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The biogeography of Indo-West Pacific tropical amphipods with particular reference to Australia*

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Abstract

The extant distribution of amphipods in the tropical Indo-Pacific can be understood only by reference to the positions of shallow seas during the past two hundred million years. Amphipods attributable to extant families, even genera, were in existence in Mesozoic times. A number of amphipod families can be recognized as Gondwanan in origin, but Laurasian families, except in fresh waters, are more difficult to identify. The tropical amphipod fauna of Australia/New Guinea is thought to have evolved *in situ* until at least 15 Ma, when the continent reached proximity with Asia. Parsimony Analysis of Endemicity of Indo-Pacific amphipod families supports this hypothesis.

Key words: Crustacea, Amphipoda, Biogeography, Indo-West Pacific, Great Barrier Reef, Australia, biogeography

Introduction

Using the paradigm of ‘dispersal and founder principle’ to explain modern marine distributions, is not tenable (Myers 1994, 1996; Heads 2005). We must attempt to understand sequences of vicariant events in earth history, if we are to understand species distributions in tropical areas. Arguments have in the past been advanced that to understand the distribution of living species, events occurring millions or tens of millions of years ago should be discounted, because supposed speciation rates would mitigate against such long time scales. We now know that this argument is untenable. Roughgarden (1995) documents a fossil *Anolis* Daudin from the Dominican Republic, dated at 20 Ma or even 40 Ma, that is indistinguishable from living Hispaniola species. Within the Amphipoda, Weitschat *et al.* (2002) have described a corophioid amphipod from Oligocene amber that, while not attributable to a known species, appears to be entirely consistent morphologically with modern corophioid taxa (see Myers & Lowry 2003).

The distribution data presented here for amphipods, illustrate important biogeographic tracks that require documentation, regardless of the geological explanation hypothesised.

World distribution patterns of the Amphipoda

One of the most characteristic biogeographic features of shallow water marine organisms, including amphipods, is the distinctive difference between the tropical fauna of the Atlantic and that of the greater Indo-Pacific. In the Amphipoda, differences are mainly at specific level with a few at generic level. Atlantic

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endemics may have originated contemporaneously with the formation of the Atlantic around 120 Ma, but at minimum must have been isolated there with the formation of the Antarctic convergence at around 22 Ma. At that time, the tropical Atlantic was separated from the tropical Indo-Pacific, by closure in the north of the Tethys through the suturing of Africa/Arabia and by low tempertaures in the south as a result of cooling of the Southern Ocean when first the Antarctic Convergence and then the circum-Antarctic current were established. This would have cut off any southern route of entry into the Atlantic for tropical Indo-Pacific forms.

Amphipods lack any distinct dispersal phase and modern distributions are therefore good 'markers' of past earth history. Taxa that occur in both the northern and southern hemispheres indicate Pangaean distributions. Disjunct distributions point to previous area connectivity or extinctions of connecting populations.

Amphipod endemicity has been shown to parallel closely that of terrestrial plants (Myers 1997) and amphipod distributions likewise have many terrestrial plant similarities. A trans-Indo-Pacific-Caribbean distribution is, for example, shown by the plant angiosperm family Myoporaceae R. Brown (Fig. 1), and by the amphipod family Neomegamphopidae Myers (Fig. 1).

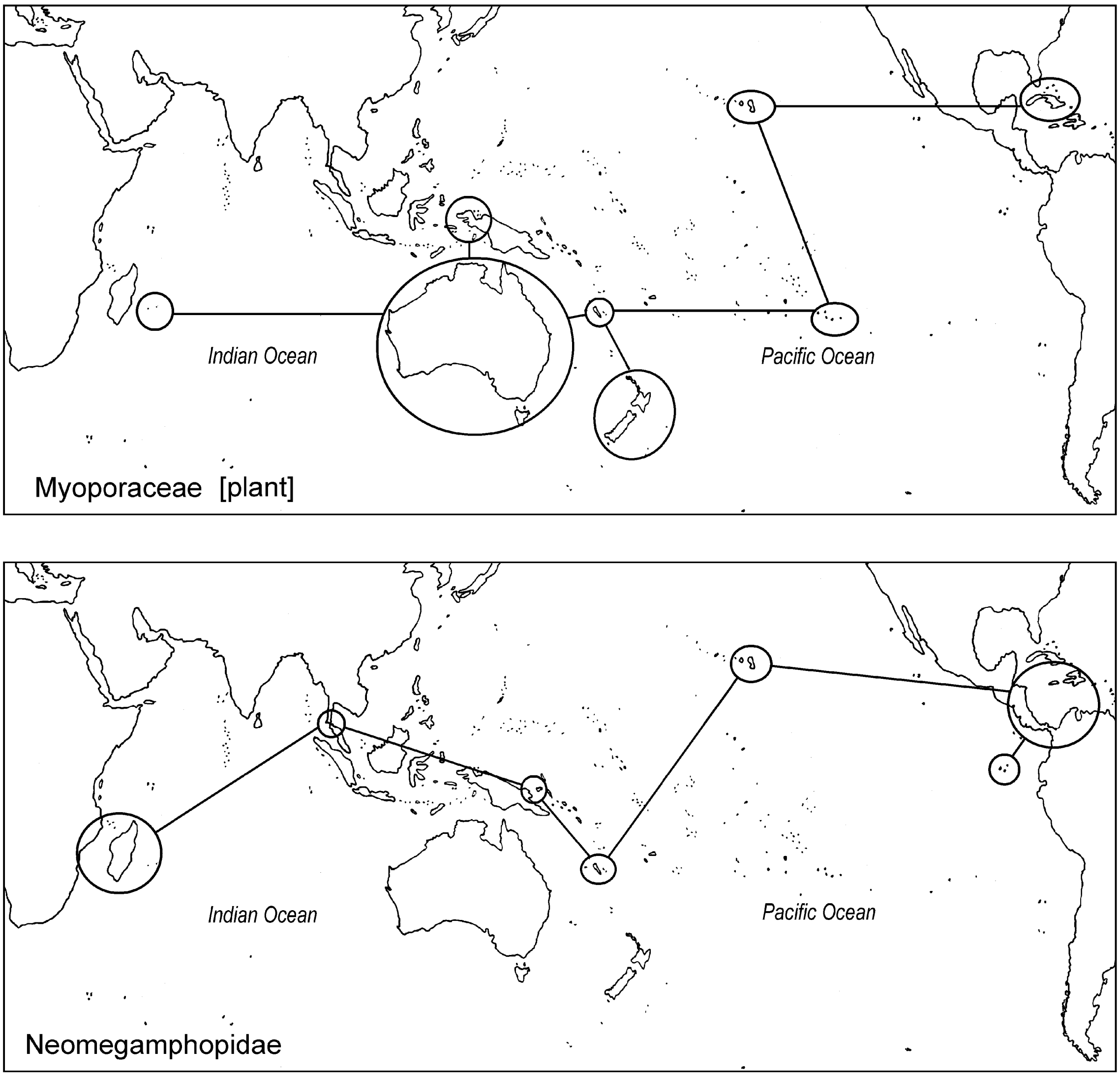

FIGURE 1. Distributions of A. The plant family Myoporaceae [plant - Angiospermae]; B. The amphipod family Neomegamphopidae.

A number of amphipod families are known only from the southern hemisphere and can therefore be assumed to be Gondwanan elements (Table 1), since Laurasian taxa would be expected to be restricted to the regions at or north of the Tethys seaway. Families ocurring in two or more Gondwanan areas must have had a common ancestor in Gondwana prior to breakup of that continent. The monotypic family Bolttsiidae Barnard & Karaman in fresh to brackish water in South Africa and in mangroves on the Great Barrier Reef, Australia (Fig. 2), is an example of a taxon with a distribution that is presumably derived from a common ancestor in Gondwana (paleoendemic). A parallel is shown by the plant genus *Cremocarpon* Baillon (Rubiaceae) that is known only from Madagascar and New Caledonia (Fig. 2). Twenty-nine families of amphipod are known only from Gondwana fragments (Table 1).

TABLE 1. Palaeoendemic amphipod families of probable Gondwana origin.

