



Biogeography of Indo-Pacific Pontoniinae (Crustacea, Decapoda): a PAE analysis

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Abstract

Aim Pontoniid shrimps are one of the most abundant coral reef associated taxa in the Indo-Pacific. Although taxonomically well known, their ecology, life history and biogeography appears virtually unstudied. The object of the present contribution is to derive a basin wide biogeographical hypothesis, using a limited number of operational geographic units (OGU).

Location Twelve OGU's were selected, spanning the entire Indo-Pacific, from the East coast of Africa and the Red Sea to the Tropical Eastern Pacific (TEP).

Methods Analysis was based on a species by OGU matrix, in which presences (1) and putative occurrences (?) were coded. Parsimony analysis of endemicity (PAE) was applied to the data set, using Dollo and Wagner Parsimony.

Results A hierarchical pattern of area relationships was derived, with the TEP occupying a basal position, Hawaii and French Polynesia occupy positions higher up in the cladogram, whilst the Melanesian OGU maintains a sister-area relationship to the crown clade. The latter consists of the Indo-Philippine area, the Australian and all Indian Ocean OGUs.

Main conclusions Pontoniinae exhibit a clear hierarchical pattern of area relationships, which is congruent with previous biogeographical studies on coral reef and other taxa. The observed pattern can be explained by a combination of dispersal and vicariant events, whilst the importance of sea level changes is recognized.

Keywords

Crustacea, Pontoniinae, Indo-Pacific, Parsimony Analysis of Endemicity.

INTRODUCTION

Pontoniinae are one of the most diverse groups of caridean shrimp taxa, worldwide there are presently 456 species known. Although they occur in almost all of the worlds' oceans (with the exception of the Antarctic and Arctic regions), they reach their highest level of species and generic diversification in the Indo-Pacific. Within the Indo-Pacific region, they are only rivalled in their species diversity by the Alpheidae; together both taxa make up more than 90% of all caridean species diversity in a given locality (Bruce, 1976). One of the most characteristic biological properties of the Pontoniinae, is their ability to form associations with a variety of host taxa. Certainly, an estimated 60–70% is involved in some form of commensal association with other taxa. Host taxa range from sponges (e.g. *Periclimenaeus*

Borradaile), sea anemones (e.g. *Periclimenes* Costa), corals (numerous genera), through to large bivalve molluscs (e.g. *Anchistus* Borradaile, *Conchodytes* Peters, *Paranchistus* Holthuis) and ascidians (e.g. *Pontonia* Latreille).

Although numerous species are known from the Indo-Pacific and in spite of work by such excellent taxonomists as Bruce and Holthuis, biogeographical studies on Pontoniinae are lacking. This may be caused by the general lack of detailed species lists for many localities or the notion that many species still remain to be discovered/described. As recently as 1990, it was stated by Bruce (1990) that only the Pontoniinae faunas of Indonesia and New Caledonia were sufficiently well studied to be compared with the Australian fauna, although it was recognized that even these must be considered incompletely known. As an example, *Periclimenella spinifera* (De Man) was quoted, one of the most widespread and abundant species, known from numerous areas (see distribution map in Myers & De Grave, 2000) but not from New Caledonia, however, the species has since (1996) been

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recorded there. Since then other checklists have appeared (e.g. Fransen, 1994 for the Seychelles; Poupin, 1998 for French Polynesia; De Grave, 2000 for Papua New Guinea), although it should be noted these are based on protracted expedition periods and may thus underestimate the true number of species in a general locality. Although no comparable studies have been carried out on caridean shrimps, estimates of the true biodiversity level in relation to the known number of species have been reported upon for coral reef inhabiting Isopoda and other peracaridean crustaceans (Kensley, 1998), with the upper limit of total species richness estimated at nearly three times the number of described species.

Given these caveats it is not surprising that the general picture that has emerged of Pontoniinae biogeography is a combination of highly endemic taxa and several widespread taxa. A distributional pattern, Pontoniinae share with numerous other Indo-Pacific marine taxa (Paulay, 1990). However, this may be an artefact, caused by the 'vagaries of field collecting'; an issue that may be solved in the future by further taxonomic work, both in poorly studied and extensively collected areas. Indeed, Gosliner & Draheim (1996) suggested that even in the latter areas, significant numbers of additional species may be found, a phenomenon not restricted to rare and/or inconspicuous species.

Nevertheless, it appears feasible to apply recently developed biogeographical analytical techniques to the existing diffuse data set in order to derive some general deductions and/or hypotheses regarding Indo-Pacific Pontoniinae biogeography.

Initially, efforts in Indo-Pacific marine biogeography were primarily concerned with delineating centres of endemism (descriptive biogeography), based on pre-set levels of endemic species in a number of taxa (e.g. Briggs, 1974; Foin, 1976), which evolved in applying phenetic methods (e.g. Hoeksema, 1989). More recently, advanced methods have been employed (analytical biogeography), such as cladistic biogeography (Wallace *et al.*, 1991; Pandolfi, 1992; van Soest & Hajdu, 1997) and parsimony analysis of endemism (PAE) (Myers, 1991; van Soest, 1994) in the unravelling of marine, biogeographical patterns. The latter techniques in combination with evidence derived from genetic studies, summarized for the Indo-Pacific region by Benzie (1999), have not only provided an analytical basis for the intuitively recognized areas of endemism, but also provided a sound footing for future marine, historical biogeography in the Indo-Pacific region.

The application of cladistic biogeography on a basin wide scale, at the species level for Pontoniinae, appears to be, at the present time, an unrealistic goal, as no published phylogenies are available for any genus. The construction of these would take an extraordinary amount of taxonomic effort. Additionally, a phylogenetic analysis at the generic level would appear unproductive for biogeographical purposes, as many genera occur outside the Indo-Pacific (e.g. *Palaemonella* Dana, *Periclimenaeus*, *Periclimenes*, *Typton* Costa), and in addition most genera are widespread within the Indo-Pacific. A biogeographical, analytical technique which does not require an *a priori* phylogeny is however,

available. The PAE technique, pioneered by Rosen (1988), applies parsimony analysis to taxa occupying two or more areas of endemism, in order to derive area relationships. The method is analogous to cladistic analysis, in that shared presence of taxa is used to describe historical relationships of areas. It has been used in the Indo-Pacific marine region by Myers (1991) and van Soest (1994), whilst several other marine applications are reported upon in the literature.

