

A revision of the higher taxonomy of the Afrotropical freshwater crabs (Decapoda: Brachyura) with a discussion of their biogeography

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The higher taxonomy of the 20 known genera of Afrotropical freshwater crabs is revised to reflect the evolutionary relationships revealed by the consensus of a series of recent morphological and molecular phylogenetic studies of the group. The Afrotropical freshwater crab genera fall into two monophyletic groups, one from Socotra with two genera (Potamidae) and another that includes the remaining 18 genera. The latter group, which includes the bulk of the region's freshwater crab fauna, forms a well-supported monophyletic clade. We recognize two monophyletic sister groups (subfamilies) within the Potamonautidae, one for seven genera from Africa (the Potamonautinae) and one for 11 genera from Africa, the Seychelles, and Madagascar (the Deckeniinae). The Deckeniinae includes two monophyletic groups (tribes), one with seven genera from Madagascar (the Hydrothelphusini), and one with four genera from Africa and the Seychelles (the Deckeniini). The Deckeniini is further divided here into two subtribes, the Deckeniina and the Globonautina. The Platythelphusidae is not recognized, and the Deckeniidae and Globonautinae are lowered in rank. There is no phylogenetic support for the continued inclusion of any genus from the Afrotropical region in the Gecarcinucidae which is treated here as an exclusively Oriental family. The Afrotropical freshwater crabs (excluding those from Socotra) form a monophyletic assemblage that has no representatives outside of the region. The wider biogeographical implications of the taxonomic revision are discussed. © 2008 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2008, **93**, 399–413.

ADDITIONAL KEYWORDS: Deckeniina – Deckeniinae – Deckeniini – Gecarcinucidae – Gecarcinucoidea – Globonautina – Hydrothelphusini – Potamoidea – Potamonautidae – Potamonautinae.

INTRODUCTION

The present work focuses on the 20 genera of freshwater crabs that occur in the Afrotropical (Ethiopian) zoogeographical region (Table 1). This region is a modern day remnant of the ancient Gondwanan supercontinent that includes the African mainland plus the major continental islands of Madagascar, the granitic Seychelles, Socotra, and the southern Arabian peninsula (Yeo *et al.*, 2007). Freshwater crabs are abundant throughout this entire region, with the exception of the driest desert areas, and all

are endemic at the genus and species levels (Bott, 1955; Ng, Števcic & Pretzmann, 1995; Cumberlidge, 1999; Apel & Brandis, 2000; Cumberlidge & Sternberg, 2002; Cumberlidge & Wranik, 2002).

Phylogenetic relationships among freshwater crabs in general and among the Afrotropical crabs in particular, have been historically neglected and as a consequence their higher-level taxonomy, phylogeny, and biogeographical affinities have been a source of disagreement among specialists. Figure 1A summarizes the higher-level taxonomic arrangement of Martin & Davis (2001) that assigns the Afrotropical freshwater crabs to five families: four in the Potamoidea (Potamonautidae, Deckeniidae, Platythel-

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Table 1. List of freshwater crab genera that occur in the Afrotropical biogeographical region with their taxonomic authorities

Potamoidea Ortmann, 1896
Potamonautidae Bott, 1970a
Potamonautinae Bott, 1970a
<i>Erimetopus</i> Rathbun, 1894
<i>Liberonautes</i> Bott, 1955
<i>Louisea</i> Cumberlidge, 1994
<i>Potamonautes</i> Bott, 1970a
<i>Potamonemus</i> Cumberlidge & Clark, 1992
<i>Sudanonautes</i> Bott, 1955
<i>Platythelphusa</i> A. Milne-Edwards, 1887
Deckeniinae Ortmann, 1897
Deckeniini Ortmann, 1897
Deckeniina Ortmann, 1897
<i>Deckenia</i> Hilgendorf, 1869
<i>Seychellum</i> Ng, Štević & Pretzmann, 1995
Globonautina Bott, 1969
<i>Globonautes</i> Bott, 1959
<i>Afrithelphusa</i> Bott, 1969
Hydrothelphusini Bott, 1955
<i>Boreas</i> Cumberlidge & Sternberg, 2002
<i>Foza</i> Reed & Cumberlidge, 2006a
<i>Hydrothelphusa</i> A. Milne-Edwards, 1872
<i>Madagapotamon</i> Bott, 1965
<i>Malagasya</i> Cumberlidge & Sternberg, 2002
<i>Marojejy</i> Cumberlidge, Boyko & Harvey, 2000
<i>Skelosophusa</i> Ng & Takeda, 1994
Potamidae Ortmann, 1896
<i>Socotra</i> Cumberlidge & Wranik, 2002 (Afrotropical)
<i>Socotrapotamon</i> Apel & Brandis, 2000 (Afrotropical)
plus 81 other genera (nine Palaeartic, 72 Oriental)

The classification proposed here is based on the phylogenetic results of Spears *et al.* (2004), Daniels *et al.* (2006), and Klaus *et al.* (2006).

phusidae, Potamidae) and one in the Gecarcinoidea (Gecarcinucidae). This contrasts with the classification by Štević, (2005) wherein all of the Old World freshwater crabs are assigned to a single family (the Potamidae) with eight subfamilies, all in the superfamily Potamoidea (Fig. 1B).

The present study arises out of the findings of a series of recent morphological and molecular phylogenetic studies (Cumberlidge, 1999; Sternberg, Cumberlidge & Rodriguez, 1999; Sternberg & Cumberlidge, 2001a, b; Spears *et al.*, 2004; Thompson, 2005; Daniels *et al.*, 2006; Klaus, Schubart & Brandis, 2006) that, despite differing in some respects, together provide a consensus view of the higher-level evolutionary relationships of the Afrotropical freshwater crabs (Fig. 2). These phylogenetic works reveal a lack of support for some of the present families of Afrotropical freshwater crabs, suggesting the need for

a radical taxonomic revision of the entire assemblage. We discuss the higher-level classification of the Gecarcinoidea proposed by Klaus *et al.* (2006) (Fig. 1C), and present an alternative classification of the 20 genera of Afrotropical freshwater crabs that more accurately reflects their evolutionary relationships (Table 1, Fig. 1D).

The discovery of new relationships for the Afrotropical freshwater crabs and the falsification of some of their traditional taxonomic assignments has profound phylogenetic implications that allow us to contribute to the debate on the origins and biogeographical affinities of these animals. Long-standing questions such as the relationships of the Malagasy freshwater crabs and the West African globonautines to those found in the Seychelles and India can now be answered. Finally, the new data permit the evaluation of the utility of the morphological characters presently used to establish the higher taxonomic categories of the Afrotropical freshwater crabs.

PHYLOGENY OF THE AFROTROPICAL FRESHWATER CRABS

The consensus phylogeny of the recent morphological (Cumberlidge, 1999; Sternberg *et al.*, 1999; Sternberg & Cumberlidge, 2001a, b) and molecular (Daniels *et al.*, 2006; Klaus *et al.*, 2006) phylogenetic studies is summarized in Figure 2. These studies, taken as a whole, bring an unprecedented level of resolution to the relationships within the Afrotropical freshwater crabs but there is less certainty regarding their affinities with the other major assemblages of freshwater crabs elsewhere in the Old World (Figs 3, 4). These molecular studies are very different in terms of the number of markers used and in their taxon sampling. For example, Daniels *et al.* (2006) collected partial sequence data from six gene loci that included four mitochondrial genes and two nuclear loci, making a total of 2643 base pairs (bp). The mitochondrial genes were two ribosomal loci, 12S rRNA (272 bp) and 16S rRNA (352 bp), and two protein-coding loci, cytochrome *c* oxidase subunit I (610 bp), and cytochrome *c* oxidase subunit II (447 bp). The nuclear loci were a protein coding gene locus (histone H3, 310 bp) and a ribosomal locus (18S rRNA, 652 bp). Daniels *et al.* (2006) used 65 freshwater crab taxa representing the Potamidae (46 species), the Gecarcinoidea (18 species), and the Pseudothelphusoidea (one species), including 14 out of 20 Afrotropical genera. Their maximum parsimony (MP) analysis was based on 956 parsimony informative characters and recovered a single shortest tree whose topology was identical to that recovered from both the maximum likelihood and Bayesian analyses. The study by Klaus *et al.* (2006)

