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Decapod Crustacean Phylogenetics

edited by

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Systematics, Evolution, and Biogeography of Freshwater Crabs

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ABSTRACT

Freshwater crabs are a large group of aquatic animals, with more than 1,280 described species worldwide found in freshwater ecosystems throughout the warmer parts of the Neotropical, Afrotropical, Palaearctic, Oriental, and Australasian zoogeographical regions. We report here on the changes in the understanding of the higher systematics of these decapods over the past 25 years associated with attempts to put freshwater crab taxonomy into a phylogenetic framework. The distributional patterns of the freshwater crabs on continents and islands are interpreted in terms of their dispersal abilities and barriers to their distribution. Theories on freshwater crab origins are discussed in the light of their phylogeny and present-day distributions. Adaptations to a permanent existence in freshwater and the adaptive radiation of freshwater crabs into such ecosystems worldwide are discussed.

1 DIVERSITY

The term ‘freshwater crab’ is most commonly used to refer to the large and diverse group of brachyurans found worldwide throughout freshwater ecosystems of inland waters of the continents in the tropics and subtropics (here called the ‘true’ freshwater crabs). However, the term ‘freshwater crab’ also has been applied commonly by different workers to such different groups of decapod crustaceans as the exclusively freshwater anomurans (Aeglidae) (Bond-Buckup et al. 2008) and even to species of predominantly marine brachyuran families (Sesarmidae, Varunidae, Hymenosomatidae) that spend time in freshwater (Ng 1988, 2004; Schubart & Koller 2005), making it necessary to distinguish here between the vernacular use of terms to refer to these very different groups of freshwater decapods. True freshwater crabs are defined here as heterotreme brachyurans that are found exclusively in freshwater habitats (never in brackish or marine environments) and that all reproduce exclusively by direct development (never with larval stages). The recent surge in taxonomic interest in this group has led to the realization that the biodiversity of freshwater crabs is not only much higher than previously thought (Martin & Davis 2001) but that they, in fact, constitute the largest natural group (18.8%) within a vastly expanded and reorganized Brachyura (Ng et al. 2008). The number of species of freshwater crabs has grown tremendously in the past 25 years, with more than 50% of all species described since 1980.

2 PHYLOGENY AND HIGHER TAXONOMY

Our understanding of freshwater crab relationships has been boosted by recent morphological and molecular studies, and the relationships of these decapods at the family, genus, and species levels are now becoming much clearer (e.g., Daniels et al. 2006; Klaus et al. 2006; Cumberlidge et al. 2008),

Table 1. Freshwater crab diversity by zoogeographical region and family.

| Family | Region | No. Genera | No. Species |
|--------------------|---|------------|--------------|
| TRICHODACTYLIDAE | Neotropical | 15 | 47 |
| PSEUDOTHELPHUSIDAE | Neotropical | 40 | 251 |
| POTAMONAUTIDAE | Afrotropical | 18 | 132 |
| POTAMIDAE | Afrotropical, Palaearctic, Oriental | 90 | 505 |
| GECARCINUCIDAE | Oriental, Australasian | 57 | 345 |
| Total: | | 220 | 1,280 |

although molecular studies on the Neotropical crabs are still not available. The most recent evaluations of freshwater crab biodiversity (Yeo et al. 2008; Ng et al. 2008) recognized more than 1,280 species of freshwater crabs worldwide (Table 1, Fig. 1).

Changes in our understanding of freshwater crab higher taxonomy in recent years (Table 2) has also meant that the number of families has been significantly reduced from the high point of 12 families recognized by Bott (1969, 1970a, b, 1972) and Cumberlidge (1999) and the eight families of Martin & Davis (2001). Recently, Cumberlidge et al. (2008) and Ng et al. (2008) assigned the freshwater crabs to only six families (Pseudothelphusidae, Potamonautidae, Potamidae, Gecarcinucidae, Parathelphusidae, and Trichodactylidae). Six other freshwater crab families, Potamocarcinidae, Deckeniidae, Platythelphusidae, Sundathelphusidae, Isolapotamidae, and Sinopotamidae, have been synonymized. The six valid families of freshwater crabs are separated into two main monophyletic lineages, each assumed to have a different (unknown) marine crab sister group (Sternberg et al. 1999). One of these lineages includes five families (Pseudothelphusidae, Potamonautidae, Potamidae, Gecarcinucidae, and Parathelphusidae), and the other includes only a single family (Trichodactylidae). Klaus et al. (2006) recently argued that the Gecarcinucidae and Parathelphusidae should be regarded as synonymous (the former having priority), supported by Klaus et al. (this

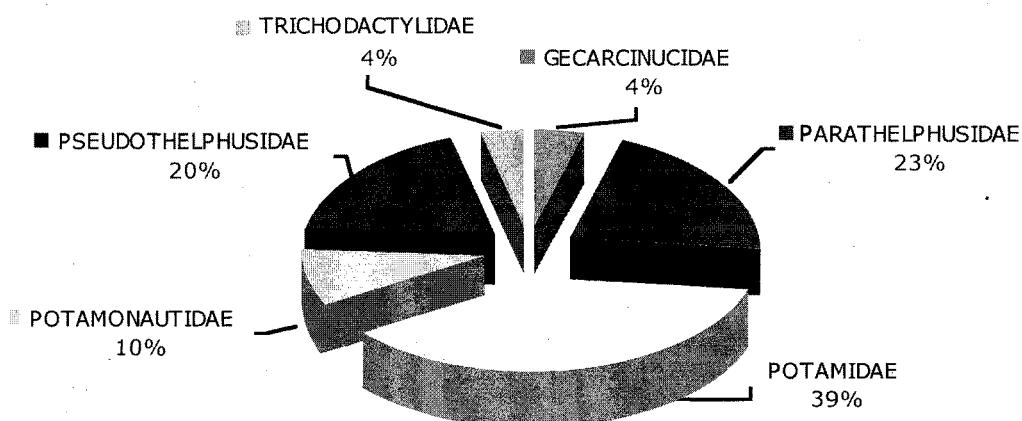
**Figure 1.** (See Color Figure 2 in the Color Insert at the end of the book.) Freshwater crab diversity (Table 2C).