The present study is concerned with deriving general, Indo-Pacific basin-wide hypotheses of Pontoniinae biogeography, as an aid to future taxonomic and biogeographical work. By highlighting historical biogeographical patterns, it is hoped that future taxonomic work may be able to concentrate in certain areas, potentially of major significance in the evolution and biogeography of Pontoniinae. In addition, hypotheses can be usefully contrasted with other marine groups in order to delineate more large-scale historical patterns across several taxa, an important aspect of marine biogeography in view of the differential dispersal patterns of many taxa.

MATERIALS AND METHODS

Initially, a species list was drawn up for Indo-Pacific localities for which recent and/or comprehensive literature was available. This resulted in more than 350 species being listed from 35 collection localities, with the number of species per locality ranging from 10 to 104. On plotting their distributions, it became quickly apparent that many species were absent from a large number of collection localities, but were present in the surrounding localities. Furthermore, if the fact that many species are commensals of other reef organisms was taken into account, it was apparent that the host species/genera occurred in a given locality, but the shrimp taxa themselves were not recorded, then this paucity of records might be reasonably assumed to be the result of a lack of collecting, rather than from true absences. To counteract this 'collection effort bias', the matrix was consolidated into several areas of endemism (Fig. 1). These areas were derived from a growing body of literature on Indo-Pacific marine biogeography, but essentially originated from the work by Briggs (1974). Although initially Briggs (1974) selected these areas on the basis of set minimum levels of endemism, separated by biogeographical barriers, since then several authors have more rigorously studied and delineated these areas. This has included analysis of species and generic distributions in molluscs (Foin, 1976) and corals (Stehli & Wells, 1971), phenetic similarity based approaches in corals (Hoeksema, 1989) and cladistic biogeographical approaches in corals (Wallace *et al.*, 1991; Pandolfi, 1992) and sponges (van Soest, 1994; van Soest & Hajdu, 1997). When superimposing area maps derived from the above studies, a relatively uniform pattern of area relationships emerges, although taxa specific differences exist, related to the dispersal capabilities of the taxa involved.

The selection of the areas in the present study is thus justified both by biogeographical congruence of previous studies and by the need to study the overall pattern with a

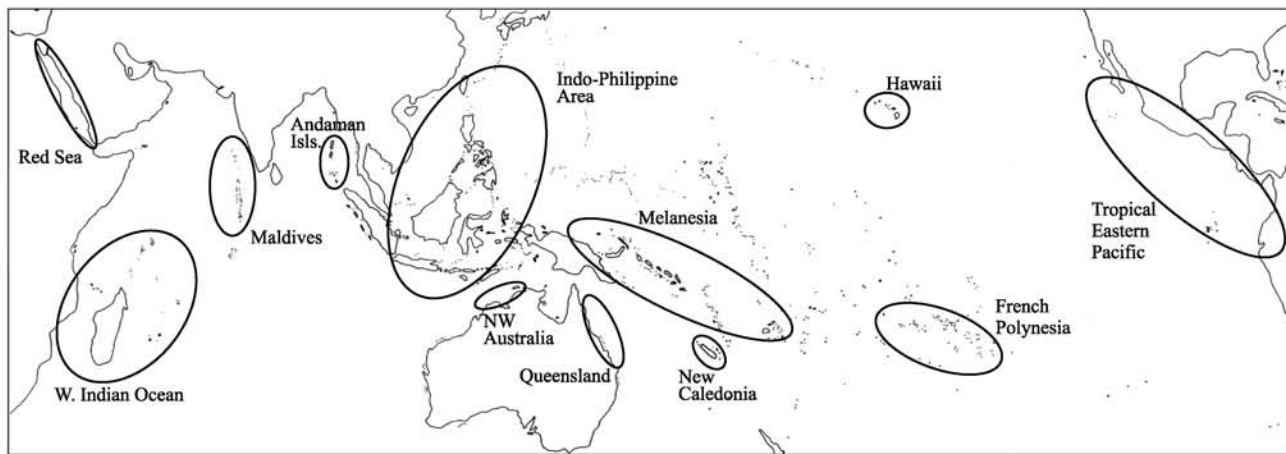


Figure 1 Delineation of operational geographic units (OGU) in the present study.

larger 'grain', thus eliminating the lack of a sufficient amount of reliable records in many smaller scale areas (smaller grain). Indeed, it has been pointed out that the areas of endemism under study, should be biogeographically meaningful (Linder & Crisp, 1995). Some bias must remain, as it is difficult to compare areas such as the entire Tropical Eastern Pacific (TEP) (comprised itself of several distinct provinces) and an area such as New Caledonia, on the basis of areal extent alone.

The resulting data set (Appendix) was analysed with PAE (Rosen, 1988). In several respects, the present study differs from the original application, but is consistent with more recent studies in their approach and with methodological advances in PAE. First, the present study differs from the original PAE application, in which localities were studied (Rosen, 1988), but is similar in its use of 'operational geographic units (OGU)' in more recent applications of PAE (van Soest, 1994; Maldonado & Uriz, 1995; van Soest & Hajdu, 1997). However, coding on the basis of OGU's does assume some degree of biogeographical non-randomness in the data set (Cracraft, 1991). Nevertheless, given the often patchy record of many finer scale species distributions, this primary assumption appears justified in the general construction of basin-wide Indo-Pacific biogeographical hypotheses for Pontoniinae.

Following Cracraft (1991) and Glasby & Alvarez (1999) both species and genera were coded in the same analysis. The main advantage of scoring multiple taxonomic levels is that area information associated with endemic species, usually filtered out in a PAE analysis, can be used for area relationships. A second advantage is that distributional data at the generic level could be used for genera with considerable taxonomic confusion, e.g. *Pontonides* Borradaile. Although at least three species of this genus occur in the study area, the status of the commonly recorded taxon, *P. unciger* Calman is doubted by several authors, and in all likelihood consists of a species complex.

