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

R. VON STERNBERG, N. CUMBERLIDGE and G. RODRIGUEZ

Abstract

Freshwater crab sister group relationships with marine eubrachyuran families were investigated. A morphology-based clades 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 superfamili 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: Eubrachyuran phylogeny – freshwater crabs – cladistic analysis

Introduction

Freshwater crabs are a diverse assemblage of eubrachyurans (Guinot 1977, 1978, 1979) distributed throughout the tropical and sub-tropical regions of Central and South America, Africa, Madagascar, southern Europe, India, Asia, and Australia. These dekapods 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 rainforest floors and dry savannas. Some species of freshwater crabs are completely aquatic, some are semi-terrestrial, and some are air-breathe that lead an arboreal existence (Rodriguez 1982; Ng 1988; Cumberlidge 1991; Cumberlidge and Sachs 1991; Rodriguez 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. Rodriguez 1992; Cumberlidge 1987, 1993, 1994, 1999; Cumberlidge and Clark 1992; Rodriguez 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 assemblies of dekapods.

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 Potamidae Ortmann 1896 and, after emendation (Opinion 712, Bull. Zool. Nomenclature 196), 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 Deckeninae, 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 Deckenidae, the Paleotropical 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 Parathelphusoidae (later emended to the Gecarcinucoidea Rathbun 1904) for the Gecarcinidae, Parathelphusidae, and Sundathelphusidae; the Potamoida Ortmann 1896 for the Deckenidae, Isolapotamidae, Potamidae, Potamonautidae, and Sinopotamidae; and the Pseudothelphusoidae 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 (envisaged 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 Sinapotamidae (Ng 1988). It would thus appear that while the Paleotropical families Deckenidae, Gecarcinidae, Parathelphusidae, Potamonautidae, and Potamidae can be defined by various apomorphies, the same cannot be said about the other Paleotropical families (the Sundathelphusidae, Isolapotamidae, and Sinapotamidae). 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; Rodri guez 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 (Rodriguez 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 Ozine or Eriphine stocks...’ within the Xanthoidea. Other proposals have tied the Potamidae and Potamonautidae with the Coryxoidae Samouel (1819) (Jamieson et al. 1997), the Pseudothelphusidae with the Panopeidae Ortmann (1893), and the Trichodactylidae with the Eriphidae 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 coryxoids and xanthooids, 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 intromitent organs (which remain sealed inside the sternum-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, Geecarcinucidae, and Parathelphusidae (Ng 1988), and the Potamonautidae (Cumberlidge 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; Cumberlidge 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 extant work of Guinot (1977, 1978, 1979) on eubrachyuran relationships (encompassing the sections Heterotremata and Thracotremata) 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 many 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 superfamly, 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 Carpiidiidae and Guinot (1979) was used to identify the flataxonid groundplan. Alcock (1898, 1899), Guinot (1978, 1979), and Rathbun (1930) were consulted for overviews of cancriad, xanthoid and portunoid character states. The aberrant ocypodoid Ucides Rathbun 1897 and the ocypodoid superfamilies Dotillinae Stimpson 1858, Helococininae H. Milne Edwards 1852, and Ocyopodinae Dana 1851 are collectively referred to here as the Ocyopodoidae. 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
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.

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, Carpiidae Ortmann 1893; Erphidiidae MacLeay 1838, Geryonidae Colosi 1923, Goneplaciidae s.l. MacLeay 1838, Hexapodidae Miers 1886, Panopeidae Ortmann 1893; Pirimelidae Alcock 1893; Platyxanthidae 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 Ocypodidae Rafinesque 1815 in the Thoracotremata. The synapomorphic 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, Bellidae (in part) Dana 1852, Calappidae (in part) de Haan 1833, Corysidae Samouelle 1819, Dorippidae de Haan 1833, Haplog rocarnidae Calman 1900, Leucosioidea Samouelle 1819, Majoidea Samouelle 1819, Palicidae Bouvier 1897, Panotheroidea MacLeay 1838, Pirimelidae Alcock 1899, Retroplumidae Gill 1894, and Thaidae 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, Pirimelidae & Mietyridae 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
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 1985a,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 eubrachyuran 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 Pseudothelphusidae/Paleotropical freshwater crabs and the Thoracotremata. The 50% majority-rule consensus tree of the 81 trees is presented in Fig. 2. The Eubrachyura 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 apomorphic 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. 1). However, the reader should note that the consensus tree presented in Fig. 2 has been modified in Figs 3 and 4: first, the Carpiilidae and Panopeidae + Xanthidae form an unresolved polytomy with the branch encompassing the remainder of the Xanthoidea, the Bythograeidae, thelphusoids, and Thoracotremata (Fig. 3); second, the grapsoid subfamily Varuninae is presented as monophyletic on the basis of sharing a character state reversal [760] (Fig 4); and third, the Potamonaustidae, Potamidae, and the [Deckeniidae, *Platythelphusa* [Gecarcinucidae, Parathelphusidae] clade are presented as forming an unresolved polytomy (Fig. 4) due to the absence of unam-
On the marine sister groups of freshwater crabs

