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Insular species of Afrotropical freshwater crabs (Crustacea: Decapoda: Brachyura: Potamonautidae and Potamidae) with special reference to Madagascar and the Seychelles

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Abstract

The evolutionary relationships between island and mainland faunas of the 24 species of insular freshwater crabs in the Afrotropical region are reviewed in the light of phylogenetic studies. Twenty insular species of freshwater crabs are endemic, and four are also found on the neighboring mainland of Africa. The Atlantic Ocean islands of Sherbro, Bioko, Príncipe, and São Tomé support five species of Potamonautidae, while the Western Indian Ocean islands of the Seychelles, Zanzibar, Pemba, Mafia, and Madagascar together have 16 species of Potamonautidae, and Socotra has three species of Potamidae. Disjunct distributions of non-endemic insular species of Afrotropical freshwater crabs with conspecifics on the mainland are the result of past lower sea levels that once united islands with the coast. The presence of endemic species of freshwater crabs on oceanic volcanic islands (such as Príncipe and São Tomé) separated from the mainland by deep seas is probably the result of transoceanic dispersal. Endemic genera of freshwater crabs found on oceanic 'Gondwanan' islands are derived from ancestral populations on the Eurasian (Socotra) or African (The Seychelles and Madagascar) mainlands that probably reached there by transoceanic dispersal, rather than their being the vicariant descendents of Gondwanan ancestors. Species of freshwater crabs found on islands in the Afrotropical region are either not unique, or are endemic at the species or genus level. The degree of endemism depends on the island's geological history: whether it is part of the continental shelf, an oceanic island of volcanic origin, or a former part of the ancient continent of Gondwana.

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Introduction

Freshwater crabs (Potamidae, Potamonautidae, Gecarcinucidae, Parathelphusidae, Pseudothelphusidae, Trichodactylidae) are a group of more than 1,280 species that comprises the largest group within the Brachyura according to the latest assessment (Ng *et al.*, 2008). Freshwater crabs have a global distribution that includes not only the tropical and subtropical inland waters of the major continents but also many dozens of islands, some of which (such as the Seychelles and Madagascar) are located considerable distances from the mainland and are separated by deep oceans (Yeo *et al.*, 2008). Monophyly of each of the families of freshwater crabs and continent-wide regional distributions make the freshwater crabs useful subjects for testing dispersalist versus vicariant biogeographic hypotheses because their range was achieved despite their limited ability to disperse long distances overland in their natural habitat. In addition, deserts, high mountain ranges, cold waters, and saltwater habitats are all significant barriers to freshwater crab distribution.

Limits to the dispersal of freshwater crabs within their natural habitats (rivers, streams, marshes, and lakes) arise from their adaptations to life in fresh water that include direct development, a reproductive strategy that lacks all free-living larval stages (Cumberlidge, 1999). Their marine crab relatives have no such limits because they produce thousands of eggs and free-swimming larval stages that are carried over long distances by ocean currents. The life cycle of freshwater crabs therefore

precludes long-distance dispersal and restricts them to the much more limited excursions made by adults within their habitats in the inland waters of continents (Ng and Rodriguez, 1995). Other factors that limit dispersal by freshwater crabs include the inability of those fully aquatic species that live in major rivers and lakes to move between river basins because they cannot survive for long out of water. Semi-terrestrial species of freshwater crabs are not limited in this way and could potentially migrate between river basins because they can breathe air as well as water and can live out of water for extended periods. However, semi-terrestrial species are limited in their dispersal and choice of habitat by their inability to tolerate prolonged submersion in deep water such as might occur in major rivers and lakes (Rodriguez, 1986). Perhaps the greatest limitation to dispersal by freshwater crabs is the fact that these strictly fresh water crustaceans are salt-intolerant and are never found naturally either in sea water or in brackish water (Cumberlidge, 1999). Despite these limitations freshwater crabs are nevertheless found throughout the inland waters of the continents and on numerous tropical islands around the world (Yeo *et al.*, 2008).

Afrotropical islands with freshwater crabs

The Afrotropical region is dominated by freshwater crabs of the Potamonautidae, a monophyletic family endemic to the Afrotropical region (Daniels *et al.*, 2006; Cumberlidge *et al.*, 2008). Islands in the Afrotropical region with freshwater crabs include those that are nearshore that were recently connected to the mainland, those that are volcanic in origin that rose up from the seabed, and those that were formerly part of the supercontinent of Gondwana. The islands off Africa differ in size, geological age, length of isolation, distance offshore, and depth of seas separating them from the mainland, as well as climate, latitude, landform, soils, and the direction of prevailing winds and currents. As a result island faunas and floras tend to be diverse and have high rates of endemism, especially large islands such as Madagascar that have been isolated for millions of years. Not all of Africa's islands have been colonized by species of freshwater crabs, but those that have possess a consistently warm and stable tropical climate.