The treatment of 'absence' of a taxon (in this case Pontoniinae) from a particular area is of crucial importance

in PAE analysis, because it has been suggested that areas having few taxa may unduly influence the analysis because they will tend to be viewed as primitive (Rosen, 1988). Although this may be the case in some instances, it is however, not certain, as several other explanations are available for areas having fewer taxa (Cracraft, 1991). As the majority of Pontoniinae are commensals, absence of certain host taxa may play a crucial role in the presence of shrimp species. The absence of a taxon from a certain area may be the result of the taxon never having occurred in the area, the taxon having gone extinct (Myers & De Grave, 2000) or the taxon having not yet been discovered (Glasby & Alvarez, 1999). The third factor is thought to be of considerable importance in the Maldives and Andaman Islands areas, where the last major collections date from Kemp (1922, 1925), with only sporadic records added since then. As the work by Kemp was carried out before the advent of SCUBA, which has played a major role in the collection and discovery of species (Bruce, 1976), it is safe to assume that numerous species await formal discovery in these areas. To a lesser extent, the Red Sea area also suffers from this, as no recent major collections have been reported upon (in spite of the excellent work by Holthuis, 1958 and Bruce & Svoboda, 1983). In view of the widespread nature of coral reef environments in the area, it again is expected that many species await discovery. In order to minimize the effects of under-collecting, attention was paid to scoring for the putative presence of a taxon in the areas, following the method of Glasby & Alvarez (1999). If a species or genus was unreported from one of those areas but had been recorded from all adjacent areas then it was scored as being present (1) in the poorly collected area. If a taxon was only reported from one adjacent area, then it was scored as '?' in the poorly collected area. A similar approach was adopted to areas, such as north-western Australia, where the host taxa are known to be present, but the relevant commensal shrimp are unreported (Bruce & Coombes, 1995). In all cases where putative presence scores were added to the matrix, every effort was made to find if the host taxa occurred in the area.

The resulting data set was further restricted to shelf species, defined as the 200 m depth limit. This could be justified, as over 90% of all Pontoniinae occur within this depth range (De Grave, unpublished data) and the fact that the majority of species are restricted to coral reef habitats. Furthermore, different evolutionary pressures may operate on deep-sea taxa as opposed to shallow water taxa (e.g. different barriers and dispersal modes), not necessarily shared by shallow water taxa. Following Rosen (1988) all taxa that occurred in all areas (plesiomorphies) were deleted from the matrix, as were all taxa, which occurred in a single area (autapomorphies). This was equally applied to taxa, which occurred in all areas, following recoding with 1 or ? (e.g. *Periclimenes soror* Nobili). An exception was made for *Palaemonella rotumana* (Borradaile), although this species occurs in the eastern Mediterranean, its occurrence there is the result of Lessepsian migration (Holthuis & Gottlieb, 1958). Similarly, *Pontoniopsis* was included in the data set, as it is clear from the description that the Atlantic species, *P. paulae* Gore does not belong to this genus. Taxa were also deleted if they were only recorded from East Africa and the Great Barrier Reef, amounting to four species (*Periclimenaeus ardeae* Bruce, *Periclimenes goniopora* Bruce, *Propontonia pellucida* Bruce, *Typton wasini* Bruce). It is clear that this level of disjunct distribution must be entirely caused by collecting efforts, as recent collections in the intervening areas have recorded taxa, previously exhibiting this type of distribution.

Taking all these caveats into account, the original data set was thus reduced to 12 OGU's and 193 taxa (species and genera combined) (Appendix).

A further assumption concerns the rooting of the cladogram. In the absence of a phylogeny for Pontoniinae, the ancestral area of the cladogram was rooted using a hypothetical area containing only zeros (Lundberg rooting). This would imply that the ancestral area would be devoid of any Pontoniinae or alternatively if the genera and species in the analysis had not yet evolved. In the absence of a fossil record for Pontoniinae, such an assumption must be made, as no alternative is available (Cracraft, 1991).

In terms of the biogeographical evolution of the taxa, both Wagner and Dollo parsimony was applied to the data (Rosen & Smith, 1988; Glasby & Alvarez, 1999). Wagner parsimony allows a taxon to appear in an area, be lost, and reappear freely; by contrast Dollo parsimony allows taxa to appear only once, but be lost as many times as necessary. Biogeographically speaking, Wagner parsimony allows for long-distance dispersal, whilst Dollo parsimony does not. All analysis were run using PAUP 4.0 (Swofford, 1998), using the branch-and-bound option and estimating confidence in the cladogram by bootstrapping (1000 replicates).

RESULTS

Levels of endemism

Based on the condensed OGU's, Pontoniinae exhibit a high degree of endemism (Table 1), with nearly half of all Indo-Pacific species only occurring in only one of the areas.

Table 1 Species level of endemism in initial and revised data matrices, showing number of species per level of endemism and percentage of total number of species. Coding for putative occurrences refers to presence in all surrounding areas (1) or present in one adjacent area (?)

No. of areas for which species are endemic	Initial coding	Coded for putative occurrences (%)	
		1	1 and ?
One area	160 (46.94)	160 (46.94)	160 (46.94)
Two areas	59 (17.20)	59 (17.20)	38 (11.08)
Three areas	31 (9.04)	31 (9.04)	28 (8.16)
Four areas	23 (6.71)	21 (6.12)	20 (5.83)
Five or more areas	69 (20.12)	71 (20.70)	96 (27.99)
Total number of species	343		

Values in parentheses are in percentages.

Conversely, this implies that approximately half of the species occur in more than one area. As PAE analysis is entirely based on shared species occurrences, this suggests that the analysis is both appropriate and justified. At the other end of the scale, approximately 20% of all species occur in more than five areas, suggesting a certain level of cosmopolitanism in some species. Indeed, numerous species occur over vast stretches of the Indo-Pacific, although not necessarily formally recorded from all intervening areas. Two of the most widespread and ubiquitous species are *P. rotumana*, considered a free-living species, although often found on living corals and *Harpiliopsis depressa* (Stimpson), a pocilloporid coral commensal (Fig. 2). In spite of such vast distribution ranges, only six species cross the eastern Pacific filter bridge (*sensu* Glynn & Ault, 2000). Although three of these species exhibit near continuous ranges, as illustrated by *Fennera chacei* Holthuis and *H. depressa* (Fig. 2), some species such as *Alloponetia iaini* Bruce and *Tuleariocaris holthuisi* Hipeau-Jacquotte (both echinoid commensal) exhibit a highly disjunct distribution (Fig. 2). Scoring for putative occurrences (Table 1) does not appreciatively change the levels of endemism of the species involved in the PAE analysis, with the largest change being noted in species occurring in five or more areas.