Fig. 1. 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. 2. 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 potamoid 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 pterygo-stomial 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 ‘potamoid’ vertical sulcus extending from the epibranchial tooth to the epimeral 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 Carpiliidae, Eriphiidae, Panopeidae, Pilumnidae, Platyxanthidae, and Xanthidae also exhibit these symplei-symplesiomorphies the Eriphiidae and Pilumnidae have state 3(0) except that these families have a somewhat reduced posterior carapace carina 3(0); 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 Trapezziidae, Bythograeidae, nontrichodactylid freshwater crabs, and Potamidae.
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 1967b). 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 thelphusid (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 Platypelphusa 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 thephusoids 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 pseudothelphusoids 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 (Eriocheir 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, Platypelphusa, 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 pereiopod 5 coxa 13(1) (Fig. 1a), which is homoplastically present in the varunines Eriocheir and Varuna.

All most parsimonious hypotheses of relationships place a clade consisting of the [varunines [Gecarcinucidae + Grapsidae s.s.] Ocyopodidae]) (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 *Euchirophoneus* H. Milne Edwards 1853; homoplastically developed in the *Trichodactylidae*).

Several apomorphies are homoplastically shared among thelphusoids and thoracotremate subclades. One most noticeable homoplasy is the presence of distinct carapace lateral carinae or striae 1(1) in the Paleotropical 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 Paleotropical 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.] Ocyopoidae clade and is a homoplasy development in the Pseudothelphusidae. The Paleotropical thelphusoids have a moderately deflexed front 4(1) that covers most of the antennular fossae (a condition also seen in the Eriphidae, 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 Ocyopodidae; Fig. 1b). This ‘grapsoid’ vertical sulcus is not topologically homologous with character 9; the epilobocerine pseudothelphusoids have both characters.

The ocyopoids have one carapace synapomorphy: the deflexed region of the carapace front has a narrowly trapezoid-to-epistomal gutter 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 ocyopoids.

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 (*Sudannonautes africanus* A. Milne-Edwards 1869, *Liberonautes chapleri* A. Milne-Edwards 1887, and *Potamonautes escorsai* Marchand 1902) to secondarily faint or absent (S. *monodi* Balss 1929, *L. paludicola* Cumberledge & 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 Paleotropical thelphusoids with reversals having occurred in subclades). Indeed, a preliminary morphological analysis of hatchlings of *Sudannonautes 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 morpholine exists for these structures, a morpholine which is a reversal of the general eubrachyuran morpholine: complete absence of suprarobital 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 Trapezidae, Bythograeidae, thelphusoids, and thoracotremes acquired fused supraorbital notches, a few parathelphusid taxa (not the majority of the reviewed family members) have redeveloped the pleiomorphic 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 pleiomorphic states for all carapace characters studied except 8 (the frontal margin clef). The frontal margin clef is highly reduced 8(1) in the trichodactylids although the front is bilobed. The placement of the Trichodactylidae within the Portunoidae (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 Cancininae and Trichodactylidae is evidence that these clades occupy basal positions within the Portunoidae.

**Epistome and mouthparts**

Sympleiomorphic character states in the Brachyura (including the Podotremata) include: a bilobed median subepistomial projection 16(0) (referred to as an ‘epistomial gutter’; Rodríguez 1992; Giuniot 1976: Fig. 8); the median projection on the posterior epistomial 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 ischiium 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 pulp 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, Xanthiidae, and of some taxa in the Eriphiidae, Plumnidae, and Trapezidae.