- A. Martin and Davis (2001)
- Superfamily Potamoidea Ortmann, 1896**
 - Family Deckeniidae Ortmann, 1897
 - Family Platythelphusidae Colosi, 1920
 - Family Potamidae Ortmann, 1896
 - Family Potamonautidae Bott, 1970a
 - Superfamily Gecarcinucoidea Rathbun, 1904**
 - Family Gecarcinucidae Rathbun, 1904
 - Family Parathelphusidae Alcock, 1910
- B. Števc̆ić (2005)
- Superfamily Potamoidea Ortmann, 1896**
 - Family Potamidae Ortmann, 1896
 - Subfamily Parathelphusinae Alcock, 1910a
 - Gecarcinucinae Rathbun, 1904
 - Globonautinae Bott, 1969
 - Seychelliinae Števc̆ić, 2005
 - Platythelphusinae Colosi, 1920
 - Potaminae Ortmann, 1896
 - Potamonautinae Bott, 1970a
 - Deckeniinae Ortmann, 1897
- C. Klaus *et al.* (2006)
- Superfamily Potamoidea Ortmann, 1896**
 - Family Potamidae Ortmann, 1896
 - Family Potamonautidae Bott, 1970a
 - Superfamily Gecarcinucoidea Rathbun, 1904**
 - Family Gecarcinucidae Rathbun, 1904
 - Subfamily Parathelphusinae Alcock, 1910a
 - Gecarcinucinae Rathbun, 1904
 - Family Deckeniidae Ortmann, 1897
 - Subfamily Deckeniinae Ortmann, 1897
 - Globonautinae Bott, 1969
 - Hydrothelphusinae Bott, 1955
- D. Present work
- Superfamily Potamoidea Ortmann, 1896**
 - Family Potamidae Ortmann, 1896
 - Family Potamonautidae Bott, 1970a
 - Subfamily Potamonautinae Bott, 1970a
 - Deckeniinae Ortmann, 1897
 - Hydrothelphusini Bott, 1955
 - Deckeniini Ortmann, 1897
 - Deckeniina Ortmann, 1897
 - Globonautina Bott, 1969
 - Superfamily Gecarcinucoidea Rathbun, 1904**
 - Family Gecarcinucidae Rathbun, 1904
 - Family Parathelphusidae Alcock, 1910a

Figure 1. Comparison of four different higher classifications of the freshwater crabs. A, Martin & Davis (2001). B, Števc̆ić (2005). C, Klaus *et al.* (2006). D, Present study.

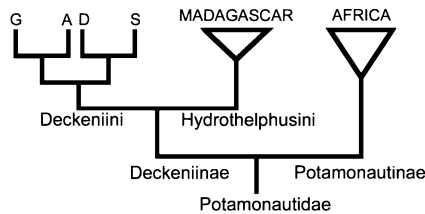


Figure 2. Consensus phylogeny for the Afrotropical freshwater crabs based on the morphological studies of Sternberg *et al.* (1999), Sternberg & Cumberlidge (2001a, b), and the molecular studies of Daniels *et al.* (2006) and Klaus *et al.* (2006). G, *Globonautes*, A, *Afrithelphusa*, D, *Deckenia*, S, *Seychellum*, MAD, seven Malagasy genera, AFR, all Potamonautine genera. For details, see Table 1.

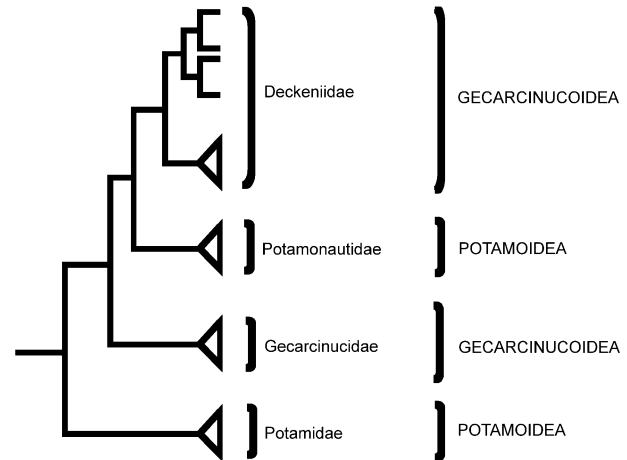


Figure 3. The higher classification of the Old World freshwater crabs proposed by Klaus *et al.* (2006) based on the phylogeny presented in that work whereby their Gecarcinucoidea (Gecarcinucidae + Deckeniidae) and their Potamoidea (Potamonautidae + Potamidae) are both paraphyletic.

collected partial sequence data from a single mitochondrial gene (16S rRNA, 536 bp) from 38 freshwater crab taxa consisting of 11 species of Potamoidea, 25 species of Gecarcinucoidea, and two species of Pseudothelphusoidea, including seven out of 20 Afrotropical genera. Their MP analysis was based on 220 parsimony informative characters that recovered a single shortest tree whose topology was different from their trees based on Bayesian analysis and Minimum Evolution.

The above two studies agree that the Afrotropical freshwater crab genera form two distinct monophyletic groups. These groups are treated here as the Potamidae and the Potamonautidae (which is

revised). There is also strong nodal support from the above phylogenetic studies for the division of the Potamonautidae into two lineages that are treated here as subfamilies. These are the Potamonautinae Bott (1970a) for seven genera from sub-Saharan Africa (*Potamonemus*, *Sudanonautes*, *Liberonautes*, *Erimetopus*, *Louisea*, *Potamonautes*, and *Platythel-*

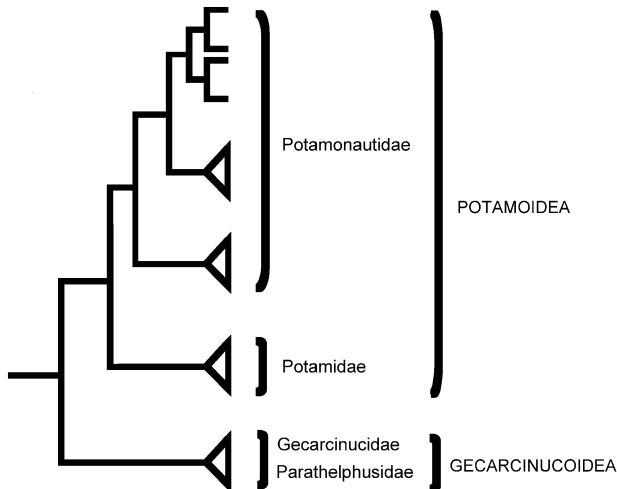


Figure 4. Higher classification of the Old World freshwater crabs based on the phylogenetic studies of Daniels *et al.* (2006) and Klaus *et al.* (2006) wherein the Potamoidea (Potamonautidae + Potamidae) and the Gecarcinucoidea (Gecarcinucidae + Parathelphusidae) are both monophyletic. For details, see Table 1.

phusa) and the Deckeniinae Ortmann, 1897 for the other 11 genera (*Deckenia*, *Seychellum*, *Globonautes*, *Afrithelphusa*, *Madagapotamon*, *Foza*, *Hydrothelphusa*, *Marojejy*, *Skelosophusa*, *Malagasya*, and *Boreas*).

