crabs to our knowledge have a mandibular palp with a bilobed terminal segment.

All members of the Deckeniidae, Pseudothelphusidae, and ocypodoids have the vertical margin of the buccal frame widened ventrally, and in some taxa the vertical margin is outwardly concave, giving the buccal frame a barrel-shaped outline 25(1). State 25(1) is interpreted as a synapomorphy for the thelphusoid clade followed by independent reversals in some gecarcinucoids, *Platythelphusa*, Potamidae, and Potamonautidae; the basis for this interpretation rests on the fact that the Pseudothelphusidae, Deckeniidae, Madagascan potamonautids, West African Globonautinae, and Indian Gecarcinucidae possess the apomorphic condition. Likewise, state 25(1) is viewed as homoplastically developed in the ancestor of the [[Gecarcinidae + Grapsidae s.s.] [Ucides + Ocypodidae]] clade. The buccal cavity is square-shaped in the varunines.

Male sternum and abdomen

The thelphusoids have traditionally been placed in the section Heterotremata (Guinot 1978) as these crabs possess strictly coxal male openings, i.e. the penis of these crabs emerges to contact the first and second gonopods via an aperture on the coxa of the fifth pereopod. Male openings on the fifth pereopod coxae constitute part of the synapomorphic groundplan of the Eubrachyura, whereas penises which emerge through a sternal aperture to contact the gonopods and never pass through apertures on the fifth pereopod coxae are synapomorphic for the Thoracotremata (Guinot 1978, 1979). A dissection of the region encompassing the fifth pereopod coxa/sternite 7–8 region in both marine and freshwater crabs revealed the male openings in *Cancer*, the portunoids, the Trichodactylidae, and the xanthoids to be strictly coxal (Guinot 1978: Fig. 3(a)). The thelphusoids present a more complicated picture as some Paleotropical taxa have male openings which approximate Guinot's (1978: Fig. 3a) 'state 4' condition although the penis passes through the coxal condyle or emerges at the base of the coxa, near or through the articular membrane (Ng, 1988).

In the Pseudothelphusidae the penis emerges very near the articular membrane and this state ‘bridges’ the heterotreme and thoracotreme conditions 28(1). Within the Thoracotremata the varunines were found to have strictly sternal penial emergence points 28(2); presenting a condition very close to that of the Gecarcinidae and *Ucides*. It was found that *Goniopsis* de Haan 1833 and *Grapsus* Lamarck 1801 in the Grapsidae s.s. have male openings in roughly the same position as that of some pseudothelphusids, i.e. the penis emerges next to the articular membrane adjacent to the coxa of pereopod 5. However, in these grapsines and in sesarmines the penis emerges through a sternal opening after passing through the articular membrane. The ocypodoids all have sternal openings near the median of sternite 7 or 8. From this it can be determined that a morphocline for penial emergence points exists within the Eubrachyura: coxal openings (heterotremes s.l.) → the penis emerges at the base of the coxa of the fifth pereopod near the articular membrane (thelphusoids) → Sorts the sternal openings are near the coxae of the fifth pereopods (gecarcinids, *Ucides*, varunines) → the sternal openings are near the median of sternites 7 or 8 (Ocypodidae). The ancestral node for the thelphusoids + Thoracotremata is interpreted here to be state 28(1) from which the thoracotrematous condition 28(2) developed (Fig. 4).

Apomorphic modifications of the male abdomen shape have occurred in a number of eubrachyuran lineages. The synapomorphic groundplan of the Geryonidae, Carcininae, Trichodactylidae, and Portunidae s.s. includes a male abdomen shaped like a (sub)equilateral triangle 29(2). Nearly all portunid subclades possess this synapomorphy although in some taxa (e.g. *Callinectes* Stimpson 1860) the male abdomen takes the form of an inverted T.

An independent synapomorphy of the male abdomen 29(1) unites the Bythograeidae, thelphusoids, and Thoracotremata. In these clades the male abdomen shape is a narrow triangle 29(1) as opposed to the plesiomorphic finger-like outline seen in xanthoids 29(0); *Ucides* and the Ocypodidae exhibit a reversal to the plesiomorphic state 29(0). Modifications of state 29(1) are seen in some thelphusoid subclades. For example, some taxa in the Parathelphusidae have an abdomen with segments a5 and a6 sharply constricted thus presenting an inverted-T outline (analogous to that seen in some portunoids) although closely related taxa have an abdominal outline which is more narrowly triangular (Bishop 1963). Some fossil carpiliids appear to have state 29(1) (Glaessner 1969) although recent taxa (*Carpilius*) have the plesiomorphic condition. Some pilumnids also have developed state 29(1).

A male telson with a triangular outline is the plesiomorphic state for this character in the Eubrachyura. A male telson with a tongue-shaped outline 30(1) is presented in Fig. 4 as a synapomorphy for the Thoracotremata, with independent reversals 30(0) in *Euchirograpsus* and *Hemigrapsus*. Within the Gecarcinucoidea, state 30(1) has arisen within some subclades of the Gecarcinucidae and Parathelphusidae and transitional states are seen in some gecarcinucids such as *Travancoriana schirnerae*.

The Cancridae, Geryonidae, Portunoidea and the xanthoid families Carpiliidae, Panopeidae, Xanthidae, and some of the Trapeziidae have abdominal segments a4 and a5 31(1) and a3 and a4 32(1) fused. The subfamily Dilocarcininae of the Trichodactylidae has states 31(1) and 32(1) whereas the Trichodactylinae has the plesiomorphic states (Rodríguez 1992). It should be noted that since abdominal segment fusion appears to have occurred in a pairwise manner, segment fusions are

coded accordingly. Sternberg (1997) hypothesized that fusion of abdominal segments a3/a4 and a4/a5 has occurred in parallel in the cancrids, geryonids, carcinines, and trichodactylids and so the groundplans for these clades were coded here as having the plesiomorphic state. The basis for this hypothesis is the fact that some trichodactylids have distinct sutures between these segments coupled with the fact that abdominal segment fusion is polymorphic in several xanthoid families (Ng 1983). The above hypothesis is largely refuted, however, by global parsimony considerations (Fig. 3). The hypothesis presented here positions states 31(1) and 31(2) at the ancestral node of the eubrachyuran families included in this study (Fig. 3), followed by character state reversals [31(0), 32(0)] at the ancestral node of the lineage including the Eriphiidae + Pilumnidae, Platyxanthidae, Trapeziidae, Bythograeidae, and thelphusoids + Thoracotremata.

Within the sterno-abdominal cavity of male eubrachyurans the synapomorphic state is for sternal sutures s4/s5 and s5/s6 to be medially interrupted 39(1), 40(1) (see Guinot 1979). The Carpiliidae & *Cancer* Linnaeus 1758 in the Cancridae have all sternal sutures complete although states 39(1) and 40(1) are found in other corystoids in addition to the bellioids, calappoids, dorippoids, hymenosomatids, leucosioids, and majoids (see Guinot 1978). Thus, interruption of sternal sutures s4/s5 and s5/s6 is most likely part of the synapomorphic groundplan of the Eubrachyura and the condition seen in the Cancridae (and possibly the Carpiliidae) is a reversal to the plesiomorphic state. The Portunoidea s.s. and Thoracotremata exhibit the most apomorphous condition with sternal sutures s6/s7 and s7/s8 medially interrupted with the interruption points well separated 41(2), 42(1). The Trichodactylidae have states 41(1) and 42(1) although some members of the Dilocarcininae have state 41(2). State 41(1) is also seen in the Geryonidae and Carcininae and the ur-portunoid (including the ur-geryonids) is postulated to have possessed this state. Furthermore, state 41(1) appears to have independently arisen in the ancestor of the [Bythograeidae [thelphusoids, Thoracotremata]] lineage. The medial interruption of sternal sutures s4/s5, s5/s6, s6/s7, and s7/s8 may not be a consequence of the ancestral widening of the sternum because portunoid and thoracotreme taxa with only moderately wide sterna (e.g. *Cardisoma* Latreille 1825 in the Gecarcinidae) display this advanced condition. (See also Magalhães and Türkay 1996a concerning the decoupling of sternal suture interruption from sternal width.) Furthermore, taxa within some reptant decapod families such as the Palinuridae and Parastacidae have all sternal sutures medially interrupted or absent with the medial termination points (when present) very well separated. Development of states 41(1,2) and 42(1) has homoplastically occurred in members of the Calappoidea, Dorippoidea, Hymenosomatidae, Leucosioidea, Majoidea, and some goneplacien grade Xanthoidea.