Table 2. Recent changes in the higher taxonomy of the true freshwater crabs. (A) Freshwater crab higher taxonomy (Bott 1970b; Cumberlidge 1999). (B) Freshwater crab higher taxonomy (Martin & Davis 2001). (C) Freshwater crab higher taxonomy (Cumberlidge et al. 2008; Ng et al. 2008). (D) Freshwater crab higher taxonomy (present work).

A. Freshwater crab higher taxonomy (Bott 1970b; Cumberlidge 1999)

Pseudothelphusoidea Ortmann, 1853
 Pseudothelphusidae Rathbun, 1893
 Potamocarcinidae
 Potamoidea Ortmann, 1896
 Potamidae Ortmann, 1896
 Potamonautidae Bott, 1970b
 Deckeniidae Ortmann, 1897
 Platythelphusidae Colosi, 1920
 Sinopotamidae Bott, 1970a
 Isolapotamidae Bott, 1970a
 Gecarcinucoidea Rathbun, 1904
 Gecarcinucidae Rathbun, 1904
 Parathelphusidae Alcock, 1910
 Sundathelphusidae Bott, 1969
 Portunoidea Rafinesque, 1815
 Trichodactylidae H. Milne Edwards, 1853

B. Freshwater crab higher taxonomy (Martin & Davis 2001)

Pseudothelphusoidea Ortmann, 1853
 Pseudothelphusidae Rathbun, 1893
 Potamoidea Ortmann, 1896
 Potamidae Ortmann, 1896
 Potamonautidae Bott, 1970b
 Deckeniidae Ortmann, 1897
 Platythelphusidae Colosi, 1920
 Gecarcinucoidea Rathbun, 1904
 Gecarcinucidae Rathbun, 1904
 Parathelphusidae Alcock, 1910
 Portunoidea Rafinesque, 1815
 Trichodactylidae H. Milne Edwards, 1853

C. Freshwater crab higher taxonomy (Cumberlidge et al. 2008; Ng et al. 2008)

Pseudothelphusoidea Ortmann, 1853
 Pseudothelphusidae Rathbun, 1893
 Potamoidea Ortmann, 1896
 Potamidae Ortmann, 1896
 Potamonautidae Bott, 1970b
 Gecarcinucoidea Rathbun, 1904
 Gecarcinucidae Rathbun, 1904
 Parathelphusidae Alcock, 1910
 Trichodactyloidea H. Milne Edwards, 1853
 Trichodactylidae H. Milne Edwards, 1853

Table 2. continued.**D. Freshwater crab higher taxonomy (present work)**

| |
|--|
| Potamoidea Ortmann, 1896 |
| Pseudothelphusidae Rathbun, 1893 |
| Potamidae Ortmann, 1896 |
| Potamonautidae Bott, 1970b |
| Gecarcinucidae Rathbun, 1904 |
| Trichodactyloidea H. Milne Edwards, 1853 |
| Trichodactylidae H. Milne Edwards, 1853 |

volume). There have been only a few phylogenetic studies on freshwater crab family-level relationships, but those that are available indicate that the lineage that includes the five families shares common ancestry, and this warrants their assignment to a single higher taxonomic unit above the family level (Sternberg et al. 1999). We consider that the most appropriate choice would be at the superfamily level, thereby keeping this group of heterotremes consistent with other groups of families elsewhere in the Brachyura (Ng et al. 2008).

This contrasts with the traditional taxonomy that assigned the 12 freshwater crab families to three different superfamilies (Bott 1969, 1970a, b, 1972): the Pseudothelphusoidea (for Pseudothelphusidae and Potamocarcinidae), the Potamoidea (for Potamidae, Potamonautidae, Deckeniidae, Platythelphusidae, Sinopotamidae, and Isolapotamidae), and the Gecarcinucoidea (for Gecarcinucidae, Parathelphusidae, and Sundathelphusidae). Bott (1970a) left the Trichodactylidae without a superfamily assignment, although Banarescu (1990) referred it to a new superfamily, the Trichodactyloidea. Ng et al. (2008) adopted a conservative approach to the higher taxonomy of the freshwater crabs and placed them in four superfamilies: Pseudothelphusoidea (with Pseudothelphusidae), Potamoidea (with Potamidae and Potamonautidae), Gecarcinucoidea (with Gecarcinucidae and Parathelphusidae), and Trichodactyloidea (with Trichodactylidae).

In view of the existing evidence, we propose to provisionally recognize here a single superfamily, the Potamoidea, for the lineage of four families of freshwater crabs (Pseudothelphusidae, Potamonautidae, Potamidae, and Gecarcinucidae). The Potamoidea as defined here is a group with a global distribution and includes species of freshwater crabs from both the New World (Pseudothelphusidae) and the Palaeotropics (Potamonautidae, Potamidae, and Gecarcinucidae). This monophyletic potamoid superfamily, however, excludes the 47 species of Neotropical river crabs assigned to the Trichodactylidae, given that the latter group of species forms a separate clade (Sternberg et al. 1999; Martin & Davis 2001; Schubart & Reuschel this volume).