Turning to the levels of endemism within each of the study areas, French Polynesia exhibits the lowest level whilst TEP exhibits the highest level (Table 2). Although both collection effort and size of the area may play significant roles in deriving these figures, other factors (ecological, biogeographical) cannot be totally discounted. Compared with other areas, the Queensland area of Australia is particularly well studied, supporting one of the highest levels of shrimp biodiversity (Table 3), yet it harbours far fewer endemic species than other equally studied areas (e.g. Indo-Philippine area, W. Indian Ocean, Table 2). New Caledonia, although harbouring less than half the number of species of the Indo-Philippine area (Table 3), nevertheless has a higher percentage of endemic species (Table 2). As expected, scoring for putative occurrences only

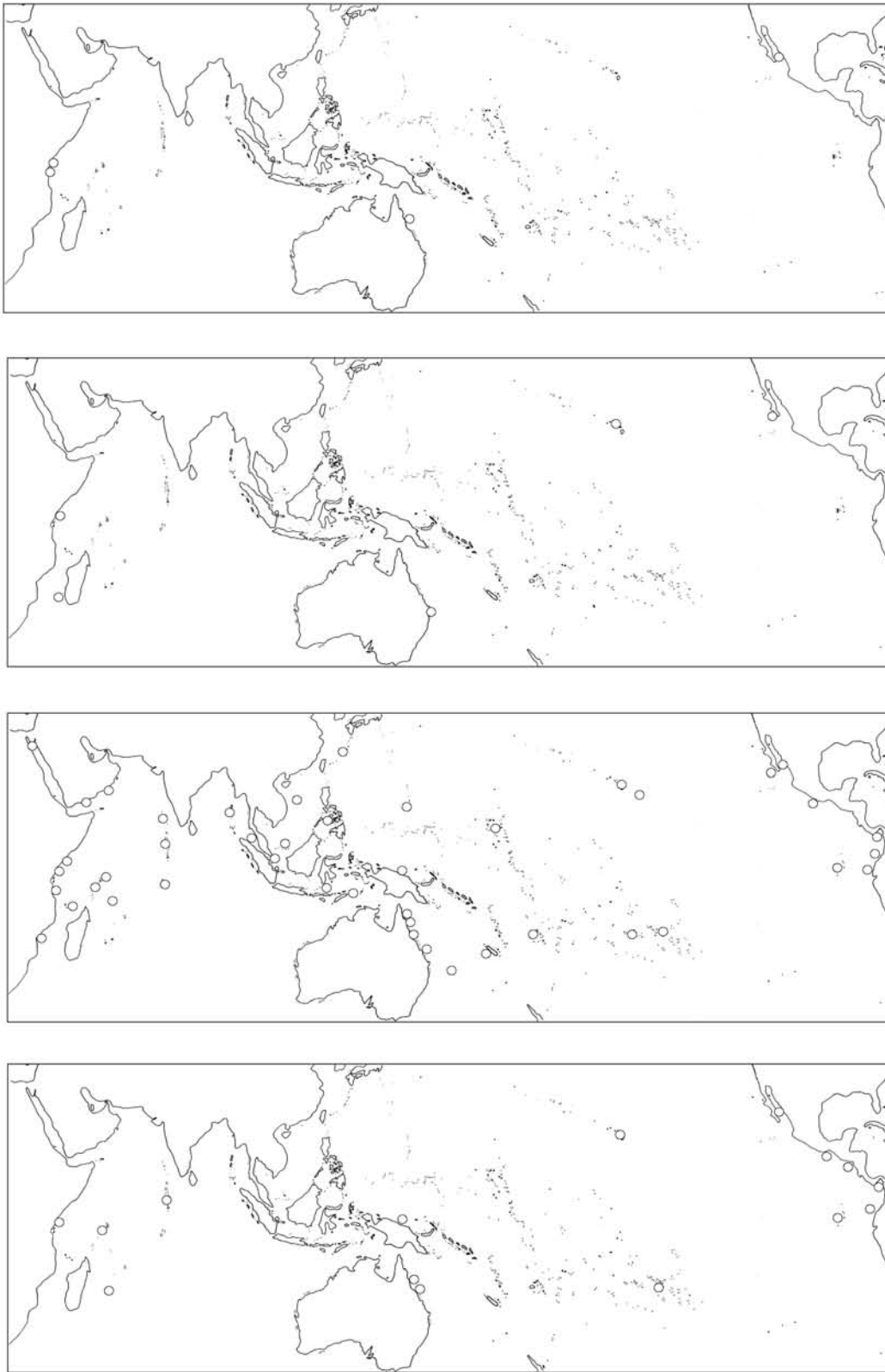


Figure 2 Distribution patterns of *Allopontonia iani* Bruce, *Tuleariocaris holthuisi* Hipeau-Jacquotte, *Harpiliopsis depressa* (Stimpson) and *Femnera chacei* Holthuis.

	No. endemic species	Percentage endemism		
		Initial coding	Coded for putative occurrences	
			1	1 and ?
Red Sea	4	7.69	7.69	3.92
W. Indian Ocean	28	18.30	18.30	18.30
Maldives	3	6.67	5.66	3.09
Andaman Isls.	2	4.55	3.92	2.11
Indo-Philippine area	35	20.35	20.35	20.23
NW Australia	23	27.71	27.38	23.71
Queensland	10	7.30	7.30	7.30
Melanesia	7	6.86	6.86	6.86
New Caledonia	17	24.29	22.67	19.77
French Polynesia	1	2.94	2.94	2.94
Hawaii	4	15.38	15.38	15.38
Tropical Eastern Pacific	26	81.25	81.25	81.25
Total	160	46.94		

Table 2 Species level endemism in each of the studied areas, with initial and revised coding (percentages calculated on the basis of the total number of species per area). For explanation of coding, see Table 1

Table 3 Recorded and putative number of species per area. For explanation of coding, see Table 1

	Recorded no. of species	Putative no. of species	
		1	1 and ?
Red Sea	52	52	102
W. Indian Ocean	153	153	153
Maldives	45	53	97
Andaman Isls.	44	51	95
Indo-Philippine area	172	172	173
NW Australia	83	84	97
Queensland	137	137	137
Melanesia	102	102	102
New Caledonia	70	75	86
French Polynesia	34	34	34
Hawaii	26	26	26
Tropical Eastern Pacific	32	32	32
Total	343		

appreciatively changes the level of endemism of the three poorly collected areas: Red Sea, Maldives and Andaman Islands, with minor changes in the NW Australia and New Caledonian areas (Table 2).