The thalpusoids + 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, *Tratancoriana schinerea* Bott 1969; and *Mainitia milleridentis* Balss 1937) have remnants of an epistomal gutter. Another synapomorphy for the thalpusoids + 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. *Varna* exhibits the plesiomorphic condition for character 20.

As pointed out by Rodriguez (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 thalpusoids, 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 thalpusoid 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 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 thalpusoids (such as *Platytelphusa* and all members of the Potamonaudeidae) uniformly possess broad, medially expanded third maxillipeds that completely fill the buccal frame. The expanded third maxillipeds of the thalpusoids are therefore decoupled from semiterrestriality and thus cannot be dismissed as convergent adaptations. It should also be noted that some arctic crabs have state 26(1) as do some belliioids (e.g. *Bellia* H. Milne Edwards 1848), calappoids, hymenosomatids, and majoids, and this is undoubtedly homoplastic with the condition seen in the thalpusoids.

The thalpusoids can be distinguished by the following set of apomorphies: the median projection on the posterior epistomial margin forms a strong triangular tooth (the epistomial tooth) that juts outward and/or downward 17(1) (Fig. 1b); a notch is present on either side of the epistomial tooth on the posterior epistomial 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 thalpusoids includes a two-segmented mandibular palp 23(1). State 17(1) is also seen in the Bythograeidae, Trichodactylidae, and ocyopodiids; although homoplastically developed in other eubrachyuran families, the epistomial tooth is a consistent feature of the thalpusoids and thus is considered an aspect of the thalpusoid synapomorphic groundplan. The notches flanking the epistomial tooth 18(1) must likewise be considered an attribute of the ur-thalpusoids as it is distinct in primitive pseudothelphusids (Epilobocercinae) and all Paleotropical thalpusoids examined. All thalpusoid families except the Potamidae and *Platytelphusa* have a two-segmented mandibular palp (Bott 1970a; Rodriguez 1986; Ng 1988; Ng et al. 1995; Ng and Rodriguez 1995; Cumberlidge 1999). It has been stated that the three-segmented mandibular palp seen in the potamids and plathythelphusids represents the ancestral condition and thus the Deckeniidae, Gecarcinucoidae, 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 *Platytelphusa*. However, a mandibular palp with a bilobed terminal segment 24(1), characteristic of the Gecarcinucoida 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 ocyopodiids 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 thalpusoid clade followed by independent reversals in some gecarcinucoids, *Platytelphusa*, 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.]/[Ocycidae + Ocyopodiidae]) clade. The buccal cavity is square-shaped in the varunines.

**Male sternum and abdomen**

The thalpusoids 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 pereiopod. Male openings on the fifth pereiopod 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 pereiopod coxae are synapomorphic for the Thoracotremata (Guinot 1978, 1979). A dissection of the region encompassing the fifth pereiopod 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. 3a). The thalpusoids present a more complicated picture as some Paleotropical taxa have male openings which approximately 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 varamines 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 Gonoiopsis 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 pereiopod 5. However, in these graspsines 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 morphcline 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 pereiopod near the articular membrane (thelphusoids) → Sorts the sternal openings are near the coxae of the fifth pereiopods (gecarcinids, Ucides, varamines) → the sternal openings are near the median of sternites 7 or 8 (Ocypodidae). The ancestral node for the thalpophusoids + 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, Trichocactyidae, 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, thalpophusoids, 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 thalpophusoid 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 carpellids appear to have state 29(1) (Gluesner 1969) although recent taxa (Car- pilus) 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 Gecarcinocidae, state 30(1) has arisen within some subclades of the Gecarcinucinae and Parathelphusidae and transitional states are seen in some gecarcinucids such as Tracancorina schirnerae.