2.1 Evolution of mandibular palp characters in the potamoid freshwater crabs

Freshwater crabs traditionally have been assigned to families and superfamilies using characters of the mandibular palp, gonopods, and frontal median triangle (Bott 1970b; Ng 1988). However, these characters may not be as reliable as previously thought. In recent years, phylogenetic character mapping of mandibular palp characters in the five potamoid freshwater crab families onto a consensus phylogeny based on morphological and molecular studies (Fig. 2) has raised doubts. Although mandibular palp characters (such as the number of segments and the form of the terminal article) are invariant in the Pseudothelphusidae, Potamidae, and Gecarcinucidae, this is not true for the Potamonautidae, where the form of the terminal article of the mandibular palp is highly variable across taxa. For example, *Seychellum* Ng, Števčić & Pretzmann, 1995, from the Seychelles

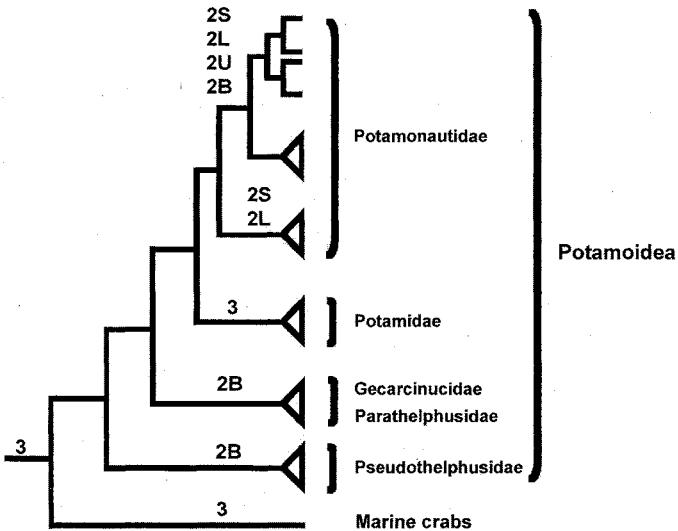


Figure 2. Phylogenetic character mapping of characters of the mandibular palp of potamoid freshwater crabs plotted onto a simplified consensus phylogeny (based on mitochondrial and nuclear DNA sequences as well as morphological data) for the freshwater crabs excluding the Trichodactylidae (after Sternberg et al. 1999; Daniels et al. 2006; and Klaus et al. 2006). The mandibular palp characters are consistent at the family level except for the Potamonautesidae. 3 = 3-segmented mandibular palp, simple terminal segment; 2S = 2-segmented, simple terminal segment; 2L = 2-segmented, terminal segment with ledge; 2U = 2-segmented, terminal segment unequal bilobed; 2B = 2-segmented, terminal segment subequal bilobed.

and *Deckenia* Hilgendorf, 1869, from East Africa have a strongly supported sister group relationship and both have a 2-segmented mandibular palp. However, the mandibular palp of *Seychellum* has a bilobed terminal segment, whereas that of *Deckenia* has a simple terminal segment. Traditional taxonomic thinking placed these two genera in different families and superfamilies (Ng et al. 1995; Štević, 2005), whereas these taxa are now both included in the Potamonautesidae (Daniels et al. 2006; Cumberlidge et al. 2008; Klaus et al. this volume). Clearly, mandibular palp characters on their own are unreliable for assigning species of Afrotropical freshwater crabs to a family, and this undermines confidence in their use as a high-weight character for the assignment of specimens to other potamoid families. In practice, mandibular palp characters remain useful for family-level placement of species of Pseudothelphusidae and Gecarcinucidae (there are no known exceptions), but there is reason to believe that these characters may be homoplastic, and as such they may not be reliable indicators of higher phylogenetic relationships.

A three-segmented mandibular palp with a simple terminal segment is generally agreed to be the common brachyuran condition and is found in nearly all heterotrematous marine crab families (unpublished data). However, only one potamoid family (Potamidae) has this form of mandibular palp, and (perhaps surprisingly) this is not positioned most basally on the phylogenetic tree (Fig. 2). Instead, it is the Pseudothelphusidae that appears as the most basal family, suggesting perhaps that the 2-segmented bilobed mandibular palp evolved early in this group (Fig. 2) and this is invariant in the family Pseudothelphusidae. The next branch in the tree is a division into two Palaeotropical lineages: (1) a branch with the Gecarcinucidae for specimens with a 2-segmented bilobed mandibular palp, and (2) a branch grouping the Potamidae and Potamonautesidae together for specimens with either a 3-segmented mandibular palp (Potamidae) or a 2-segmented mandibular palp (Potamonautesidae). Members of the Potamidae all have a 3-segmented mandibular palp with a simple terminal segment, while members of the Potamonautesidae have a 2-segmented palp with a terminal segment

that exhibits a variety of forms (either simple, or with a small ledge, or bilobed) in different species and genera (Cumberlidge et al. 2008). The only possible explanation for the 3-segmented mandibular palp with a simple terminal segment that is diagnostic of the Potamidae at the moment is that it appears to be a reversal of the apomorphic 2-segmented palp back to the plesiomorphic condition.

2.2 Evolution of gonopod 1 characters in the potamoid freshwater crabs

The gonopod 1 (G1) morphology of potamoid and trichodactylid freshwater crabs has become modified in the course of life in freshwater, and it is now distinctly different from each other and from the G1 of most marine crabs in both of these freshwater crab lineages. Because the marine sister group of the freshwater crabs is unknown, it is difficult to theorize about the original form of the gonopods seen in freshwater crabs. This search is hampered by the specialized and highly derived G1 seen in many families of marine heterotremes and thoracotremes (see Guinot 1977, 1978, 1979). Nevertheless, a stout columnar 3-segmented G1 is typical of many marine crabs, and no marine crabs have the four-part (4-segmented) G1 as seen in Palaeotropical freshwater crabs. Within the five families of potamoid freshwater crabs, the Pseudothelphusidae are the most basal, indicating that the stout 3-segmented G1 (Rodriguez 1982) may be closest to the marine crab ancestral form. However, the G1 of pseudothelphusids is distinguished from the superficially similar G1 of marine crabs such as panopeids (see Martin & Abele 1986) and pseudorhombilids (see Ng et al. 2008) by the highly ornamented and lobed distal end, the degree of complexity of which is not found in any other brachyurans. In contrast, the three Palaeotropical families of freshwater crabs (Potamidae, Potamonautidae, and Gecarcinucidae) usually share a similar 4-part G1 — the three segments seen in all brachyurans, plus a distinct terminal article (Bott 1970b). Within the Palaeotropical freshwater crab families, G1 characters are by no means uniform, and differences in G1 morphology are sufficient to distinguish between families in most cases. For example, both the Potamidae and Potamonautidae have a G1 with a long symmetrical tapered terminal article that may possess complex folds and lobes (Ng & Naiyanetr 1993; Cumberlidge 1999; Dai 1999; Ng 2004). Members of the Gecarcinucidae may have a simple terminal article but often also lack one, in which case the distal part sometimes displays a variety of different forms (Bott 1970b; Ng & Naiyanetr 1993; Ng 1988, 2004; Dai 1999).