PAE

A total of 191 taxa were included in the PAE analysis, representing 54% of all species and genera occurring in the Indo-Pacific region. Under Dollo parsimony, a single most parsimonious cladogram was generated, with tree length (TL) = 399 and consistency index (CI) = 0.479 (Fig. 3); under Wagner parsimony a single cladogram was generated, with TL = 336 and CI = 0.568 (Fig. 4). Both cladograms are very similar in the position of basal clades, but differ largely in their resolution of the crown clades. Under the no dispersal

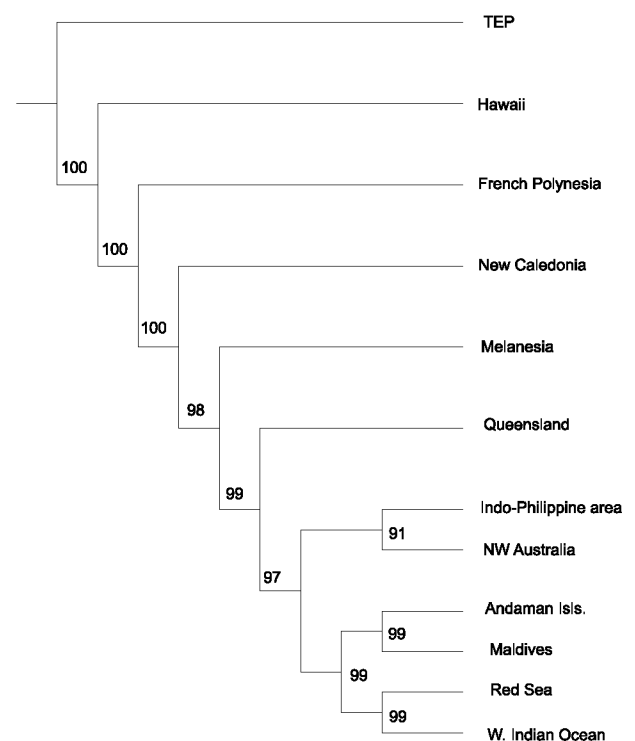


Figure 3 Single minimum-length PAE area cladogram under Dollo parsimony assumption of all OGU. Bootstrap values are indicated as a percentage, TEP refers to Tropical Eastern Pacific.

assumption (Dollo parsimony), Queensland forms a sister-area of all the Indian Ocean and the Indo-Philippine areas (excluding Melanesia); with the Indo-Philippine area + NW Australia forming a sister-area of all Indian Ocean areas. Furthermore, the Red Sea + W. Indian Ocean form a sister-area to the central Indian Ocean areas (Fig. 2). In contrast, under the dispersal assumption (Wagner parsimony), the

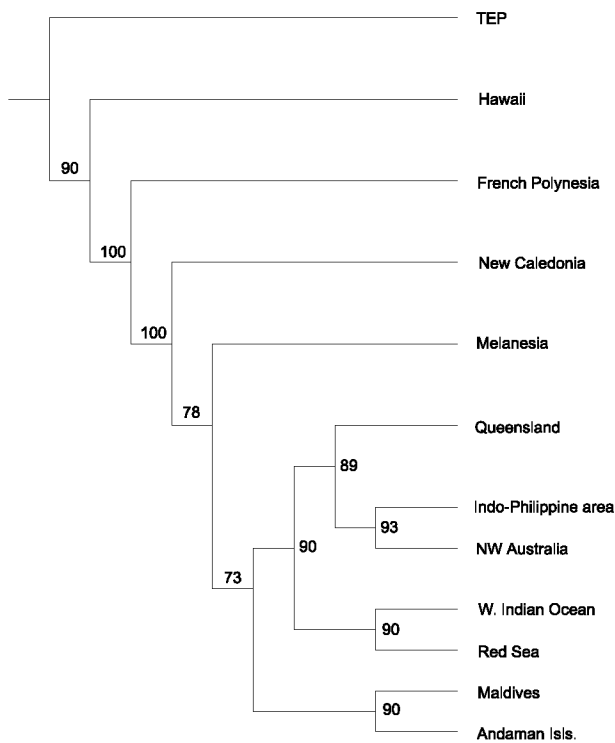


Figure 4 Single minimum-length PAE area cladogram under Wagner parsimony assumption of all OGU. See Fig. 3 for explanation.

central Indian Ocean areas form a sister-area to the remainder of the Indian Ocean areas and Indo-Philippine areas (excluding Melanesia), both forming sister-areas to each other (Fig. 4).

As the low level of recent records in the Central Indian Ocean areas (Maldives and Andaman Islands) and the Red Sea may have unduly influenced the analysis (in spite of the putative coding), these three areas were deleted from the matrix and the PAE analysis re-run. Under Dollo parsimony, a single cladogram was generated (TL = 351, CI = 0.541, Fig. 5); whilst under Wagner parsimony a single cladogram was also generated (TL = 309, CI = 0.615, Fig. 6). Both cladograms are virtually identical in topology to the original analysis, taking into account the excluded areas. Both reduced data set cladograms only differ in the positions of Queensland and the W. Indian Ocean, with Queensland forming a sister-area of W. Indian Ocean + NW Australia + Indo-Philippine area under the no-dispersal assumption; whilst the positions of the Queensland and W. Indian Ocean areas are reversed under the dispersal assumption.

DISCUSSION

Limitations of the study

Limitations are associated with both the recorded geographical distribution of taxa and the use of PAE. Limitations

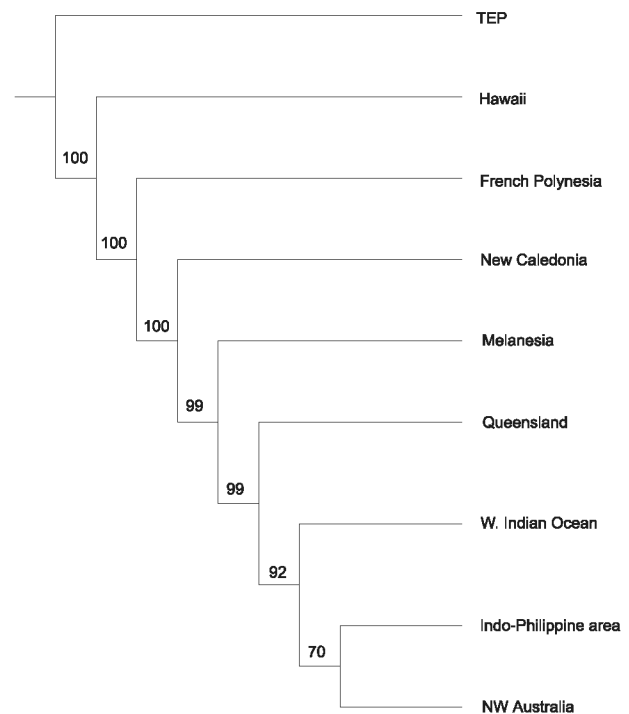


Figure 5 Single minimum-length PAE area cladogram under Dollo parsimony assumption; Red Sea, Maldives and Andaman Isls. excluded. See Fig. 3 for explanation.