Afrotropical freshwater crabs are found on sev-

eral islands in the Western Indian Ocean (Socotra, Seychelles, Zanzibar, Pemba, Mafia, and Madagascar) and comprise three species of Potamidae and 16 species of Potamonautidae. Another five species of Potamonautidae are found on West African islands in the Atlantic Ocean (Sherbro, Bioko, Príncipe, and São Tomé). A total of 20 insular species in the Afrotropical region are endemic, while four are also found on the neighboring mainland of Africa (Fig. 1, Table 1).

Socotra has three species, *Socotra pseudocardisoma* (Cumberlidge and Wranik, 2002), *Socotrapotamon socotrensis* (Rathbun, 1904), and *S. nojidensis* Apel and Brandis, 2000 (Potamidae: Potaminae). The granitic islands in the Seychelles host one species, *Seychellum alluaudi* (Bouvier, 1898) (Potamonautidae: Deckeniinae), and Zanzibar, Pemba, and Mafia host one species, *Potamonautes obesus* (A. Milne-Edwards, 1868) (Potamonautidae: Potamonautinae). The largest island in the Western Indian Ocean, Madagascar, has the most diverse freshwater crab fauna comprising 14 species of potamonautids (Ng and Takeda, 1994; Cumberlidge *et al.*, 2002; Cumberlidge and Sternberg, 2002; Cumberlidge *et al.*, 2004; Reed and Cumberlidge, 2006a; Daniels *et al.*, 2006; Cumberlidge *et al.*, 2008). The Atlantic Ocean side of Africa has insular species of potamonautine Afrotropical freshwater crabs on Bioko (*Sudanonautes granulatus* (Balss, 1929) and *S. floweri* (de Man, 1901)), Príncipe (*Potamonautes princeps* (Cumberlidge, Clark and Baillie, 2002)), and São Tomé (*P. margaritarius* (Rathbun, 1904)). In addition, Sherbro Island near the coast of Sierra Leone is home to one species, *Afrithelphusa leonensis* (Cumberlidge, 1987) (Potamonautidae: Deckeniinae).

Freshwater crabs are absent from the Cape Verde Islands, Annobon (Pagalu), the coralline Seychelles, the Comoros, Inacha, Mauritius, Rodrigues, and Réunion. The absence of freshwater crabs from Afrotropical islands can best be understood in terms of the island's size, age, and distance from the mainland. Most of the islands that lack freshwater crabs were never connected to the mainland and are either coralline or volcanic in origin; none are ancient fragments of Gondwana. For example, the volcanic island of Annobon (Equatorial Guinea) is 350 km offshore, small (only 17 km²), and young (4.8 My old). Similarly, the three remote islands in the colder South Atlantic (Tristan da Cunha, St. Helena, and Ascension) are all extremely far

