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FRESHWATER ANIMAL DIVERSITY ASSESSMENT

Global diversity of crabs (Crustacea: Decapoda: Brachyura) in freshwater

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Abstract An assessment of the global freshwater crab diversity is presented. A total of 1,476 species in 14 families are currently known from all zoogeographical regions (except Antarctica), including 1,306 species in eight exclusively freshwater families (Pseudothelphusidae, Trichodactylidae, Potamonautidae, Deckeniidae, Platythelphusidae, Potamidae, Gecarcinucidae and Parathelphusidae). Estimates of true freshwater crab diversity including likely numbers of undescribed taxa suggest that the field remains largely in a "discovery" phase. Main ideas on the origins, diversification, and phylogeny of true freshwater crabs are briefly discussed. The economic importance of freshwater crabs is also highlighted.

Keywords Global assessment · Freshwater crab · Diversity · Crustacea · Decapoda · Brachyura · Species estimates

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Freshwater Animal Diversity Assessment

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Introduction

Of the more than 6,700 known species of brachyuran crabs, over 1,300 are true freshwater crabs. True freshwater crabs are regarded as those that have adopted freshwater, semi-terrestrial or terrestrial modes of life, and are characterized by their ability to complete their life cycle independently of the marine environment. These crabs are currently assigned to eight exclusively freshwater families—Pseudothelphusidae and Trichodactylidae (Mexico, Central and South America), Potamonautidae (Africa and Madagascar), Deckeniidae and Platythelphusidae (East Africa), Potamidae (North Africa, southern Europe, Asia), Gecarcinucidae (Seychelles, Asia), and Parathelphusidae (Asia, Australasia) (Martin & Davis, 2001). Wholly or primary freshwater taxa undergo direct development in which the large, yolky eggs hatch directly into juvenile crabs. Crabs found in

freshwater also include numerous euryhaline species or secondary freshwater species from primarily marine brachyuran families (e.g. Sesarmidae, Varunidae, Hymenosomatidae). Although these freshwater species are fully adapted to freshwater/terrestrial living, most do not have direct development in their life cycle (though highly abbreviated development occurs in some) and most possess one or more larval stages. The diversity of these taxa is also assessed in this chapter (Tables 1 and 2), but the emphasis will be placed on the true freshwater crabs.

Freshwater crabs belong to the Order Decapoda, the crustacean group that also includes lobsters, prawns, crayfish and hermit crabs, which share the characteristic presence of five pairs of thoracic legs (pereiopods). In freshwater crabs the first pereiopods are modified as pincers (chelipeds), and the remaining four pairs are relatively unspecialised walking legs (Fig. 1). The general body plan of freshwater crabs consists of a head, thorax and abdomen, with the head and thorax (cephalothorax) covered by a broad carapace, and the abdomen reduced, flattened and flexed under the thoracic sternum. In adults, the male abdomen is slim and narrow, and is either triangular or T-shaped, while the female abdomen is broad and round and covers nearly the entire thoracic sternum. Adult males bear two pairs of abdominal appendages (pleopods) that are modified into copulatory structures known as gonopods. Gonopod structure is taxonomically important, especially because the external morphology of freshwater crabs tends to be rather conservative (see Ng, 1988; Cumberlidge, 1999, for details).

Freshwater crabs are found in the tropics and subtropics in most parts of the world, and occur in a wide variety of aquatic and terrestrial habitats. These decapods are present in almost all freshwater bodies, from clear, fast-flowing montane streams to sluggish lowland rivers and streams, as well as in peat and freshwater swamps, stagnant ponds and rice fields, and even in pools in tree holes and leaf axils. A fair number are also adapted to live in caves. Among the primarily aquatic freshwater crabs, some (e.g. potamids) are entirely adapted to living in fresh water, and are not thought to be able to survive for long in salt water, while others (e.g. parathelphusids) are more tolerant of saline conditions, and can survive immersion in salt water for short periods of time. Terrestrial species may occur well away from permanent freshwater sources, either moving among the forest floor litter or, in some cases, even climbing trees (Ng, 1988; Ng & Tay, 2001; Cumberlidge et al., 2005). These freshwater crab species do not require regular immersion in fresh water and can obtain water either from food, from drinking dew or casual water, or by capillary or osmotic uptake from moist substrata. In the present chapter, such species are also categorised as "freshwater-dependent" species (see later; Table 1).

Freshwater crabs are primarily nocturnal, preferring to remain hidden during the day in sheltered places and foraging mostly at night. They are mostly omnivorous scavengers, mainly feeding on plant matter, but some are opportunistic carnivores, feeding either on live prey such as fish and prawns or on dead animals that they encounter (Ng, 1988; unpub.), and cannibalism is not uncommon (unpub.). Crabs themselves also constitute an important food resource for many species of fishes, birds, caymans, turtles and mammals (see Ng, 1988; Magalhães, 2003).