Family	India	S.Africa/	Madagascar	Australia	New Zealand	S. America	Antarctic/ sub Antarctic
Bolttsiidae		+		+			
Cardenioidae							+
Cheidae						+	
Chiltoniidae		+		+	+		
Clarenciidae							+
Condukiidae				+	+		
Dussartiellids*			+				
Falklandellids*						+	
Kotumsaridae	+						
Membrilopids*	+	+					
Neoniphargidae				+			
Pagetinidae							+
Paragammaropsidae							+
Paracrangonyctidae					+		
Paraleptamphopidae					+		
Paramelitidae		+		+			
Perthiidae				+			
Phoxocephalopsidae				+		+	
Plioplateidae		+					
Pseudamphilochidae						+	
Pseudingolfiellids*						+	+
Sanchoidae				+			
Sternophysingidae		+					
Temnophliantidae		+					
Tulearidae			+				
Urohaustoriidae				+		+	
Vicmusiidae				+			+
Wandinidae			+	+			
Zobrachoidae				+		+	

* *= Unformalised family*

By contrast it is difficult to recognise marine families of Laurasian (Laurentia + Eurasia) origin (Table 2). The large superfamily Gammaroidea (about 18 families) appears to be Laurasian being distributed across the entire northern hemisphere, principally in freshwaters but also in brackish and marine waters. It is absent from the southern hemisphere, apart from the enigmatic *Praefalklandella* Stock & Platvoet from the Falkland Islands that is considered a gammaroid only because it possesses gammarid-like calceoli which may be a homoplasy.

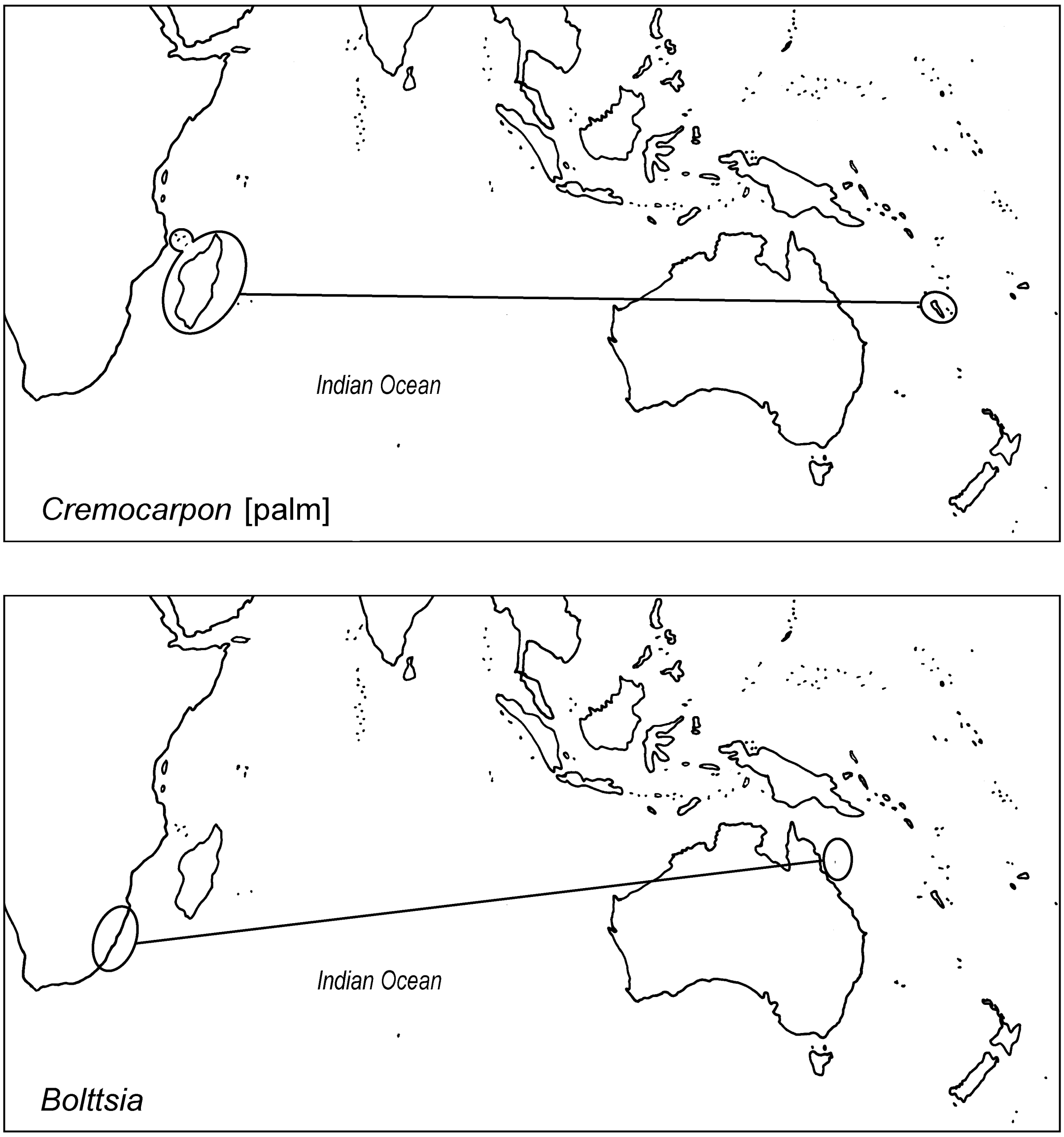

FIGURE 2. Gondwanan distributions of: A. *Cremocarpon* [plant - Rubiaceae]; B. *Bolttsia*.

TABLE 2. palaeondemic amphipod superfamily and families of probable Laurasia origin.

Taxon	N. Pacific	Europe/Med. Middle east	Asia	Indo-Malayia	China Seas	Japan
Gammaroidea	+	+	+			+
Niphargidae		+				
Cressidae		+				
Haustoriidae	+	+			+	
Lucioblividae						+
Priscomilitariidae					+	+
Sinurothoidae					+	

Freshwater or largely freshwater families in italics

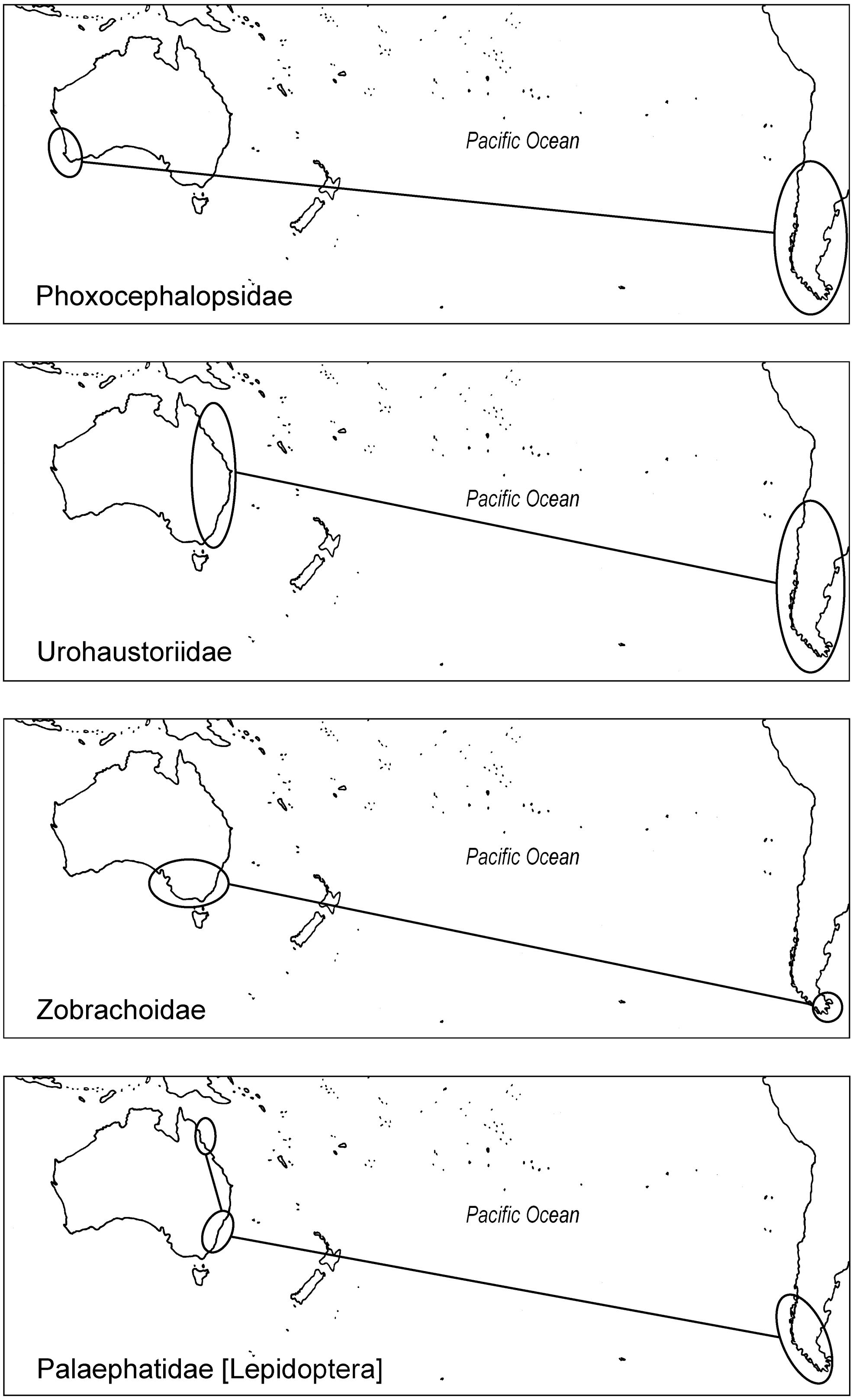

FIGURE 3. Trans-Pacific tracks of: A. Phoxocephalopsidae; B. Urohaustoriidae; C. Zobrachoidae; D. Palaephatidae [Lepidoptera].