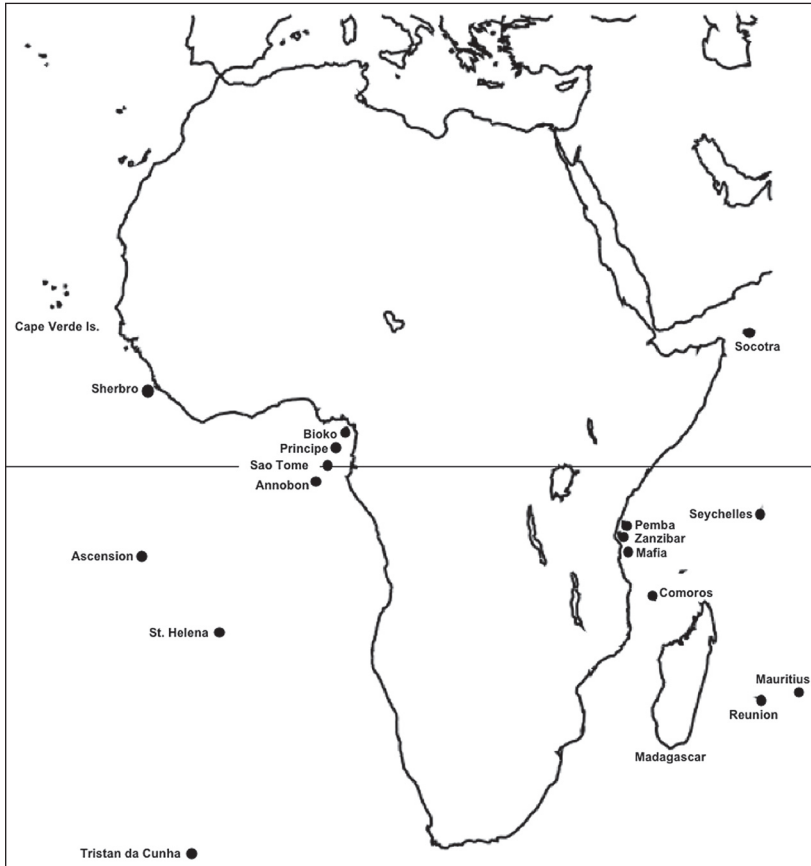


Fig. 1. Map showing the major islands in the Afrotropical region.

from the mainland, small in size, and surrounded by cold seas.

Continental islands

Freshwater crabs that occur on nearshore (continental shelf) islands that are separated from the mainland by relatively shallow seas are assumed to have reached there in the past (either in the Tertiary or Quaternary) at times when sea levels were more than 100 m lower than today, thereby uniting today's islands with the mainland. In such cases, there is no requirement for freshwater crabs to have crossed a sea water barrier to reach an island.

Sherbro island

Sherbro island (670 km²) (Sierra Leone) lies in the Atlantic Ocean 8 km off the coast of West Africa, and is separated from the mainland by the shal-

low waters of the Sherbro Strait. The disjunct distribution of the potamonautid freshwater crab *Afrithelphusa leonensis* on Sherbro island and on the nearby mainland in Sierra Leone undoubtedly reflects a relatively recent isolation event of this continental shelf island that can be attributed to past changes in sea level (Cumberlidge 1987, 1999).

Bioko

Bioko (2,017 km²) (Equatorial Guinea) is located in the Gulf of Guinea about 40 km from Cameroon, 100 km from southern Nigeria and 160 km northwest of continental Equatorial Guinea. This volcanic island has forested mountains (3,308 m asl), a recent history of connection to the mainland, and supports two species of freshwater crabs, *Sudanonautes floweri* and *S. granulatus*, neither of which is endemic (Cumberlidge, 1993, 1995, 1999). Today both of these species are distributed over a wide area of West and Central Africa that includes

Table 1. The major islands in the Afrotropical region and their freshwater crab fauna.

* endemic species; ** = endemic genus; # sp. = number of species.

Island	Origin Island	km ² Area	km Distance	# sp.	Family	Genus and Species
Madagascar	Gondwanan	590,000	400	14**	Potamonautidae	<i>Boreas uglovi</i>
Madagascar	Gondwanan	590,000	400		Potamonautidae	<i>Foza raimundi</i>
Madagascar	Gondwanan	590,000	400		Potamonautidae	<i>Hydrothelphusa agilis</i>
Madagascar	Gondwanan	590,000	400		Potamonautidae	<i>Hydrothelphusa bombetokensis</i>
Madagascar	Gondwanan	590,000	400		Potamonautidae	<i>Hydrothelphusa goudoti</i>
Madagascar	Gondwanan	590,000	400		Potamonautidae	<i>Hydrothelphusa madagascariensis</i>
Madagascar	Gondwanan	590,000	400		Potamonautidae	<i>Hydrothelphusa vencesi</i>
Madagascar	Gondwanan	590,000	400		Potamonautidae	<i>Madagapotamon humberti</i>
Madagascar	Gondwanan	590,000	400		Potamonautidae	<i>Malagasya antongilensis</i>
Madagascar	Gondwanan	590,000	400		Potamonautidae	<i>Malagasya goodmani</i>
Madagascar	Gondwanan	590,000	400		Potamonautidae	<i>Marojejy longimerus</i>
Madagascar	Gondwanan	590,000	400		Potamonautidae	<i>Skelosophusa eumeces</i>
Madagascar	Gondwanan	590,000	400		Potamonautidae	<i>Skelosophusa gollhardi</i>
Madagascar	Gondwanan	590,000	400		Potamonautidae	<i>Skelosophusa prolixa</i>
Seychelles	Gondwanan	454	480-1600	1**	Potamonautidae	<i>Seychellum alluaudi</i>
Socotra	Gondwanan	3625	400	3*	Potamidae	<i>Socotra pseudocardisoma</i>
Socotra	Gondwanan	3625	400		Potamidae	<i>Socotrapotamon socotrensis</i>
Socotra	Gondwanan	3625	400		Potamidae	<i>Socotrapotamon nojiensis</i>
Zanzibar	Continental	1660	35	1	Potamonautidae	<i>Potamonautes obesus</i>
Mafia	Continental	394	48	1	Potamonautidae	<i>Potamonautes obesus</i>
Pemba	Continental	984	56	1	Potamonautidae	<i>Potamonautes obesus</i>
Bioko	Continental	2017	40	2	Potamonautidae	<i>Sudanonautes granulatus</i>
Bioko	Volcanic	2017	40		Potamonautidae	<i>Sudanonautes floweri</i>
Principe	Volcanic	128	250	1*	Potamonautidae	<i>Potamonautes principe</i>
Sao Tome	Volcanic	836	300	1*	Potamonautidae	<i>Potamonautes margaritarius</i>
Sherbro	Continental	670	8	1	Potamonautidae	<i>Afrithelphusa leonensis</i>
Rodrigues	Volcanic	108	1900	0	No FWC	No FWC
Réunion	Volcanic	5500	1500	0	No FWC	No FWC
Cape Verde Is.	Volcanic	4000	500	0	No FWC	No FWC
Mauritius	Volcanic	1865	1900	0	No FWC	No FWC
Comoros	Volcanic	1862	500	0	No FWC	No FWC
Tristan da Cunha	Volcanic	201	2816	0	No FWC	No FWC
Aldabra	Volcanic	155	600	0	No FWC	No FWC
St. Helena	Volcanic	122	2720	0	No FWC	No FWC
Ascension	Volcanic	90	1700	0	No FWC	No FWC
Annobon	Volcanic	17	350	0	No FWC	No FWC