All thelphusoids have sternal sutures s4/s5 and s5/s6 medially interrupted. Sternal suture s6/s7 is interrupted in some gecarcinucoids, *Platythelphusa*, the Potamidae, Potamonautidae and the Pseudothelphusidae and the hypothesis presented here has state 41(2) synapomorphic for the thelphusoids + Thoracotremata, with reversals to state 41(0) seen in thelphusoid subclades. Sternal suture s7/s8 is interrupted 42(1) in some Gecarcinucoidea, Potamidae, and Pseudothelphusidae although this may be due to obsolescence of the medial region of the suture as opposed to true interruption.

The overall shape of the male sternum in thelphusoid families, particularly the Potamonautidae and Pseudothelphusidae,

is strikingly similar to that of the Carpiliidae (Guinot 1968a: Pl. 1). This carpiliid sternal conformation (for lack of a better term) is a symplesiomorphy in the Eubrachyura and the orbicular sternal outline seen in the Portunoidea s.l., Bythograeidae, varunines, Grapsidae s.s., thelphusoids such as *Gubernatoriana* Bott (1970b); goneplacien grade xanthoids, and ocpodoids was undoubtedly independently derived from this groundstate. The carpiliid sternum seen in most thelphusoids thus cannot be used to support a sister group relationship between these freshwater crabs and the xanthoids or cancrids. On average, the width of the thelphusoid sternum is wider than that seen in cancrids and most xanthoids and some thelphusoids have a sternum that is similar in shape to that of *Cardisoma* and *Ucides*, with the sternum of these thoracotremes topologically closer to the carpiliid condition than to the form seen in, e.g. the sesarmines and ocpodoids.

Sternites s1 and s2 are very reduced 43(1) in ocpodoids, forming a small triangular 'chip' just anterior the termination point of the male sterno-abdominal cavity which terminates at the s2/s3 sternite boundary 44(2). These two synapomorphies underscore the monophyly of this ocpodoid clade. The ocpodoids and the Gecarcinidae + Grapsidae s.s. clade form a sister group based upon another sternal synapomorphy: sternites s3 and s4 have semicircularly indented lateral margins giving this region of the sternum something of an hourglass shape 45(1).

Termination of the male sterno-abdominal cavity near the midregion of sternite 4 is a symplesiomorphic state in the Eubrachyura. Within the many members of the Thoracotremata (some varunines, sesarmines, and Gecarcinidae) and the Gecarcinoidea, the male sterno-abdominal cavity terminates at or very near the s3/s4 sternite boundary 44(1). Indeed, state 44(1) constitutes a synapomorphy for the Gecarcinidae and Parathelphusidae (among other states not discussed here). State 44(1) is hypothesized to have been independently developed in the *Eriocheir* + *Varuna* clade and the [[Gecarcinidae + Grapsidae s.s.] Ocpodoidea] lineage.

First gonopods

All (or almost all) Paleotropical thelphusoids have a four-part gonopod 1, whereby the two distal parts comprise the subterminal segment (the 'endopod' of Guinot 1979) and a distinct and synapomorphic spout-like additional terminal member 35(1) which in freshwater crab parlance is referred to as the terminal segment (Ng 1988) or terminal article (Cumberlidge 1999). The additional terminal 'segment' of these thelphusoids actually constitutes a pseudo-segmentation of the endopod, which consists of the subterminal segment (the endopod proper) plus the terminal article (Cumberlidge 1999). State 35(1) provides solid evidence for the monophyly of the Paleotropical thelphusoids.

The synapomorphic groundplan of the Eubrachyura includes a first gonopod endopod/subterminal segment which is narrowly conical, a conformation seen, e.g. in the corystoids, calappoids, and eriphiids. The Geryonidae, Trichodactylidae, and Portunoidea have a first gonopod endopod/subterminal segment which is shaped like a 'v': the base of the endopod is very stout with the middle region constricted, and the apical region tapers to a point that is directed medially 33(1). In *Carcinus* and in many portunoids the distal half of the endopod forms a needle-like stylus whereas in the geryonids and trichodactylids the distal half of the gonopod is considerably thinner

than the base but not as exaggeratedly so as in, for example, *Callinectes*.

At another extreme is the very slender first gonopod endopod/subterminal segment of the Panopeidae, Pilumnidae, and Xanthidae 38(1). State 38(1) is positioned as a synapomorphy for the Panopeidae and Xanthidae and homoplastically developed in the Pilumnidae. This hypothesis does not seem convincing given the very similar areolations of the carapace surface in these three families; however, resolution of xanthoid familial relationships is far beyond the scope of this paper.

Unlike the Paleotropical thelphusoids, the first gonopod endopod/subterminal segment in the Pseudothelphusidae lacks a terminal article 35(0). All members of this family have an extremely stout first gonopod endopod/subterminal segment with numerous small lobes and terminal processes (Rodríguez 1982). The pseudothelphusid subfamily Epilobocerinae has the least derived first gonopods and the first gonopod endopod/subterminal segment of these crabs is comparable (homologous) to that of marine taxa. While differing in what may turn out to be significant details, the stout and conical first gonopod endopod/subterminal segment of the Epilobocerinae and the first gonopod endopod/subterminal segment seen in the varunines, Gecarcinidae, and Grapsidae s.s. have some similarities in terms of overall topology and state 34(1) is postulated to be part of the synapomorphic groundplan of the thelphusoids + Thoracotremata. The difficulty with this hypothesis is that the first gonopod endopod/subterminal segment of the pseudothelphusids and the Paleotropical thelphusoids has a very disparate topology, although this segment is stout and complex in some Asiatic potamids (Bott 1970b). The most parsimonious hypotheses position the Pseudothelphusidae as the sister group of the Paleotropical thelphusoids and this raises the question of how the distinct gonopod types are structurally interrelated. Some other eubrachyuran families such as the Hymenosomatidae encompass several distinct first gonopod types (Guinot 1997) and thus gonopodal disparity alone cannot be used to negate a sister group relationship between the Pseudothelphusidae and Paleotropical clades.

Two first gonopod states indicate the monophyly of the Thoracotremata. First, in all thoracotremes examined dense setae cover the apex of first gonopod endopod/subterminal segment 36(1). Second, in all thoracotremes examined the apex of first gonopod endopod/subterminal segment has a chitinous flange 37(1) (described in detail by Crane 1975). With respect to state 34(1) constituting the groundplan of the thelphusoids + Thoracotremata, it is possible that the field of apical spines seen in the pseudothelphusids are modified setae and thus homologous with state 36(1) in the thoracotremes.

Pereiopods 1–5

Four character states of pereiopods 2–5 are synapomorphic for the thelphusoids + Thoracotremata, namely, the merus of pereiopods 2–5 is distinctly triangular in cross-section 46(1), i.e. posterior margins are present (unlike in most heterotremes; Fig. 1c); the superior meral surface bears carinae or striae 47(1) (Fig. 1d) (indistinct in *Varuna*) which can be secondarily modified with granulation; a 'trough' or groove runs immediately parallel to the anterior margin of the merus 48(1) (Fig. 1d; reduced in some thelphusoids); and the dactylus of pereiopods 2–5 has rows of corneous spines 49(1). The Trichodactylidae is the only group of freshwater crabs lacking corneous spines on the dactylus of pereiopods 2–5. Some of the Grapsidae s.s. examined in this study lack corneous spines on the propodus

of pereopods 2–5 (but these segments do have very stiff black setae). Examination of the benthic marine varunine *Euchi-rograpsus* and the littoral grapsine *Grapsus* revealed distinct corneous spines on the dactylus of pereopods 2–5 and this is taken to represent the basic thoracotreme condition. The long, thick setae seen on the dactylus of pereopods 2–5 in some of the Grapsidae s.s. appears to be an autapomorphic modification of the short, blunt corneous spines seen, for example in all the thelphusoids, *Euchi-rograpsus*, and the Gecarcinidae; some of the spines observed on *Euchi-rograpsus* exhibit a conformation intermediate between that of *Grapsus* and the stiff setae seen, for example, on *Goniopsis*. Other thoracotremes (some varunines and the ocypodoids) have lost spines on the dactylus of pereopods 2–5 completely.