Diversity and endemicity

Known global diversity

There are currently a total of 238 genera and 1,476 species of known freshwater crabs from 14 families (including 1,306 true freshwater crab species in eight families: Pseudothelphusidae, Trichodactylidae, Potamonautidae, Deckeniidae, Platythelphusidae, Potamidae, Gecarcinucidae and Parathelphusidae) (as of 1st August 2006). The species and genus diversity of primary as well as secondary freshwater species are listed by zoogeographical regions (sensu Cox, 2001) in Tables 1 and 2, respectively. The total number of species or genera of certain families listed in the last column of Tables 1 and 2, respectively, do not tally with the sum of species or genera from each zoogeographical region because some taxa occur in more than one region (see later, Tables 1 and 2 footnotes).

Table 1 also lists separately the number of "freshwater-dependent" species (WDpt). In the context of the present volume, our assessment of the freshwater crab species required grouping them into two broad ecological categories to reflect their different habitat preferences and degrees of their association with freshwater habitats, viz., "real aquatic" species and "freshwater-dependent"

Table 1 Global species diversity of freshwater crabs

Family	PA		NA		NT		AT		OL		AU		PAC		World[c]	
	Total FW	WDpt	Total FW	WDpt	Total FW	WDpt	Total FW	WDpt	Total FW	WDpt	Total FW	WDpt	Total FW	WDpt	Total FW	WDpt
[a]Potamidae[d]	86	–	–	–	–	–	3	1	435	58	–	–	–	–	509	59
[a]Potamonautidae	–	–	–	–	–	–	115	9	–	–	–	–	–	–	115	9
[a]Deckeniidae	–	–	–	–	–	–	2	2	–	–	–	–	–	–	2	2
[a]Platythelphusidae	–	–	–	–	–	–	9	–	–	–	–	–	–	–	9	–
[a]Parathelphusidae[e]	4	–	–	–	–	–	–	–	243	14	52	8	–	–	298	22
[a]Gecarcinucidae	–	–	–	–	–	–	8	6	36	3	–	–	–	–	44	9
[a]Pseudothelphusidae	–	–	16	–	262	3	–	–	–	–	–	–	–	–	278	3
[a]Trichodactylidae	–	–	–	–	51	–	–	–	–	–	–	–	–	–	51	–
[b]Gecarcinidae[f]	–	–	3	3	9	9	9	9	8	8	6	6	8	8	20	20
[b]Hymenosomatidae[g]	1	–	–	–	1	–	1	–	8	–	9	–	3	–	22	–
[b]Ocypodidae	–	–	–	–	–	–	–	–	2	–	–	–	–	–	2	–
[b]Sesarmidae[h]	2	–	–	–	14	14	1	1	72	68	15	13	7	7	101	95
[b]Goneplacidae	–	–	–	–	–	–	–	–	–	–	2	–	2	–	4	–
[b]Varunidae[i]	4	–	–	–	3	–	1	–	14	–	5	–	4	–	21	–
Total[j]	97	–	19	3	340	26	149	28	818	151	89	27	24	15	1476	219

Total FW: Aquatic + "freshwater dependent" species. WDpt: "freshwater-dependent" species (see text under "Known global diversity" for definition). PA: Palaearctic, NA: Nearctic, NT: Neotropical, AT: Afrotropical, OL: Oriental, AU: Australasian, PAC: Pacific Oceanic Islands

[a] True (or primary) freshwater crab family

[b] Secondary freshwater crab family

[c] "World" refers to the actual total number of freshwater species, which may not necessarily be the sum of the totals for each zoogeographical region as some species occur in more than one region (see text)

[d] Potamidae—15 species with Palaearctic/Oriental distributions

[e] Parathelphusidae—1 species with Palaearctic/Oriental distribution

[f] Gecarcinidae—13 species with various overlapping distributions (3 Nearctic/Neotropical + 4 Afrotropical/Neotropical + 4 Afrotropical/Oriental/Australasian/Pacific + 2 Oriental/Australasian/Pacific)

[g] Hymenosomatidae—1 species with Neotropical/Australasian distribution

[h] Sesarmidae—6 species with various overlapping distributions (1 Palaearctic/Oriental/Australasian + 1 Afrotropical/Oriental/Australasian + 1 Oriental/Australasian + 2 Oriental/Australasian/Pacific + 1 Australasian/Pacific)

[i] Varunidae—7 species with various overlapping distributions (3 Palaearctic/Oriental + 1 Palaearctic/Afrotropical/Oriental/Australasian/Pacific + 3 Oriental/Australasian)