the neighboring lowland coastal regions of Nigeria, Cameroon, Equatorial Guinea and Gabon (Cumberlidge 1999). These two species may have reached Bioko overland at a time when sea levels were lower and this island was united with the mainland.

Zanzibar (*Unguja*), Mafia, and Pemba

A single species of potamonautid, *Potamonautes obesus*, is found on the islands of Zanzibar, Mafia, and Pemba (Tanzania) and across a wide area of East Africa that includes the lowland coastal re-

gions of Somalia, Kenya, Tanzania, and Mozambique (Reed and Cumberlidge, 2006b). Zanzibar (1,660 km²) and Mafia (394 km²) are nearshore continental shelf islands that lie 35 km and 48 km respectively from the coast of Tanzania. Today they are separated by shallow seas but in the recent past they were connected to the mainland of Africa (50,000 years ago and again 10,000 years ago) (Kingdon, 1989). It is likely that the ancestors of *P. obesus* may have reached Zanzibar and Mafia at a time when low sea levels permitted overland dispersal. Pemba (984 km²) the third of the Tanzanian spice islands, is located 56 km off the coast and is

much older than the other Tanzanian islands, dating back to the Miocene; it is separated from the mainland continental shelf by an 800 m deep trench that is at least several million years old (Kingdon, 1989). The presence of *P. obesus* on Pemba (which would not have been connected to the mainland even in the Tertiary or Quaternary when sea levels were much lower than they are today) suggests possible transoceanic dispersal to this island perhaps by natural rafts.

Oceanic 'Gondwanan' islands

There is disagreement about the origins of freshwater crabs on oceanic islands that were once part of Gondwana. Some authors have ruled out overseas colonization because saltwater has long been assumed to be an effective barrier to dispersal by freshwater crabs, and instead have proposed hypotheses that favored Gondwanan ancestry made disjunct today by Mid-Cretaceous vicariant events associated with continental break-up (Rodriguez, 1986; Ng *et al.*, 1995; Ng and Rodriguez, 1995). The long-held assumptions of Gondwanan ancestry and Indian affinities for freshwater crabs found on the Seychelles and Madagascar have been challenged recently by the molecular phylogenetic study of Daniels *et al.* (2006) that included genera from Africa, Madagascar, the Seychelles, India and Socotra (Cumberlidge *et al.*, 2008). This study, and that of Klaus *et al.* (2006), gave new insights into the relationships of the Afrotropical freshwater crabs found on the islands in the Indian Ocean. In addition, Daniels *et al.* (2006) provided new estimates of divergence times that were not congruent with the geological history of this part of Gondwana (whereby Madagascar-Seychelles-India split from Africa in the Mid-Cretaceous over 160 Mya) (Rabinowitz *et al.*, 1983). In summary, the majority of available evidence supports hypotheses that insular species of freshwater crabs on oceanic islands in the Afrotropical region reached their present distribution by transoceanic dispersal rather than vicariance (Daniels *et al.*, 2006; Cumberlidge *et al.*, 2008).