The occurrence of prominent carinae on the dorso-external surface of the merus of pereopod 1 50(1), a sharply defined inferior margin of the merus of pereopod 1 52(1), and a carpus of pereopod 1 with a rugose surface 53(1) are robust synapomorphies for the thelphusoids + Thoracotremata. One possible synapomorphy for a [Bythograeidae [thelphusoids + Thoracotremata]] clade is the presence of rows of irregular teeth along the dorso-interior margin (facing the crab) of the merus of pereopod 1 51(1). *Hemigrapsus* and the pseudothelphusids show the plesiomorphic condition for character 53. Furthermore, state 51(1) has been secondarily lost in the Deckeniidae, *Platythelphusa*, and gecarcinucoids, in the thelphusoid lineage, and *Hemigrapsus* in the thoracotreme clade.

Three synapomorphies of the pereopods were also determined for the Portunoidea (including the Trichodactylidae). The portunoid groundplan includes: a spatulate dactylus on pereopod 5 55(1), fine setae on the margins of the propodus and dactylus of pereopods 2–5 56(1), and a broad and flat propodus of pereopod 5 57(1). Character states 55(1), 56(1), and 57(1) were independently developed in *Eriocheir* and *Varuna* and in the latter taxon pereopods 3 and 4 also have a spatulate, seminant dactylus. Characters 55 and 57 have been further modified in the Podophthalminae and Portuninae in which the dactylus of pereopod 5 is very broad and flat 55(2) as is the propodus of pereopod 5 57(2); in addition, in these portunid subfamilies the merus of the dorsointerior margin of the cheliped has regularly spaced, large curved teeth 59(1).

Eriocheir and *Varuna* have another possible pereopodal synapomorphy: the dorsal margin of the merus of pereopod 4 has a very sharp subdistal spine 54(1).

Guinot (1968a) and Ng (1983) discussed the phylogenetic significance of the degree of fusion of the ischiobasis of pereopod 1 with the merus of pereopod 1. Fusion of the cheliped ischiobasis and merus with subsequent reduction of the articulation joint is seen in both the Carpiliidae and Eriphiidae 58(1). All other eubranchyurans examined have very distinct regions of articulation between the ischiobasis and merus of the cheliped 58(0) and it appears that state 58(1) arose twice (Fig. 3). The finding that all thelphusoids have a well-defined joint between the ischiobasis and merus of the cheliped is a serious argument against the derivation of this clade from *within* the Carpiliidae or Eriphiidae.

Transversely oval 'oziine' carapace outline

One possible apomorphy linking the thelphusoids with the xanthoids that is alluded to in the literature (e.g. Alcock 1898), is the transversely oval carapace outline characteristic of many xanthoids and some thelphusoids, particularly the oziines in the family Eriphiidae and the pseudothelphusids (see carapace

outline in Fig. 1a). This 'oziine' carapace outline 60(1) is not a plesiomorphy as it is a highly derived end-product of carcinization (Guinot 1979). Paleotropical thelphusoids, however, exhibit an array of carapace morphologies, some species having an oziine outline with other taxa exhibiting a carapace conformation reminiscent of grapsids and gecarcinids [a 'grapsoid' carapace outline 61(1)]. These characters were not included in the parsimony analysis because of the high degree of variability in carapace shape observed within the families studied, although the distributions of the character states are presented in Fig. 5. It is clear that the oziine carapace outline maps onto the consensus tree as a plesiomorphic condition for the thelphusoids, and grapsoid-like carapace outlines are polymorphically present in this freshwater crab lineage.

Discussion

On the basis of the above cladistic evidence, several important points emerge. First, the true freshwater crabs of the world consist of two distinct phylogenetic groups: the Trichodactylidae, which comprises a basal clade of the Portunoidea (Rodríguez 1992), and what has been termed here the 'thelphusoid clade'. Second, it is apparent that, aside from vague phenetic resemblances in a few instances, no true freshwater crabs can be systematically positioned within or adjacent to the Xanthoidea or within or adjacent to other primitive heterotrematous groups. On the contrary, the closest marine sister group of the thelphusoids is most likely the Thoracotremata. However, this by no means rules out the possibility that the thelphusoids (and thoracotremes) originated from some underived xanthoid or bythograeid-like clade (Fig. 2; see below). And third, the 'male openings' of the thelphusoids are intermediate (at least in some taxa) between the heterotreme and thoracotreme conditions (Guinot 1979). These points raise important questions about the relationships of the Heterotremata and Thoracotremata and about the monophyly (versus para- or polyphyly) of the various subclades in these sections. Each of these points is discussed briefly below. In addition, the biogeographic implications of the hypothesis presented is considered below, as is the general topic of the origin, groundplan, and diversification of the freshwater crabs.

Paraphyly of the freshwater crabs

The freshwater crabs have long been assumed by many authors to be (at least in part) a para- or polyphyletic assemblage (Ortmann 1902; Colosi 1921; Bott 1955, 1969, 1972; Bishop 1963; Pretzmann 1973; Rodríguez 1986; Ng et al. 1995; Ng and Rodríguez 1995; Guinot et al. 1997). This assumption was based on a number of factors including: (1) a knowledge of the limited dispersal capabilities of freshwater crabs, (2) the largely pantropical distribution of the freshwater crabs, (3) the lack of pre-Tertiary fossils of freshwater crabs, (4) the presumed post-Cretaceous radiation of the Heterotremata and Thoracotremata (which would argue against plate tectonics playing a role in the modern distribution of freshwater crabs), and (5) the disparate morphologies of the first gonopod within and between families.

Recently, however, the argument for polyphyly has been replaced with proposals for the monophyly of all freshwater crab families whereby sister group relationships have been posited for the Pseudothelphusidae + Gecarcinucoidea and the Potamoidea (specifically the Eupotamonea) + Trichodactylidae (Rodríguez 1986; Ng et al. 1995; Ng and Rodríguez 1995).

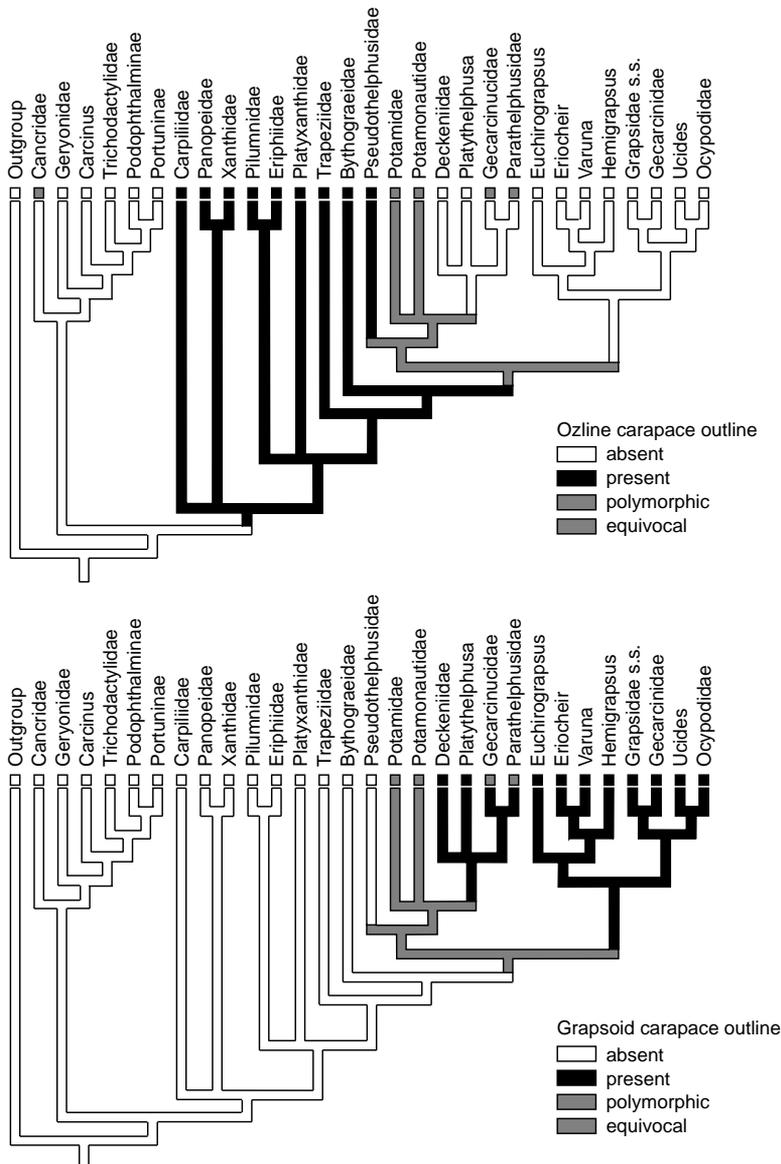


Fig. 5. Distribution of 'ozline' and 'grapsoid' carapace outlines among eubrachyuran taxa