[j] Total—43 species with various overlapping distributions (see above for details)

Table 2 Global genus diversity of freshwater crabs

Family	PA	NA	NT	AT	OL	AU	PAC	World[c]
[a]Potamidae[d]	9	–	–	2	72	–	–	78
[a]Potamonautidae	–	–	–	12	–	–	–	12
[a]Deckeniidae	–	–	–	1	–	–	–	1
[a]Platythelphusidae	–	–	–	1	–	–	–	1
[a]Parathelphusidae[e]	1	–	–	–	35	9	–	42
[a]Gecarcinucidae	–	–	–	4	10	–	–	14
[a]Pseudothelphusidae[f]	–	2	41	–	–	–	–	41
[a]Trichodactylidae	–	–	15	–	–	–	–	15
[b]Gecarcinidae[g]	–	2	3	4	4	4	4	6
[b]Hymenosomatidae[h]	1	–	1	1	3	2	2	6
[b]Ocypodidae	–	–	–	–	1	–	–	1
[b]Sesarmidae[i]	1	–	3	1	7	4	3	10
[b]Goneplacidae[j]	–	–	–	–	–	1	2	2
[b]Varunidae[k]	2	–	2	1	7	4	2	9
Total[l]	14	4	65	27	139	24	13	238

PA: Palaearctic, NA: Nearctic, NT: Neotropical, AT: Afrotropical, OL: Oriental, AU: Australasian, PAC: Pacific Oceanic Islands

[a] True (or primary) freshwater crab family

[b] Secondary freshwater crab family

[c] "World" refers to the actual total number of freshwater genera, which may not necessarily be the sum of the totals for each zoogeographical region as some genera occur in more than one region (see text)

[d] Potamidae—5 genera with Palaearctic/Oriental distributions

[e] Parathelphusidae—3 genera with various overlapping distributions (1 Palaearctic/Oriental + 2 Oriental/Australasian)

[f] Pseudothelphusidae—2 genera with Nearctic/Neotropical distributions

[g] Gecarcinidae—6 genera with various overlapping distributions (1 Nearctic/Neotropical + 1 Nearctic/Afrotropical/Neotropical/Oriental/Australasian/Pacific + 1 Afrotropica/Neotropical + 2 Afrotropical/Oriental/Australasian/Pacific + 1 Oriental/Australasian/Pacific)

[h] Hymenosomatidae—2 genera with different overlapping distributions (1 Palaearctic/Oriental/Pacific + 1 Neotropical/Oriental/Australasian)

[i] Sesarmidae—4 genera with various overlapping distributions (1 Palaearctic/Oriental/Australasian + 1 Afrotropical/Oriental/Australasian/Pacific + 2 Oriental/Australasian/Pacific)

[j] Goneplacidae—1 genus with Australasian/Pacific distribution

[k] Varunidae—6 genera with various overlapping distributions (1 Palaearctic/Oriental + 1 Palaearctic/Afrotropical/Oriental/Australasian/Pacific + 3 Oriental/Australasian + 1 Oriental/Pacific)

[l] Total—29 genera with various overlapping distributions (see above for details)

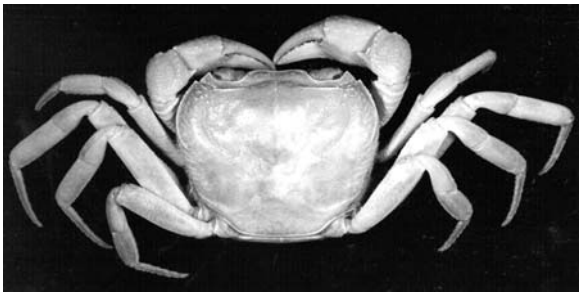

Fig. 1 Habitus

species. "Real aquatic" species are ones that are dependent on freshwater habitats to complete their life cycle i.e. part or all of the life cycle occurs in the water. Thus, adopting a practical approach, this study has included under "real aquatic" species all fully aquatic as well as semi-terrestrial species that are generally found in and around (or associated with) traditional freshwater environments (streams, rivers, lakes, ponds, swamps). Under "freshwater-dependent" species (WDpt), this work has included the more terrestrial species in which the adults are not

primarily found in and around (or associated with) traditional freshwater environments, but are nevertheless dependent on wet/humid terrestrial environments for survival e.g. tree-climbing crabs, forest floor dwellers, dry cave dwellers. These include many so-called terrestrial crabs that have juvenile stages that can occur in water.