There are a number of possible reasons why there are so few recogniseable Laurasian marine endemics. The Indo-Pacific tropical coasts of Eurasia were largely obliterated by the suturing of Gondwanan fragments. The African, Arabian and Indian plates now border much of the the northerly coasts of the Indian Ocean. Only the Eurasian plate shallow seas from the Gulf of Thailand to the Japan Sea represent the ancient southern coasts of tropical Eurasia, and even here the craton has accreted a number of allochthonous terranes. Amphipods living on southern Eurasian coasts would have become integrated with those of the arriving Gondwanan fragments thus greatly diminishing any hope that we might now recognise Laurasian endemics. Secondly, many of the Gondwanan endemics are still isolated on the Gondwanan fragments, whereas, few opportuinities remain for isolation along Eurasian coasts. The extant tropical Eurasian coastline between the Gulf of Thailand and the sea of Japan does still harbour a few endemic families that probably represent Eurasian palaeoendemics. These include the Priscomilitariidae and the Sinurothoidae.

Trans-Pacific tracks

Several amphipod families e.g. the Phoxocephalopsidae Barnard & Clark, Urohaustoriidae Barnard & Drummond and Zobrachoidae Barnard & Drummond (Fig. 3) have south Pacific distributions, occuring in South America and Australia. These distributions mirror those of other organisms such as the Lepidopteran family, Palaephatidae Davis (Fig. 3).

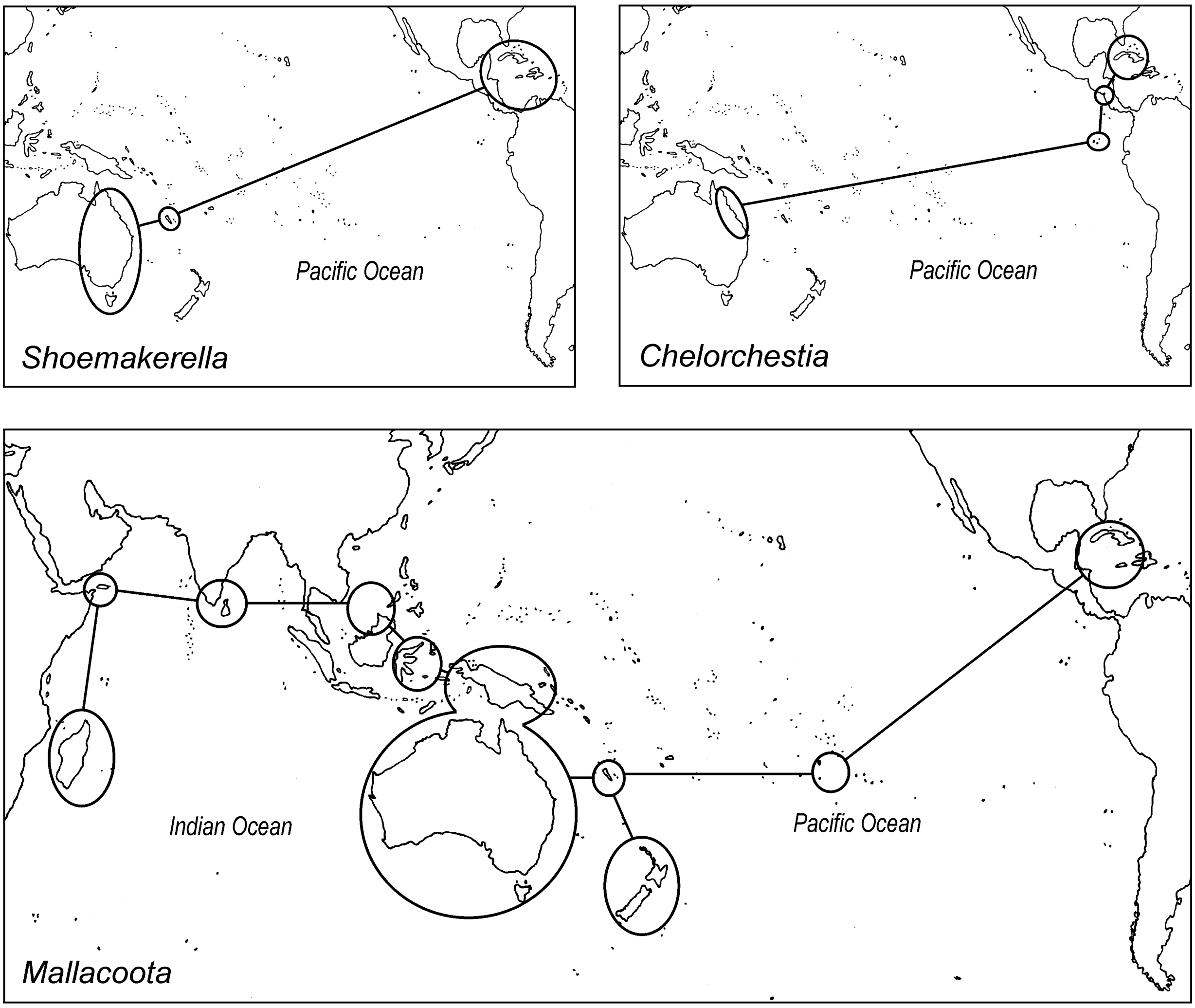

FIGURE 4. Trans-Indo-Pacific tracks of: A. *Shoemakerella*; B. *Chelorchestia*; C. *Mallacoota*.

Trans-Indo-Pacific-Caribbean tracks

A number of amphipod taxa show distributions which encompass the central Indo-Pacific and Caribbean. The family Neomegamphopidae Myers (Fig. 1), is distributed from East Africa to the Caribbean, including Malaysia, New Guinea, New Caledonia and Hawaii (but not Australia). This may be part of the broader track shown by the plant family Myoporaceae (Fig. 1), which also includes Australia, New Zealand and Japan. A number of amphipod genera, such as the semi-terrestrial talitrid *Chelorchestia* Bousfield, the marine maerid *Mallacoota* J. L. Barnard, the marine lysianassid *Shoemakerella* Pirlot (Fig. 4) and the oligohaline/freshwater sebid *Seborgia* Bousfield (see Holsinger, 1998) all fall within the generalised track of the Myoporaceae. In the mid Cretaceous, the new Pacific plate was small and the Ontong-Java and Gorgona plateaux were in place in the mid-Pacific. The distribution of, and longevity of, shallow seas on the Ontong-Java plateau is unknown, but fossil wood has been discovered there indicating the existence at some time, of emergent land (Meffre, Crawford & Quilty, 2007). According to Chicangana (2005) and Kerr & Tarney (2005), during the Cretaceous, the Ontong-Java plateau moved westwards and eventually accreted with the Solomons, while the Gorgona plateau moved north-East and collided with north-west South America/Caribbean at about 45 Ma. The Caribbean plateau, which formed in the vicinity of the present day Galapagos hot spot, collided with the proto-Caribbean arc and north-east South America around 80 Ma. These terrane movements may explain the distributions of amphipods such as *Shoemakerella* and *Chelorchestia* and particularly *Seborgia*, which is known only from Texas and from Rennell Island in the Solomon Islands.

Trans North Pacific tracks

The genera *Aoroides* Walker (Fig. 5). and *Pachynus* Bulycheva (Fig. 5) are found around the Pacific rim from North America to Japan, Indonesia, New Guinea and eastern Australia. *Aoroides* also occurs in Hawaii, but apparently nowhere else on the Pacific Plate. This distribution could be linked to allochthonous terranes which are found around the North American and Asian cratons. Hawaii has an anomalous amphipod fauna, with links to the eastern Pacific and Caribbean (Myers 1991). It is possible that the hotspot was overrun at some point in the past by a terrane, island arc, micro continent (Nur & Ben Avraham 1977) or basaltic plateau, although none has so far been identified.

Trans-Indian Ocean tracks

The families Bolttsiidae Barnard & Karaman (Fig. 2) and Wandinidae Lowry & Stoddart (Fig. 8), and the genera *Exampithoe* K.H. Barnard, *Wallametopa* J.L. Barnard (Fig. 6), and Unyapheonoides J.L. Barnard, exhibit trans-Indian Ocean distributions occurring in Africa/Madagascar and Australia/New Guinea. These amphipod taxa may belong to a generalised track which includes the plant genus *Dietes* (Iridaceae) which occurs in South Africa and on Lord Howe Island off Australia and the palm sub-family Ceroxyloideae Drude. This latter plant sub-family shows the same Madagascar-Australia distribution as *Exampithoe*, but continues across the Pacific to include Pacific South and Central America and the Caribbean (Fig. 6). Trénel et al. (2007), consider that Gondwanan vicariance is unlikely to be an explanation for basic disjunctions in the tribe Ceroxyleae and they propose alternative explanations, such as a mid-Tertiary trans-Atlantic/trans-African dispersal track or “lemurian stepping stones”. Any hypothesis of dispersal needs to explain how taxa with such different dispersal modes as terrestrial plants and marine amphipods could accomplish such congruent distribution patterns.