The divisions within the Potamonautinae are still not clear, and this subfamily is not further divided in the present work. On the other hand, the Deckeniinae forms two distinct lineages (recognized here as tribes) named the Hydrothelphusini (type genus: *Hydrothelphusa* A. Milne-Edwards, 1872) from Madagascar, and the Deckeniini (type genus: *Deckenia* Hilgendorf, 1869) from West Africa, East Africa, and the Seychelles (Figs 2, 5B). The Hydrothelphusini is a monophyletic group of seven Malagasy freshwater crab genera (Table 1) that is well supported by both morphological studies (Cumberlidge & Sternberg, 2002) and molecular studies (Spears *et al.*, 2004; Thompson, 2005; Daniels *et al.*, 2006; Klaus *et al.*, 2006). The sister group of the Hydrothelphusini is the Deckeniini which includes African (*Globonautes*, *Afrithelphusa*, and *Deckenia*) and Seychellian (*Seychellum*) genera, thereby unexpectedly uniting four taxa of morphologically disparate freshwater crabs from geographically discontinuous regions that are currently separated at the family or subfamily levels (Fig. 1A, B). The Deckeniini comprises two distinct groups (recognized here as subtribes) that are named the Deckeniina and the Globonautilina. The Deckeniina includes *Deckenia* from East Africa and its sister genus *Seychellum* from the Seychelles, so linking genera that were previously referred to two different families, the Deckeniidae

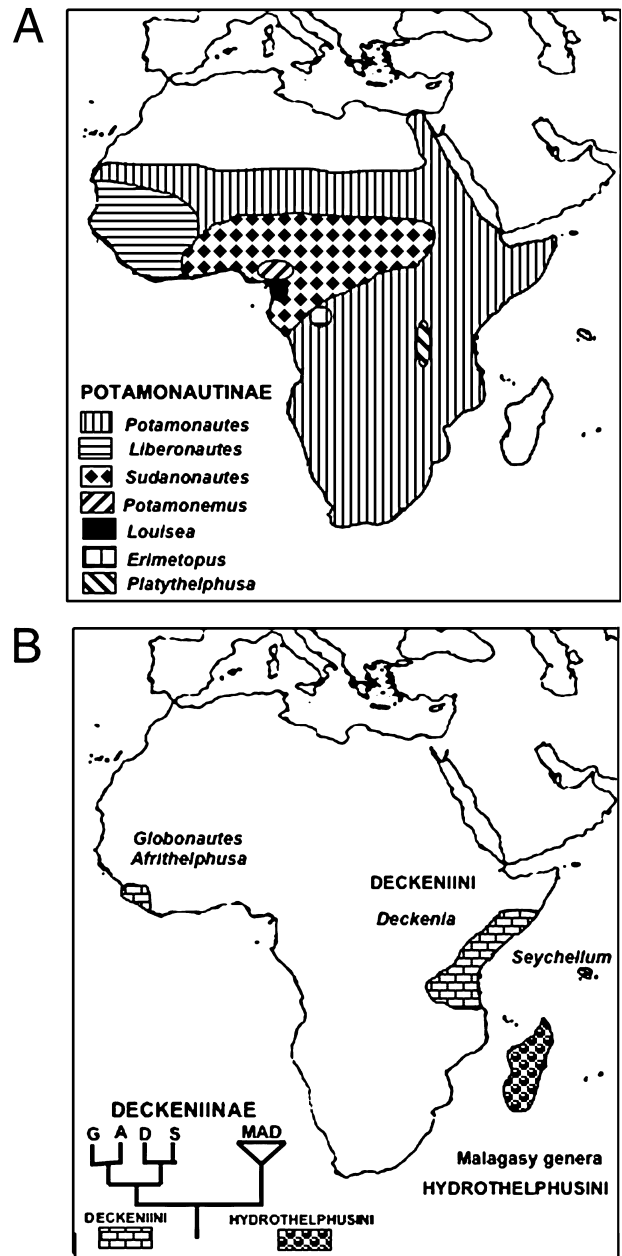


Figure 5. A, distribution of the genera included here in the Potamonautinae with a summary of the phylogenetic relationships within the family Potamonautidae. B, distribution of the genera included here in the Deckeniinae with a summary of their phylogenetic relationships. G, *Globonautes*, A, *Afrithelphusa*, D, *Deckenia*, S, *Seychellum*, MAD, seven Malagasy genera. For details, see Table 1.

and Gecarcinucidae, respectively (Bott, 1955, 1960; Ng *et al.*, 1995). The Globonautilina includes *Globonautes* and *Afrithelphusa* from West Africa that were previously assigned to the Gecarcinucidae (Bott, 1969, 1970b; Cumberlidge, 1999) although this family

assignment was questioned by Cumberlidge (1999). A close evolutionary relationship between the freshwater crabs of Madagascar, West Africa, East Africa, and the Seychelles is a surprising finding, which raises a number of important morphological and biogeographical questions.

TAXONOMY AND SYSTEMATIC AFFINITIES AMONG AFROTROPICAL FRESHWATER CRABS

Morphological characters of the mandible, first gonopod, carapace, sternum, and abdomen of freshwater crabs have long been used to make both family and superfamily taxonomic assignments and to infer evolutionary and biogeographical relationships (Bott, 1955, 1965, 1970a, b; Rodriguez, 1982, 1992; Ng, 1988; Cumberlidge, 1999; Dai, 1999; Števíč, 2005). However, the utility of some of these characters for taxonomy and phylogeny has recently been challenged, especially for the Afrotropical crabs (Guinot, Jamieson & Tudge, 1997; Cumberlidge, 1999; Cumberlidge & Sternberg, 2002; Daniels *et al.*, 2006; Klaus *et al.*, 2006). Ironically, it is the mandibular palp characters that are most widely used for higher-level classifications (Alcock, 1909a, b, 1910a, b; Calman, 1913; Bott, 1955, 1965, 1970a, b; Ng, 1988; Ng *et al.*, 1995), and which have historically been afforded significant taxonomic weight, that have become the most dubious (Cumberlidge, 1999; Cumberlidge & Sternberg, 2002; Daniels *et al.*, 2006; Klaus *et al.*, 2006).

Bott's (1955) landmark monographic work on the African freshwater crabs assigned three genera (*Potamonautes*, *Sudanonautes* and *Liberonautes*) to the then family Potamonidae. Bott (1955) included *Platythelphusa* and *Erimetopus* in different subgenera of *Potamonautes*, assigned most of the Malagasy taxa to the subfamily Hydrothelphusinae, and assigned the species from the Seychelles to the Deckeniidae. Later works by Bott (1959, 1960, 1965, 1969, 1970a, b) developed this classification further and recognized three families with three subfamilies in Africa and Madagascar: the Potamonautidae (Hydrothelphusinae), Deckeniidae, and Gecarcinucidae (Globonautinae and Gecarcinucinae).

Bott (1965, 1970a) considered that the Malagasy freshwater crab fauna included a mix of taxa with different phylogenetic and biogeographical affinities and used mandibular palp characters to assign the three genera recognized then to two families and three subfamilies. *Madagapotamon*, which has a simple ('African') mandibular palp, was assigned to the Potaminae, and *Hydrothelphusa*, which has a bilobed mandibular palp, was assigned to the

Hydrothelphusinae (*sensu* Bott, 1955), and viewed as intermediate between African and Indian taxa. Finally, *Gecarcinautes* was treated (incorrectly) by Bott (1960, 1965) as if all members had a bilobed mandibular palp and was assigned to the Oriental Gecarcinucidae (Gecarcinucinae), together with West African and South African taxa (Bott, 1965, 1969, 1970a, b). The latter assignment inferred a close phylogenetic relationship between Afrotropical and Oriental taxa, with the Malagasy freshwater crabs forming a transitional group linking African and Indian faunas (Rodriguez, 1986; Ng & Rodriguez, 1995; Ng *et al.*, 1995).