Estimated global biodiversity

Two methods are proposed here for estimating the global diversity of true freshwater crabs:

(1) Based on extrapolation. Estimated global diversity of true freshwater crabs: 2,155 species

Yeo & Ng (1999) used the species number per unit area of Thailand (1.8×10^{-4} species/km^2) as a reference for estimating the fauna for the whole of Indochina. These authors applied this ratio to Indochina [=Thailand, Laos, Cambodia, Vietnam and Myanmar] (1,939,320 km^2), and obtained a working estimate of 349 species for this region. There are currently 212 species known from Indochina (Yeo & Ng, unpub.) which gives an approximate ratio of actual to estimated species of 1:1.65. The 13 species of freshwater crabs known from Madagascar give a similar estimate (Cumberlidge & Sternberg, 2002). Although simplistic, no similar objective estimates have been attempted thus far. Applying a ratio of actual to estimated species of 1:1.65 to the known true freshwater crab global diversity from the previous section (1,306 species), gives an estimated global diversity of 2,155 species. Given that Indochina lies in one of the most species-rich areas of the global range of freshwater crabs, this figure may tend to be an overestimate. Considering the large numbers of undescribed species known and/or likely to be discovered in the near future, freshwater crab taxonomy must be regarded as still being in its "discovery" phase. The cumulative curves of new species described over time for the two South American crab families suggests that the diversity of the Pseudothelphusidae is still far from being well-known because the curve (Fig. 2a) is still ascending. On the other hand, the curve for the trichodactylids (Fig. 2b) seems to have already reached an asymptote, suggesting at least for this group, the discovery phase is ending. The several phases of tectonic uplift that affected most of the western and northern

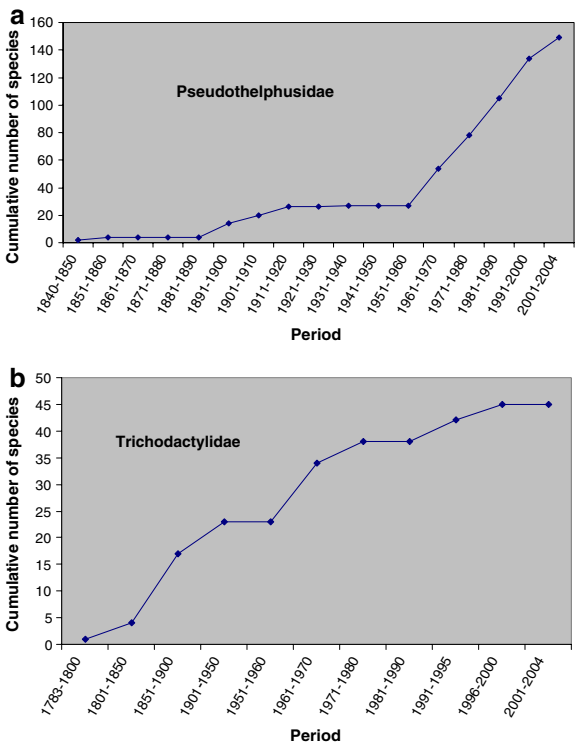

Fig. 2 Cumulative number of South American species of: (**a**) Pseudothelphusidae described since 1840; and (**b**) Trichodactylidae described since 1783

margins of South America produced many vicariance events (Lundberg et al., 1998) that could account for the high diversification of the pseudothelphusids along the Andes. Pseudothelphusids are usually distributed in mountainous regions with restricted distributional ranges and there still are several unexplored areas in the Andes, Guyana and the Central Brazilian Massifs from where new taxa are still being found. Species of trichodactylids usually have extensive ranges along the relatively uniform, tectonically stable lowlands of the continent's huge hydrographic basins, have not speciated as much as the pseudothelphusids, and the number of new species of trichodactylids still awaiting discovery is expected to be low.

(2) Based on numbers of as yet undescribed species known. Estimated global diversity of true freshwater crabs: 1,430 species.

This estimate is based simply on the total number of described and undescribed species of true freshwater crabs known to the authors. The breakdown of these estimates by family is as follows: Potamidae

(570 species); Potamonautidae (135 species); Deckeniidae (3 species); Platythelphusidae (12 species); Parathelphusidae (310 species); Gecarcinucidae (60 species); Pseudothelphusidae (289 species) and Trichodactylidae (51 species). The disparity between the overall estimates obtained using this method versus the extrapolation method is probably accentuated by the fact that some of our family level estimates here are conservative. Reality is probably somewhere in between, which means that there are at least 128–846 more species yet to be described/discovered. A more accurate system of estimating species numbers is clearly needed.

Distribution and zoogeography

The vast majority of true freshwater crab species are point endemics owing to their generally limited dispersal abilities, relatively low fecundity, and stenotopic habits. Most genera of true freshwater crabs are endemic to their respective zoogeographical regions (sensu Cox, 2001; see below).