Socotra

Socotra (3,625 km²) (Republic of Yemen) lies in the Western Indian Ocean 350 km south of the Arabian peninsula, 400 km east of Somalia, and 1,600 km

north of the Seychelles and is separated from nearby landmasses by deep seas. The Socotra archipelago comprises the main island and three smaller islands, and has mountains that reach 1,525 m asl. Socotra is an African Gondwanan continental fragment that is part of the Afrotropical region, and has experienced a long period of geological isolation. Socotra's fauna and flora are generally more closely linked with Africa than with the Arabian peninsula, but this is not the case for the island's endemic freshwater crab fauna which have Palaearctic rather than Afrotropical affinities (Daniels *et al.*, 2006; Cumberlidge *et al.*, 2008). Interestingly, the two potamid genera found on Socotra are not part of the main African potamonautid freshwater crab radiation and morphological studies place their affinities with the Palaearctic and Oriental Potaminae (Apel and Brandis, 2000; Cumberlidge and Wranik, 2002; Yeo and Ng, 2003). Interestingly, the molecular study of Daniels *et al.* (2006) contradicts this assumption, and positions *Socotra* close to *Johora tiomanensis* (Ng and Tan, 1984) from Palau Tioman, Malaysia and *Geothelphusa albogilva* (Shy, Ng and Yu, 1994) from Taiwan (both Potamiscinae). The presence on Socotra of three endemic species and two endemic genera of potamid freshwater crabs (*Socotra pseudo-cardisoma*, *Socotrapotamon socotrensis*, and *S. nojiddensis*) that belong to a Eurasian family is most likely the result of dispersal to the island either from the Middle East (if Potaminae) or from southeast Asia (if Potamiscinae). Overseas rafting is a possible route of transportation to Socotra from either one of these mainland centers, while Apel and Brandis (2000) have argued for overland dispersal via the Middle East to Socotra at a time when the region was much less arid.

The Seychelles

The Seychelles are a group of more than a hundred granitic and coralline islands, cays, and atolls in the Indian Ocean that extend between 160 and 1,300 km north of Madagascar, 480 and 1,600 km east of Africa (Tanzania, Kenya, and Somalia), and some 3,000 km from India. The long isolation of the Seychelles (75 million years) and the great distance from the mainland has resulted in a highly endemic flora and fauna that includes *Seychellum alluaudi* a morphologically unique genus and species of freshwater crab (Ng *et al.*, 1995). This species is found only on the four largest granitic Gondwanan islands

(Mahé, Praslin, Silhouette and La Digue) (with a combined area of only 454 km²) that lie 1,600 km off the coast of Africa, and it is absent from the more recent but still isolated coralline Seychelles islands (Ng *et al.*, 1995). The presence of the same species of freshwater crab on these four remote islands in the Seychelles is probably the result of their more recent isolation from each other by present day high sea levels. Until recently, the granitic Seychelles consisted of a much larger Gondwanan landmass (55,000 km²) known as the Seychelles Bank, when past sea levels were more than 100 m lower than at present. Today most of this land is submerged and only the terrestrial communities on the hilltops (where *Seychellum* is found) survived, presumably because the higher elevations remained above the surface when the oceans rose to their present levels.

How *Seychellum* came to be on the Seychelles in the first place has been the subject of disagreement over the years. Authors that discount the possibility of oceanic dispersal by freshwater crabs (Rodriguez, 1986; Ng *et al.*, 1995; Ng and Rodriguez, 1995) have explained the presence of these decapods on the Seychelles by simple vicariance, arguing that freshwater crab ancestors already lived on this part of Gondwana before it fragmented. On the other hand, the morphological and molecular evidence that can now be brought to bear over the question of the origins of *Seychellum* favors accidental overseas dispersal over vicariance (Daniels *et al.*, 2006; Cumberlidge *et al.*, 2008). For example, the closest affinities of *Seychellum* are with ancestral East African Deckeniinae rather than with African Potamonautinae or Indian Gecarcinucidae (Daniels *et al.*, 2006; Klaus *et al.*, 2006; Cumberlidge *et al.*, 2008). The phylogenetic relationships between Seychellian freshwater crabs and those from Madagascar, Africa, and India therefore do not fit the temporal framework of Gondwanan fragmentation in the Mesozoic whereby Madagascar-Seychelles-India split first from Africa, followed millions of years later by the break-up of the Seychelles and India. In addition, the divergence time estimates for the Afrotropical clade (78.6-75.03 Mya), the *Seychellum/Deckenia* clade (75 Mya), and the Malagasy clade (43.5-39 Mya) indicate Upper/Late Cretaceous or Eocene origins for these lineages (Daniels *et al.*, 2006) that are not congruent with the dates for continental break-up. The fact that *Seychellum* and *Deckenia* (East Africa) today occur on opposite sides of a

deep oceanic barrier argues for overseas dispersal rather than vicariance. The common ancestor of these two genera was presumably living on the African mainland (where *Deckenia* still occurs) (rather than Madagascar or India) and was carried to the Seychelles by accidental transoceanic dispersal. The distance between the coast of Africa and the granitic Seychelles today is about 1,600 km, but this would have been considerably shorter in the Upper/Late Cretaceous.