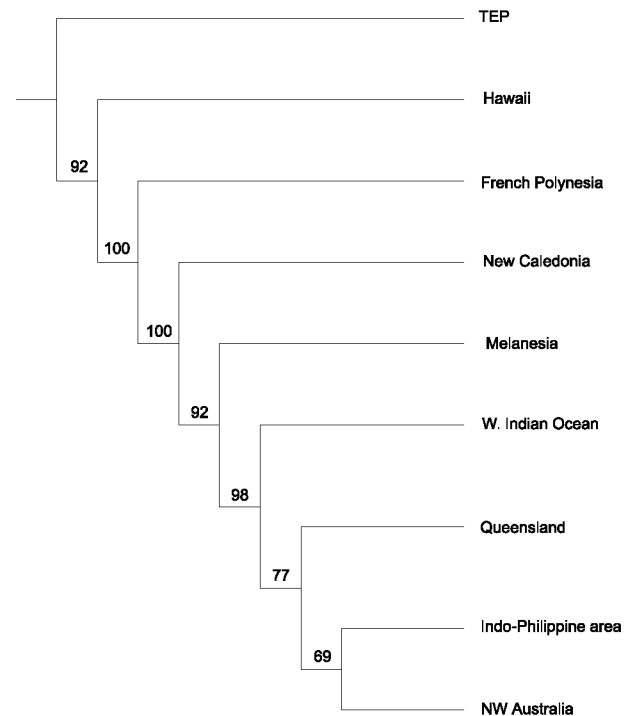


Figure 6 Single minimum-length PAE area cladogram under Wagner parsimony assumption; Red Sea, Maldives and Andaman Isls. excluded. See Fig. 3 for explanation.

concerned with the taxa themselves centre on poor collecting efforts (not uncommon in many Indo-Pacific taxa), lack of knowledge of the dispersal potential of larval and adult stages and unresolved taxonomic problems. Limitations concerned with the analytical procedure are because of quantity of available data and the exclusion of endemic taxa to a single area.

Although recent studies have improved our biogeographical and taxonomic knowledge of Indo-Pacific Pontoniinae, it is clear that numerous gaps still exist. For instance, many commensal species are not formally recorded from areas where their host species are known to exist. This not only applies to the cryptic species, living endo-commensally in bivalves and tunicates (Bruce & Coombes, 1995), but also to many species living ecto-commensally on corals and sponges and free-living species. An experienced taxonomist/collector can in some dives easily collect upwards of 30–40 species at any given locality, provided that healthy and well established reefal ecosystems are present. Based on far more conspicuous taxa than shrimps, Gosliner & Draheim (1996) noted that the number of Hawaiian opisthobranch molluscs nearly doubled over a period of 4 years, because of the persistent efforts of a single collector. Given the need for destructive sampling of host species as a requirement to collect Pontoniinae and the limitations of SCUBA diving in terms of catch-per-unit effort, some bias must be present in the known distributions of many species. The question remains how much this bias affects the underlying biogeographical signal. In the present analyses, this has been partly resolved by coding for putative occurrences.

Virtually nothing is known about the dispersal potential of both larval and adult stages of Pontoniinae. Although it is generally assumed that Pontoniinae (with few exceptions) have planctonic stages, the duration of these is unknown. Given the unique commensal relationship of many Pontoniinae, it is imprudent to speculate on larval duration by comparison with related groups. Nevertheless, it can be speculated upon that successful colonization by many taxa depends on finding a suitable host, providing further emphasis on the success of the colonization phase, following dispersal. Given the commensal nature of many Pontoniinae adult dispersal must be limited, although short-range dispersal has been alluded to by the rare discovery of commensal species away from their host taxa. Long-range dispersal is more unlikely, unless aided by external agents, such as coral rafts (Jokiel, 1984), ship fouling and other drifting objects.

Unresolved taxonomic problems in Pontoniinae are perhaps few in comparison with many other taxa, largely because of the effort by A. J. Bruce. Nevertheless, some taxonomic problems are outstanding, such as the genus *Pontonides* and the status of some species of the *Periclimenes grandis* (Stimpson) complex (see Chace & Bruce, 1993), as well as the monophyletic nature of *Periclimenes*, the largest genus in the group.

It has been suggested that PAE analysis relies on quantity of data, rather than quality (van Soest, 1994; Glasby & Alvarez, 1999); with the latter suggesting that eighty species

is the minimum for a successful analysis. Preliminary analyses during the present study would support this. Although a certain number of species included in each analysis may exhibit a biogeographically anomalous or conflicting signal, it is implicitly assumed in PAE that, as long as the historical biogeographical signal is strong enough, good hypotheses will result (Glasby & Alvarez, 1999). The present study has attempted to overcome some of these shortcomings, by selectively deleting certain taxa (e.g. *Pontonides unciger*, probably a species complex) and by adding putative occurrences to the data set.

In common with other analytical biogeographical methods, PAE has the disadvantage of not being able to utilize information associated with taxa occupying a single area of endemism (i.e. only one of the included OGU's in the analysis). Rather, PAE relies on the information that if two areas share a certain taxon, these areas must be more closely related than areas not sharing this taxon. Although this assumption has been criticized by Myers & De Grave (2000), the technique remains useful, as it bypasses phylogenetic information of the taxa concerned, and has certain advantages over phenetically based approaches. Rosen (1988, 1992), Rosen & Smith (1988) and Cracraft (1991) discuss other limitations of the technique, including the selection of an ancestral area and ways of dealing with homoplasy and area plesiomorphy. Although some of these analytical limitations have been addressed in the present study, it is possible that analytical artefacts resulting from the inclusion of OGU's with few taxa remain problematic. For instance, although the TEP harbours 32 species (Wicksten & Hendrickx, 1992; Wicksten & Hernández, 2000), the majority of these are endemic to the region, with only three remaining in the analysed matrix (*P. soror* was excluded after putative coding). Alternatively, the position of these regions at the base of the cladograms may be a reflection of an underlying historical biogeographical pattern.