The distribution of freshwater crab diversity across the main zoogeographical regions (sensu Cox, 2001) adopted in this volume is illustrated in Table 1 (species), Table 2 (genera), and Fig. 3 (total and true freshwater crabs). It should be noted, however, that the phylogeographical patterns of some taxa are not always reflected by this categorisation. One such anomaly is with the family Potamidae, in which the two subfamilies have relatively distinct distributions: Potaminae is clearly a Palaearctic group with the main diversity in southern Europe/North Africa/Near East/Middle East, while Potamiscinae is an Oriental group with the main diversity in East and Southeast Asia. These two groups are only linked by the potamids of the northwestern Oriental Region, where their distributions overlap around parts of Myanmar and northeastern India (Yeo & Ng, 2003). Following strictly the zoogeographical regions of Cox (2001), however, a significant proportion of East Asian

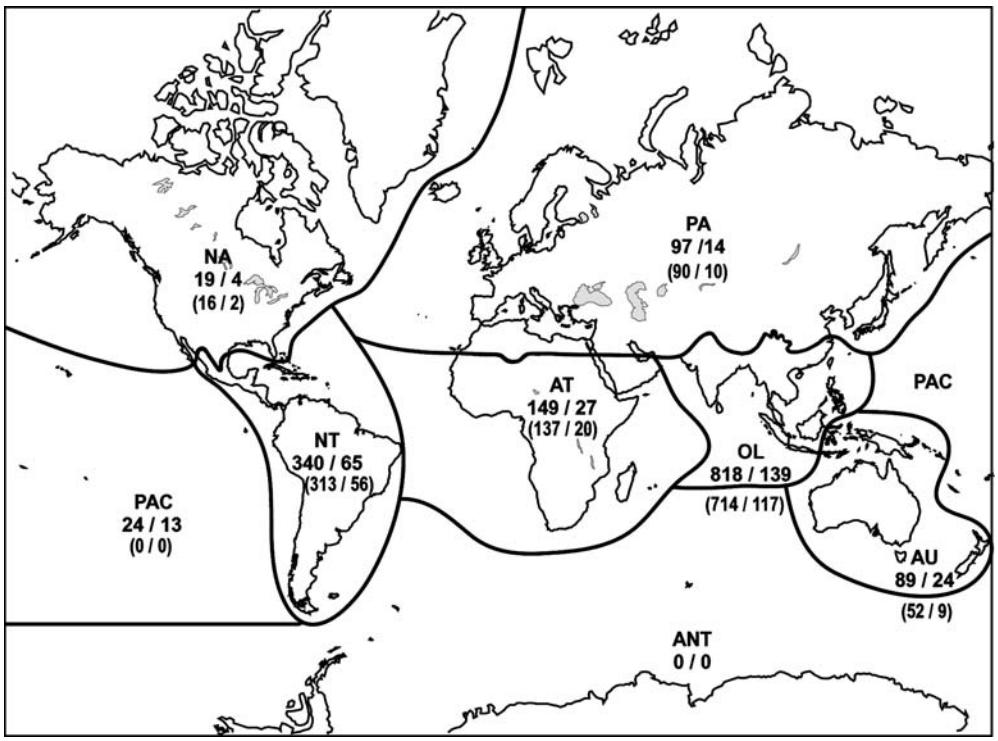

Fig. 3 Map of zoogeographical regions sensu Cox (2001) showing total freshwater crab distribution (Species number/Genus number). True freshwater crab distribution is shown in parentheses. (PA—Palaearctic; NA—Nearctic; AT—Afrotropical; NT—Neotropical; OL—Oriental; AU—Australasian; PAC—Pacific Oceanic Islands; ANT—Antartica)

potamiscines will fall into the Palaearctic region (together with potamines) instead.

Furthermore, a small group (two genera with three species) of potamids on the island of Socotra off the horn of Africa that is clearly affiliated with the Paleartctic potamines falls misleadingly under the Afrotropical region instead. Similarly, the definition in this volume of the Neotropical region as "excluding highlands of Mexico" and the Nearctic as "including highlands of Mexico", ends up assigning pseudothelphusids found in the Mexican highlands to the Nearctic region despite their Neotropical affinities.

In addition, not all taxa are restricted to a single zoogeographical region (e.g. *Aparapotamon grahami* and *Geothelphusa* spp. [Potamidae] occur in both Palaearctic and Oriental regions; and *Parathelphusa* and *Sundathelphusa* [Parathelphusidae] occur in both Oriental and Australasian regions). The families containing species and/or genera that have distributions which overlap adjacent zoogeographical regions are: Potamidae, Parathelphusidae, Pseudothelphusidae, Gecarcinidae, Hymenosomatidae, Sesarmidae, Goneplacidae and Varunidae. Because of this, as mentioned earlier, the "World" totals listed in the last column of Tables 1 and 2 for these families are less than the sum of the number of taxa from each zoogeographical region on the map (Fig. 3) or in the corresponding row of each table (see Tables 1 and 2 footnotes).