The Cancridae, Geryonidae, Portunoida and the xanthoid families Carpillidae, Panopeidae, Xanthidae, and some of the Trapeziidae have abdominal segments a4 and a5 31(1) and a3 and a4 32(1) fused. The subfamily Didocarcininae of the Trichocactyidae has states 31(1) and 32(1) whereas the Trichocactyidae 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 cancriids, 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 xanthid 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 Eriphiiidae + Pilumnidae, Platyanxhidae, Trapeziidae, Bythograeidae, and thalpophusoids + 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 Carpillidae & 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 bellidoids, calappoids, dorippoids, hymenosomatids, leucosioids, and majaoids (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 Carpillidae) is a reversal to the plesiomorphic state. The Portunoida s.s. and Thoracotremata exhibit the most apomorphic condition with sternal sutures s6/s7 and s7/s8 medially interrupted with the interruption points well separated 41(2), 42(1). The Trichocactyidae have states 41(1) and 42(1) although some members of the Didocarcininae 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 [thalpophusoids, 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 stern (e.g., Caridisoma 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 median termination points (when present) very well separated. Development of states 41(1, 2) and 42(1) has homoplastically occurred in members of the Callappoidea, Dorippoidea, Hymenosomatidae, Leucosioida, Majoidea, and some gonoplenic grade Xanthoidea.

All thalpophusoids have sternal sutures s4/s5 and s5/s6 medially interrupted. Sternal suture s6/s7 is interrupted in some gecarcinocoids, Platythelphusa, the Potamidae, Potamonautidae and the Pseudothelphusidae and the hypothesis presented here has state 41(2) synapomorphic for the thalpophusoids + Thoracotremata, with reversals to state 41(0) seen in thalpophusoid subclades. Sternal suture s7/s8 is interrupted 42(1) in some Gecarcinocidae, 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 thalpophusoid families, particularly the Potamonautidae and Pseudothelphusidae,
is strikingly similar to that of the Carpiidae (Guinot 1968a: Pl. 1). This carapillid sternal conformation (for lack of a better term) is a sympleiomorphy in the Eubrachyura and the orbicular sternum outline seen in the Portunoida s.l., Bythograeidae, varunines, Grapsidae s.s., thalassophaidae such as Gubernatoriana Bott (1970b); goneplacien grade xanthoids, and ocypodoids was undoubtedly independently derived from this groundstate. The carapillid sternum seen in most thelphaidae 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 thalassophaid sternum is wider than that seen in cancrids and most xanthoids and some thalassophaid have a sternum that is similar in shape to that of Cardisoma and Ucides, with the sternum of these thoracotremes topologically closer to the carapillid condition than to the form seen in, e.g. the sesarmines and ocypodoids.

Sternites s1 and s2 are very reduced 43(1) in ocypodoids, 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 ocypoid clad. The ocypodoids and the Gecarcinidae + Grapsidae s.s. clad 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 synapomorphic state in the Eubrachyura. Within the many members of the Thoracotremata (some varunines, sesarmines, and Gecarcinidae) and the Gecarcinucoidea, 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 Gecarcinucidae and Parathelphusidae (among other states not discussed here). State 44(1) is hypothesized to have been independently developed in the Eriocheir + Varuna clad and the [Gecarcinidae + Grapsidae s.s.] Ocypodoidea lineage.

First gonopods

All (or almost all) Paleotropical thalassophaid 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 parable is referred to as the terminal segment (Ng 1988) or terminal article (Cumberlidge 1999). The additional terminal ‘segment’ of these thalassophaid 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 thalassophaid.

The synapomorphic groundplan of the Eubrachyura includes a first gonopod endopod/subterminal segment which is narrowly conical, a conformation seen, e.g. in the corynoids, calappoids, and eriophaidae. The Geryonidae, Trichodactylidae, and Portunoida 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 mediadly 33(1). In Carcinus and in many portunoids the distal half of the endopod forms a needle-like stylus whereas in the geryonoids 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 thalassophaid, the first gonopod endopod/subterminal segment in the Pseudepilophthalmidae 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 (Rodriguez 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 all thalassophaid + Thoracotremata. The difficulty with this hypothesis is that the first gonopod endopod/subterminal segment of the pseudothelphusid and the Paleotropical thalassophaid has a very disparate topology, although this segment is stout and complex in some Asiatic potamids (Bott 1970b). The most parsimonious hypotheses position the Pseudepilophthalmidae as sister group of the Paleotropical thalassophaid 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 Pseudepilophthalmidae 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 thalassophaid + Thoracotremata, it is possible that the field of apical spines seen in the pseudothelphusid 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 thalassophaid + 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 ‘tough’ or groove runs immediately parallel to the anterior margin of the merus 48(1) (Fig 1d; reduced in some thalassophaid); and the dactylus of pereiopods 2–5 has rows of corneous spines 49(1). The Trichodactylidae are 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 pereiopods 2–5 (but these segments do have very stiff black setae). Examination of the benthic marine varunine *Euchiro`rapsus* and the lithoral grapside *Grapsus* revealed distinct corneous spines on the dactylus of pereiopods 2–5 and this is taken to represent the basic thoracotremate condition. The long, thick setae seen on the dactylus of pereiopods 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, *Euchirograpsus*, and the Gecarcinidae; some of the spines observed on *Euchirograpsus* 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 pereiopods 2–5 completely.