Some versions of the above monophyly hypothesis (Ng et al. 1995) propose an ancient origin for the ancestral population of all the freshwater crab families (approximately 120 million years ago, prior to the fragmentation of Gondwanaland), whereby the Potamoidea + Trichodactylidae constituted the ancestral stock which gave rise to the Pseudothelphusidae + Gecarcinucoidea. This latter hypothesis (Rodríguez 1986; Ng et al. 1995; Ng and Rodríguez 1995) assigns high taxonomic weight to the structure of the mandibular palp and third maxilliped, but overlooks a number of problems associated with biogeographic relationships, dispersal capabilities, and the somatic and genital disparity between the thelphusoid families and subfamilies. It has recently been argued (Cumberlidge 1999) that the mandibular palp of freshwater crabs exhibits several distinct character states and that not all conditions can be assumed to be homologous. Such a finding clearly weakens any hypothesis of monophyly based solely upon this one character. Ultimately, the polyphyletic and monophyletic hypotheses for the origin and diversification of the freshwater crabs suffer from the same

underlying problem: the failure to identify plausible marine outgroups that could enable the determination of plesiomorphic and apomorphic states for many characters, coupled with a rigorous cladistic analysis.

The results of the present cladistic analysis support the earlier conclusions of Rodríguez (1986, 1992) who pointed out that the Trichodactylidae are phylogenetically distinct from both the Pseudothelphusidae and most Palearctic thelphusoids. That author also postulated the origin and systematic placement of the Trichodactylidae within the Portunoidea. Rodríguez (1992) identified several putative synapomorphies which tied the Trichodactylidae to the portunoid subfamily Carcininae and to the Portunoidea as a clade. Recent systematic revisions of the Trichodactylidae (Magalhães and Türkay 1996a,b,c) found no evidence to argue against portunoid affinities of this family and it is clear that the most parsimonious hypotheses of cladistic relationships (Fig. 2) positions this family basally within the portunoid clade. However, no sister group relationship could be established between the Carcininae and Trich-

odactylidae as the diagnostic characters of these clades are symplesiomorphies within the Portunoidea. Given that the Carcininae may well be a 'catch-all' pseudotaxon for underived portunoids, all that can be stated is that the Trichodactylidae most likely separated from the main portunoid clade prior to the diversification of the Caphyrinae, Catoptrinae, Macropipinae, Podophthalminae, and Portuninae. The fossil record of clades such as the Portuninae extends back to the mid Cretaceous period (100–65 million years ago; Glaessner 1969) so, if the hypothesis presented here has any validity, the Trichodactylidae must have emerged prior to this time. Rodriguez (1992) postulated a southern Tethys Sea origin for the clade beginning before 120 million years ago based upon a consideration of vicariant events. An open research question is the relationship of the Trichodactylidae to the Geryonidae which was thought by Manning and Holthuis (1981) to be a possible sister taxon of the Portunoidea, an idea supported from the results of this study. Indeed, the first gonopod of some trichodactylids is nearly identical in morphology to that of some geryonids (Guinot 1969c) and this may point to a closer relationship between these two families *vis-à-vis* the Carcininae.

The monophyly of the thelphusoid clade was not falsified by this study. Indeed, the present preliminary cladistic analysis points to the monophyly of this clade with seven synapomorphies, four of which are unique: 9(2), 17(1), 18(1), 22(1), 23(1), 25(1), and 26(1). The monophyly of the Paleotropical thelphusoids is strongly supported by six synapomorphies, two of which are unique: 1(1), 2(1), 4(1), 12(1), 13(1), and 35(1). Other synapomorphies for the Paleotropical groups can also be discerned (in preparation). It suffices here to state that despite the morphological disparity of thelphusoid taxa, hypotheses postulating a polyphyletic derivation of the thelphusoid families from various marine heterotrematous clades appear to have little support.

The question of whether the thelphusoids diverged in freshwater environments from an ancestral freshwater group or whether several or many thelphusoid subclades independently (and at different times) invaded freshwater systems is a separate issue from monophyly. The urthelphusoid clade could well have been monophyletic in the sense of possessing a certain constellation of synapomorphies and yet could have been widespread and marine with euryhaline capabilities. It thus becomes important to tease apart the different concepts used in the evolutionary scenarios for the freshwater crabs published or implied by some workers (e.g. Colosi 1921; Bott 1955, 1969, 1972; Pretzmann 1973).

The Thoracotremata as the marine sister taxon of the thelphusoids

It is interesting to note that H. Milne Edwards (1837) was the first carcinologist to point out the similarities between the thelphusoids and the Thoracotremata. The thelphusoids formed in H. Milne Edwards' opinion a 'satellite' of the Grapsinae. Alcock (1898, 1899), likewise, wrote: 'The Telphusidae are the highest Cyclometopes [=heterotremes], and approach the *Catometopa* [=Thoracotremata] . . .' (his italics) (1899: 3). Elsewhere in the work he states, in an overview of the Cyclometopa: '*Telphusidae*, in which the form is grapsoid, . . .' (1898: 69). It is clear however, that although Alcock noted the grapsid-like habitus of the thelphusoids, he was inclined to place them adjacent to primitive xanthoids (Eriphiidae) implying thereby that such grapsoid-like features were convergences. The position of the male openings (see above) of the thelphusoids was

apparently the key argument for linking these crabs with underived heterotremes.

The most parsimonious trees position the thelphusoids and thoracotremes as sister groups (Figs 2 and 4). The homoplastic states [e.g. 1(1) and 2(1)] shared between the thelphusoids (particularly the Paleotropical taxa) and the grapsids and gecarcinids, suggests to us that these homoplasies might constitute underlying synapomorphies (Saether 1979, 1983; Sluys 1989). While we are well aware that many cladists are loath to acknowledge underlying synapomorphies, the morphological similarity of many Paleotropical thelphusoid taxa to gecarcinids and grapsids is very evident (see, e.g. the plates in Bott 1970b). Indeed, *Gecarcinus* H. Milne Edwards 1844 (family Gecarcinidae) was originally placed in the Gecarcinidae (Alcock 1900).

The square carapace, prominent carapace lateral carinae 1(1) and carapace wall carinae 2(1), deflexed carapace front 4(1), flattened meri of pereopods 2–5 with carinae on the superior surface 47(1), for example, give many Paleotropical thelphusoid taxa (e.g. *Mainitia* and *Gubernatoriana*) a very grapsid-like appearance (as do the hatchlings of *Potamonautes* MacLeay 1838 and *Sudanonautes* Bott 1955). And aside from the first gonopod morphology, the gecarcinids and grapsines appear typologically closer to the thelphusoids than to many varunines. In this context it should be noted that the recent spermatozoal study of *Varuna* relative to other thoracotremes by Jamieson et al. (1996) implied that this genus is distinct from the Grapsidae s.s. and from other thoracotremes. These authors proposed (as one of three explanatory hypotheses) that the Varuninae s.l. represents a clade independent of the other grapsids, a possibility supported by this study. It would thus appear that the Grapsidae are para- or polyphyletic and the possibility of a closer relationship between the thelphusoids and the Gecarcinidae + Grapsidae s.s. *vis-à-vis* the varunines cannot be dismissed.