Major historic processes leading to global biodiversity patterns

Sternberg et al. (1999) summarised the hypotheses for the origin and diversification of the true freshwater crabs into the polyphyletic, archaic and phylogenetic schools. The polyphyletic school (e.g. Bott, 1955; Pretzmann, 1973) considered that the freshwater crab families originated from a number of different marine ancestors; in this case, morphological similarities would be the result of convergence, not common ancestry.

In the archaic population school, vicariance has been suggested as the key mechanism and the breakup of Gondwanaland a key historic process. The pseudothelphusoid and gecarcinucoid freshwater crabs share a two-segmented bilobed mandibular palp (a presumptive synapomorph) and freshwater crab taxa with this character are found today in the majority of Gondwanan fragments (South America, Africa, Madagascar, the Seychelles, India, Southeast Asia, and Australasia). Crabs are postulated to have had a Gondwanan origin with present day distribution patterns resulting from the breakup of the supercontinent (Rodríguez, 1986; Ng & Rodríguez, 1995; Ng et al., 1995; Yeo & Ng, 1999). There is, however, no paleontological support for this view and there is incongruence with regard to what is known about Brachyuran evolution. Daniels et al. (2006), however, argue that the two-segmented bilobed mandibular palp may be a convergent character, and the pseudothelphusoid and gecarcinucoids may not be that closely related. Bănărescu (1990) proposed long distance transoceanic dispersal as an alternative mechanism to explain the largely insular distribution of the Parathelphusidae in Sundaic Southeast Asia. However, this has been challenged by Ng & Rodríguez (1995), who argued that Bănărescu's ideas made dubious assumptions about the ecology and origins of the Parathelphusidae (and about the phylogeny of all freshwater crabs). The dominance of gecarcinucoid crabs in the Indian peninsula (and the absence of potamids) could also be explained as the result of their long isolation on a Gondwanan continental fragment before it collided with continental Asia (where potamids are found in large numbers).

In contrast to the above hypotheses, the phylogenetic school (Sternberg et al., 1999, following Colosi's (1921) ideas) suggested that the pseudothelphusoid, gecarcinucoid, and potamoid freshwater crabs form a monophyletic group that may have had a more recent, post-Gondwanan origin. Here the present global distribution pattern is thought to be the result of colonisation of the tropical continental margins from a common ancestral marine group consisting of a monophyletic thoracotreme clade widely distributed along littoral areas of the southern Tethys Sea during the Cretaceous that eventually gave rise to the modern families after independent diversification into the freshwater environments. This post-Gondwanan (Cretaceous) transoceanic dispersal hypothesis was most recently supported by molecular evidence presented by Daniels et al. (2006) based on work carried out with emphasis on Afrotropical freshwater crabs. Another hypothesis recently proposed by

Klaus et al. (2006) suggested that gecarcinucoid crabs originated in Africa and reached South Asia via transoceanic dispersal and a series of theorised "stepping-stone" islands. The available evidence might now suggest a mixture of vicariance and dispersal, although consensus has still to be reached in this complex issue. Clearly, there are many ideas and hypotheses being proposed, a sure sign that there is increasing interest in using freshwater crabs for biogeographic studies.

The current Eurasian distribution of the Potamidae shows that one subfamily (Potaminae) occurs in western Eurasia (in North Africa, southern Europe, Socotra, the Middle East and the Himalayas), and one subfamily (the Potamiscinae) is in Southeast Asia, China and Japan. There is reason to believe that this distributional pattern may be the result of dispersal from a continental Asian origin (Yeo & Ng, 2003). A trend is apparent in the relative distributions of these two subfamilies that suggests potamids may have spread westwards into Eurasia (as potamines) and southwards into insular Southeast Asia (as potamiscines) from a continental Asian origin. Additional circumstantial evidence for this trend is seen in the distinct decline in potamid diversity westward from Southeast Asia, whereby southern Europe has only one genus (*Potamon*) and East Asia has some 40 genera. The distributional trend shown by potamines and potamiscines corresponds to a similar trend shown by freshwater crab superfamilies discussed by Yeo & Ng (1999).