2.3 The Potamoidea

The Potamoidea, as redefined here, is now a freshwater crab superfamily with a very wide distributional range that stretches from the tropical and subtropical parts of the Americas across to Africa, Eurasia, Indonesia, and Australia. Possible alternatives to characters of the mandibular palp and G1 as indicators of family and superfamily level groupings of the Potamoidea include the following suite of synapomorphic characters of the carapace, mouthparts, sternum, and pereiopods (Sternberg et al. 1999). The anterolateral margin of the carapace has a distinct exorbital tooth and a distinct epibranchial tooth; the margin behind the epibranchial tooth is well defined, convex, and lined with numerous small teeth or tubercles (which in some species may be secondarily lost); there is a vertical (= cervical) sulcus on the carapace sidewall dividing the suborbital from the subhepatic regions, beginning just posterior to the epibranchial tooth and extending inferiorly to meet the longitudinal (= pleural) sulcus on the sidewall of the carapace. The antennae are short and are only half the length of the eyestalk. The third maxillipeds are broad and fill the entire buccal field; the medial margins of the ischium and merus of the third maxillipeds are vertical and touch along their entire length; there is a distinct, triangular epistomial tooth on the lower margin of the epistome, and the epistomial tooth is flanked by incisions. The median septum of the endophragmal system is interrupted between interosternites 4/5, 5/6, 6/7, but interosternite 7/8 is complete and not medially erased. The anterior-inferior margin of the merus of pereiopod 1 (cheliped) has distinct, irregular teeth; the

dorsal surface of the merus of pereiopods 1–5 are rugose (either vague or distinct); and the dactyli of pereiopods 2–5 have at least four longitudinal rows of distinct corneous spines.

2.4 *The Trichodactylidae*

The Trichodactylidae is a freshwater crab family found primarily in the drainage basins of the Amazon, Orinoco, and Paraguay-Parana rivers in South America, with a small number of taxa distributed in Mexico and Trinidad (Rodriguez 1992; Magalhães & Türkay 1996a, b, c). The Trichodactylidae are morphologically unusual crabs that form a well-defined monophyletic group that is sharply isolated systematically. Other than direct development and a strict freshwater habitat, the trichodactylids have little in common morphologically with the Potamoidea as defined here. We list below the likely synapomorphies for the Trichodactylidae that include characters of the carapace, mouthparts, sternum, pereiopods, and G1 based on Magalhães (2003) and Sternberg & Cumberlidge (2003). The medial margins of the third maxillipeds meet along the midline, and the meri are slim and do not fill the entire buccal frame when closed; the endopod of maxilliped 1 has a distinct portunoid lobe (Rodriguez 1992). The antennae are long, either equal to or longer than the length of the eyestalk. The dactyli of the walking legs (P2–P5) have fields of dense soft setae rather than corneous spines. The median septum of the endophragmal system is dorsoventrally reduced, and interosternite 7/8 is extensively interrupted medially (Sternberg & Cumberlidge 2003). The male abdomen is broadly triangular with segments a3–a5 often fused. G1 is in three parts and is tubular (Sternberg 1998).

2.5 *Marine crab sister group of the Potamoidea and Trichodactylidae*

Other decapods such as crayfish (Astacoidea and Parastacoidea) that live exclusively in freshwater have identifiable (extant) marine lobster-like relatives (e.g., the Nephropoidea: Nephropsidae). The exclusively freshwater Aeglidae are included in the same anomuran superfamily (Galatheoidea) as the Galatheidae and other marine anomurans (Crandall 2007). However, the marine sister group of the Potamoidea (as defined here) has proven difficult to identify, and the identity of the closest living relatives of the potamoid freshwater crabs is still the subject of much active discussion (Sternberg et al. 1999; Sternberg & Cumberlidge 2003). This knowledge is necessary to both understand the evolutionary history of the freshwater crabs and to establish the proper placement of the group within the Brachyura.

According to several morphological studies (Sternberg et al. 1999, Sternberg & Cumberlidge 2001a, b) and preliminary molecular evidence (T. Spears pers. comm.) a possible candidate for the marine sister group of the potamoids would be an unspecified basal member of the Grapoidea (which may now be extinct). In support of this hypothesis, Sternberg et al. (1999) listed a number of apomorphic characters that are shared by grapsoids (thoracotremes) and potamoids (heterotremes). These include a pair of epigastric crests on the anterior carapace, a pair of postorbital crests on the anterior carapace, clear exorbital and epigastric teeth on the anterolateral margins of the carapace, a posterior carina (a long raised line) running parallel with the posterolateral margin of the carapace, fields of carinae (short raised lines) on the posterolateral surfaces of the carapace, fields of carinae on the carapace sidewalls, a vertical sulcus on the carapace sidewall, a distinct triangular epistomial tooth, a notch flanking the epistomial tooth, a pereiopod 2–5 merus with a triangular cross-section, an anterior trough (groove) running parallel to the superior margin, and fields of carinae on the sides.