Madagascar

Madagascar (590,000 km²) today lies about 400 km from the east coast of southern Africa (Mozambique) and became separated from Africa 165-121 Myr ago and from the Seychelles and India 88-63 Myr ago (Rabinowitz *et al.*, 1983; Storey *et al.*, 1995). The long period of isolation of Madagascar's original Gondwanan fauna together with additions by dispersal events over the years have produced a unique endemism on this island that includes an impressive number of species of freshwater crabs. The seven endemic genera and fourteen endemic species of Malagasy freshwater crabs are unevenly distributed on the island and are most diverse in Antsiranana Province in northern Madagascar, an area with both dry and moist forests that includes the Tsaratanana and Marojejy mountains (Ng and Takeda, 1994; Cumberlidge and Sternberg, 2002; Cumberlidge *et al.*, 2004; Cumberlidge *et al.*, 2005; Reed and Cumberlidge, 2006a; Daniels *et al.*, 2006; Cumberlidge *et al.*, 2008). The tropical rainforest on the mountainous eastern side of the island has a lower freshwater crab species diversity, while crabs are completely absent from vast areas the island on the western side (where the vegetation consists of dry deciduous forests) and in the far south (which is arid spiny desert) (Cumberlidge *et al.*, 2004).

The fourteen species of Malagasy freshwater crabs are so striking in their morphological variety that they have been assigned to seven genera (Cumberlidge *et al.*, 2000; Cumberlidge and Sternberg, 2002; Reed and Cumberlidge, 2006a; Cumberlidge *et al.*, 2008). They are also sufficiently morphologically divergent from the freshwater crab fauna elsewhere in the Afrotropical region to have been assigned to two different families by some authors (Bott, 1960, 1965, 1969a, 1970a; Ng *et al.*, 1995). These authors argued that the Malagasy freshwater crabs comprised two separate lineages, one group

with supposedly African affinities that they placed in the Potamonautidae, and the other group with supposedly Indian and Seychellian (Gondwanan) affinities that they placed in the Gecarcinucidae. This arrangement meshed with the view that it was the fragmentation of the Gondwanan supercontinent that carried the freshwater crabs to their present position on Madagascar and not transoceanic rafting (Bott, 1960, 1965; Ng *et al.*, 1995; Ng and Rodríguez, 1995). Vicariance hypotheses require that freshwater crabs found on Gondwanan continental fragments have phylogenetic relationships that are congruent with a shared history of continental break-up. However, this two-family hypothesis for the Malagasy freshwater crabs was not supported by the morphological study of Cumberlidge and Sternberg (2002), or by the molecular study of Daniels *et al.* (2006), which both concluded that all Malagasy taxa form a single monophyletic lineage that was part of the African Potamonautidae (Cumberlidge *et al.*, 2008). Daniels *et al.* (2006) identified the sister group of the Malagasy freshwater crabs to be a clade consisting entirely of African genera that were included in the African Potamonautidae by Cumberlidge and Sternberg (2002) and Cumberlidge *et al.* (2008). The consensus phylogeny (based on molecular and morphological evidence) is not congruent with the affinities predicted by Gondwanan break-up, and supports African origins for the Malagasy freshwater crabs (Daniels *et al.*, 2006; Cumberlidge *et al.*, 2008). In addition, the molecular divergence estimates provided by Daniels *et al.* (2006) indicated that the Malagasy freshwater crabs diverged from their African relatives about 43.5–39 Mya, long after the separation of Madagascar from Africa. The available data indicate that the Malagasy freshwater crabs most likely descended from a transoceanic migrant from Africa during the Eocene (Palaeogene) when the distance between the coast of Africa and northwest Madagascar would have been considerably shorter than it is today (400 km).