Rodríguez (1982, 1986) explained the current distribution of Neotropical pseudothelphusids by vicariance events and secondary dispersion. In his hypothesis, based on Rosen's (1976) model for Caribbean biogeography, an ancestral group that occupied the Proto-Antillean archipelago, characterised by a plesiomorphic character of the third maxilliped (presence of long exognath), gave rise to two different groups after the Caribbean Plate drifted northeastward between Central and South America during the late Mesozoic and Cenozoic: the Epilobocerinae in the Antilles and the Strengerianini in northern Colombia. Based on sympatries and geographic morphoclines in somatic and gonopodal characters, Rodríguez (1986) distinguished three distinct chorological series that would have radiated from a dispersal centre in northern Colombia towards Central America and Mexico (Pseudothelphusini and Potamocarcinini), northern and eastern South America (Kingsleyini) and the southern Andes (Hypolobocerini).

The South American trichodactylids are phylogenetically separate from all other freshwater crab families which points to an independent invasion of this habitat by the group's supposedly marine portunoid ancestors (Rodríguez, 1992; Sternberg et al., 1999; Martin & Davis, 2001). The morphological cladistic analysis of Sternberg et al. (1999) identified grapsids as probable sister taxa to the non-trichodactylid freshwater crabs, which contradicted the assertions of earlier authors (Bott, 1955) who suggested ancestry from marine crab groups such as the Xanthoidea or the Portunoidea. There is, however, still some uncertainty about freshwater crab origins and relationships.

In addition to vicariance and dispersal, distributional limits of true freshwater crabs are also influenced by a host of other factors that interact with these two key processes. These include abiotic factors such as climate, hydrology, topography and altitude as well as biotic factors such as habitat vegetation and inter-specific competition (see Rodríguez, 1986; Ng, 1988; Barbaresi & Gherardi, 1997; Cumberlidge, 1999; Dai, 1999; Rodríguez & Suárez, 2004; Magalhães et al., 2005; Marijnissen et al., 2005).

Phylogeny

The recent surge in alpha taxonomic descriptions of freshwater crabs has been accompanied by an increase in interest in their phylogenetic relationships and higher taxonomy. Most studies in the late 20th century have accepted the traditional morphology-based classification system proposed by Bott (1970) comprising three superfamilies and eleven families. This has been challenged over the last decades by some workers who questioned the superfamily system and synonymised three families, namely Sundathelphusidae, now a junior synonym of Parathelphusidae (Ng, 1988; Chia & Ng, 1998); and Isolapotamidae and Sinopotamidae, both now junior synonyms of Potamidae (Ng, 1988; Dai, 1999; Yeo & Ng, 2003). Brandis (2002) had recently argued for the revalidation of the families Isolapotamidae and Sinopotamidae for two

apparently discreet monophyletic potamid taxa; however, this was challenged by Yeo & Ng (2003) who suggested that Brandis' (2002) groupings might instead be infra-familial clades within the Potamidae (subfamily Potamiscinae).

Morphological cladistic studies (e.g. Sternberg et al., 1999; Cumberlidge, 1999; Sternberg & Cumberlidge, 1999, 2001) argue for recognising the remaining eight families in two main lineages. These authors argued that the true freshwater crabs are paraphyletic and consist of two distinct lineages: (1) the monophyletic Trichodactylidae in the predominantly marine superfamily Portunoidea and (2) a monophyletic group consisting of all remaining freshwater crab families assigned to three superfamilies, viz., Potamoidea (Potamidae, Potamonautidae, Deckeniidae, Platythelphusidae), Gecarcinucoidea (Parathelphusidae, Gecarcinucidae) and Pseudothelphusoidea (Pseudothelphusidae). Various authors have expressed doubts about the existing family classification and it is clear that there is still much to be done before a reasonable consensus can be reached. Most recently, Daniels et al. (2006) have suggested that some of these families may be artificial, while Brandis (2002), and Klaus et al. (2006) and Cumberlidge et al. (2007) have each offered different systems of higher classification. We have erred on the side of "conservativeness" in the system adopted here. The differences between workers will only encourage more morphological and molecular work to help resolve the conflicting views to the classification of these animals. Currently, there are few other molecular phylogenies of freshwater crabs and those available have a limited geographical scope (e.g. Japan: Segawa, 2000; Taiwan: Shih et al., 2004, 2007; South Africa: Daniels et al., 2002; India and Sri Lanka: Bossuyt et al., 2004; East Africa: Marijnissen et al., 2006; Malay Peninsula: Yeo et al., 2007). The status of the phylogenetic relationships of the freshwater crabs is, therefore, still controversial in the face of incongruent morphological and molecular studies and is the subject of ongoing work by several research groups including the present authors. For convenience, we follow the higher taxonomy of the freshwater crabs proposed by Martin & Davis (2001).