The sperm of the Paleotropical thelphusoids *Potamon* Savigny 1816 and *Potamonautes* have been investigated within the context of the Eubrachyura (Guinot et al. 1997). These authors identified several synapomorphies (elongation of the two centrioles, the almost parallel placement of the centrioles, cleistospermy, and the wide inner acrosome zone) which support the monophyly of the Potamidae + Potamonautidae. However, no apomorphic states were identified which would link these thelphusoids to any heterotrematous clade (the overall structure of the sperm was nonetheless found to be typical for the Eubrachyura). A cladistic analysis of spermatozoal and morphological data (Jamieson 1994) found *Potamonautes* to be most parsimoniously placed basal to the xanthoid clade, although this relationship was based upon only two unambiguous apomorphies (one quantitative): an acrosome length-width ratio of 0.9 and a well developed periopercular rim. That the potamoids cannot be subsumed within the Xanthoidea was indicated by their lacking a xanthoid spermatozoal synapomorphy, the 'xanthid ring' (Jamieson 1994; Guinot et al. 1997). The combined results of the investigations presented by Jamieson (1994) and by Guinot et al. (1997) support the idea that the potamoids are members of the section Heterotremata, but they revealed no close relationship between these freshwater crabs and either the portunoids, majids, or xanthoids. However, those authors identified several apomorphies shared between the potamoids and the thoracotremes. The spermatozoon of *Potamon*, for example, was found to lack an unambiguous acrosomal ray zone (as was that of *Potamonautes* and the fresh-

water goneplacid *Australocarcinus* Davie 1988) and was found to possess a perforated operculum (which is nonperforated in xanthoids and portunoids). These characters of the spermatozoon are conditions typical of the Thoracotremata (although the operculum is perforate in the Podotremata, corystoids, and majids; Guinot et al. 1997). Reduction of the thickened ring, a robust synapomorphy of the spermatozoon of the Gecarcinidae and Grapsidae s.s., was also found in the potamoids (Guinot et al. 1997). The results of the above spermatozoal studies revealed that a tier of possible synapomorphies is shared between at least some of the thelphusoids and a subgroup of the Thoracotremata. Characters interpreted by those investigators as homoplasies between the potamoids and thoracotremes can, given the cladistic hypothesis presented here, equally represent synapomorphies with various degrees of generality. Thus, if the poorly defined (absent) acrosomal ray zone of the spermatozoa and the perforated spermatozoon operculum are interpreted as synapomorphies they would in general support a [varunine [thelphusoids [Gecarcinidae + Grapsidae s.s.]]] arrangement. The reduced thickened ring would support the sister group relationship [thelphusoids [Gecarcinidae + Grapsidae s.s.]]. Guinot et al. (1997) indicate that the potamoids are excluded from the Thoracotremata, but add that the relationships of the potamoids with other heterotremes are poorly resolved. The morphological data presented here suggest a similar conclusion except that the thelphusoids are either the sister taxon of the Thoracotremata or the sister taxon of some of the thoracotremes, should the Thoracotremata be found to be paraphyletic (as was suggested by Rice 1980; see also Jamieson et al. 1996).

Origin, groundplan, and diversification of the thelphusoids in light of previously published evolutionary hypotheses

Understanding the origin and diversification of the thelphusoids depends to a large extent upon reconciling morphological character state distributions with biogeographical evidence. Two schools of thought exist on how to reconcile the two. The first is what we term here the polyphyletic hypothesis which was outlined by Bott (1955, 1969, 1972) and by Pretzmann (1973) and briefly touched upon by Guinot et al. (1997). The second is what we term here the archaic population hypothesis which was proposed by Ng et al. (1995) and Ng & Rodríguez (1995).

The polyphyletic hypothesis of Bott (1955, 1969, 1972) and Pretzmann (1973) interprets the modern distribution of thelphusoid taxa to be the result of the independent migration of preadapted heterotrematous lineages into freshwater environments from the Tethys Sea, probably during the Tertiary (around 65 million years ago). This hypothesis explains thelphusoid synapomorphies as the result of similar selective pressures, rather than common ancestry. Indeed, Pretzmann (1973) argued that the different tribes and even genera within the Pseudothelphusidae each had a different marine ancestor (Rodríguez 1986). Bott (1955, 1969, 1972) and Pretzmann (1973) apparently discounted the notion of an archaic freshwater thelphusoid ancestral group, but it is unclear whether these authors proposed a strict polyphyly of the thelphusoids because their discussions dealt only with the invasion of the freshwater environment and did not consider the marine lineages that gave rise to the various freshwater crab families. Whatever their actual phylogenetic views on the thelphusoids, it is clear that both Bott and Pretzmann were heavily influenced by the neo-Darwinian 'selection narratives' of the early mid portion of this

century (Croizat 1964) and, consequently, tended to subordinate morphological data to historical speculations.

In sharp contrast to the polyphyletic school, the archaic population hypothesis of Rodríguez (1986), Ng & Rodríguez (1995) and Ng et al. (1995) interprets the modern distribution of the thelphusoid families as the result of vicariance events associated with the fragmentation of an archaic continental mass more than 120 million years ago which resulted in the isolation of ancestral populations of freshwater crabs. These authors proposed an hypothesis whereby the freshwater crabs of the world originated from two monophyletic groups: (1) Potamoidea + Trichodactylidae, and (2) Gecarcinucoidea + Pseudothelphusidae. These authors suggested that the ancestors of the freshwater crabs originated on a single southern landmass (Gondwana) at sometime in (before?) the early Cretaceous. They explain the present day distribution of the freshwater crabs in terms of the splitting up of Gondwana and the separation of the descendants of these ancestral crabs on the southern continents and islands of tropical America, Africa, Madagascar, the Seychelles, and India.

This archaic population hypothesis was developed by the above authors by interpreting evidence from comparative anatomy, relying mainly on studies of the Asian and American freshwater crab faunas. The hypothesis makes several testable predictions based on evidence from characters of the mandibular palp (Rodríguez 1986; Ng et al. 1995), the third maxilliped (Rodríguez 1986; Ng & Rodríguez 1995), and the structure of the male openings (Ng & Rodríguez 1995).

Ng et al. (1995) noted the following points arising from the mandibular palp structure of freshwater crabs: (1) the Potamoidea have a plesiomorphic third-segmented mandibular palp 23(0) with an unmodified terminal segment 24(0) which represent the plesiomorphic states of the characters; (2) the Deckeniidae, Gecarcinucoidea, Potamonautidae, and Pseudothelphusidae are united by a two-segmented mandibular palp 23(1); and (3) the Gecarcinucoidea and Pseudothelphusidae are in turn united by the bilobed terminal segment of the mandibular palp 24(1). Ng et al. (1995) considered the two-segmented mandibular palp with a bilobed terminal segment to be unique to the Gecarcinucoidea and Pseudothelphusidae, so that crabs with state 24(1) essentially have a Gondwanan distribution in the Paleotropics and Neotropics. The present distribution of crabs with a bilobed mandibular palp across today's southern continents is explained by postulating that these crabs must have been present 120 million years ago (early Cretaceous) on the single southern continental landmass of Gondwana. This would be at a time before Gondwana began to split up, separating South America, India, Madagascar, the Seychelles, Australasia, and Antarctica from Africa. Furthermore, these authors postulated that these bilobed crabs were derived from freshwater crabs with a single terminal segment of the mandibular palp ('the potamoids') that were present even earlier. If supported, this idea has important implications for estimating the age of the freshwater crabs and, by implication, the age of the Eubrachyura as a whole.

Ng & Rodríguez (1995) cite the form of the exopod of the third maxilliped as additional evidence for a Gecarcinucoidea + Pseudothelphusidae clade. They write: 'The presence of species with reduced exognaths (an apomorphy connected with their advanced adaptation to fresh water life) in America, Africa, and India is a strong argument for a monophyletic origin of several families of these same species, and is also evidence of a former Gondwanan distribution, and shows that the trans-

formation of buccal appendages had already begun in mid-Cretaceous times in a basic group whose modern representatives are the American Pseudothelphusidae and the African Gecarcinucidae.'