Klaus *et al.* (2006) also proposed that freshwater crabs reached Madagascar and the Seychelles from Africa in the past by rafting across oceanic distances that were shorter than today, but they differed in their estimates of the timing of this event and in the way it may have happened. Klaus *et al.* (2006) argued that freshwater crabs reached these islands during the Oligocene 28 Mya when sea levels were 150–200 m lower than today and when significant portions of the continental shelves as well as the

Mascarene Plateau, Seychelles Bank, and Chagos/Laccadive Plateau were emergent. Klaus *et al.* (2006) also suggested that freshwater crabs may have reached Madagascar and the Seychelles from Africa indirectly by rafting via intervening small emergent islands and seamounts that served as ‘stepping stones’. Those authors further suggested that freshwater crabs in the Seychelles reached India via the Chagos/Laccadive Plateau during the Oligocene but this is considered unlikely here because Daniels *et al.* (2006) found no close relationship between any Afrotropical genera (Potamonautidae) and Indian and southeast Asian genera (representing the Gecarcinucidae and Parathelphusidae).

Oceanic volcanic islands

While there is more than one explanation (overseas dispersal or vicariant origins) for how freshwater crabs came to be on oceanic ‘Gondwanan’ islands, there is little debate about the presence of freshwater crabs on oceanic volcanic islands: it is assumed that crabs reached there by overseas dispersal. However, it would seem that large stretches of saltwater present a formidable, but not entirely impenetrable, barrier to freshwater crab dispersal.

Príncipe and São Tomé

The volcanic islands of Príncipe (128 km²) and São Tomé (836 km²) (São Tomé and Príncipe) lie 250 km and 300 km from the mainland and both have forested mountains that reach 948 and 2,024 m asl respectively. Príncipe rose out of the sea about 31 Mya (Oligocene), while São Tomé dates back to about 14 Mya (Miocene). The presence of an endemic species of potamonautid freshwater crab on each of these islands (*Potamonautes princeps* on Príncipe, and *Potamonautes margaritarius* on São Tomé) means that each species is the product of a separate dispersal event from the mainland, presumably by natural rafts. Colonization of each island separately is the most likely because there is no morphological evidence that these species are closely related to each other and therefore no reason to assume that there was any island-to-island transfer (the distance between the closest islands is 146 km). While both taxa are endemic at the species level, the genus is distributed widely not only in the nearby coastal countries but also throughout sub-Saharan

Africa (Cumberlidge, 1999; Cumberlidge *et al.*, 2002). Measey *et al.* (2007) have recently proposed that amphibians and other salt-intolerant animals found on oceanic islands in the Gulf of Guinea reached there by rafting aided by favorable surface currents and by surface waters of reduced salinity (rather than by storms, birds, or rafts alone). Those authors argued that low-salinity ‘freshwater paths’ in the surface layers of the ocean (formed either by catastrophic events or by wet periods in climatic history) lasted long enough to be capable of transporting salt-intolerant continental animals to isolated oceanic islands.

Transoceanic dispersal by freshwater crabs

It would seem that oceanic dispersal, rather than Gondwanan break-up and a simple vicariant history, produced present-day freshwater crab distributions on the three oceanic ‘Gondwanan’ islands in the Western Indian Ocean, and on the two volcanic islands in the Atlantic considered here. Island colonization preceded by accidental transoceanic dispersal of freshwater crabs to oceanic islands requires that these strictly freshwater decapods survive both periods of submergence in sea water and exposure out of water for two or more weeks. The fact that freshwater crabs are salt-intolerant and are never found naturally in saltwater habitats argues for their accidental displacement perhaps during storms violent enough to dislodge large masses of vegetation that would be carried down rivers and out to sea. Transoceanic dispersal would also require favorable ocean currents, and successful colonization on arrival would require the ability to establish viable populations in the freshwater ecosystems of the new island habitat.

A number of authors have offered their opinions on the physiological resistance of freshwater crabs to high salinity, and have concluded that in general gecarcinucoids are salt tolerant but that potamoids are not (Bott, 1969b, 1970b; Haig, 1984; Klauss *et al.*, 2006; Yeo *et al.*, 2008). However, there have been only a few actual studies on the physiological response of freshwater crabs to salt water and their survival times in different salinities, and those that are available contradict the above opinions. For example, experiments on species of Potamoidea from Africa and Europe demonstrated that freshwater crabs do indeed have the ability to osmoregulate in

brackish and full strength sea water, and that they can survive for between one to two weeks (Shaw, 1958a, b; Morris and Van Aardt, 1998). The recent comparative study of groups of potamids and parathelphusids from Thailand exposed to sea water for different periods of time found no major differences between these families in either survival time or osmoregulatory ability (Esser, 2007; Esser and Cumberlidge, in prep.).