Bott (1955) estimated that the age of freshwater crabs was about 65 million years, with an origin between the end of the Cretaceous and the beginning of the Tertiary for the African Potamonautidae. Later, in agreement with Rodríguez (1986) that New World pseudothelphusoids and Old World gecarcinucoids share a synapomorphy (a bilobed mandibular palp), Ng et al. (1995) suggested that the freshwater crabs possessing this synapomorph were at least 120 million years old by inference, corresponding to the timing of the split between South America and Africa. More recently, Daniels et al. (2006) estimated that Afrotropical crabs radiated some 75.03–78.6 million years ago. The fossil evidence, however, does not support any of the above proposed age estimates, with the oldest known fossil from the Upper Tertiary in northern India and Europe being not much older than 23 mya (Bott, 1955; Glaessner, 1969). Ng et al. (1995), however, warned against making firm conclusions based on this dearth of fossils, commenting that, "the rarity and difficulty of forming (and finding) freshwater fossils is well known".

One of the key processes driving freshwater crab diversification is likely to be allopatric speciation resulting from geographic isolation. This is helped by the relatively low fecundity and poor dispersal abilities of freshwater crabs; and is often facilitated by the habitat heterogeneity and numerous ecological niches and microhabitats afforded by the complicated topography and hydrology of their

Fig. 4 Freshwater crabs (*Somanniathelphusa dangi*: Parathelphusidae) being sold as food in a rural market in northern Vietnam

environments. Nevertheless, the significance of sympatric speciation cannot be discounted, especially for lacustrine species (e.g. *Platythelphusa* in the African Rift Valley Lakes (Cumberlidge et al., 1999; Marijnissen et al., 2006); and *Parathelphusa* and allies in the Sulawesi lakes (Chia & Ng, 2006)). All these factors have led to a high degree of endemism in freshwater crabs.

Human-related issues

Economic and medical uses

Freshwater crabs are an important protein source and are consumed in many parts of the world. Ng (1988) noted that in Thailand, large potamids and parathelphusids are occasionally eaten by locals. Yeo & Ng (1998) commented that potamids are important in the diet of rural and hill tribes of northern Vietnam (Fig. 4). Freshwater crabs are also consumed for purported medicinal and tonic properties, including treatment of stomach ailments and physical injuries (Dai, 1999). In South America, indigenous groups use freshwater crabs, particularly large pseudothelphusids, for food (Finkers 1986).

Medically, freshwater crabs are important because they are intermediate hosts to the parasitic lung fluke, *Paragonimus* (Platyhelminthes) which causes paragonimiasis. This dangerous disease affects humans when they consume infected crabs (Ng, 1988; Dai, 1999; Cumberlidge, 1999). Rodríguez & Magalhães (2005) listed the pseudothelphusid species reported as hosts for *Paragonimus* and discussed its occurrence in the neotropics. Although proper cooking would kill the parasite, many of the more rural communities prefer to consume freshwater crabs half-raw (Ng, 1988; Dai, 1999).

Freshwater crabs are sometimes sold in the aquarium trade. These are usually the more colourful Indochinese potamids e.g. *Demanietta khirikhan, Pudaengon arnamicai, Terrapotamon abbotti*, although less gaudy parathelphusids like *Heterothelphusa fatum* are also sold. The trichodactylid crab, *Dilocarcinus pagei*, is captured for bait in game fishing of large catfishes in the Pantanal Matogrossense, a swampy area in the Paraguay River basin (Magalhães, 2000). The impact of these activities on the freshwater crab fauna, however, is low as demand is low and collection irregular.

Threats and conservation issues

Based on a recent assessment of the conservation status of Malaysian freshwater crabs, a few patterns emerged (Ng & Yeo, 2007). The restricted distributions of most of the freshwater crab species pose serious problems for conservation. Fortunately, for the time being, the species with the most restricted distributions are often those that inhabit offshore islands or mountains, areas that are generally less immediately impacted by man. The loss of natural forest as a result of land development and agriculture has generally affected lowlands more severely. However, many lowland species (e.g. *Parathelphusa maculata*) may have survived because they have relatively wider distributions. Specialist species (e.g. obligate cavernicoles like *Cerberusa caeca*), and highland taxa (e.g. *Johora grallator*) are at higher risk because they have a restricted range and are less tolerant of habitat changes. A similar study was made of the Sri Lankan fauna by Bahir et al. (2005), and of the Tanzanian and Southern African freshwater crabs by Reed & Cumberlidge (2006) and Cumberlidge & Daniels (2007).

The conservation of freshwater crabs will depend primarily on preserving large enough natural forest areas to maintain the good water quality of the original streams. Thus, the need to establish more nature reserves and national parks, together with careful planning and development is imperative.

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