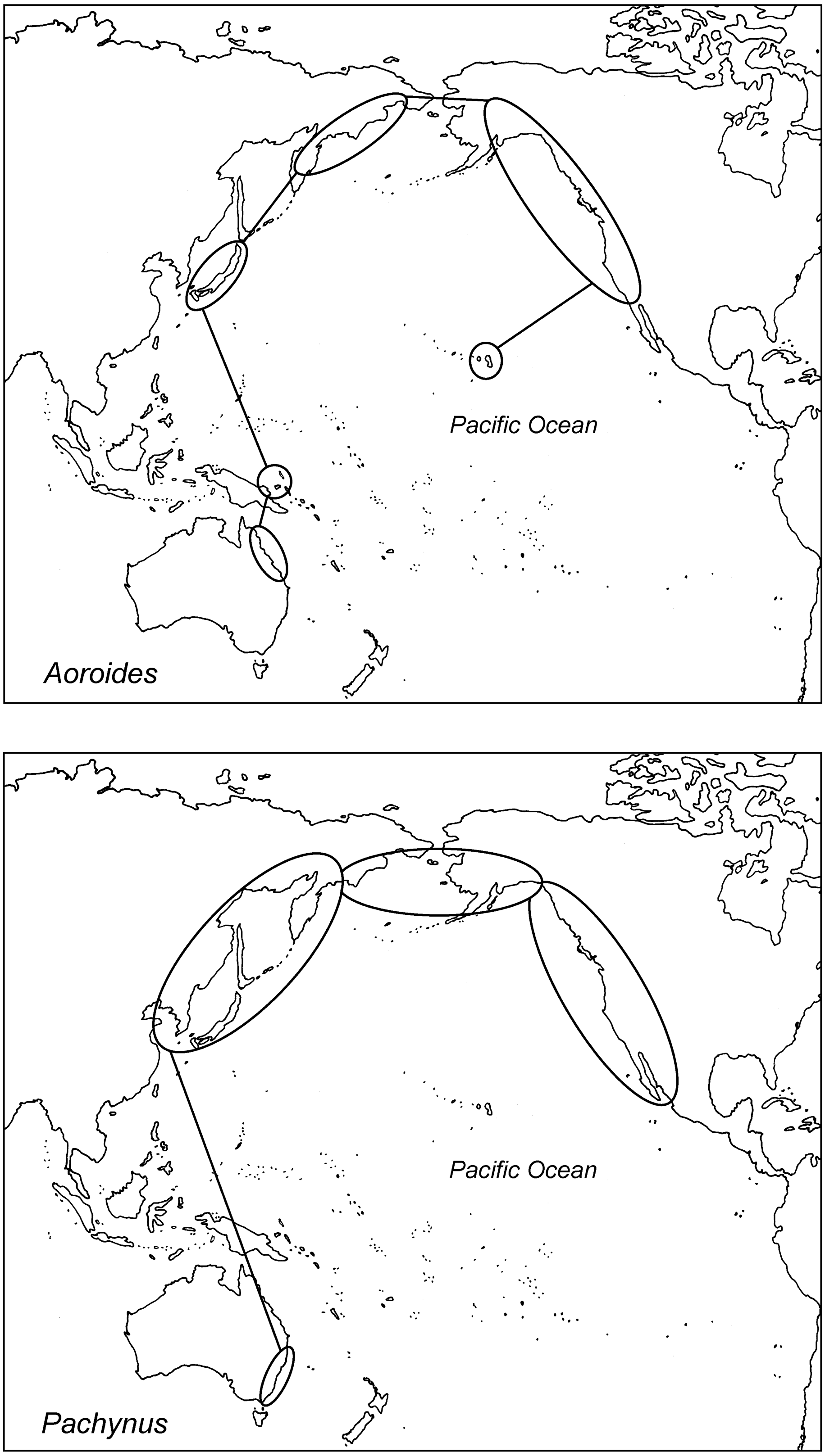

FIGURE 5. North Pacific rim distributions of: A. *Aoroides*; B. *Pachynus*.

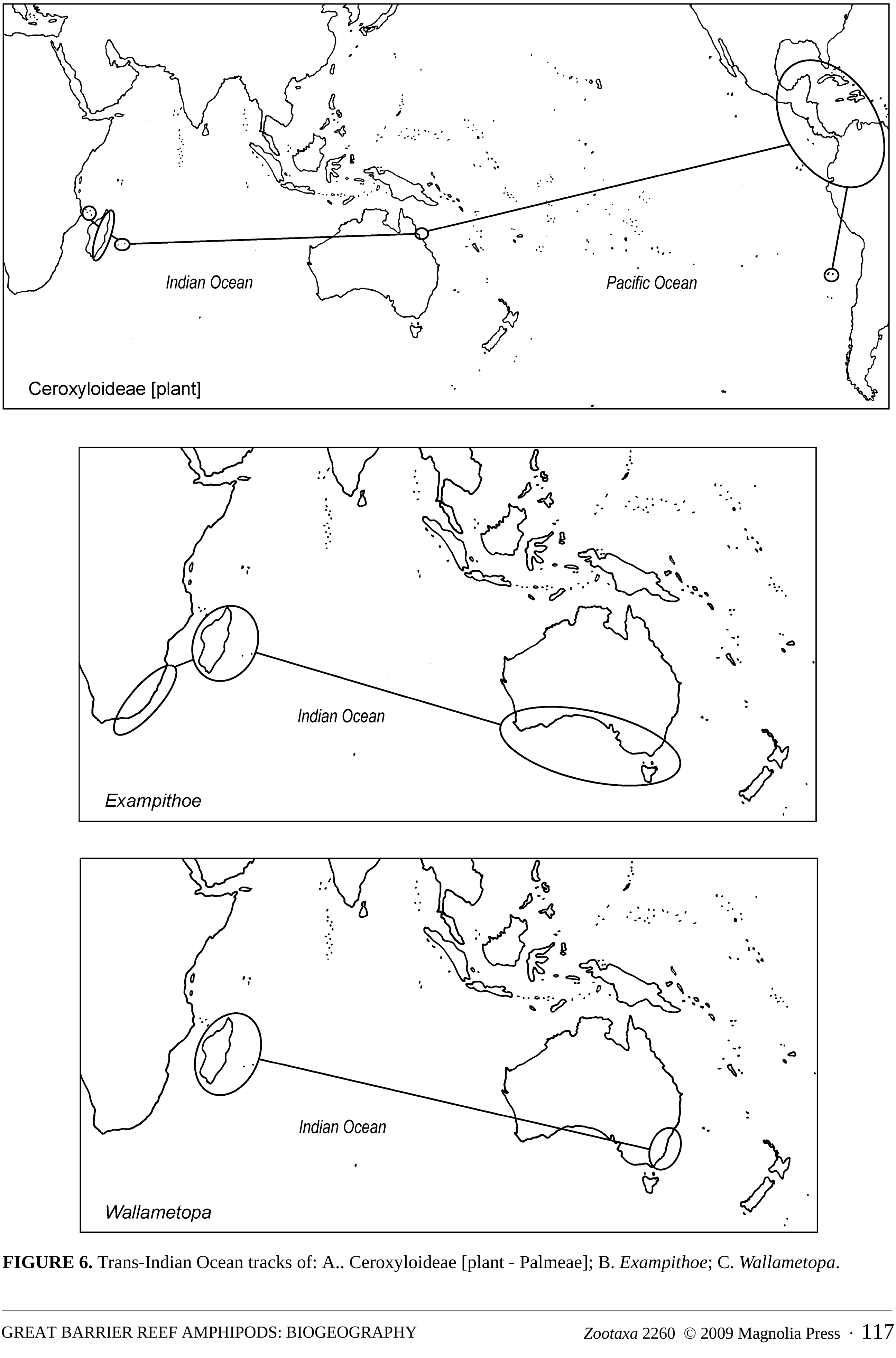

FIGURE 6. Trans-Indian Ocean tracks of: A.. Ceroxyloideae [plant - Palmeae]; B. *Exampithoe*; C. *Wallametopa*.