However, our review of this character in African, Asian, and American freshwater crabs indicates that it is likely that the loss of the flagellum on the exopod of the third maxilliped is a parallelism which has arisen more than once in a number of different families of freshwater crabs, and is not a strict apomorphy supporting the single ancestry of the Gecarcinucoidea + Pseudothelphusidae. The exopod (exognath) of the third maxilliped of freshwater crabs exists in three different forms. The first is a third maxilliped with a long exopod which has a long flagellum. This form is found in all Trichodactylidae (Rodríguez 1992; Magalhães and Türkay 1996a,b,c), all Liothelphusinae, all Gecarcinucinae, all Parathelphusidae, most Potamidae (Bott 1970b; Ng 1988), and in most Potamonautidae (Bott 1955; Cumberlidge 1999). This type of third maxilliped is the plesiomorphic state in the Brachyura. The second form is a third maxilliped with a long exopod which completely lacks a flagellum. This form is found in a number of African freshwater crab genera such as *Globonantes* Bott 1959 (Cumberlidge 1991), *Afrithelphusa* Bott 1969 (Cumberlidge 1996a,b), *Louisea* Cumberlidge 1994 (Cumberlidge 1994), *Potamonemus* Cumberlidge and Clark 1992 (Cumberlidge 1993), and some species of *Liberonantes* Bott 1955 (Cumberlidge 1999). This type of third maxilliped is also found in some Asian Potamidae (Bott 1970a,b), and in the more primitive Pseudothelphusidae (*Epilobocera*) from the Caribbean (Rodríguez 1982). The third form of the third maxilliped is where the exopod not only lacks a flagellum, but is itself greatly reduced in size. This form is found almost exclusively in the Pseudothelphusidae from Central and South America (Rodríguez 1982). Since the loss of the flagellum of the exopod of the third maxilliped has occurred several times in different families and superfamilies of freshwater crabs on different continents it is likely that this feature is of limited significance for delimiting thelphusoid relationships. In short, the form of the third maxilliped alone does not support the idea that widely distributed freshwater crabs form a single monophyletic group (Gecarcinucoidea + Pseudothelphusidae).

Ng & Rodríguez (1995) also include the structure of the male openings as evidence for a Gecarcinucoidea + Pseudothelphusidae clade. They write: 'This hypothesis of two monophyletic groups for the origin of the majority of freshwater crabs is further supported by the study of the structure of their sexual openings (Rodríguez 1992), a character of fundamental phylogenetic significance in the Brachyura (Guinot 1977, 1978, 1979).'

The evidence from the study of the structure of the male openings cited by Ng & Rodríguez (1995) could be interpreted differently, and does not directly support the hypothesis for the origin of freshwater crabs from two monophyletic groups. According to those authors the Pseudothelphusidae have a rudimentary penial groove located on the posterior margin of episternite 7 and the anterior margin of sternite 8, while the Trichodactylidae and Parathelphusidae have a penial groove located along sternite 8. However, this character, if interpreted as a synapomorphy, would argue for the inclusion of *Somanniathelphusa* (Parathelphusidae) and the Trichodactylidae in the same superfamily (either the Gecarcinucoidea or the Potamoidea). The African Potamonautidae and Globonautinae both lack a penial groove on sternite 8. These African fresh-

water crabs have the plesiomorphic state with respect to this character. (There is a trace of a penial groove in the Deckeniidae, but this alone does not necessarily imply a relationship between this family and the Pseudothelphusidae and Trichodactylidae.)

The archaic population hypothesis predicts that the hierarchical taxonomic sequence of thelphusoid families should be congruent with the vicariant tectonic events leading to the modern distribution of the various freshwater crab families. Marine dispersal or long distance land migrations would be unlikely given that the ancestral thelphusoid population had already acquired direct development and maternal care and was already restricted to the freshwater environment. One would therefore expect to see a cladogram that is topologically congruent with the sequence: Pangaea → [Gondwana], [Laurasia] → [[Africa, Madagascar], [Australia, South America, New Zealand]], [Laurasia] → [[Africa, Madagascar], [New Zealand [Australia, South America]]], [Laurasia].

The Gecarcinucoidea of Bott (1970b) and the Pseudothelphusidae fall into three geographical groups (1) the mainly Southeast Asian Parathelphusidae, (2) the mainly Indian and Southeast Asian Gecarcinucidae, and (3) the neotropical Pseudothelphusidae. The only way that the proposed sister group relationship of the Gecarcinucoidea and Pseudothelphusidae (suggested by Ng et al. 1995) can be reconciled with the geological evidence and with the concept of an archaic population is to postulate that the potamoid ancestor of these families was already in existence prior to the separation of Laurasia from Gondwanaland and long before the separation of South America and Africa. Clearly, if this hypothesis is correct, 'higher' eubrachyurans would need to have been present in the Tethys Sea much longer than 120 million years ago. Given the sparse fossil record for freshwater crabs, extending only to the late Tertiary (Ng et al. 1995), and given that most of the fossil evidence supports a Cretaceous/post Cretaceous origin and 'radiation' of the Eubrachyura (e.g. Glaessner 1969), the archaic population school has virtually no paleontological support. The cladistic results suggest that whereas the thelphusoids are most likely monophyletic, the pseudothelphusids bifurcated soon after the emergence of the thelphusoids and the Asian and Australasian crabs are the sister group of the African clades (in preparation). In short, vicariant events do not easily explain thelphusoid biogeography.

In light of the above, all parsimonious hypotheses of relationships position the Bythograeidae as the sister group of the thelphusoids + Thoracotremata (Fig. 2). While we are not convinced of this relationship (see also Guinot 1988), it is important to note that Williams (1989; cited in Guinot 1989) argued for a post-Mesozoic origin of the bythograeids. Indeed, Williams is quoted as stating: 'There is no way in which the Bythograeidae can be aligned directly with the Mesozoic crabs . . . the Bythograeidae are "modern" (Guinot 1989: 892). If this can be said of the bythograeids, it is even more applicable to the thelphusoids and thoracotremes which are very "modern" in all characters and which cannot be derived from any Mesozoic taxon.

A new phylogenetic hypothesis

The phylogenetic hypothesis favored here for the origin, groundplan, and diversification of the thelphusoids is a modified version of that proposed by Colosi (1921). Colosi compared the biogeography of the freshwater crab families with the age of the respective freshwater basins the different families and

subfamilies now inhabit, and concluded that the various freshwater crab lineages (except the trichodactylids) are not archaic but rather had a recent (post-Cretaceous) derivation from a morphologically and phylogenetically advanced group of brachyurans. Colosi (1921) proposed that all the freshwater crabs originated from a widespread marine crab clade that was morphologically heterogeneous for some characters, and which independently invaded freshwater systems in different areas at different times. Colosi, like Croizat (1964), derived his ideas from Rosa (1918) who postulated that widespread biogeographical distributions of taxa with limited dispersal capabilities could be most parsimoniously explained by differentiation of a formerly widespread monophyletic yet polymorphic ancestral group, instead of by migrations from 'centers of origin' (Heads 1985). In this case, however, the vicariant disruption of the widespread ancestral heterotrematous clade giving rise to modern thelphusoids would not have involved plate tectonics as such, but rather the restriction (stranding) of thelphusoid populations to brackish water or freshwater systems, as has happened with some of the Goneplacidae (Davie and Guinot 1996) and with other freshwater crustaceans (Stock 1993; 1994).

The alternative hypothesis to those presented by both the polyphyletic school (Ortmann 1902; Bott 1955, 1969, 1972; Pretzmann 1973; Guinot et al. 1997) and by the archaic population school (Ng et al. 1995; Ng & Rodríguez 1995) is the following. A widespread, predominantly littoral, marine ur-thoracotreme clade emerged during the Cretaceous. This ur-thoracotreme clade would have had a pancoastal distribution along the southern Tethys Sea. In addition, this clade would have been monophyletic in the sense of possessing the following synapomorphies: a straight carapace front lacking a medial cleft 8(1), no epistomal gutter 16(1), a slender third maxilliped exopod 20(1), a penis that emerges next to the coxal/sternum articular membrane of pereopod 5 28(1), a prethoracotreme first gonopod endopod/subterminal segment which is stout and columnar 34(1), the s6/s7 sternal sulcus medially interrupted with the points of interruption well separated 41(2), the merus of pereopods 2–5 with a triangular cross section 46(1), the superior margin of the merus of pereopods 2–5 with carinae-striae 47(1), the anterior margin of the merus of pereopods 2–5 with a trough parallel to this margin 48(1), the dactylus of pereopods 2–5 with corneous spines 49(1), the merus of the cheliped with carinae on the dorsal external margin 50(1), the merus of the cheliped with a sharp inferior margin 52(1), and the cheliped carpal surface with distinct rugosities 53(1). This hypothetical group bifurcated into the Thoracotremata (or subclades of the section) and the ur-thelphusoid clade. The modern biogeographical distribution of thelphusoid families would thus be explained by different populations (with generic or subfamilial level distinctions) of the ur-thelphusoid clade undergoing differentiation in both marine and freshwater environments. That is, some thelphusoid families would have had an independent diversification in the freshwater or estuarine environment whereas others would have diverged after entering freshwater. This would imply that the adaptations to freshwater or semiterrestrial existence in these different families would have occurred in parallel. Indeed, the production of relatively few, large yolky eggs by strictly freshwater decapods is a convergent feature, occurring repeatedly in monophyletic clades (e.g. Hymenosomatidae; Guinot 1997; Palaemonidae; Pereira 1989). Thus, if the thelphusoids are demonstrated to be strictly monophyletic, there is still no reason to postulate a strictly freshwater origin for the group.