Cumberlidge & Sternberg's (2002) revision of the Malagasy freshwater crabs placed the island's entire fauna in the African Potamonautidae (with no Malagasy taxa in the Gecarcinucidae which they viewed as an Oriental family). Those authors radically altered the membership of *Hydrothelphusa*, synonymized *Gecarcinautes* under *Potamonautes*, and established two new genera, *Malagasya* and *Boreas*. Cumberlidge & Sternberg (2002) restricted the use of the mandibular palp characters to the genus level and grouped the genera as: those sharing a simple terminal segment (*Madagapotamon*), those with a small basal ledge on the terminal segment (*Skelosophusa* and *Boreas*), and those sharing a bilobed terminal segment with a medium-sized anterior lobe (*Hydrothelphusa*, *Malagasya*, and *Marojejy*). Another Malagasy genus (*Foza*) with a mandibular palp that has a bilobed terminal segment with a medium-sized anterior lobe, was recently added by Reed & Cumberlidge (2006a). Cumberlidge & Sternberg (2002) viewed the Malagasy freshwater crab fauna as a single lineage with affinities to Africa, and found no support for any close relationships to taxa in West Africa, South Africa, the Seychelles, or India. Studies such as those of Cumberlidge (1999) and Cumberlidge & Sternberg (2002) questioned the unconditional use of mandibular palp characters for making higher-level taxonomic assignments of the Afrotropical freshwater crabs, and cast doubt on the classification schemes of Bott (1955, 1965, 1970a, b) and others (Ng *et al.*, 1995) that relied heavily on such characters.

The distribution of the mandibular palp characters between the genera of Afrotropical freshwater crabs is summarized in Table 2. This character is useful for separating potamids (such as *Socotra* and *Socotrapotamon*) with a three-segmented mandibular palp, from the rest of the Afrotropical genera (which all have a two-segmented mandibular palp). However, other mandibular palp characters are less useful within the potamonautids because the terminal segment of the two-segmented palp exhibits four different configurations: (1) simple (*Potamonautes*, *Sudanonautes*, *Potamonemus*, *Erimetopus*, *Platythelphusa*, *Deckenia*,

Table 2. List of freshwater crab genera that occur in the Afrotropical region with their distribution by region, taxonomic assignment, and mandibular palp characters

Genus	Distribution	Superfamily	Family	Subfamily	Tribe	Number of segments	Simple	Simple with anterior ledge	Bilobed, anterior lobe 0.5× posterior lobe	Bilobed, anterior lobe subequal to posterior lobe
<i>Erimetopus</i>	Central Africa	Potamoidea	Potamonautidae	Potamonautinae	None	2	X			
<i>Liberonautes</i>	West Africa	Potamoidea	Potamonautidae	Potamonautinae	None	2		X		
<i>Louisa</i>	West Africa	Potamoidea	Potamonautidae	Potamonautinae	None	2		X		
<i>Platyhelphusa</i>	Lake Tanganyika	Potamoidea	Potamonautidae	Potamonautinae	None	2	X			
<i>Potamonautes</i>	All Africa	Potamoidea	Potamonautidae	Potamonautinae	None	2	X			
<i>Potamonemus</i>	West Africa	Potamoidea	Potamonautidae	Potamonautinae	None	2		X		
<i>Sudanautes</i>	West and Central Africa	Potamoidea	Potamonautidae	Potamonautinae	None	2	X			
<i>Deckenia</i>	East Africa	Potamoidea	Potamonautidae	Deckeniinae	Deckeniini	2	X			
<i>Globonautes</i>	West Africa	Potamoidea	Potamonautidae	Deckeniinae	Deckeniini	2				X
<i>Afrithelphusa</i>	West Africa	Potamoidea	Potamonautidae	Deckeniinae	Deckeniini	2				X
<i>Seychellum</i>	Seychelles	Potamoidea	Potamonautidae	Deckeniinae	Deckeniini	2			X	
<i>Madagapotamon</i>	Madagascar	Potamoidea	Potamonautidae	Deckeniinae	Hydrothelphusini	2	X			
<i>Boreas</i>	Madagascar	Potamoidea	Potamonautidae	Deckeniinae	Hydrothelphusini	2		X		
<i>Skelosophusa</i>	Madagascar	Potamoidea	Potamonautidae	Deckeniinae	Hydrothelphusini	2		X		
<i>Foza</i>	Madagascar	Potamoidea	Potamonautidae	Deckeniinae	Hydrothelphusini	2			X	
<i>Hydrothelphusa</i>	Madagascar	Potamoidea	Potamonautidae	Deckeniinae	Hydrothelphusini	2			X	
<i>Malagasya</i>	Madagascar	Potamoidea	Potamonautidae	Deckeniinae	Hydrothelphusini	2			X	
<i>Marojejy</i>	Madagascar	Potamoidea	Potamonautidae	Deckeniinae	Hydrothelphusini	2			X	
<i>Socotra</i>	Socotra	Potamoidea	Potamidae	Deckeniinae	None	3	X			
<i>Socotrapotamon</i>	Socotra	Potamoidea	Potamidae	Potaminae	None	3	X			

Table 3. Family level classification and revised family level of the Old World freshwater crabs (Martin & Davis, 2001) showing the number of genera and species (in parentheses), and the zoogeographical region(s) where each occurs

Family	Afrotropical totals	Palaeartic totals	Oriental totals	Australasian totals	Total totals
Family level					
Potamonautidae	12 (115)	–	–	–	12 (115)
Deckeniidae	1 (2)	–	–	–	1 (2)
Platythelphusidae	1 (9)	–	–	–	1 (9)
Gecarcinucidae	4 (8)	–	10 (36)	–	14 (44)
Potamidae	2 (3)	9 (86)	72 (432)	–	83 (521)
Parathelphusidae	–	1 (4)	35 (243)	9 (52)	45 (299)
Total	20 (137)	10 (90)	117 (711)	9 (52)	156 (990)
Revised family level					
Potamonautidae	18 (134)	–	–	–	18 (134)
Potamidae	2 (3)	9 (86)	72 (432)	–	83 (521)
Parathelphusidae	–	1 (4)	35 (243)	9 (52)	45 (299)
Gecarcinucidae	–	–	10 (36)	–	10 (36)
Total	20 (137)	10 (90)	117 (711)	9 (52)	156 (990)

and *Madagapotamon*) (Bott, 1965; Ng *et al.*, 1995; Cumberlidge, 1999; Cumberlidge & Sternberg, 2002; Cumberlidge & Reed, 2004); (2) simple, with a small basal ledge at the junction between the two segments (*Liberonautes*, some *Sudanonautes*, some *Potamonautes*, *Louisea*, *Skelosophusa*, and *Boreas*) (Cumberlidge, 1999; Cumberlidge & Sternberg, 2002); (3) bilobed, with a small anterior lobe, about 0.5× the terminal segment length (*Hydrothelphusa*, *Malagaysa*, *Marojejy*, *Foza*, and *Seychellum*) (Ng *et al.*, 1995; Cumberlidge & Sternberg, 2002; Reed & Cumberlidge, 2006a); and (4) bilobed, with a large subequal anterior lobe (*Globonautes* and *Afrithelphusa*) (Cumberlidge, 1999).

SYSTEMATICS

None of the Afrotropical freshwater crab families currently defined on the basis of characters of the mandibular palp forms a natural group (Cumberlidge, 1999; Sternberg *et al.*, 1999; Sternberg & Cumberlidge, 2001a,b; Daniels *et al.*, 2006; Klaus *et al.*, 2006) indicating that the higher taxonomies of this group proposed by Martin & Davis (2001) and Števcic (2005) may be artificial (Fig. 1A, C, Table 2). It should be noted that the bilobed two-segmented mandibular palp with a terminal segment with a subequal anterior lobe that is used to assign specimens to the Neotropical Pseudothelphusidae (Rodriguez, 1982, 1992) and the Oriental Parathelphusidae (Bott, 1970b; Ng, 1988; Dai, 1999), and the three-segmented palp with a simple terminal segment used to recognize the Old World Potamidae (Bott, 1970b; Ng, 1988; Dai, 1999; Brandis, Storch & Türkay, 2000; Brandis,

2000, 2002; Števcic, 2005) are invariant throughout each of these three monophyletic families, and the validity of these groups is not thrown into question by the present study.