Palaeobiogeography of the Amphipoda

Early Jurassic.—200 Ma. Amphipods of modern appearance were well established and widespread around Pangaea. There was more or less shallow-water continuity between all the continents, but there is no reason to doubt that local endemism occurred. South-eastern and north-western coasts of Gondwana may, for example, have had different amphipod faunas. Ancestors of such genera as *Elasmopus* Costa, *Ampelisca* Kroyer and *Tryphosella* Bonnier, that are widespread in all oceans from the Arctic to the Antarctic, in the Atlantic, Pacific, Indian and Southern oceans today, probably originated at this time, somewhere around Gondwana.

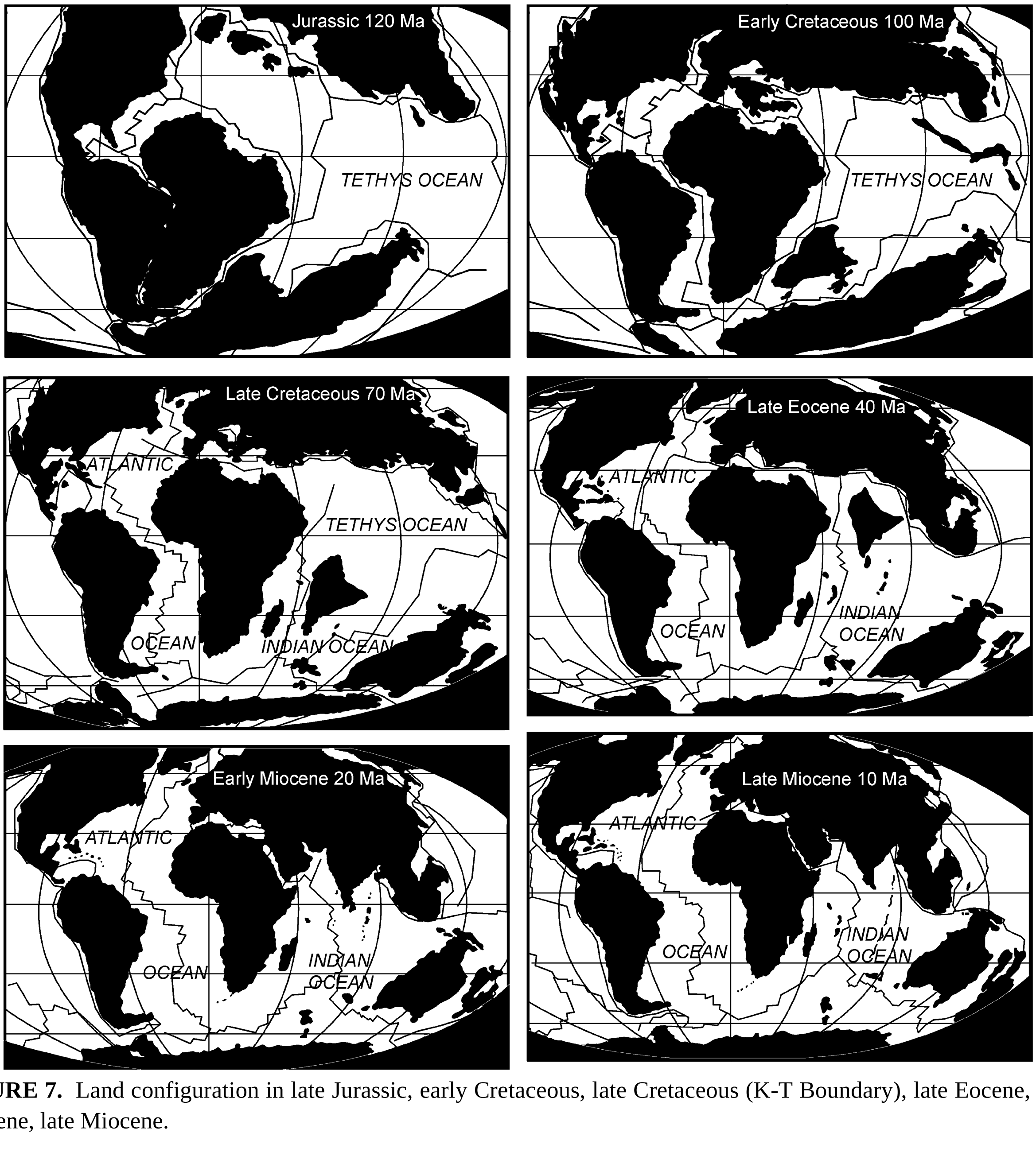

FIGURE 7. Land configuration in late Jurassic, early Cretaceous, late Cretaceous (K-T Boundary), late Eocene, early Miocene, late Miocene.

Late Jurassic.—150 Ma (Fig. 7). Pangea begins to rift apart, and amphipod genera start to differentiate in Gondwana and Laurasia, as the Tethys Sea develops between these two super-continents. A group of taxa with bicarinate urosomes (*Hoho* Lowry & Fenwick, *Ifalukia* J.L. Barnard, *Mallacoota* J. L. Barnard (Fig. 4) and *Parelasmopus* Stebbing Fig. 8) derived from a Pangean proto-*Elasmopus*, speciate in Gondwana. Today, *Mallacoota* (Fig. 4) is the most widespread of these genera. It occurs in Madagascar and Mauritius in the western Indian Ocean, at Abd-el-Kuri on the Arabian plate, in southern India, in the Nansha Islands in the

South China Sea, in Sulawesi, in Australia (including Lord Howe Island), in New Caledonia, in New Zealand, in Fiji and in Cuba and Brazil. *Parelasmopus* (Fig. 8) has a similar distribution to *Mallacoota,* except that it does not occur in New Zealand or in the Caribbean. It is not known from Fiji, but it does occur in Tonga. *Ifalukia* is known only from Ifaluk atoll in Micronesia, while *Hoho* is known only from New Zealand and south-east Australia. The mainly Gondwanan distribution of the these four taxa suggests that they may have started to evolve along the Gondwana shores of the Tethys, but if that is true, their occurrence in the South China Sea requires explanation. The greater geographic distribution and much higher species diversity in Gondwana than in Laurasia does not, *per se*, indicate origin, but, their occurrence in a number of isolated Gondwana fragments, does support an origin in Gondwana before the super-continent rifted. A Gondwana origin requires one range expansion into Laurasia, whereas a Laurasian origin requires multiple range expansions into isolated Gondwanan fragments. There is an anomaly in that their occurrence in widespread Gondwana fragments indicates that they evolved before the breakup of Gondwana (>100Ma) yet their absence from the Atlantic suggests that they evolved after the closure of the Tethys (<35 Ma). One explanation may be that they started to evolve on Gondwana shores before the breakup of Gondwana, moved northwards with the drifting fragments and by the time the fragments came into contact with shallow Laurasian seas, the tropical Atlantic had closed off. Shallow sea environments in the Mesozoic and early Tertiary were no more ‘uniform’ than they are today. Biogeographic barriers would have occurred everywhere and we cannot begin to know the extent of topographic and ecological factors that affected amphipod ranges in those times. All we can hypothesise with some support, is that if they occur today in what are now isolated shallow seas around New Zealand, and Madagascar, then they must have been in place in Gondwana before these areas separated. Why they did not apparently enter the Atlantic (more parsimonious than the hypothesis of total extinction of both of the two widespread genera) is probably related to historical biogeographic barriers at a scale too small to be discerned from this perspective of time. It would follow, from this hypothesis, that their occurrence in the South China Sea must be secondary and result from more recent range expansion.

Trans-Indian ocean genera such as *Bolttsia* Griffiths, found only in South Africa and Australia (Fig. 2), *Wallametopa* J.L. Barnard (Fig. 6) and *Unyapheonoides* J.L. Barnard found only in Madagascar and Australia and *Pseudocyphocaris* Ledoyer found only in Madagascar and Papua New Guinea, must also have been in existence before the formation of the Indian Ocean.

The family Maxillipiidae Ledoyer comprises two genera that live in association with gorgonacean corals and in seagrass beds. The genus *Maxillipius* Ledoyer occurs in Madagascar, Papua New Guinea, the Great Barrier Reef and Hainan Island in the South China Sea, while the other genus *Maxillipides* Ledoyer is endemic to New Caledonia (Fig. 8). The maxillipiids must have been in existence for at least 150 Ma, because after this time, links between Madagascar and Australia/New Caledonia no longer existed. The Wandinidae Lowry & Stoddart (Fig. 8), exhibit a similar distribution. This family is comprised of two genera, *Pseudocyphocaris* in Madagascar and New Guinea and *Wandin* in Australia (GBR) and New Caledonia. New Caledonia, New Guinea and Eastern Australia along with the Bismarcks/Solomons form part of an important geological 'edge' of Gondwana and the biota of these areas represent a globally significant biological 'edge' marked by basal endemics (Heads, 2008).

Late Cretaceous.—80 Ma (Fig. 7). The south Atlantic was now formed and extended to Antarctica. In the North, America-Greenland-Europe were still continuous.