The hypothesis briefly presented here for the origin, ground-plan, and diversification of the thelphusoids has several heuristic benefits. At a minimum it accords with the cladistic evidence concerning the marine sister groups of the thelphusoids. It also dispenses with large-scale polyphyletic scenarios and with some of the arguments required by extreme versions of the archaic population hypothesis. And perhaps most importantly, it allows the morphological evidence to be considered *in toto*, freed from conceptual limitations about what constitute freshwater adaptations.

The evidence presented here indicates that the Thoracotremata is the most likely candidate marine sister group of the nontrichodactylid freshwater crabs. While it is likely that the thelphusoids + Thoracotremata originated from some xanthoid-like (bythograeid-like?) progenitor, there is as of yet no cladistic evidence linking either clade to a specific xanthoid family. Indeed, with the exception of the Carpiliidae and part of the Eriphiidae, all of the xanthoid (and cancrid + portunoid) families are too derived to posit an ancestry of the thelphusoids from within one of these families. However, there are a number of heterotreme taxa which do not fit within any of the traditional families and which appear to share one or more apomorphies with the thelphusoids (in particular the pseudothelphusids); for example, the goneplacid subfamily Pseudoziinae Alcock 1898 (Ng & Wang 1994). Such intermediate taxa warrant further detailed study which is far beyond the scope of the present analysis. It nevertheless appears that the Grapsidae s.l. would be the most parsimonious choice of outgroup for resolving sister group relationships within the thelphusoid clade. The thoracotremes are morphologically an heterogeneous group and the Grapsidae likely constitutes a para- or polyphyletic group. Areas of future research include: (1) identifying which grapsid subclade is the most likely sister taxon of thelphusoids, (2) resolving the heterotreme-thoracotreme distinction, and (3) identifying the sister group of the thelphusoids + Thoracotremata.

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Zusammenfassung

Über die marinen Schwestergruppen der Süßwasserkrabben (Crustacea: Decapoda: Brachyura)

Die Schwestergruppenbeziehungen der Süßwasserkrabben mit den Familien der marinen Eubranchyuren wurden untersucht. Eine auf morphologischen Merkmalen basierende Analyse wurde an Vertretern der Familien Deckeniidae, Gecarcinidae, Parathelphusidae, Potamidae, Potamonautidae, Pseudothelphusidae und Trichodactylidae der Süßwasserkrabben durchgeführt, wobei eine representative Auswahl von marinen heterotremen und thoracotremen Brachyuren als mögliche Geschwistergruppen eingesetzt wurde. Eine Monophylie der Süßwasserkrabben in weiterem Sinn kann ausgeschlossen werden. Die Familie Trichodactylidae und die marine Unterfamilie Carcininae bilden eine ursprüngliche Gruppe innerhalb der Überfamilie Portunoidea. Die Monophylie der Pseudothelphusidae und der paläotropischen Süßwasserkrabben wird bestätigt, wobei diese Klade eine Schwestergruppe der Thoracotremata (Gecarcinidae, Grapsidae s.l. und Ocypodoidea) ist. Der Ursprung, der Grundbauplan und dessen Abwandlung bei den Süßwasserkrabben wird in Zusammenhang mit den früher veröffentlichten Szenarien ihrer Evolution diskutiert.

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Appendix 1. Listing and current systematic placement of freshwater crab taxa used in the cladistic analysis. The classification of paleotropical crabs follows Bott (1970b).

- Deckeniidae** Ortmann 1897
Deckenia mitis Hilgendorf 1869 — Tanzania
- Gecarcinucidae** Rathbun 1904
Gecarcinucinae Rathbun 1904
Barytelphusa cunicularis (Westwood 1836) — India
Gecarcinus jacquemonti (H. Milne Edwards 1844) — Bombay, India
- Globonautinae** Bott 1969
Globonautes macropus (Rathbun 1898) — Liberia
- Liotelphusinae** Bott 1969
Sartoriana blanfordi (Alcock 1909) — Bengal, India
Travancoriana schirnerae (Bott 1969) — India
- Parathelphusidae** Colosi 1920
Ceylonthelphusinae Bott 1969
Ceylonthelphusa rugosa (Kingsley 1880) — Sri Lanka
- Parathelphusinae** Colosi 1920
Palawanthelphusa pulcherrima (de Man 1902) — Borneo, Sarawak
Parathelphusa (Mesotelphusa) celebensis de Man 1892 — Sulawesi
- Somanniathelphusinae** Bott 1968
Siamthelphusa improvisa (Lanchester 1901) — Malaysia, Thailand
Sommaniatelphusa bangkokensis (Ng and Naiyanetr 1993) — Thailand
- Spiralothelphusinae** Bott 1968
Irmengardia pilosimana (Roux 1936) — Malaysia
Oziothelphusa senex (Fabricius 1798) — South India, Sri Lanka
Spiralothelphusa hydrodroma (Herbst 1794) — South-east India,

Sri Lanka

Potamidae Ortmann 1896*Potamon fluviatilis algeriense* Bott 1967 — Morocco**Potamonautidae** Bott 1970a*Potamonautes aloystisabaudiae* (Nobili 1906) — Uganda*Potamonautes obesus* (A. Milne-Edwards 1868) — Tanzania*Sudanonautes faradjensis* (Rathbun 1921) — Zaire*Platythelphusa armata* A. Milne-Edwards 1887 — Lake

Tanganyika, East Africa

Pseudothelphusidae Rathbun 1893**Epilobocerae** Smalley 1964*Epilobocera sinuatifrons* A. Milne-Edwards 1866 — Puerto Rico**Pseudothelphusinae** Rathbun 1893*Fredius reflexifrons* (Ortmann 1897) — Brazil*Kingsleya latifrons* (Randall 1840) — Brazil*Hypolobocera chilensis* (H. Milne Edwards & Lucas 1844) — Peru**Sundathelphusidae** (= Parathelphusidae) Bott 1969*Archipelothelphusa grapsoides* (H. Milne Edwards 1853) —

Philippines

Holthuisana (Austrothelphusa) transversa (Martens 1868) —

Australia

Holthuisana festiva (Roux 1911) — New Guinea*Mainitia mainitensis* (Balss 1937) — Philippines*Perithelphusa rouxi* Bott 1970b — Central Borneo*Sendleria gloriosa* (Balss 1923) — Bismark Archipelago*Sundathelphusa aruana* (Roux 1911) — Lesser Sunda Islands**Trichodactylidae** H. Milne Edwards 1853*Sylviocarcinus pictus* (Pretzmann 1968) — Brazil*Valdivia serrata* (White 1847) — Brazil**Appendix 2. Listing and current systematic placement of marine outgroup taxa used in the cladistic study.****Heterotremata** Guinot 1977**Bythograeoidea** Williams 1980**Bythograeidae** Williams 1980*Austinograea alayseae* (Guinot 1989)**Corystoidea** Samouelle 1819**Cancridae** Latreille 1803*Cancer (Metacarcinus) borealis* (Stimpson 1859)**Xanthoidea** Macleay 1838**Carpiliidae** Ortmann (1893)*Carpilius corallinus* (Herbst 1783)**Eriphiidae** MacLeay 1838*Eriphia gonagra* (Fabricius 1781)*Menippe mercenaria* (de Haan 1833)*Ozius reticulatus* (Desbonne & Schramm 1867)**Panopeidae** Ortmann 1893*Panopeus purpureus* (Lockington 1877)*Nanoplax xanthiformis* (A. Milne Edwards 1880)**Pilumnidae** Samouelle 1819*Pilumnus dasypodus* (Kingsley 1879)*Pilumnus sayi* (Rathbun 1897)**Trapeziidae** Miers 1886*Trapezia cymodoce* (Latreille 1825)**Xanthidae** Macleay 1838*Eucratodes agassizii* (A. Milne-Edwards 1880)*Pseudomedeus agassizii* (A. Milne-Edwards 1880)