SUPERFAMILY GECARCINUCOIDEA RATHBUN, 1904

The superfamily Gecarcinucoidea (Martin & Davis, 2001) currently includes two families, the Gecarcinucidae (for four genera with eight species from Africa and the Seychelles and ten genera with 36 species from India and South-east Asia), and the Parathelphusidae (for one genus with four species from the Palaeartic region, 35 genera and 243 species from the Oriental region, and nine genera and 52 species from the Australasian region) (Fig. 1A, Table 3; Yeo *et al.*, 2007). The present work recognizes these same two families but revises the membership of the Gecarcinucidae, which is treated as an exclusively Oriental family that includes ten genera with 36 species from India and South-east Asia, and none from the Afrotropical region, and leaves the Parathelphusidae unchanged (Fig. 1D, Table 3). This latter arrangement is supported by recent morphological and molecular studies (Cumberlidge, 1999; Sternberg *et al.*, 1999; Sternberg & Cumberlidge, 2001a, b; Daniels *et al.*, 2006; Klaus *et al.*, 2006). The proposal by Klaus *et al.* (2006) (Figs 1C, 3) that the Gecarcinucoidea be revised to include an Oriental family (the Gecarcinucidae) and an Afrotropical family (their revised Deckeniidae) is in conflict with the consensus molecular and morphological phylogenies of Daniels *et al.* (2006), Thompson (2005), and Klaus *et al.* (2006), which do not position any of the Afrotropical

genera close to any of the Oriental genera (Figs 2, 4). Furthermore, the Gecarcinucoidea of Klaus *et al.* (2006: table 1, figs 6–8) is paraphyletic because it excludes their revised Potamonautidae (which is the sister group of their revised Deckeniidae), and so fails to include all of the descendants of the common ancestor of the Gecarcinucoidea (Figs 1C, 3). The morphological support for the classification of the Gecarcinucoidea of Klaus *et al.* (2006: table 1) is also not convincing because mapping the gonopod 2 character on to the molecular phylogenies provided in that same work indicates that this character is convergent at the taxonomic levels at which it is applied, despite the (subjective) arrangement shown in Klaus *et al.* (2006: fig. 5).

SUPERFAMILY POTAMOIDEA ORTMANN, 1896

The superfamily Potamoidea of Martin & Davis (2001) includes four families: the Potamidae from the Afrotropical region (two genera, three species), Palaearctic region (nine genera, 86 species), and Oriental region (72 genera, 432 species), the Potamonautidae (for 12 genera with 115 species from Africa and Madagascar), the Deckeniidae (for one genus with two species from East Africa), and the Platythelphusidae (for one genus with nine species from Lake Tanganyika) (Fig. 1A, Table 2). The present work revises the Potamoidea to include two families: the Potamidae, which is unchanged here, and the Potamonautidae which here comprises 18 genera with 134 species that are all endemic to the Afrotropical biogeographical region (Fig. 1D, Table 3). The Potamoidea is revised here to accommodate these changes that include no longer recognizing the Platythelphusidae as a valid family, and lowering the rank of the Deckeniidae and the Globonautinae (Table 1, Figs 1D, 4).

The phylogenies presented by Sternberg & Cumberlidge (2001a, b) and Daniels *et al.* (2006: fig. 1) group the Potamidae and the Potamonautidae (in the present sense) as sister groups within the same clade (the Potamoidea) (Fig. 4), although there is not strong nodal support in this respect. One apomorphy diagnostic for the Potamoidea as defined here is a distinct gonopod 1 terminal article with a broad dorsal membrane, a character which sets this superfamily apart from members of the Gecarcinucoidea that have a gonopod 1 which is either lacking a dorsal membrane or has only a rudimentary one. However, the Potamoidea may be revised in the future because the phylogenies presented by Klaus *et al.* (2006: figs 7, 8) do not group the Potamidae and the Potamonautidae together in the same clade (Fig. 3), making their concept of the Potamoidea paraphyletic, although there is not strong nodal support for that arrangement. Finally, there is no support for the classification

proposed by Števcíć (2005) whereby all of the Old World freshwater crabs are included in a single family and superfamily (the Potamidae, Potamoidea), which places the Afrotropical freshwater crab genera in five out of eight subfamilies (Fig. 1B).

FAMILY POTAMIDAE ORTMANN, 1896

Diagnosis: Mandibular palp three-segmented with a simple terminal segment; lateral margin of each antennular fossa filled by second and third segments of antenna.

Distribution: Southern Europe, North Africa, East and South-east Asia including Socotra (Yeo & Ng, 2003).

Remarks: Yeo & Ng (2003) and Yeo *et al.* (2007) recognized the family Potamidae for all European and Asian potamid crabs comprising 83 genera and 521 species (Table 3). The Potamidae have a more or less continuous distribution ranging from southern Europe and North Africa across to East and South-east Asia, including Socotra (Ng, 1988; Ng & Naiyanetr, 1993; Dai, 1999; Yeo & Ng, 1999; Apel & Brandis, 2000; Cumberlidge & Wranick, 2002). Yeo & Ng (2003) divided the Potamidae into two subfamilies on the basis of differences in the structure of the eighth thoracic sternite. These two subfamilies are: (1) the Potaminae Ortmann, 1896 (from North Africa, Socotra, and western Eurasia) that is recognized by a narrow transverse ridge that interrupts the longitudinal median line at the suture between sternites 7 and 8 on the eighth thoracic sternite, and (2) the Potamiscinae Bott, 1970a (from East and South-east Asia) that is recognized by the lack of any trace of a transverse ridge at the suture between sternites 7 and 8 on the eighth thoracic sternite, whereby the longitudinal median line is completely uninterrupted in the posterior sternum. In the Afrotropical region, the Potamidae is represented by two genera, *Socotra* and *Socotrapotamon*. Both genera are endemic to Socotra Island, Yemen, and their thoracic sternal characters indicate that they belong to the subfamily Potaminae that includes the potamids from Europe, the Middle East and the Himalayas (Brandis *et al.*, 2000; Yeo & Ng, 2003). This is an interesting finding because, although Socotra lies approximately 400 km off the coast of Somalia, the affinities of its freshwater crabs lie with the Potaminae, and not with the Asian Potamiscinae or the potamonautids from Africa, the Seychelles, or Madagascar (Cumberlidge & Wranick, 2002; Yeo & Ng, 2003).

FAMILY POTAMONAUTIDAE BOTT, 1970A

Diagnosis: Mandibular palp 2-segmented. Lateral margin of each antennular fossa filled by second segment of antenna.

Distribution: Africa (except for Western Sahara, Morocco, Algeria, Tunisia and Libya), the granitic Seychelles (Mahe, Praslin, Silhouette, and La Digue), and Madagascar (Cumberlidge, 1999; Cumberlidge *et al.*, 2004; Reed & Cumberlidge, 2006a).