The occurrence of prominent carinae on the dorso-external surface of the merus of pereiopod 1 50(1), a sharply defined inferior margin of the merus of pereiopod 1 52(1), and a carpus of pereiopod 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 carapace) of the merus of pereiopod 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, *Platytyphlops*, and gecarcinucoids, in the thelphusoid lineage, and *Hemigrapsus* in the thoracotreme clade.

Three synapomorphies of the pereiopods were also determined for the Portunoidea (including the Trichactidaeidae). The portunoid groundplan includes: a spatulate dactylus on pereiopod 5 55(1), fine setae on the margins of the propodus and dactylus of pereiopods 2–5 56(1), and a broad and flat propodus of pereiopod 5 57(1). Character states 55(1), 56(1), and 57(1) were independently developed in *Eriocheir* and *Varuna* and in the latter taxon pereiopods 3 and 4 also have a spatulate, seminatant dactylus. Characters 55 and 57 have been further modified in the Podophthalminae and Portuninae in which the dactylus of pereiopod 5 is very broad and flat 55(2) as is the propodus of pereiopod 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 pereiopodal synapomorphy: the dorsal margin of the merus of pereiopod 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 pereiopod 1 with the merus of pereiopod 1. Fusion of the cheliped ischiobasis and merus with subsequent reduction of the articulation joint is seen in both the Carpillidae and Eriphidae 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 Carpillidae or Eriphidae.

Transversely oval ‘ozine’ 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 Eriphidae and the pseudothelphusids (see carapace outline in Fig. 1a). This ‘ozine’ carapace outline 60(1) is not a plesiomorphy as it is a highly derived end-product of carinization (Guinot 1979). Paleotropical thelphusoids, however, exhibit an array of carapace morphologies, some species having an ozine 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 ozine 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 Trichactylidae, 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 paraphyly) 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 + Gecarcinucoidae and the Potamoidea (specifically the Eupomatonea + Trichodactylidae (Rodríguez 1986; Ng et al. 1995; Ng and Rodríguez 1995).
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 Paleotropical 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 Turkay 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 Portunidea. Given that the Cininae 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 Caphrynidae, 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 Portunidea, 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 telphusoid 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 telphusoids 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 telphusoid taxa, hypotheses postulating a polyphyletic derivation of the telphusoid families from various marine heterotrematous clades appear to have little support.

The question of whether the telphusoids diverged in freshwater environments from an ancestral freshwater group or whether several or many telphusoid 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 telphusoids

It is interesting to note that H. Milne Edwards (1837) was the first carcinologist to point out the similarities between the telphusoids and the Thoracotremata. The telphusoids formed in H. Milne Edwards’ opinion a ‘satellite’ of the Grapsinae. Alcock (1898, 1899), likewise, wrote: ‘The Telphusidae are the highest Cyclometopidae, etc., and approach the Carcinomidae [ = 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 grapsoid-like habits of the telphusoids, he was inclined to place them adjacent to primitive xanthoids (Eriphididae) implying thereby that such grapsoid-like features were convergences. The position of the male openings (see above) of the telphusoids was apparently the key argument for linking these crabs with underived heterotremes.