If the grapsoid sister group hypothesis of Sternberg et al. (1999) were to be supported by further studies, then the common ancestor (a heterotreme marine crab) gave rise to two monophyletic lineages, one that is exclusively freshwater that resulted in the several heterotreme potamoid crab families extant today, and the other, mostly marine, that produced a number of thoracotreme families. Interestingly, the predominantly marine families Sesarmidae and Grapsidae (all thoracotremes) resemble the true freshwater crabs in that both are mainly tropical and subtropical groups with a

circumglobal distribution. In addition, a number of inland and coastal species of sesarmids spend large parts of their life cycle in freshwater habitats, and some have large eggs and abbreviated development (Hartnoll 1964; Soh 1969; Schubart & Cuesta 1998; Cuesta et al. 1999; Ng 2004). One species of sesarmid (*Geosesarma notophorum*) even has direct development similar to that seen in all true freshwater crabs, and this species never needs to return to the sea to complete its life cycle (Ng & Tan 1995). Interestingly, there are no known species of Grapsidae *sensu stricto* (see Ng et al. 2008) that are freshwater, although there are several terrestrial species that live near coasts. None have abbreviated or direct development. Similarly, although many members of the Varunidae (another major grapsoid group) live in freshwater, all need to return to the sea to release their small eggs. The predominantly marine brachyuran family Hymenosomatidae (false spider crabs, Majooidea) also has a few exclusively freshwater species, some of which reproduce by direct development (Ng & Chuang 1996).

A lack of knowledge also surrounds the identity of the marine sister group of the Trichodactylidae. A basal (possibly extinct) member of the Portunoidea has been suggested based on morphological evidence (Rodriguez 1992, Sternberg & Cumberlidge 2003), but this persuasive idea is not supported by preliminary molecular studies of selected species of modern portunids (Schubart et al. this volume). However, that study was also unable to shed light on the possible identity of the marine sister group of the trichodactylids (and therefore on the proper placement of this family within the Brachyura), and to date, this remains unknown.

3 DISTRIBUTION

The massive increase in our knowledge of the taxonomy of freshwater crabs worldwide has led to a refinement of the understanding of the distribution patterns of families, genera, and species, which are now the most resolved they have ever been. It is clear that freshwater crabs have a circumglobal distribution that is restricted to tropical and subtropical freshwater ecosystems. Cold temperatures, arid lands, deserts, high mountains, and large tracts of oceans are all barriers to the dispersal of true freshwater crabs, and these decapods are never found naturally in aquatic ecosystems that have even low levels of salt water. These warm-water decapods are represented in the Neotropical, Afrotropical, Oriental, Palaearctic, and Australasian zoogeographic regions and are absent from the Nearctic and Antarctic regions and from the cooler temperate zones of the Palaearctic, Neotropical, and Australasian regions (including New Zealand). Elsewhere in the tropics, freshwater crabs are completely absent from all remote oceanic islands in the Pacific (such as the Galapagos islands, the Hawaiian archipelago, the Society Islands) and from the remote oceanic islands in the Atlantic and Indian oceans.

Some families of freshwater crabs (e.g., the Pseudothelphusidae and Trichodactylidae) are restricted to the Neotropical zoogeographical region, and no species of Palaeotropical crabs are found in that region naturally. The same family-level endemism is largely true for the freshwater crabs found in the Afrotropical region: all belong to the Potamonautesidae, except for three species of potamids on the island of Socotra. However, family-level endemism at the continental/zooogeographical region level is not seen in the Palaearctic, Oriental, and Australasian regions, where the parathelphusids are found in all three regions, and the potamids and gecarcinucids are found only in the Palaearctic and Oriental regions (and are both absent from the Australasian region).

3.1 The Neotropical region

Freshwater crabs are found throughout the Neotropical region in Central America (from Mexico to Panama and several Caribbean islands) and South America (from Colombia to Argentina). This region hosts two phylogenetically unrelated monophyletic lineages (families) of freshwater crabs — the Pseudothelphusidae (with 251 species) and the Trichodactylidae (with 47 species). Each of these families has representatives throughout the warmer parts of Central and South

America (from Mexico to northern Argentina), including the islands in the Caribbean and Pacific, and both families are absent from the cooler parts of the region (Chile, southern Argentina). Our present knowledge of the Pseudothelphusidae comes in large part from the landmark monograph by Rodriguez (1982) that brought together a literature that is widely scattered across time and in many different journals. Since then there have been a number of important contributions dealing with aspects of this family from specialists working in Central America (Alvarez 1989; Alvarez et al. 1996; Alvarez & Villalobos 1997, 1998, 1990, 1991, 1994, 1998), the Colombian Andes (Campos 2005 and publications therein), Venezuela and the Caribbean (Rodriguez 1992), and the Amazon (Rodriguez & Magalhães 2005). As for the Trichodactylidae, our present knowledge is based largely on the monographs of Rodriguez (1992), Magalhães & Türkay (1996a, b, c), and Magalhães (2003). The rate of description of new species of trichodactylids is now slowing compared to the past (Yeo et al. 2008), and this may indicate that we are close to knowing the true diversity of this family.

3.2 The Afrotropical region

The Afrotropical region is dominated by the endemic family Potamonautidae (with 132 species), which is distributed throughout the African continent and its associated islands in the Atlantic and western Indian Ocean (except for Socotra Island, where there are three endemic species with affinities to the Palaearctic-Oriental Potamidae). The first authors to treat the freshwater crab fauna of the Afrotropical region as a whole were Rathbun (1904, 1905, 1906), Chace (1942), and Bott (1955, 1965), and these works are still used by many as the standard taxonomic references for this group. Elsewhere in Africa recent taxonomic revisions are available for the freshwater crab faunas of West Africa (Cumberlidge 1999), Tanzania (Reed & Cumberlidge 2006), Lake Tanganyika (Cumberlidge et al. 1999; Marijnissen et al. 2004), Angola (Cumberlidge & Tavares 2006), southern Africa (Cumberlidge & Daniels 2008), and the Nile basin (Cumberlidge 2008), but large geographic areas such as Central Africa and East Africa are still in need of taxonomic revision. Recent works by Daniels et al. (2006), Cumberlidge et al. (2008), Yeo et al. (2008), and Cumberlidge (2008) have all advanced our knowledge of the phylogeny, higher classification, and biodiversity of the freshwater crabs of the Afrotropical region.