Esser (2007) and Esser and Cumberlidge (in prep.) found that potamid and parathelphusid freshwater crabs are indeed capable of short-term survival for at least two weeks when exposed to sea water, which would be long enough to survive a short oceanic journey clinging to drifting vegetation. Indeed, many species of African freshwater crabs are semi-terrestrial, have well developed air-breathing capabilities, are resistant to desiccation, and do not require permanent submergence in fresh water (Cumberlidge, 1986, 1991, 1999). This is especially true for the majority of Deckeniinae that includes *Deckenia*, *Seychellum*, *Afrithelphusa*, and *Globonautes* plus the Malagasy genera, all of which have pseudolungs (Cumberlidge and Sternberg, 2002; Cumberlidge *et al.*, 2008). If adequately protected against desiccation, these animals are at least potentially capable of surviving for the relatively long periods away from fresh water involved in crossing distances of up to 500 km (Cumberlidge, 1986, 1991, 1999). A single ovigerous female freshwater crab landing on an island with freshwater ecosystems available would potentially be able to ensure a viable number of males and female offspring needed for successful colonization. This is because she typically carries between 200 and 500 fertilized eggs in her abdominal brood pouch, and because each egg eventually releases a hatchling crab without producing any of the free-living larval stages seen in marine crabs.

Transoceanic dispersal by rafting should be viewed as a rare and accidental occurrence in animals that avoid prolonged contact with sea water, despite the physiological ability of freshwater crabs to be able to withstand periods spent drifting on the open ocean clinging to vegetation, and then to be able to successfully colonize the new island habitat. Overseas dispersal by rafting has also been proposed to explain the origins of a range of vertebrates (amphibians, reptiles, and mammals) currently found on the Seychelles and Madagascar (Raxworthy, 2002; Vences *et al.*, 2003, 2004; Yoder *et al.*, 2003; Poux *et al.*, 2005; Yoder and Nowak, 2006).

Discussion

The origins of species of freshwater crabs found on continental and oceanic islands elsewhere in the world, such as the Neotropics (Rodríguez and López, 2003) and southeast Asia (Brandis, 2002), are comparable to the findings presented here for the Afrotropical region. For example, one species of Trichodactylidae (*Dilocarcinus dentatus* (Randall, 1839)) from Trinidad and four species of Pseudothelphusidae are present on continental islands in three areas of Central and South America (Rodríguez and López, 2003). The disjunct distributions of widespread species such as *Eudaniela garmani* (Rathbun, 1898) on Trinidad and Margarita Island as well as the Venezuelan mainland have been attributed to lower sea levels during the Pleistocene that united these islands with the coast. Similarly, the presence of the endemic species *Microthelphusa odaealcae* (Bott, 1970c) on Trinidad, and the endemic *Potamocarcinus roatanensis* on Roatan Island off the coast of Honduras have been attributed to prior land access during lowered sea levels in the Tertiary followed by isolation when sea levels returned to higher levels.

Six endemic species of pseudothelphusids are found on oceanic islands in the Caribbean (five species of *Epilobocera* on Cuba, Hispaniola, Puerto Rico, and La Croix) (Rodríguez and Williams, 1995), and *Guinotia dentata* (Latreille, 1828) in the Lesser Antilles islands of Guadeloupe, Dominica, Martinique, St. Lucia and St. Vincent (Rodríguez and López, 2003). Rodríguez (1986) viewed the presence of crabs on these oceanic islands to be the result of a primitive Gondwanan distribution made disjunct by Mid-Cretaceous vicariant events associated with continental break-up. Finally, the presence of the endemic *Hypolobocera gorgonensis* von Prael (1983) on Gorgona island off the Pacific coast of Colombia has been attributed to accidental dispersal through natural rafts because the island is separated from the mainland by a channel that is 200 to 1,000 m deep, which precludes a connection during minimal sea levels in the Quaternary (Rodríguez and López, 2003).

In southeast Asia the distribution patterns of species of Potamidae found on major continental islands of the Sunda shelf (e.g., Sumatra, Java, Borneo, the Philippines, Okinawa, Hainan) are thought to reflect the palaeogeographic and palaeoclimatic conditions of this region during the Tertiary and

Quaternary at times when low sea levels created land bridges between islands (Brandis, 2002). Similar conclusions were reached to explain the distribution patterns of species of potamid freshwater crabs found on islands in the Mediterranean (Brandis *et al.*, 2000).

In conclusion, species of freshwater crabs found on islands in the Afrotropical region (and elsewhere in the world) are either not unique, or are endemic at either the species or genus level. This in turn depends on the island's geological history: whether it is part of the continental shelf, an oceanic island of volcanic origin, or a former part of the ancient continent of Gondwana.

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