Hierarchical patterns

Perhaps not surprisingly, in all analyses the TEP forms a sister-area to the entire Indo-West Pacific (IWP) area. Although few species are shared between these two areas, which may unduly affect the PAE analysis, it can be assumed that this relationship is a true expression of a biogeographical relationship. This is supported by the numerous other marine taxa, exhibiting a similar relationship. Throughout the Cenozoic, the eastern Pacific Barrier has probably been limiting dispersal (Grigg & Hey, 1992), as a result the TEP faunal composition of many taxa is fundamentally different from the IWP. The origin of TEP biota has been extensively debated in the past, with both vicariance and dispersal hypotheses put forward. In a recent review of TEP coral biogeography, Glynn & Ault (2000) discussed these and concluded that the coral fauna consists of three distinct elements: (1) the majority of taxa are Indo-Pacific migrants that reached the TEP by long distance dispersal after the closure of the Central American seaway (c. 3.7–3.0 Ma), (2)

several endemics which evolved relatively recently and (3) some relict species with close affinity to west Atlantic ancestral stocks. This appears to be a plausible hypothesis for Pontoniinae as well, although the proportion of each category is quite different. Of the currently known 32 TEP species, only 6 (i.e. 18.75%) are shared with the IWP. As nothing is known about the larval longevity of these species (and Pontoniinae in general), their mode of dispersal can only be speculated upon. It is however, noteworthy that three of these [*F. chacei*, *H. depressa*, *Harpiliopsis spinigera* (Ortmann)] are commensals of pocilloporid corals; with *Pocillopora* corals being the most commonly recorded corals on rafting objects (Jokiel, 1984, 1989, 1990). Although no actual shrimps have been recorded from rafts, DeVantier (1992) did record a single crab species, amongst many other groups. The majority of TEP Pontoniinae are endemics, amounting to nearly 84%, the highest number of any Pacific area. Unfortunately no phylogenetic analysis has been carried out of the species concerned, hence their evolutionary affinities are unclear. Nevertheless, in the genus *Periclimenta*, species are found with close affinities to Caribbean species, whilst the sponge dwelling species *Typton tortugae* McClendon occurs in both the TEP and in the western Atlantic, proving evidence for a biogeographical link through the Central American seaway.

Within the IWP, Hawaii forms a sister-area to all remaining areas in all analyses, whilst French Polynesia forms a further sister-area to all remaining inclusive areas.

The basal position in the PAE analyses of Hawaii is probably linked to its long geological history, as the Hawaiian-Emperor Chain has been in existence since at least 70 Ma (oldest non-subducted seamount), with present islands being dated at 1–28 Ma (Grigg, 1997). Nevertheless, it is only since the middle Oligocene that gyral circulation strengthened in the north Pacific and coral colonization could take place (Grigg, 1997). The Hawaiian fauna also appears to be a mixture of relatively widespread species, as a result of dispersal aided by the western boundary current system, and perhaps relatively recently evolved endemic species. In contrast to Hawaii, French Polynesia harbours more species, but with the lowest level of endemism within the study area. As the atolls and reefal systems in this area are relatively young, being dated at between 0.30 and 4.80 Ma (Diraison *et al.*, 1991) and as the main current system feeding into the area is the South Equatorial current originating in the western part of the Pacific, it is assumed that both these factors contributed to the low number of species encountered and the very low level of endemism. The number of coral species is also low (50–100) compared with the Indo-Philippine area (>400) (Veron, 1995), lending support to the potential lack of successful colonization.

In all PAE analyses, New Caledonia forms a sister-area to all remaining IWP areas. New Caledonia is an old Gondwana land fragment, which drifted apart together with New Zealand from the rest of the Australian block by at least 60 Ma occupying its present location by about 30 Ma (Burrett *et al.*, 1991). Throughout this period, New Cale-

donia has been separated from nearby islands and reefs by deep water basins and by poorly developed current gyres. This probably explains the high levels of endemism encountered, as genetic interchange of ancestral stock was probably limited by these factors, aiding in speciation.

Melanesia maintains a stable position in all PAE analyses, forming a sister-area to all remaining IWP areas. This area consists of the margin of the Pacific Plate and essentially comprises of a string of 'stepping stones' throughout much of its geological history (Burrett *et al.*, 1991). At the north-western end (region of Irian Jaya), this area connects quite seamlessly with the Indo-Philippine area, whilst the South Equatorial and the Equatorial Counter current systems provide a good vehicle for dispersal along the chain. During the glacial pulses of the Pleistocene this area was not connected to the Indo-Philippine area, as the Timor Sea became episodically dry, whilst strong seasonal and non-seasonal barriers were present in the eastern part of present-day Indonesia (Fleminger, 1986; Voris, 2000). Possibly, these land barriers resulted in changes in current strength and direction south of Melanesia, further isolating the area from Queensland. It therefore appears probable that following the abatement of glacial pulses, dispersal may have followed rapidly, but the present pontoniid fauna of Melanesia still bears testimony to this period of isolation of the western part of the IWP. The low levels of endemism may partly be linked to the absence of comprehensive studies from many localities in this area, with only the northern coastline of Papua New Guinea being adequately sampled (De Grave, 2000).

The crown clades of the PAE analyses are less resolved, with specific areas taking different positions, according to the restrictions of the particular analysis. A number of general observations can however, be made. Under Wagner parsimony (dispersal allowed) Queensland is a sister-area of NW Australia and the Indo-Philippine areas combined, whilst Queensland forms a sister-area of all western IWP areas under Dollo parsimony (no dispersal). The closure of the Timor Sea during the glacial pulses of the Pleistocene (Fleminger, 1986; Voris, 2000) effectively isolated Queensland from the western part of the IWP, with potential dispersal during interglacial periods, as a result of the Indonesian throughflow current. Essentially, the analytical restrictions applied (Dollo vs. Wagner) explains the position of Queensland in the cladograms. There is a relatively clear disjunction between the western parts of the Indian Ocean and the Indo-Philippine + NW Australia areas. These two regions have been separated by deep water, with a low density of 'stepping stones' since the opening of the proto-Indian Ocean in the late Jurassic. Although strong seasonally driven currents may have enabled successful dispersal, mainly from west to east along the Equatorial Counter current. Perhaps because of these dispersal routes, the Maldives and Andaman Islands occupy an intermediate position between these two regions in the cladograms, as they do in present day geography. Certainly, strong monsoon-driven currents exist in the Indian Ocean region, enabling both west to east and vice versa dispersal. Evidence

for this hypothesis can be found in the faunal affinity (number of species shared, expressed as a percentage of the Maldives or Andaman Islands species richness) of both regions with the surrounding areas. For the Maldives, these percentages are 86.4% for the W. Indian Ocean and 77.3% for the Indo-Philippine area, whilst for the Andaman Islands these are 81.8% and 90.9%, respectively. As the Pontoniinae fauna of these two areas is imperfectly known, more solid hypotheses cannot be derived.