The most parsimonious trees position the telphusoids and thoracotremes as sister groups (Figs 2 and 4). The homoplasic states [e.g. 1(1) and 2(1)] shared between the telphusoids (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 telphusoid taxa to gecarcinids and grapsids is very evident (see, e.g. the plates in Bott 1970b). Indeed, Gecarcinucinae H. Milne Edwards 1844 (family Gecarcinucidae) 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 pereiopods 2–5 with carinae on the superior surface 47(1), for example, give many Paleotropical telphusoid taxa (e.g. Mainitia and Gubernatoriana) a very grapsid-like appearance (as do the hatchlings of Potamonauta MacLeay 1838 and Sudanonautes Bott 1955). And aside from the first gonopod morphology, the gecarcinids and grapsines appear typologically closer to the telphusoids 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 telphusoids and the Gecarcinidae + Grapsidae s.s. vis-à-vis the varunines cannot be dismissed.

The sperm of the Paleotropical telphusoids Potamon Savigny 1816 and Potamonauta 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 telphusoids 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 Potamonauta 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, majdis, or xanthoids. However, those authors identified several apomorphies shared between the potamoids and the thoracotremes. The spermatozoos of Potamon, for example, was found to lack an unambiguous acrosomal ray zone (as was that of Potamonauta 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, cory- stoids, and majids; Guinot et al. 1997). Reduction of the thick- ened 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 sper- matozoa1 studies revealed that a tier of possible syn- apomorphies 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 [variform [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 pre- sented here suggest a similar conclusion except that the thel- phusoids are either the sister taxon of the Thoracotremata or the sister taxon of some of the thoracotremes, should the Tho- racotremata 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 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 thel- phusoid taxa to be the result of the independent migration of preadapted heterotrematous lineages into freshwater environ- ments from the Tethys Sea, probably during the Tertiary (around 65 million years ago). This hypothesis explains thel- phusoid synapomorphies as the result of similar selective pres- sures, rather than common ancestry. Indeed, Pretzmann (1973) argued that the different tribes and even genera within the Pseudothelphusidae each had a different marine ancestor (Rod- ríguez 1986). Bott (1955, 1969, 1972) and Pretzmann (1973) apparently discounted the notion of an archaic freshwater thel- phusoid 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 sub- ordinate 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) Potamonidae + 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 separ- aration of the descendents of these ancestral crabs on the south- ern continents and islands of tropical America, Africa, Mad- agascar, 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 predicitions based on evidence from characters of the man- dibular palp (Rodríguez 1986; Ng et al. 1995), the third maxil- liped (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 Pot- amidae 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 Deck- eniidae, Gecarcinucoidea, Potamonautidae, and Pseudo- thelphusidae 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-seg- mented 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 dis- tribution in the Paleotropics and Neotropics. The present dis- tribution 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 spec- ies 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-
The 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 Gecarcinucinae + Pseudothelphusidae. The exopod (exogonath) 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 Lithophthalmidae, all Gecarcinucinae, all Parathelphusidae, most Potamidae (Bott 1970b; Ng 1988), and in most Potamonautidae (Bott 1985a; 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 Globonanthes 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 Liberonautes 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 (Epibocera) 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 Somathelphusa (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 freshwater 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. Glassner 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 trichocoracids) 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 05(0), a slender third maxilliped exopod 20(1), a penis that emerges next to the coxal/sternum articular membrane of pereiopod 5 28(1), a prethoracotremere 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 pereiopods 2–5 with a triangular cross section 46(1), the superior margin of the merus of pereiopods 2–5 with carinae-striae 47(1), the anterior margin of the merus of pereiopods 2–5 with a trough parallel to this margin 48(1), the dactylus of pereiopods 2–5 with concomous 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 sub-clades 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; Pretzmann 1986). 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 accounts for 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 nontrichocoracid 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 Carpiidae and part of the Erphidiidae, all of the xanthid (cancond + putronuid) 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 heterogenous 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 the thelphusoids, (2) resolving the heterotreme-thoracotreme distinction, and (3) identifying the sister group of the thelphusoids + Thoracotremata.