Remarks: The most recent configuration of the Potamonautidae [type genus: *Potamonautes* MacLeay, 1838] (Cumberlidge, 1999; Martin & Davis, 2001; Cumberlidge & Sternberg, 2002) recognized 12 genera and 115 species of freshwater crabs from Madagascar and sub-Saharan Africa (Fig. 1A, Table 3). The Potamonautidae is revised here (Figs 1C, 2, 4, Tables 1–3) to comprise a well-supported clade consisting of 18 genera and 134 species that are all endemic to the Afrotropical region (*Erimetopus*, *Liberonautes*, *Potamonautes*, *Platythelphusa*, *Potamonemus*, *Sudanonautes*, *Louisea*, *Deckenia*, *Seychellum*, *Globonautes*, *Afrithelphusa*, *Madagapotamon*, *Foza*, *Hydrothelphusa*, *Marojejy*, *Skelosophusa*, *Malagasya* and *Boreas*). This arrangement differs from the former composition of this family because it now includes *Deckenia*, *Platythelphusa*, *Globonautes*, *Afrithelphusa* and *Seychellum* (Fig. 1C, Table 3). *Deckenia* (the type genus of the Deckeniidae Ortmann, 1897), *Platythelphusa* (the type genus of the Platythelphusidae Colosi, 1920), *Hydrothelphusa* (the type genus of the Hydrothelphusinae Bott, 1955), and *Globonautes* (the type genus of the Globonautinae Bott, 1959) are all included here in the Potamonautidae Bott, 1970a, and priority is suppressed under current ICZN rules because the junior name Potamonautidae Bott, 1970a, has a broader usage than any of the other names. In addition, the inclusion of *Platythelphusa* within the genus *Potamonautes* (Potamonautidae) raises doubts about the continued recognition of the genus *Platythelphusa* (see below).

Figure 2 summarizes the phylogenetic insights suggested by the work of several authors (Cumberlidge, 1999; Sternberg *et al.*, 1999; Sternberg & Cumberlidge, 2001a, b; Daniels *et al.*, 2006; Klaus *et al.*, 2006). The inclusion of *Seychellum* (Seychelles) in the Potamonautidae (and its removal from the Gecarcinidae) represents a change from the classification proposed by Ng *et al.* (1995) and Martin & Davis (2001), and also involves a revision of the Gecarcinidae. In addition, the type genus of the Deckeniidae Ortmann, 1897 [*Deckenia* Hilgendorf, 1869] and the type genus of the Globonautinae Bott, 1959 [*Globonautes* Bott, 1959] are both transferred here to the Deckeniinae (Potamonautidae) (Table 1), and the family group names Deckeniidae and the Globonautinae are both lowered in rank. The Potamonautidae is divided here into two distinct groups (subfamilies),

the Potamonautinae and the Deckeniinae (Fig. 1C, Table 3).

SUBFAMILY POTAMONAUTINAE BOTT, 1970A

Type genus: *Potamonautes* MacLeay, 1838; by original designation.

Diagnosis: Members of the subfamily Potamonautinae are recognized as follows. When the second gonopod is viewed in cross section, the dorsal side of the junction between the subterminal segment and terminal article has a setose spoon-like structure that does not extend round to the ventral side (Klaus *et al.*, 2006). In addition, when the terminal article of the second gonopod is viewed in cross section the edges of both the dorsal and ventral margins are long, curve inward, and their tips overlap forming a closed dorsal tube (Klaus *et al.*, 2006). Although the above gonopod 2 characters are found in *Potamonautes*, *Liberonautes* and *Platythelphusa* (Potamonautinae), they are also found in *Potamon* (Potamidae) (Klaus *et al.*, 2006) a fact that would restrict their use at higher taxonomic levels. Mandible characters are incongruent within the Potamonautinae and have limited use for defining this subfamily (Cumberlidge, 1999; Cumberlidge & Sternberg, 2002). *Platythelphusa* (the type genus of the Platythelphusidae Colosi, 1920) and *Hydrothelphusa* (the type genus of the Hydrothelphusinae Bott, 1955) are included here in the Potamonautinae Bott, 1970a, and priority is suppressed under current ICZN rules because the junior name Potamonautidae Bott, 1970a, has a broader usage than both of these other names.

Distribution: Africa (except for Western Sahara, Morocco, Algeria, Tunisia, and Libya) (Figs 2, 5A).

Remarks: The Potamonautidae as conceived of here comprises two major evolutionary lineages (recognized as subfamilies) that represent two separate radiations of the freshwater crabs within the Afrotropical region. The Potamonautinae is established to represent one of these lineages (Figs 2, 5A) and comprises seven genera (*Erimetopus*, *Liberonautes*, *Louisea*, *Potamonautes*, *Potamonemus*, *Sudanonautes*, *Platythelphusa*) from all parts of sub-Saharan Africa that form a well-supported clade (Daniels *et al.*, 2006; Klaus *et al.*, 2006). The current taxonomic assignment of *Platythelphusa* to the Platythelphusidae (Cumberlidge *et al.*, 1999; Marijnissen *et al.*, 2004) or the Platythelphusinae (Števíć, 2005) is uncertain. The molecular phylogenies of Marijnissen *et al.* (2006) and Daniels *et al.* (2006) indicate that *Platythelphusa* is a monophyletic group of crabs nested within the large genus *Potamonautes*. This

raises questions as to the validity of the family Platythelphusidae and even the genus *Platythelphusa* because its continued generic recognition would render *Potamonautes* as currently understood a paraphyletic group. However, a definitive decision on this question is beyond the scope of the present work, and while the genus *Platythelphusa* is still recognized here, there is no support for the continued recognition of the family Platythelphusidae.

Louisea from Cameroon is provisionally included here in the Potamonautinae, despite the fact that Cumberlidge (1999) tentatively placed *Louisea* in the Globonautinae with an uncertain family placement. This little-known genus has so far not been included in any of the available molecular studies and until it is, its higher-level taxonomic assignment will remain provisional. A similar provisional assignment applies to *Erimetopus* from Central Africa (Cumberlidge & Reed, 2004) because this too has so far not been included in any of the available molecular studies.

The potamonautine freshwater crabs undoubtedly comprise a monophyletic group, but the mandibular palp characters of these animals vary greatly between genera (Table 3). For example, most taxa have a mandibular palp with a simple terminal segment (*Erimetopus*, *Potamonemus* and *Platythelphusa*, and most species of *Potamonautes*) while a few have a simple terminal segment with a small anterior ledge (*Louisea*, *Liberonantes*, *Potamonantes brincki*, some *Sudanonantes*). None have a bilobed mandibular palp. Nevertheless, the variability of mandibular palp characters between the genera (and in some cases such as *Sudanonantes*, within the genus) means that these characters have a more limited use for defining higher taxonomic groups than has been assumed in the past.

SUBFAMILY DECKENIINAE ORTMANN, 1897

Type genus: Deckenia Hilgendorf, 1869, by original designation. The name Deckeniinae Ortmann, 1897, is available and is assigned here to the family Potamonautidae. This subfamily was originally limited to *Deckenia* from East Africa. Klaus *et al.* (2006) assigned the Malagasy freshwater crabs (although they only examined three genera in their study) to the Hydrothelphusinae and included this subfamily in their revised family Deckeniidae Ortmann, 1897. In the present work, the Deckeniinae is expanded to include all Madagascan genera, plus *Seychellum* (Seychelles), *Deckenia* (East Africa), and *Globonantes* and *Afrithelphusa* (West Africa).

Diagnosis: Members of the subfamily Deckeniinae are recognized as follows. When the second gonopod is viewed in cross section, the spoon-like structure at

the junction between the subterminal segment and terminal article completely surrounds the gonopod and lacks setae (Klaus *et al.*, 2006). In addition, when the terminal article of the second gonopod is viewed in cross section, the dorsal margin is either reduced or missing while the ventral margin is long and curves upward and inward to create the lateral groove. The ventral margin achieves different degrees of enclosure of the lateral groove within this group from completely open (*Afrithelphusa*), to partly closed (*Seychellum*), to almost closed (*Hydrothelphusa*, *Malagasya* and *Madagapotamon*), but it is never completely closed as in the Potamonautinae and *Potamon* (Klaus *et al.*, 2006). All of the genera that have been examined in the Deckeniinae as configured here possess a pair of pseudolungs in the branchial chambers above the gills (Sternberg & Cumberlidge, 2001a). Mandible characters are inconsistent within the Deckeniinae and have limited use for defining this group.