The existence of abelisaurid dinosaur fossils in Madagascar, South America and India (Sampson *et al.* 1998) indicates that these three landmasses were connected until late in the Cretaceous. India and Madagascar were probably linked with the Kerguelen and Seychelles plateaux (Rage, 2003). That we cannot recognise a suite of taxon synapomorphies between Madagascar and India may be a result partly of extinctions in India as it sutured with Eurasia and the two faunas came into contact and partly due to range expansion of the fauna into other regions thus obliterating the ‘signature’. In the eastern Pacific, the Guererro-Caribbean plateau was consolidating with Central America (Mann *et al.*, 2006).

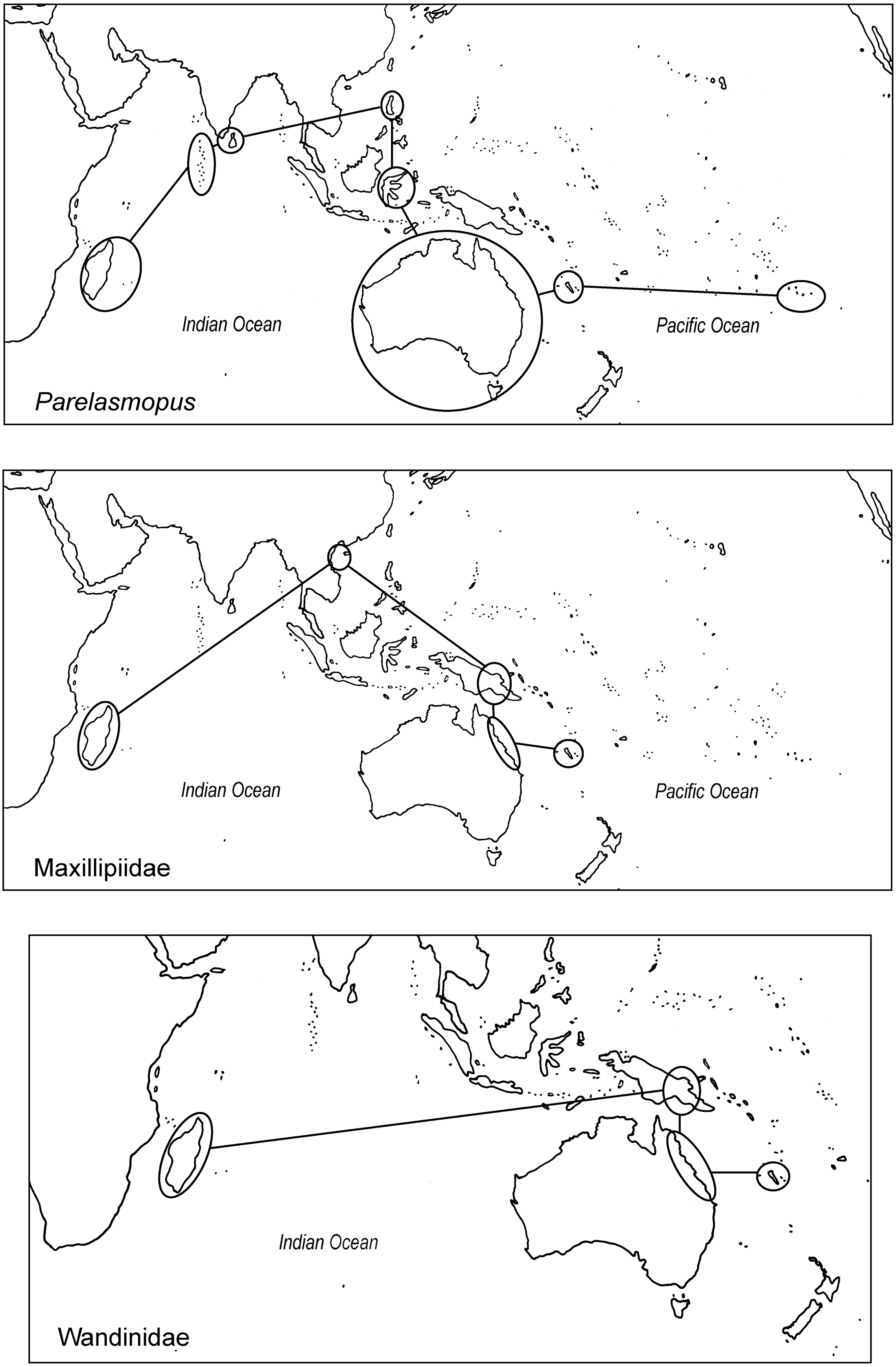

FIGURE 8. Distributions of A. *Parelasmopus*, B. Maxillipiidae, C. Wandinidae.

KT Boundary.—67 Ma (Fig. 7). All Gondwanan fragments were separated, allowing isolated evolution of amphipods on each fragment. Examples of endemic taxa at the family level are the Sternophysingidae Holsinger and Temnophliantidae Griffiths in South Africa, the Kuriidae J.L. Barnard in Arabia, the Tulearidae Ledoyer in Madagascar, the Cheidae Thurston and Ipanemidae Thomas & Barnard in Brazil, the Miramarassidae Lowry in Cuba, the Kotumsaridae Missouli, Holsinger & Raddy in India, the Sinurothoidae Ren in the South China Sea, the Sanchoidae Lowry & Barnard and Sicafodiidae Just in eastern Australia, the marine family Rakiroidae Myers & Lowry along with the two freshwater families Paracrangonyctidae Bousfield and Phreatogammaridae Bousfield in New Zealand, and the Paragammaropsidae Myers & Lowry and Pseudamphilochidae Schellenberg in West Antarctica.

Endemics at the generic level include *Gbroidea* Lowry & Azman, *Austropheonoides* J.L. Barnard, *Narapheonoides* J.L. Barnard, *Bamarooka* Lowry & Stoddart, *Virgammaropsis* Myers and *Graciliphotis* Myers and *Wonga* Lowry & Stoddart, in Australia; *Orstomia* Myers in New Caledonia; *Neocyproidea* Hurley and *Paraleptamphopus* Stebbing, in New Zealand; *Hoplopleon* K.H. Barnard and *Unguja* Griffiths in South Africa and *Dikwa* Griffiths from South Africa and the Scotia Arc.

Late Eocene.—35 Ma (Fig. 7). India sutured with Laurasia and put the Gondwanan and Laurasian amphipod lineages into contact again for the first time in more than 75 million years. This must have been a period of increased extinctions, as a result of competition between the two faunas (see previous).

Miocene–Present.—20 Ma-Present (Fig. 7). Until the Miocene, the amphipod fauna continued to evolve across the Indo-Pacific, uninterrupted by Australia/New Guinea, which detached from Antarctica in the Paleocene, moved northwards through the Eocene and only reaching the proximity of Asia by the late Miocene. The first interchange of amphipods between the Australian plate and the Asian/Philippine plates then became possible. The Iciliidae Dana may have evolved either in Australia/New Guinea or in Asia. This family would have expanded its range onto the adjacent plate after the two docked in the Miocene/Pliocene (Fig. 9). The Tethys Sea was interrupted (c. 18 Ma), isolating the Indo-Pacific from the Atlantic.

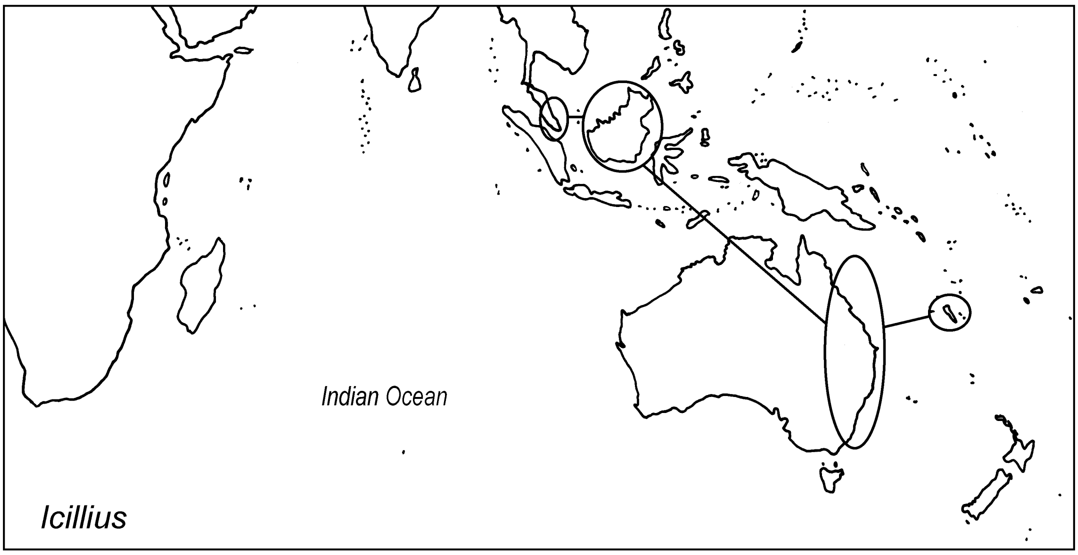

FIGURE 9. The distribution of *Iciliius*.