Acknowledgements

Appreciation is extended (in arbitrary order) to Dr Celio Magalhães (Instituto Nacional de Pesquisas de Amazônia, Brazil) for donating specimens of Stylokiaprosus pictus, Valdivia serrata, Freuds reflexions and Kingdeyia laitffons to N.C. Dr Michael Türkay (Forschungsinstitut Senckenberg, Frankfurt a. M., Germany) loaned the Indian and Southeast Asian gecarcinoids, sundathelphusids, and parathelphusids to R.V.S. Specimens of Potamonathus aloysiaabandiae from Uganda were kindly donated by Professor Rolf Garms of the Bernhard Nocht Institute for Tropical Medicine, in Hamburg, Germany. Specimens of Sudamamans farahrensis were collected by Dr Louise Bourgault of Northern Michigan University, and the specimens of Platythelphusa armata from Lake Tanganyika were loaned by Ian Roger Bills of the JLB Smith Institute of Ichthyology in Grahamstown, South Africa. Dr Peter K. L. Ng (National University, Singapore) is thanked for sending to us many reprints, and Dr Daniele Guinot (Museum National d'Histoire Naturelle, Paris) is especially appreciated for providing reprints, for helpful discussions on heterotretem-thoracotreme distinctions, and for loaning specimens of the Bythograeidae, Dotillidae, Helococciinae, and Varaminae. Thanks also to Trefor Williams, of the Department of Environmental and Evolutionary Biology, University of Liverpool, UK, who kindly donated the specimens of Potamonattus obesus and Deckenia mitsis from East Africa and Potamon fluitans algierense from Morocco. Finally, we thank Dr Engelhoff and an anonymous reviewer for their constructive criticisms of an earlier version of this paper.
Zusammenfassung
Über die marinen Schwestergruppen der Süßwasserkrabben (Crustacea: Decapoda: Brachyura)


References
Croizat, L., 1964: Space, time, form: the biological synthesis. Published by the author, Caracas.
- 1994: Loutsea, a new genus of fresh-water crab (Brachyura, Pota-


Appendix 2. Listing and current systematic placement of marine outgroup taxa used in the cladistic study.

Heterotremata Guinot 1977

Bythograeoida Williams 1980

Bythograeidae Williams 1980

Austrothelphusa australis (Guinot 1989)

Corythoidea Samouelle 1819

Cancridae Latreille 1803

Cancer (Metacarcinus) borealis (Stimpson 1859)

Xanthidae Malceay 1838

Carpiidae Ortmann 1893

Carpiulus coronellus (Herbst 1783)

Eriphidae MacLeay 1838

Eriphia gonagra (Fabricius 1781)

Menippus mercenarius (de Haan 1833)

Oziza reticulata (Desbonne & Schramm 1867)

Panopidae Ortmann 1893

Panopites purpureus (Lockington 1877)

Nanoanax hirsutus (A. Milne-Edwards 1880)

Pilumnidae Samouelle 1819

Pilumina dasypoda (Kingsley 1879)

Pilumnus sayi (Lockington 1877)

Trapeziidae Miers 1886

Trapezia cymodoce (Latreille 1825)

Xanthidae Malceay 1838

Eucratodes agassizii (A. Milne-Edwards 1880)

Pseudomedaeus agassizii (A. Milne-Edwards 1880)

Superfamily Uncertain

Geryonidae Colosi 1923

Chaceon fenneri (Manning & Holthuis 1971)

Portunoida Rafinesque 1815

Portunidae Rafinesque 1815

Carcinidae MacLeay 1838

Carcinus maenas (Linnaeus 1758)

Podophthalminae Borradaile 1907

Euphylax robustus (A. Milne-Edwards 1874)

Portuninae Rafinesque 1815

Callinectes arcuatus (Ordway 1863)

Portunus iridescentes (Rathbun 1893)

Thoracotremata Guinot 1977

Gecarcinoidea Dana 1851

Gecarcinidae Dana 1851

Cardisoma crassum (Smith 1870)

Gecarcinus quadratus (Sauvage 1853)

Grapsoida Dana 1851

Grapsidae Dana 1851

Grapsinae Dana 1851

Geograpus lividus (A. Milne Edwards 1837)

Goniopsis pulchra (Lockington 1877)

Grapsus grapsus ( Lamarck 1801)

Pachygrapsus transversus. (Gibbes 1850)

Sesarmae Dana 1852

Armasies ricordi (A. Milne Edwards 1853)

Aratus pisonii (A. Milne Edwards 1837)

Chiromantes harsedi (Desmarest 1825)

Metagrapsus curvatus (A. Milne Edwards 1853)