Distribution: The Deckeniinae are endemic to the Afrotropical region and are represented in West Africa (Liberia, Guinea, Sierra Leone), East Africa (Tanzania, Kenya, Somalia), the granitic Seychelles, and Madagascar (Cumberlidge, 1999; Cumberlidge *et al.*, 2004; Reed & Cumberlidge, 2006a, b) (Figs 2, 5B).

Remarks: The Deckeniinae is the second major evolutionary lineage within the Potamonautidae (Figs 2, 5B) and comprises a well-supported clade that unites genera from East and West Africa (*Deckenia*, *Globonantes*, and *Afrithelphusa*), the Seychelles (*Seychellum*), and Madagascar (*Madagapotamon*, *Boreas*, *Skelosophusa*, *Malagasya*, *Marojejy*, *Foza*, *Hydrothelphusa*) (Spears *et al.*, 2004; Thompson, 2005; Daniels *et al.*, 2006; Klaus *et al.*, 2006). The Deckeniinae is subdivided here into two lineages (tribes) named the Hydrothelphusini (type genus: *Hydrothelphusa* A. Milne-Edwards, 1872) from Madagascar, and the Deckeniini (type genus: *Deckenia* Hilgendorf, 1869) from West Africa, East Africa, and the Seychelles (Figs 2, 5B). The suggestion by Klaus *et al.* (2006) that the Malagasy freshwater crabs should be placed in the Hydrothelphusinae and that this subfamily be assigned to a revised Deckeniidae (Figs 1C, 3) is not accepted here.

TRIBE HYDROTHELPHUSINI BOTT, 1955

Type genus: Hydrothelphusa A. Milne-Edwards, 1872, by original designation. The name Hydrothelphusini is derived from the subfamily level name Hydrothelphusinae Bott, 1955. This tribe is assigned here to the subfamily Deckeniinae in the family Potamonautidae, in contrast to Števíć (2005), who assigned the

Hydrothelphusini to the subfamily Potamonautinae of the Potamidae. The present definition of the Hydrothelphusini includes *Madagapotamon*, *Boreas*, *Skelosophusa*, *Malagasya*, *Marojejy*, *Foza*, and *Hydrothelphusa* that are all endemic to Madagascar (Cumberlidge & Sternberg, 2002; Reed & Cumberlidge, 2006a).

Diagnosis: Members of the Hydrothelphusini are recognized as follows. When viewed in cross section, the ventro-lateral margin of the terminal article of the second gonopod of *Hydrothelphusa*, *Madagapotamon*, and *Malagasya* is short (approximately half the width of the tissue area and its cuticle) and curves sharply upward and inward with the tip ending just before making contact, thereby forming a partly enclosed groove with a dorsal opening rather than a completely enclosed tube (Klaus *et al.*, 2006; Fig. 4). The medial part of the ventral face of the subterminal segment of gonopod 1 has a distinct disto-medial rounded triangular shoulder close to the junction with the terminal article (Cumberlidge & Sternberg, 2002; Reed & Cumberlidge, 2006a). Mandible characters are inconsistent within the Hydrothelphusini and have limited use for defining this group.

Distribution: Madagascar (Cumberlidge *et al.*, 2004; Reed & Cumberlidge, 2006a).

Remarks: Both morphological and molecular studies arrange the seven genera of Malagasy freshwater crabs in a well-supported clade, indicating that these taxa form a monophyletic group (Cumberlidge & Sternberg, 2002; Spears *et al.*, 2004; Thompson, 2005; Daniels *et al.*, 2006; Klaus *et al.*, 2006). The available evidence indicates that the common ancestor of the Malagasy freshwater crabs most likely lived in Africa, belonged to the Deckeniinae (rather than the Potamonautinae), and reached Madagascar from the Africa rather than from the Seychelles. Enforcing monophyly of the Malagasy genera and the African genera in the Potamonautinae resulted in a statistically worse topology, and the idea that the Malagasy genera are more closely related to the Potamonautinae than to other members of the Deckeniinae can be rejected with confidence (Daniels *et al.*, 2006). The Malagasy freshwater crabs undoubtedly comprise a monophyletic group but the mandibular palp characters of these animals vary greatly between genera (Table 2). For example, there are taxa with a mandibular palp with a simple terminal segment (*Madagapotamon*), those with a simple terminal segment with a small anterior ledge (*Boreas* and *Skelosophusa*), and those with a bilobed terminal

segment (*Malagasya*, *Marojejy*, *Foza*, and *Hydrothelphusa*) (Cumberlidge & Sternberg, 2002; Reed & Cumberlidge, 2006a).

TRIBE DECKENIINI ORTMANN, 1897

Type genus: *Deckenia* Hilgendorf, 1869, by original designation. The Deckeniini is derived from the family level name Deckeniidae Ortmann, 1897 (type genus: *Deckenia* Hilgendorf, 1869) and this tribe is assigned here to the subfamily Deckeniinae in the family Potamonautidae. Up to this point, the Deckeniidae had been limited to the two species of *Deckenia* from East Africa (Bott, 1955; Ng *et al.*, 1995). Klaus *et al.* (2006) expanded the Deckeniidae to include three subfamilies, the Deckeniinae (from East Africa and the Seychelles), the Globonautinae (from West Africa), and Hydrothelphusinae (from Madagascar), and assigned the Deckeniidae to the superfamily Gecarcinucoidea. That classification is not accepted here. The present definition of the Deckeniini includes *Seychellum* (Seychelles), *Deckenia* (East Africa), and *Globonautes* and *Afrithelphusa* (West Africa).

Diagnosis: Members of the Deckeniini are recognized by a buccal frame whose margins are narrowest dorsally and widest ventrally (Sternberg & Cumberlidge, 2001a).

Distribution: West Africa (Liberia, Guinea, Sierra Leone), East Africa (Tanzania, Kenya, Somalia), the granitic Seychelles (Mahe, Praslin, Silhouette, and La Digue) (Figs 2, 5B).

Remarks: The tribe Deckeniini is a monophyletic group that includes *Deckenia*, *Seychellum*, *Globonautes*, and *Afrithelphusa* (Figs 2, 5B). It is not easy to find morphological characters that unite the West African *Globonautes* and *Afrithelphusa* with either *Deckenia* or *Seychellum*, and characters of the mandible and gonopod 2 are inconsistent within the Deckeniini (Ng *et al.*, 1995; Cumberlidge, 1999; Klaus *et al.*, 2006) and have limited use for defining this group. For example, three genera of the Deckeniini have a mandibular palp with a bilobed terminal segment, whereas that of *Deckenia* is simple. The Deckeniini includes genera that occur in widely separate geographical regions, and which have strikingly unusual morphological characters so different from each other that they conceal underlying evolutionary relationships suggested by molecular studies. As such, each of these genera is itself distinct and can be easily distinguished by reference to the existing diag-

noses that are available in Ng *et al.* (1995), Cumberlidge (1999), and Reed & Cumberlidge (2006b).

SUBTRIBE DECKENIINA ORTMANN, 1897

Type genus: *Deckenia* Hilgendorf, 1869, by original designation.

Diagnosis: Members of the Deckeniina are recognized by first maxilliped endopods that are formed into long respiratory tubes, and by a distinctly lobed frontal margin (Ng *et al.*, 1995).

Distribution: East Africa (Tanzania, Kenya, Somalia) and the granitic Seychelles (Mahe, Praslin, Silhouette, and La Digue) (Figs 2, 5B).