Gondwana and its descendent components. *120 Ma–Present*

On Gondwanan fragments, the evolution of tropical shallow-water amphipods ocurred in isolation for millions of years, as the plates, carrying the land masses and their surrounding shallow seas, migrated northwards from Antarctica towards Eurasia. Some Gondwanan fragments have remained isolated to this day e.g. Madagascar (for about 80 Ma, see Sampson *et al.*, 1998), some e.g Australia/New Guinea have been (in theory) open to recent (<10 Ma) faunal interchange (see the example of *Mallacoota* described earlier), while others such as India, have had the potential for faunal interchange (with Europe) around 35 Ma when it docked with Eurasia. Because amphipods, like all peracaridans, have no larval dispersive phase, range expansion can occur only by normal ‘means of survival’ (Croizat 1958). Species will extend their range inexorably (given million of years) until they come across an insurmountable biogeographic barrier. To shallow water marine amphipods, the deep sea is just such an insurmountable barrier. It is clear, therefore, that amphipods will have evolved in isolation in each of the Gondwanan fragments until it docked with, or at least gained shallow-sea contiguity with, another shallow-water area.

Eurasia

The arrival of Gondwana amphipods in Eurasia in the early Tertiary will have had far reaching consequences for the endemic lineages. Much of the old Eurasian shore-line no longer exists. Almost the entire northern Indian ocean now consists of Gondwanan fragments (Africa, Arabia and India). In the east, from the Gulf of Thailand through the South China Sea, the East China Sea and the Sea of Japan, the Eurasian craton has been accreted by allochthonous terranes, each bringing with it its own mixture of amphipod lineages and thus further obliterating the original ‘signature’ of it’s amphipod fauna.

The continuity of the Tethys was interrupted in the late Eocene/early Miocene by the continents of India and Africa. The distribution of the genus *Tethylembos* Myers 1988, appears to be Tethyan (Fig. 10). The two extant species, *T. vigueiri* Myers in the Mediterranean and *T. japonicus* Ariyama, in Japan. both occur within, or adjacent to, the Tethys seaway. They were presumably vicariated by the closure of the Tethys in the early Miocene. The fresh-water amphipods of the Ponto-Caspian are also thought to be Tethyan relictuals (Pjatakova & Tarasov 1996).

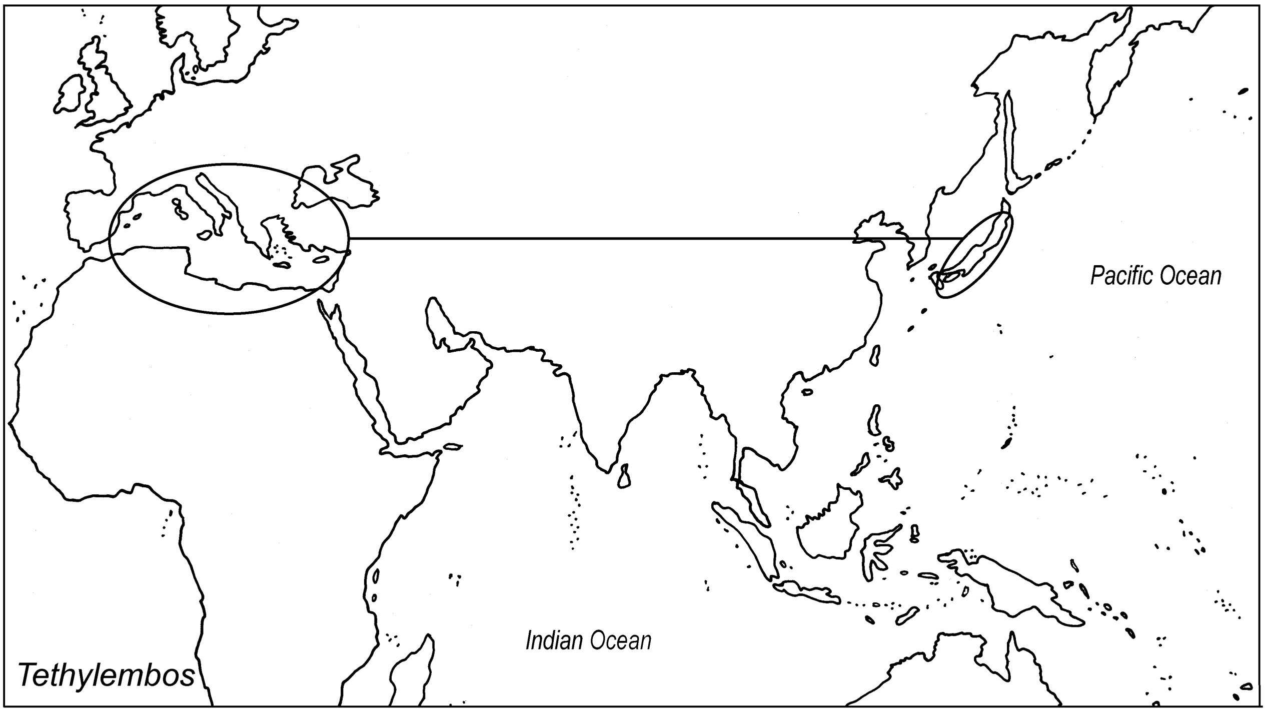

FIGURE 10. The distribution of *Tethylembos*.

The formation of the Australian amphipod fauna

At the KT boundry (Fig. 7), Australia, still connected to or in close proximity with Antarctica, was bathed fairly uniformly in warm seas (18–20°C), as equatorial currents were deflected down the eastern sides of southern continents transferring heat from low to high latitudes. The Southern Ocean was warm, Antarctica was unglaciated and Australia’s climate was warm and wet with little zonation. Amphipods living in Australia’s shallow seas at that time, would have been adapted to warm-temperate or almost sub-tropical conditions. Australia finally broke away from Antarctica, allowing the development of a circum-polar current in the late Eocene around 40 Ma, and the Antarctic convergence became established around 22 Ma (Kennett et al., 1975). This blocked the equatorial currents, and temperature gradients became established between northern and southern Australia. As Antarctica began to cool, Australia moved northwards. By the early Miocene, New Guinea was in tropical waters at around 20ºS. By 14 Ma the Antarctic ice sheet had reached its greatest dimension, but by this time, the Australian continent lay not far south of its current latitude.

A warm temperate amphipod fauna was widespread around Australian coasts during the late Eocene, and was probably not dissimilar to that of southern Australia today. As Australia moved progressively northwards, the evolution of a tropical amphipod fauna in the north and a warm-temperate fauna in the south, would have begun, initiating the distinctive partitioning of the amphipod fauna into temperate and tropical components that is in evidence today. In the late Miocene, about 5-10 Ma, Australia/New Guinea came into close proximity with Asia, allowing for the first time, the potential to exchange shallow-water marine organisms with Indo-Pacific shallow seas (*Kamaka* Derzhavin with four species occuring from Kamchatka to Vietnam and three sibling species, one in PNG one on the Great Barrier Reef and one in Sulawesi, may be an example of a genus that has expanded its range into northern Australia). There was a cooling episode (ice house) in the late Pliocene as the Pliocene-Pleistocene glacial-interglacial pattern became established, but at this stage northern Australia was firmly anchored in the tropics. In Australia, the amphipod fauna, like the terrestrial fauna and flora has evolved *in situ* for at least 30 million years.

Parsimony Analysis of endemicity of Indo-Pacific amphipods

The Australian plate supports a very high level of endemicity, in excess of 80% (Table 3), This supports the hypothesis that a high proportion of the marine amphipod fauna of Australia has been derived from *in situ* evolution. If this hypothesis is correct, we might expect the tropical amphipod fauna of northern Australia to be more closely related to the temperate amphipod fauna of southern Australia, than it is to the tropical amphipod fauna of any other tropical areas in the Indo-Pacific-Caribbean.

TABLE 3. Amphipod endemicity recorded in IndoPacific reef systems.

Great Barrier Reef	78%
Hawaii	62%
Madagascar (Ledoyer, 1982)	61%
India	45%

To test this hypothesis of area homology, a Parsimony Analysis of Endemicity (PAE) was carried out on 47 genera of marine amphipods (Appendix 1) that are endemic to Australia (tropical and temperate) and to the Indo-West Pacific - Caribbean. Garzon-Orduna et al., (2008) have raised doubts regarding conclusions that interpret PAE trees as area cladograms, but they acknowledge that it is a useful tool for establishing hypotheses of primary homology between areas, which is the sole function of this analysis. Regions selected for analysis were 1. Tropical Australia-New Guinea; 2. Temperate Australia; (both Australian Plate); 3. New Caledonia; 4. Fiji (both Gondwana fragments); 5. India (Indian plate); 6. Andaman Sea, western Wallacea, South China Sea, East China Sea, Japan, Korea (Asian Plate); 7. Tropical eastern Africa, Madagascar, Mascarenes (African Plate) and 8. Micronesia and Polynesia (Pacific Plate). The Philippines plate was omitted from the analysis due to insufficient data. Genera that also occur outside these areas were eliminated from the analysis (symplesiomorphies) as were genera occurring in only one region (autapomorphies). Genera were treated as 'characters' of each region, with 'states' being 'present' or 'absent' and a PAUP analysis was run with a heuristic search.