Superfamily Uncertain

Geryonidae Colosi 1923*Chaceon fenneri* (Manning & Holthuis 1971)**Portunoidea** Rafinesque 1815**Portunidae** Rafinesque 1815**Carcininae** MacLeay 1838*Carcinus maenas* (Linnaeus 1758)**Podophthalminae** Borradaile 1907*Euphylax robustus* (A. Milne-Edwards 1874)**Portuninae** Rafinesque 1815*Callinectes arcuatus* (Ordway 1863)*Portunus iridescens* (Rathbun 1893)**Thoracotremata** Guinot 1977**Gecarcinoidea** Dana 1851**Gecarcinidae** Dana 1851*Cardisoma crassum* (Smith 1870)*Gecarcinus quadratus* (Saussure 1853)**Grapsoidae** Dana 1851**Grapsinae** Dana 1851*Geograpsus lividus* (H. Milne Edwards 1837)*Goniopsis pulchra* (Lockington 1877)*Grapsus grapsus* (Lamarck 1801)*Pachygrapsus transvs.* (Gibbes 1850)**Sesarminae** Dana 1852*Armases ricordi* (H. Milne Edwards 1853)*Aratus pisonii* (H. Milne Edwards 1837)*Chiromantes huzardi* (Desmarest 1825)*Metagrapsus curvatum* (H. Milne Edwards 1853)*Sesarma aequatoriale* (Ortmann 1894)*Sesarma reticulatum* (Say 1817)**Varuninae** Alcock 1900*Eriocheir sinensis* (H. Milne Edwards 1853)*Euchirograpsus americanus* (A. Milne-Edwards 1880)*Hemigrapsus nudus* (Dana 1851)*Varuna litterata* (Fabricius 1798)**Ocypodoidea** Fabricius 1798

Family Uncertain

Ucides occidentalis (Ortmann 1898)**Ocypodidae** Fabricius 1798**Dotillinae** Stimpson 1858*Dotilla mictyroides* (H. Milne Edwards 1852)*Scopimera globosa* (de Haan 1835)**Heloeeciinae** H. Milne Edwards 1852*Heloeecius cordiformis* (H. Milne Edwards 1837)**Ocypodinae** Fabricius 1798*Ocypode gaudichaudii* (H. Milne Edwards & Lucas 1843)*Uca festae* (Nobili 1902)*Uca galapagensis galapagensis* (Rathbun 1902)*Uca heteropleura* (Smith 1870)*Uca pugilator* (Bosc 1802)*Uca vocator ecuadoriensis* (Herbst 1804)**Appendix 3. Characters and character states used in the cladistic analysis.**

1. Carapace lateral carinae: absent (0), present, (1).
2. Carapace sidewall carinae: absent (0), present (1).
3. Oblique carina running divergently subparallel to the posterior half of the carapace margin: absent (0), present, moderately developed (1), distinct (2).
4. Carapace frontal margin: horizontally projecting (0), moderate downward deflexion (1), deflexed downward vertically (2).
5. Deflected region of carapace front trapezoidal to spatulate in outline: absent (0), present (1).
6. Epigastric lobes positioned anterior to the supraorbital margins: absent (0), present (1).
7. Carapace orbital notches: present (0), absent (1).
8. Carapace front straight, lacking median cleft: absent (0), present (1).
9. 'Potamoid' vertical sulcus on carapace sidewall subhepatic region: absent (0), present (1), distinct (2).
10. 'Grapsoid' vertical sulcus on carapace sidewall subhepatic region, flanking the outer orbital margin: absent (0), present (1).
11. Carapace posterior margin carina: high and sharp (0), narrow and distinct (1), low and indistinct (2).
12. Postorbital crest: absent (0), present (1).
13. Distinct posterior carina parallel to posterolateral margin of the carapace and anterior to the space for the pereopod 5 coxa: absent (0), present (1).
14. Carapace frontal margin with large, blunt teeth: absent (0), present (1).
15. Transverse epibranchial carina: absent (0), present (1).
16. Epistomal gutter: present (0), very reduced or absent (1).
17. Triangular median projection on subepistomal margin, epistomal 'tooth': absent or low (0), present (1).
18. Epistomal tooth flanked by a notch on either side: absent (0), present (1).

19. Endostomial ridges: absent (0), present (1).
 20. 3rd maxilliped exopod: robust, width 0.5–0.35X ischium width (0), thin, width < 0.35X ischium width (1).
 21. ‘Portunoid lobe’, 1st maxilliped endopod: absent (0), present (1).
 22. 1st maxilliped endopod extending laterally considerably beyond endostomial ridges: absent (0), present (1).
 23. Mandibular palp: 3-segmented (0), 2-segmented (1).
 24. Terminal segment of mandibular palp bilobed: absent (0), present (1).
 25. Buccal frame vertical margin: straight (0), ventrally widened or concave (1).
 26. 3rd maxillipeds completely enclosing buccal cavity: absent (0), present (1).
 27. 3rd maxillipeds very constricted at the region of ischium-merus articulation: absent (0), present (1).
 28. Primary penial emergence point, ‘male openings’: via aperture on pereopod 5 coxa (0), at base of pereopod 5 coxa, on or near articular membrane (1), via sternal aperture (2).
 29. Male abdomen outline: finger-like (0), narrowly triangular (1), broadly triangular (2).
 30. Male telson outline: (sub)triangular (0), tongue-shaped (1).
 31. Fusion, male abdominal segments a4 & a5: absent (0), present (1).
 32. Fusion, male abdominal segments a5 & a6: absent (0), present (1).
 33. Gonopod 1 subterminal segment outline: narrowly conical (0), 6-shaped (1).
 34. Gonopod 1 subterminal segment stout, conical: absent (0), present (1).
 35. Gonopod 1 terminal article: absent (0), present (1).
 36. Gonopod 1 subterminal segment apex with dense setae: absent (0), present (1).
 37. Chitinous flange present on gonopod 1 subterminal segment apex: absent (0), present (1).
 38. Gonopod 1 subterminal segment long, very slender: absent (0), present (1).
 39. Male sternal sulci s4/s5 interrupted: absent (0), present (1).
 40. Male sternal sulci s5/s6 interrupted: absent (0), present (1).
 41. Male sternal sulci s6/s7 interrupted: absent (0), present (1), distantly separated (2).
 42. Male sternal sulci s7/s8 interrupted: absent (0), present (1).
 43. Sternites 1 and 2 very reduced: absent (0), present (1).
 44. Male sterno-abdominal cavity anterior termination point: middle of s4 (0), at s3/s4 boundary (1), near s2/s3 boundary (2).
 45. Lateral margins of sternites 3 and 4 distinctly concave, s3-s4 with an ‘hour-glass’ shape: absent (0), present (1).
 46. Merus, pereopods 2–5, triangular in cross-section, posterior margins present: absent (0), present (1).
 47. Merus, pereopods 2–5, with carinae-striae on superior surface: absent (0), present (1).
 48. Merus, pereopods 2–5, with anterior ‘trough’ on superior surface: absent (0), present (1).
 49. Dactylus, pereopods 2–5, with corneous spines: absent (0), present (1).
 50. Merus, pereopod 1, with carinae on dorsal, external face: absent (0), present (1).
 51. Merus, pereopod 1, with irregular teeth on dorsal, interior margin: absent (0), present (1).
 52. Merus, pereopod 1, with sharp and distinct inferior margin: absent (0), present (1).
 53. Carpus, pereopod 1, with rugose superior surface: absent (0), present (1).
 54. Merus, pereopod 4, with sharp subdistal spine on superior margin: absent (0), present (1).
 55. Dactylus, pereopod 5: styliform (0), spatulate (1), broad, leaf-like (2).
 56. Pereopod 5 margins lined with fine (silky) setae: absent (0), present (1).
 57. Propodus, pereopod 5: narrow (0), broad (1), very broad, flat (2).
 58. Joint between pereopod 1 ischio-basis and merus indistinct: absent (0), present (1).
 59. Merus, pereopod 1, with large, curved, and regularly spaced teeth on dorsal, interior margin: absent (0), present (1).
 60. Carapace outline transversely oval or egg-shaped in outline, ‘oziine’ carapace shape: absent (0), present (1).
 61. Carapace outline ‘grapsoid’: absent (0), present (1).

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