3.3 The Palaearctic region

In the vast Palaearctic region, freshwater crabs (Potamidae) are found only on its warmer southern margins stretching from North Africa to northern China and northern Japan, but these are not endemic to the region because they are also found in the Oriental region. The Palaearctic region is dominated by species of the family Potamidae, and potamonautids and gecarcinucids (Table 2D) are largely absent. The Potamidae is divided into two subfamilies (the western Palaearctic Potaminae and the eastern Palaearctic and Oriental Potamiscinae) whose distributional ranges overlap in northeast India and Myanmar (Yeo & Ng 2003). Freshwater crabs occur in the warmer freshwater habitats bordering the Mediterranean, the Middle East, the Himalayas, China, and Japan, and are not found in the colder, more northerly parts of the region. For example, freshwater crabs are absent from the Palaearctic region in Asia north of the Himalayas, Tibet, northern China, and the Korean peninsula, with the exception of a few species of potamids (subfamily Potamiscinae) found on the main islands of Japan (Dai 1999). In contrast, the southern islands of Japan (the Ryukyu Islands including Okinawa) and Taiwan lie in the Oriental region, and these have a rich freshwater crab fauna (mainly potamids). Potamid freshwater crabs of the subfamily Potaminae are found in Myanmar, the Himalayan states of north India, and Nepal, Pakistan, Afghanistan, the Middle East, southeastern Europe, and North Africa, which represents a wide distribution that (except for Myanmar) lies in the Palaearctic region (Brandis et al. 2000). Most of Europe lacks freshwater crabs except for a few species found in Italy, Greece, the Balkans, and the Black Sea region (Brandis et al. 2000). In North Africa, which is dominated by the Sahara desert, a single species of potamid is found along the

Mediterranean side of the Atlas Mountains in Morocco, Algeria, and Tunisia, but Libya completely lacks freshwater crabs. Most of Egypt also lacks freshwater crabs, except for the Sinai Peninsula, which has a single species of potamid (Potaminae), and the Nile valley, which has two species of Afrotropical potamonautid crabs (Bott 1970b; Williams 1976; Cumberlidge 2008).

3.4 The Oriental region

The Oriental region is home to three phylogenetically distinct monophyletic lineages of freshwater crabs recognized here as natural families — the Potamidae and Gecarcinucidae (including Parathelphusidae). Each of these families has representatives throughout the warmer parts of this region, both on the mainland and on most of the nearby islands. Crabs of the vastly diverse and widely distributed family Potamidae are found throughout the Oriental region as well as being well represented in the Palaearctic region. Potamids are completely absent from peninsular India south of the Ganges. The Potamidae reaches its greatest diversity in the Oriental region (which hosts about 450 out of the more than 500 species) (Dai 1999; Yeo & Ng 2007; Yeo et al. 2008). The southern boundary of the distributional range of the Potamidae is marked by Wallace's Line, whereby the islands of the Sunda Shelf (Sumatra, Java [only the western part], Borneo) and the southern Philippines have potamids, but the islands to the east of this (from Lombok to Sulawesi and eastwards to Australasia) all lack them. Besides mainland Asia, the Potamidae in the Oriental region (subfamily Potamiscinae) has representatives on many of the smaller islands in the South China Sea, the Yellow Sea, and the East China Sea. Smaller numbers of potamids (subfamily Potamiscinae) are found in the Palaearctic region in northern China and Japan, and there are several species (subfamily Potaminae) found in the Himalayas, the Middle East, southern Europe, and North Africa (Brandis et al. 2000). Interestingly, there are three species of potamids found in the Afrotropical region on the island of Socotra (Apel & Brandis 2000; Cumberlidge & Wranik 2002). The newly defined Gecarcinucidae, including the Parathelphusidae of Ng et al. (2008) (*sensu* Klaus et al. this volume) has a total of 345 species and is very diverse in the Oriental region (Sri Lanka, northeast India, Myanmar, Indochina, Thailand, Malaysia, Indonesia, Taiwan, the Philippines) but is also well represented in the Australasian region as far east as northern Australia and the Solomon islands (Bott 1970b; Yeo & Ng 1999; Bahir & Yeo 2007).

3.5 The Australasian region

Wallace's Line marks the edge of the continental margin at the Sunda Shelf and divides the Australasian and Oriental regions. Bali, Borneo, and the Philippines lie on the western (Oriental) side and Lombok and Sulawesi lie on the eastern (Australasian) side. The Australasian zoogeographical region stretches from the Lesser Sunda Islands (Lombok, Flores, and Sambawa) and Sulawesi eastward to include the Moluccas and the Aru Islands, New Guinea and its neighboring islands, and Australia. The Australasian region is relatively poor in freshwater crab species compared to the neighboring Oriental region. All freshwater crabs found in Australasia belong to the family Gecarcinucidae, and potamids are completely absent from this region. Sulawesi and New Guinea are the largest islands in this region and have the highest diversity of freshwater crab species. It would appear that the gecarcinucid freshwater crabs found in these islands today are all derived from ancestral southeast Asian forms that dispersed east across the seawater barrier represented by Wallace's Line (see Klaus et al. this volume for discussion). The deep water of the Lombok Strait between the islands of Bali and Lombok and the Philippines and Sulawesi has always represented a significant seawater barrier, even when lower sea levels linked many of the now-separated islands in this region with the landmasses on either side. Freshwater crab diversity in Australasia is highest in Sulawesi, Moluccas, and New Guinea and declines towards Australia. In Australia, only seven species of freshwater crabs (all in the endemic genus *Astrothelphusa*) are found in the northern tropical and subtropical parts of the continent, although several more species remain

undescribed (P.J.F. Davie, pers. comm.). They are absent in southern and western Australia, Tasmania, and New Zealand. This distribution pattern strongly suggests that crabs entered Australia relatively recently from New Guinea, presumably during periods of lowered sea level (corresponding to the Pleistocene Ice Ages) when Australia and New Guinea were connected across the Torres Strait. Presumably the ancestors of *Austrohelphusa* crossed to the forested Cape York Peninsula and from there dispersed over time throughout the river systems of northeastern Australia, spreading in all directions and eventually reaching most of inland and coastal Queensland, the Lake Eyre basin, and the Darling River drainage system in western New South Wales. The southern boundary of the distribution of *Austrohelphusa* was presumably established by the cooler, more temperate climates in the south and the lack of water in the west.