In the cladogram (Fig. 11), there are two major clades, one including both temperate and tropical Australia along with New Caledonia, the other including all the other tropical Indo-Pacific areas. Tropical Australia (which includes New Guinea*)* is therefore shown to be a sister area to temperate Australia supporting the hypothesis of *in situ* evolution of the Australian Amphipoda. In this cladogram (Fig. 12), Australia (temperate and tropical together) is defined by seven taxa, *Ceina* Della Valle, *Doowia* Barnard & Drummond, *Limnoporeia* Fearn-Wannan, *Nagada* Lowry & Stoddart, *Narapheonoides* J.L. Barnard, *Narunius* Barnard & Drummond and *Prosocratus* Barnard & Drummond; the clade Australia plus New Caledonia is defined by *Aborolobatea* Ledoyer, *Bamarooka* Lowry & Stoddart and *Wandin* Lowry & Stoddart. On the other side of the tree, the clade African plate plus Indian plate is defined by one taxon, *Indischnopus* Barnard & Drummond; the clade African plate plus Indian plate plus Pacific plate is defined by four taxa, *Aloiloi* J.L. Barnard, *Kanaloa* J.L. Barnard, *Konatopus* J.L. Barnard and *Ledoyerella* Myers.

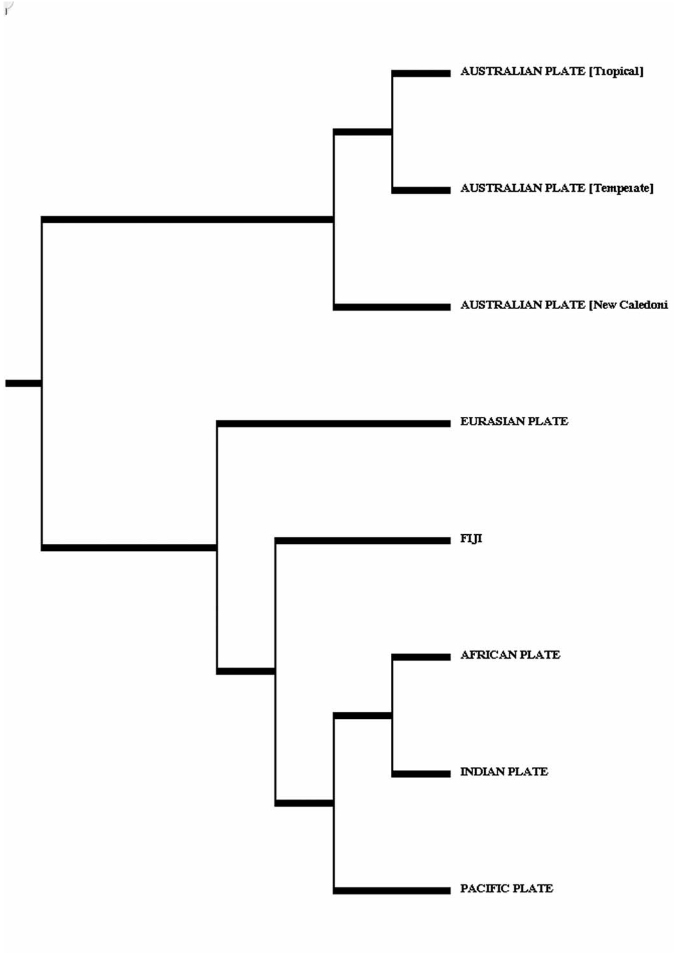

FIGURE 11. PAE Cladogram of 47 genera of marine amphipods from the Indo-Pacific (see text for details)

Discussion

The fragmentation of Gondwana 150 Ma, resulted in a distinctive amphipod fauna and high endemicity evolving in Gonwanaland fragments such as Madagascar, India, Australia, New Caledonia and New Zealand. The disjunct distribution of extant amphipod genera in shallow seas surrounding continents/islands once part of Gondwana, points to a Jurassic origin for these genera. The distribution of many disjunct amphipod taxa parallel the disjunct distributions of terrestrial plants suggesting that the same bigeographic barriers apply to amphipods, and presumably other peracarid crustaceans, as they do to terrestrial plants. Many marine amphipod genera are readily attributable to origins on the supercontinent Gondwana, but few marine amphipod genera can be identified as having evolved on the supercontinent Laurasia. This may be partly due to obliteration of much of the old Laurasian coastline by suturing of the continents of Africa, Arabia and India and by the fusion of numerous allochthonous terranes, events which scarcely impacted on the isolated Gondwanan fragments. In addition, many of the Gondwanan endemics are still isolated on the Gondwanan fragments, whereas opportunities for isolation along Eurasian coasts are few.

Amphipods of modern appearance were well established and widespread around Pangaea in the early Jurassic (200 Ma), when there was more or less shallow-water continuity between all the continents. Modern trans-Indian Ocean and trans-Pacific Ocean endemics represent forms which evolved during this period. In the late Jurassic as Gondwana and Laurasia rifted apart, amphipods evolved independently in the two super-continents and some of these lineages can be recognised today. At the KT boundary (66 Ma), the isolated Gondwana fragments were evolving endemic forms, many of which remain as endemic families today. During the Late Cretaceous/Early Eocene (65–50Ma), the Gondwanan fragments were separated, allowing isolated evolution of amphipods on each fragment. The late Eocene (35 Ma), when India sutured with Laurasia, was a period of raised extinction rates as a result of competition between faunas that had been isolated from one another for 75 million years. The Tethys Sea was interrupted, isolating the Indo-Pacific from the Atlantic and vicariating taxa such as *Tethylembos*.

In the Miocene (20 Ma) until the present, the first interchange of amphipods between the Australian plate and the Asian/Philippine plates became possible. The Australian fauna would consequently be expected to consist primarily of paleaoendemic Australian amphipods perhaps ‘overlain’ by a few recent Asian range expanders. A PAE analysis demonstrates strong biotic isolation and *in situ* evolution of Amphipoda within Australia/New Guinea.

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APPENDIX 1

List of amphipod genera used in Parsimony Analysis of Endemicity (PAE).

Aborolobatea Ledoyer, 1984
Aloiloi J.L.Barnard, 1970
Anoediceros Pirlot, 1932
Azotostoma J.L.Barnard, 1965
Bamarooka Lowry & Stoddart 2002
Birubius J.L.Barnard & Drummond 1976
Bolttsia Griffiths, 1976
Ceina Della Valle, 1893
Ceinina Stephensen, 1933
Doowia J.L.Barnard & Drummond, 1987
Endevoura Chilton, 1921
Exampithoe K.H.Barnard, 1926
Glossomaera Krapp-Schickel, 2009
Haustoriopsis Schellenberg 1938
Icilius Dana, 1852
Indischnopus J.L.Barnard & Drummond 1979
Iphiplateia Stebbing, 1899
Kamaka Derhavin, 1923
Kanaloa J.L.Barnard, 1970
Konatopus J.L.Barnard, 1970
Ledoyerella Myers, 1973
Lelehua J.L.Barnard, 1970
Leucothoella Schellenberg, 1928
Limnoporeia Fearn-Wanan, 1968
Maxillipius Ledoyer, 1973
Metatiron Rabindranath, 1972
Moolapheonoides J.L.Barnard, 1974
Nagada Lowry & Stoddart, 1995
Narapheonoides J.L. Barnard. 1972
Narunius J.L.Barnard & Drummond, 1982
Nihotunga J.L.Barnard, 1972
Ochlesis Stebbing, 1910
Paracalliope Stebbing, 1899
Paralepechinella Pirlot, 1933
Paranamixis Schellenberg, 1938
Plumithoe J.L.Barnard & Karaman, 1991
Procyphocaris J.L.Barnard, 1961
Prosocratus J.L.Barnard & Drummond, 1982
Protophoxus K.H.Barnard, 1930
Tepidopleustes Karaman & J.L.Barnard, 1979
Tropischyrocerus Just 2009
Unyapheonoides J.L.Barnard, 1972
Wallametopa J.L.Barnard, 1974
Wandin Lowry & Stoddart 1990
Wildus J.L.Barnard & Drummond, 1978
Wombalano Thomas & J.L.Barnard, 1991
Yulumara J.L.Barnard, 1972