Remarks: A number of studies (Cumberlidge & Sternberg, 2002; Spears *et al.*, 2004; Daniels *et al.*, 2006; Klaus *et al.*, 2006) indicate strong support for a sister group relationship between *Deckenia* and *Seychellum* and this is recognized here as the subtribe Deckeniina. The superficial similarity between the mouthparts and frontal region of *Deckenia* and *Seychellum* prompted Milne-Edwards & Bouvier (1893) and Bott (1955) to assign *Seychellum* (as a species of *Deckenia*) to the Deckeniidae. By contrast, Ng *et al.* (1995), who relied upon mandibular palp characters, assigned *Deckenia* to the Deckeniidae but reassigned *Seychellum* to the Gecarcinucidae. However, it is now becoming clear that mandible characters are inconsistent within the Afrotropical freshwater crabs in general and have only limited use for defining this group as a whole. For example, *Deckenia* has a two-segmented mandibular palp with a simple terminal segment that is typical of that seen in almost all genera found in Africa (Cumberlidge, 1999), whereas *Seychellum* has a two-segmented mandibular palp with a bilobed terminal segment (Ng *et al.*, 1995). It should be noted that the anterior lobe of the bilobed mandibular palp of *Seychellum* is not the same size as that of *Globonautes* and *Afrithelphusa*. For example, the anterior lobe in *Seychellum* is only half as big as the posterior lobe (Ng *et al.*, 1995; Cumberlidge, 1999; Cumberlidge & Sternberg, 2002) and is similar to that seen in the bilobed genera from Madagascar (*Malagasya*, *Hydrothelphusa*, *Marojejy*, *Foza*) (Cumberlidge & Sternberg, 2002; Reed & Cumberlidge, 2006a). By contrast, the mandibular palp of *Globonautes* and *Afrithelphusa* from West Africa has two subequal lobes, similar to that seen in the Oriental parathelphusids (Bott, 1970b), the Neotropical pseudothelphusids (Rodriguez, 1982), and some (but not all) of the Indian gecarcinucids (Bott, 1970b).

It is notable that there is no support from molecular phylogenetic studies (Thompson, 2005; Daniels

et al., 2006; Klaus *et al.*, 2006) for a close affinity between *Seychellum* and any Indian freshwater crab genus in the Gecarcinucidae, despite the fact that these taxa all share a bilobed mandibular palp (Bott, 1970b). Moreover, enforcing monophyly of *Seychellum* and the Oriental Gecarcinucidae genera resulted in a statistically worse topology, and the idea that *Seychellum* is more closely related to the Indian genera than to other members of the Deckeniinae can be rejected with confidence (Daniels *et al.*, 2006).

SUBTRIBE GLOBONAUTINA BOTT, 1969

Type genus: *Globonautes* Bott, 1959, by original designation.

Diagnosis: Members of the Globonautina are recognized by a distinctly bilobed mandibular palp with a large (subequal) anterior lobe and by the lack of a flagellum on the exopod of the third maxilliped (Cumberlidge, 1999).

Distribution: West Africa (Guinea, Liberia, Sierra Leone) (Figs 2, 5B).

Remarks: There is no doubt that *Globonautes* and *Afrithelphusa* are closely related to each other based on strong morphological (Cumberlidge, 1999) and molecular (Klaus *et al.*, 2006) evidence. *Globonautes* and *Afrithelphusa* from West Africa were formerly assigned to the subfamily Globonautinae (Gecarcinucidae) (Bott, 1969, 1970a, b). The morphological cladistic analysis carried out by Cumberlidge (1999) resulted in an equivocal assignment for *Globonautes* and *Afrithelphusa* and the Globonautinae was listed in that work as an uncertain subfamily, and doubtfully allied to the Gecarcinucidae. The Globonautinae is here lowered in rank from subfamily to subtribe following the transfer of *Globonautes* Bott, 1959; the type genus of the Globonautinae from the Gecarcinucidae to the Deckeniinae (Potamonautidae).

BIOGEOGRAPHICAL IMPLICATIONS

The consensus phylogeny (Fig. 2) provides support for the recognition of all 20 freshwater crab genera that are currently known from the Afrotropical region. The present day distribution of the genera from the Afrotropical region (Fig. 5A, B) is broadly summarized in Table 2.

According to the molecular clock estimates of Daniels *et al.* (2006) the common ancestor of the potamonautid freshwater crabs entered African inland waters during the upper Cretaceous about 78 Mya. These crabs subsequently radiated throughout the

entire continent dividing over time into two distinct evolutionary lineages, recognized here as the Potamonautinae and the Deckeniinae. The phylogenetic studies indicate that the taxa found on some of the ancient continental islands of the Seychelles and Madagascar have their closest affinities with ancestral deckeniines rather than with the potamonautines (or the gecarcinucids). Similarly, the two genera found on Socotra are not part of this main African potamonautid freshwater crab radiation and have affinities with the Palaearctic and Oriental Potaminae (Apel & Brandis, 2000; Cumberlidge & Wranik, 2002; Yeo & Ng, 2003).

Over time, the Deckeniinae separated into two lineages, the Deckeniini (*Globonautes*, *Afrithelphusa*, *Deckenia* and *Seychellum*) and the Hydrothelphusini (all Malagasy genera). The Deckeniini were presumably once widely dispersed across Africa but, today, they are represented by only a few species that survive in marginal habitats in the Upper Guinea forests of West Africa, the marshy freshwater wetlands of coastal East Africa, and the small rivers of the granitic Seychelles in the Indian Ocean. The Deckeniini in East and West Africa live alongside the more widely distributed and abundant species that belong to the other great African lineage, the Potamonautinae. Madagascar, the Seychelles, and India split from Africa over 160 Mya (Rabinowitz, Coffin & Falvey, 1983), which means that the ancestors of *Seychellum* must have crossed the Indian Ocean separating East Africa from the Seychelles islands (perhaps on driftwood accidentally carried by ocean currents). Similarly, the common ancestor of the Malagasy Hydrothelphusini crossed the ocean between mainland Africa and Madagascar during the Oligocene approximately 44 Mya according to Daniels *et al.* (2006).

There is no phylogenetic evidence (either morphological or molecular) to justify the inclusion of any Afrotropical freshwater crab taxa in the Gecarcinucoidea. Specifically, we can find no support for the idea that any of the Afrotropical taxa with a bilobed mandibular palp that were formerly assigned to the Gecarcinucidae (*Globonautes*, *Afrithelphusa*, *Seychellum*, *Malagasya*, and *Hydrothelphusa*) are closely allied to any Oriental taxa. For example, the Indian gecarcinucid genera with a bilobed mandibular palp and the bilobed Afrotropical genera (*Globonautina*) are each part of distinct groups positioned on different parts of the phylogenetic tree (Daniels *et al.*, 2006; Klaus *et al.*, 2006).

The inclusion by Klaus *et al.* (2006) of some Afrotropical genera in the Gecarcinucoidea (as their Deckeniidae) and other Afrotropical genera in the Potamoidea (as their Potamonautidae) makes both of these superfamilies paraphyletic (Fig. 4) and, as such,

devalues their usefulness for biogeographical theorizing. Indeed, the totality of the morphological and molecular evidence suggests that the Gecarcinucoidea as revised here (Fig. 4) is an exclusively Oriental taxon that most likely arose somewhere else other than Africa, Madagascar, and the Seychelles. This casts doubt on the assertion by Klaus *et al.* (2006) that Africa was the centre of origin of the Gecarcinucoidea and eliminates the need to posit elaborate scenarios for the dispersal of freshwater crabs across the Indian Ocean separating the Seychelles from India (Klaus *et al.*, 2006). The present conclusions (i.e. that the Potamonautidae is an exclusively Afrotropical family, and that the Gecarcinucidae is a wholly Oriental taxon with no Afrotropical members) are based on independent phylogenetic studies and require fewer assumptions about long-distance dispersal across saltwater barriers to explain the present day distribution patterns of these exclusively freshwater decapod crustaceans.

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