4 BIOGEOGRAPHY

The realization that five families of freshwater crabs may share common ancestry has revolutionized the way that these brachyurans are now viewed, because their worldwide distribution on continents and islands today includes vast tracts of ocean in between. These crabs are not only found on every continent in the tropics; these exclusively freshwater animals are also found on most of the large and small offshore islands associated with the continents. All around the world freshwater crab families include species found on offshore islands, and some species have a distribution that includes both the mainland and nearby islands. In many cases, the presence of freshwater crabs on islands near continental landmasses can best be explained by past sea level changes that created land bridges. However, there are a number of islands with established freshwater crab faunas that have never been connected to the mainland, even when sea levels were at historical lows. In the latter cases it is clear that freshwater crabs must have somehow crossed tracts of seawater to reach these islands, perhaps in a similar way to that proposed for amphibians on oceanic islands (Measey et al. 2007).

Single ancestry for the potamoid freshwater crabs has profound implications for biogeographical theories, as does a detailed knowledge of the global distribution and phylogenetic relationships within this group. However, an important piece of information — the age of origin of the freshwater crabs — is still not available. The oldest known freshwater crab fossil (see Feldmann et al. 2007) is still quite recent. Equally important is the lack of knowledge of the physiological abilities of the freshwater crabs to survive in seawater (it is widely assumed that they cannot survive for long). Single ancestry for the potamoid freshwater crabs could be explained by postulating a colonization event by a marine crab ancestor into the freshwaters of a single continent followed by a worldwide overland radiation (see Ng et al. 1995). This would require an ancient origin for the freshwater crabs because it would have to have taken place in the Jurassic (about 250 mya) when the continents were fused into a single landmass (Pangaea). In this scenario, crabs could have established a global distribution without crossing tracts of seawater, because they were carried to their present positions on fragmenting and drifting continents. However, there is no evidence that freshwater crabs, or even the Eubrachyura for that matter, are that old.

However, other explanations must be sought if freshwater crabs first evolved after the initial breakup of Pangaea into Laurasia and Gondwana (200 mya). In this case it is necessary to postulate at least two separate colonization events by marine crabs (one into Laurasian freshwaters and one into Gondwanan freshwaters). An even later origin of freshwater crabs after the further fragmentation of these two landmasses into smaller continental fragments (160—80 mya) would require either a separate colonization of each landmass by multiple marine crab ancestors or a single colonization event by a marine crab ancestor followed by overseas dispersal across oceanic barriers by its freshwater crab descendants to reach each of the widely separated continents. However, neither of the preceding scenarios is congruent with the phylogenetic relationships of the freshwater crab families found today in the Neotropics, Afrotropics, and the Indian subcontinent (i.e., on the continental plates that were once part of Gondwana), and they are not congruent with the sequence of continental breakup predicted by geological data. This argues against vicariance theories that postulate that

freshwater crabs are an ancient group present on Gondwana before continental breakup that reached its present distribution when continents separated and moved. Vicariance theories of biogeography do not require the assumption that crabs crossed one or more seawater barriers (Rodriguez 1986; Ng et al. 1995; Ng & Rodriguez 1995).

Alternately, present-day distribution patterns could be explained by a separate colonization of the freshwaters of each continental landmass during the Cenozoic by members of a single widespread marine crab ancestral stock living in the circumtropical Tethys Sea from the Neotropics to the Pacific. Single ancestry and a recent origin for freshwater crabs require that explanations be sought for explaining present-day distributions on widely separated continents and islands with seawater barriers in between. Sternberg et al. (1999) theorized that potamoid freshwater crabs descended from a widespread freshwater-adapted marine crab ancestor that had a global distribution across the shallow tropical seas from tropical America to Southeast Asia. This was at a time before the closing of the Mediterranean Sea and before the collision of India with Asia, when the Atlantic, Indian, and Pacific oceans formed a continuous water body around the tropics. At this time, ancestral crabs living in different parts of the range of the same widespread species entered suitable freshwater ecosystems in the Neotropical, Afrotropical, Palaearctic, and Oriental regions. Once established in freshwater, these colonizers lost their ability to survive in seawater and effectively became isolated in freshwater habitats over time. Evolution in isolation in each of these regions led to their radiation, adaptation, and speciation to produce monophyletic groups in each of these continents. Freshwater crabs then spread slowly throughout continental freshwaters and also colonized many of the offshore islands. This process led to the development of morphologically distinct lineages of freshwater crabs in each of the zoogeographic regions that are separable at the family level. The founder effect on islands led to some freshwater crabs' becoming morphologically atypical, and in some cases this led taxonomists to recognize higher taxa or make family-level transfers for some of the more apomorphic species (e.g., in Madagascar, the Seychelles, and East Africa) (Bott 1960, 1965; Ng et al. 1995; Cumberlidge et al. 1999, Števčić 2005), all of which later proved to belong to the same family (Daniels et al. 2006; Cumberlidge et al. 2008).

4.1 Colonization of freshwater

Today, there are several species of catadromous marine crabs such as *Varuna litterata* (Varunidae) that have wide distributional ranges over tens of thousands of sq. km. of ocean, and that have the physiological ability to live both in the sea and in freshwater habitats for long periods of time. For example, *Varuna litterata* ranges from East Africa and Madagascar in the Indian Ocean to Japan and Polynesia in the Pacific Ocean. These catadromous brachyurans have free-living larval stages that require saltwater for development, and all need to return to the sea to breed, a strategy that has the advantage of achieving a wide dispersal range when developing larvae are carried long distances by ocean currents.