Sesarma aequatoriale (Ortmann 1894)

Sesarma reticulatum (Say 1817)

Varuninae Alcock 1900

Eriocheir sinensis (A. Milne Edwards 1853)

Euchirograpsus americanus (A. Milne Edwards 1880)

Hemigrapsus nudus (Dana 1851)

Varuna littorata (Fabricius 1798)

Ocypodoida Fabricius 1798

Family Uncertain

Ucides occidentalis (Ortmann 1898)

Ocypodidae Fabricius 1798

Dotillinae Stimpson 1858

Dotilla mictyroidea (A. Milne Edwards 1852)

Scopimera globosa (de Haan 1835)

Helocoeinae H. Milne Edwards 1852

Helocoeus cordiformis (H. Milne Edwards 1837)

Ocyopodinae Fabricius 1798

Ocyode gandiahaudii (H. Milne Edwards & Lucas 1843)

Uca festae (Nobili 1902)

Uca galapagensis galapagensis (Rathbun 1902)

Uca heteropleura (Smith 1870)

Uca pupillator (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 front carina: absent (0), present (1).
3. Oblique carina running divergently subparallel to the posterior half of the carapace margin: block (0), present, moderately developed (1), distinct (2).
4. Carapace front margin: horizontally projecting (0), moderate downward deflexion (1), deflexed downward vertically (2).
5. Deflected region of carapace front tranzeoidal to spoutulate in outline: absent (0), present (1).
6. Maxilar lobes positioned anterior to the supraorbital margins: absent (0), present (1).
7. Carapace orbital carinae: present (0), absent (1).
8. Carapace front straight, lacking median cleft: absent (0), present (1).
9. ‘Posterior’ vertical sulcus on carapace front subhepatic region: absent (0), present (1), distinct (2).
10. ‘Grapsoid’ vertical sulcus on carapace front 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 pereiopod 5 coxa: absent (0), present (1).
14. Carapace front margin with large, blunt teeth: absent (0), present (1).
15. Transverse epibranchial carina: absent (0), present (1).
16. Epistomal gutter: absent (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 pereiopod 5 coxa (0), at base of pereiopod 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: subtriangular (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. Stermites 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, pereiopods 2–5, triangular in cross-section, posterior margins present: absent (0), present (1).
47. Merus, pereiopods 2–5, with carinae-striae on superior surface: absent (0), present (1).
48. Merus, pereiopods 2–5, with anterior ‘trough’ on superior surface: absent (0), present (1).
49. Dactylus, pereiopods 2–5, with conical spines: absent (0), present (1).
50. Merus, pereiopod 1, with carinae on dorsal, external face: absent (0), present (1).
51. Merus, pereiopod 1, with irregular teeth on dorsal, interior margin: absent (0), present (1).
52. Merus, pereiopod 1, with sharp and distinct inferior margin: absent (0), present (1).
53. Carpus, pereiopod 1, with rugose superior surface: absent (0), present (1).
54. Merus, pereiopod 4, with sharp subdistal spine on superior margin: absent (0), present (1).
55. Dactylus, pereiopod 5: styliform (0), spatulate (1), broad, leaf-like (2).
56. Pereiopod 5 margins lined with fine (silky) setae: absent (0), present (1).
57. Propodus, pereiopod 5: narrow (0), broad (1), very broad, flat (2).
58. Joint between pereiopod 1 ischio-basis and merus indistinct: absent (0), present (1).
59. Merus, pereiopod 1, with large, curved, and regularly spaced teeth on dorsal, interior margin: absent (0), present (1).
60. Carapace outline transversly oval or egg-shaped in outline, ‘ozine’ carapace shape: absent (0), present (1).
61. Carapace outline ‘grapsoid’: absent (0), present (1).

Authors’ addresses: Dr N. Cumberlidge (for correspondence), Department of Biology, Northern Michigan University, Marquette, Michigan, 49855–5341, USA. E-mail: Ncumberl@nmu.edu; Dr R. von Sternberg and Dr G. Rodriguez, Centro de Ecología, Instituto Venezolano de Investigaciones Científicas, Apartado 21827, Caracas 1020-A, Venezuela. E-mail: Grodrigu@oikos.ivic.ve and Rsternbe@oikos.ivic.ve