The first step in the colonization of freshwaters must have involved the development of the physiological ability to osmoregulate and gain some control over the movement of ions and water in and out of the body. The ability of marine crabs to osmoregulate in low-salinity environments encompasses adaptations ranging from short-term survival in brackish water to long-term colonization of freshwater. These were presumably the stages through which the ancestors of the true freshwater crabs passed on their way to becoming exclusively freshwater organisms. Once the ancestors of freshwater crabs had become fully adapted to freshwater, they would have lost their ability to survive for long in seawater. The best "analogy" in the modern crabs would probably be genera of Sesarmidae like *Geosesarma*, whose members are all freshwater or semiterrestrial and species have varying larval strategies, from eggs hatching into planktotrophic larvae, very advanced zoeae, megalopae or even direct development (see discussion in Ng et al. 2004).

Another important adaptation to life in freshwater was the ability of freshwater crabs to complete their life cycle without returning to the sea to release eggs and larvae. Like other freshwater

decapods (such as crayfish and many species of palaemonid and atyid shrimps), the ancestors of freshwater crabs evolved direct development and could remain in freshwater habitats year round without having to return to the sea to release their larvae. The lack of dispersive planktonic larval stages restricted the dispersal abilities of freshwater crabs, and their distributional ranges in freshwater habitats necessarily became much smaller. Oceans now became barriers to their dispersal rather than facilitators. The result was that freshwater crab populations became reproductively isolated much more easily, and this isolation led to their adaptation, speciation, and diversification over time.

4.2 Theories on origins

There is some morphological, molecular, and fossil evidence (Sternberg et al. 1999; Daniels et al. 2006; Brösing 2008) that the evolution of freshwater crabs from a brachyuran heterotreme stock happened sometime in the Late Cetaceous/early Cenozoic. The study by Brösing (2008) provided a temporalized cladogram that estimated the divergence time of the potamoids (represented by a potamonautid terminal taxon) from marine crab stock just prior to the Cretaceous-Tertiary boundary. If this estimate of freshwater crab origins is supported by further studies, then the potamoids appeared well after major tectonic events such as the breakup of Pangaea that separated the northern continent (Laurasia) from the southern continent (Gondwana). Similarly, freshwater crabs were therefore not present on the continents when the Laurasian supercontinent broke up into the Nearctic from the Palaearctic landmasses. It also follows that freshwater crabs were not present when Gondwana began to fragment, first splitting off the South American landmass from the western coast of Africa, and then splitting off the Madagascar-Seychelles-India landmass from the eastern coast of Africa, followed by the eventual breakup of Madagascar-Seychelles-India.

A Late Cetaceous/early Cenozoic origin of the freshwater crabs would mean that these decapods colonized freshwaters at a time when the continental landmasses of North America, South America, Africa, and India were all islands, and when the southern margins of the Eurasian landmass were fragmented and constituted a series of small shifting plates. At this time the warm, shallow Tethys Sea formed a continuous marine connection between all of these landmasses around the equator from the Americas to Asia, joining the Atlantic with the Indian and Pacific oceans. This continuous marine connection was later broken when the Mediterranean Sea closed, separating the Atlantic and Indian oceans, and when peninsular India collided with Eurasia.

The collision of India with Asia had a big impact on the three families of freshwater crabs that are found today in Eurasia, India, and the Oriental region. It is likely that these three families were well established in these areas long before the Indian collision with Asia and the building of the Himalayas. For example, the Gecarcinucidae most likely evolved in isolation on peninsular India (where it is most diverse today) and was already present before this landmass collided with Asia. There probably were no gecarcinucids on the mainland of Asia before the contact with India. This is consistent with today's distribution pattern of this family, where there are now only a handful of gecarcinucid taxa to the east of peninsular India (in Myanmar, Thailand, Malaysia, and Sarawak) and where there is a similar tapering off of diversity to the west (in Pakistan, Afghanistan, and Iran). This pattern is most likely the result of the subsequent gradual spread of gecarcinucids out of India following the collision of India with Eurasia. It is significant that there are still no potamids in peninsular India today, an observation that is consistent with the fact that the potamids evolved on the mainland of Asia and were never able (for some reason) to disperse south into India despite the favorable habits for them there.

The present-day distribution pattern of the Potamidae indicates that it most likely evolved in the warmer eastern parts of the Palaearctic landmass (where it is most diverse today) and was widely distributed in the freshwater ecosystems along the southern shores of the Tethys Sea from Europe to southeast Asia before the collision of India with Asia. Potamids most likely evolved when India was still an island continent, which would explain their absence there to this day. The high numbers of

potamid taxa found to the east of India (in Myanmar, Indochina, Malaysia, China, the Sunda Shelf Islands, the Philippines, Taiwan, and Japan) and the relatively few taxa found to the west of India (stretching from Pakistan to North Africa) are likely the result of the isolation of the eastern and western potamids after the collision of peninsular India with Eurasia. The building of the Himalayan mountains likely eliminated most of the potamids already living along the collision zone and became a barrier to subsequent potamid dispersal, after which the western potamids (Potaminae) evolved separately from the eastern potamids (Potamiscinae) (see Shih et al. in press).

With regard to the rest of Gecarcinucidae (the Parathelphusidae in Ng et al. 2008), it is possible they first evolved in Southeast Asia (Myanmar, Thailand, Indochina, Malaysia, southwest China) where it is most diverse today (see also Klaus et al. this volume). The number of gecarcinucid taxa declines eastwards from this center towards China and Taiwan and westwards (in northern India), but the family is well represented in the Philippines, most of the islands in the Sunda Shelf, the Indonesian islands east of Java, and in the chain of Indonesian islands as far east as New Guinea and northern Australia and the Solomons. The collision of India with Eurasia no doubt explains the decline and then absence of this family west of Myanmar, but the origin of the rich gecarcinucid fauna of Sri Lanka is difficult to explain (Ng & Tay 2001; Bossuyt et al. 2004). The southeasterly dispersal of gecarcinucids from southeast Asia to the Philippines and northern Australia is likely the result of their subsequent spread across marine barriers over time because the landmasses in this part of the world between the Sunda Shelf and Australia are greatly divided and dominated by islands (see also Klaus et al. this volume).

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