In conclusion, Pontoniinae exhibit broad biogeographical patterns, which are in congruence with previous broad scale patterns of many Indo-Pacific taxa (e.g. Hoeksema, 1989; Wallace *et al.*, 1991; van Soest, 1994). A close correlation is observed between the biogeographical pattern of other coral reef associated taxa and Pontoniinae, undoubtedly linked to the commensal nature of Pontoniinae, many of which are commensal on these taxa. More biogeographical studies of marine taxa are needed, before general hypothesis about Indo-Pacific marine biogeography can be put forward. It is however, clear that the explanation of the observed patterns cannot be explained by vicariance or dispersal in isolation, but that an integrated approach, including sea level changes, vicariant events and dispersal events, is needed to explain the observed historical biogeographical patterns.

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BIOSKETCH

Sammy De Grave works on the taxonomy and biogeography of several groups of caridean shrimps. Current research is focusing on the biodiversity of coral reef associated Pontoniinae, including their biogeography and patterns in their description. Other research strands include taxonomy, phylogeny and biogeography of the genus *Crangon* and allied taxa.

Appendix Distribution of taxa across operational geographical units (OGU), including putative occurrences (? and 1). For details of putative scoring see text. OGU's: W. Indian Ocean (A), Red Sea (B), Maldives (C), Andaman Islands (D), Indo-Philippine area (E), Melanesia (F), NW Australia (G), Queensland (H), New Caledonia (I), French Polynesia (J), Hawaii (K) and Tropical Eastern Pacific (L)

	A	B	C	D	E	F	G	H	I	J	K	L
<i>Allopontonia iani</i> Bruce	1	?	0	0	0	0	0	1	0	0	0	1
<i>Anapontonia denticauda</i> Bruce	1	?	?	?	1	0	0	1	0	0	0	0
<i>Anchiopontonia hurii</i> (Holthuis)	0	0	0	0	0	1	0	0	1	1	0	0
<i>Anchistus Borradaile</i>	1	1	1	1	1	1	1	1	1	1	0	0
<i>Anchistus australis</i> Bruce	0	0	0	0	1	1	1	1	1	0	0	0
<i>Anchistus custoides</i> Bruce	0	0	0	0	1	1	0	1	0	0	0	0
<i>Anchistus custos</i> (Forskål)	1	1	1	1	1	1	1	1	1	0	0	0
<i>Anchistus demani</i> Kemp	1	?	1	1	1	1	?	1	1	1	0	0
<i>Anchistus gravieri</i> Kemp	0	0	0	0	0	0	0	1	1	0	0	0
<i>Anchistus miersi</i> (De Man)	1	1	1	1	1	1	?	1	1	1	0	0
<i>Anchistus pectinis</i> Kemp	1	?	?	1	1	0	0	1	1	0	0	0
<i>Apopontonia</i> Bruce	1	?	1	?	?	1	1	1	1	0	0	0
<i>Apopontonia dubia</i> Bruce	0	0	0	0	0	1	0	1	1	0	0	0
<i>Apopontonia falcirostris</i> Bruce	1	?	1	?	?	1	0	1	0	0	0	0
<i>Araiopontonia odontorhyncha</i> Fujino & Miyake	0	0	0	0	1	1	0	0	0	0	0	0
<i>Chernocaris placunae</i> Johnson	0	0	0	0	1	0	1	0	0	0	0	0
<i>Conchodytes</i> Peters	1	1	1	1	1	1	1	1	1	1	0	0
<i>Conchodytes biunguiculatus</i> (Pauls'on)	1	1	?	1	1	1	0	0	0	0	0	0
<i>Conchodytes maculatus</i> Bruce	0	0	0	0	1	0	1	0	0	0	0	0
<i>Conchodytes meleagrinae</i> Peters	1	1	1	1	1	1	1	1	1	1	1	0
<i>Conchodytes monodactylus</i> Holthuis	0	0	0	0	1	1	1	1	0	0	0	0
<i>Conchodytes nipponensis</i> (de Haan)	0	0	0	1	1	0	1	1	0	0	0	0
<i>Conchodytes tridacnae</i> Peters	1	1	1	1	1	1	?	1	1	1	1	0
<i>Coralliocaris</i> Stimpson	1	1	1	1	1	1	1	1	1	1	0	0
<i>Coralliocaris brevirostris</i> Borradaile	0	0	0	0	0	1	0	1	0	0	0	0
<i>Coralliocaris graminea</i> (Dana)	1	1	1	1	1	1	1	1	1	1	0	0
<i>Coralliocaris macrophthalma</i> (H. Milne Edwards)	1	1	0	0	0	0	0	0	0	0	0	0
<i>Coralliocaris nudirostris</i> (Heller)	1	1	0	0	1	1	0	0	1	1	0	0
<i>Coralliocaris pavonae</i> Bruce	1	?	0	0	0	1	0	0	0	0	0	0
<i>Coralliocaris superba</i> (Dana)	1	1	1	1	1	1	?	1	1	1	0	0
<i>Coralliocaris venusta</i> Kemp	1	1	1	1	1	1	?	1	?	0	0	0
<i>Coralliocaris viridis</i> Bruce	1	?	1	1	1	1	1	?	1	0	0	0
<i>Dasella</i> Lebour	0	0	0	0	1	0	1	1	0	0	0	0
<i>Dasycaris</i> Kemp	1	?	?	?	1	0	0	1	1	0	0	0
<i>Dasycaris ceratops</i> Holthuis	1	?	?	?	1	0	0	1	0	0	0	0
<i>Dasycaris symbiotes</i> Kemp	0	0	0	0	1	0	0	0	1	0	0	0
<i>Dasycaris zanzibarica</i> Bruce	1	?	?	?	1	0	0	1	1	0	0	0
<i>Epipontonia</i> Bruce	0	0	0	0	0	0	1	1	0	0	0	0
<i>Eupontonia noctalbata</i> Bruce	1	?	0	0	1	0	0	0	0	0	0	0
<i>Exoclimenella</i> Bruce	0	1	1	?	1	1	0	0	0	1	0	0
<i>Exoclimenella denticulatus</i> (Nobili)	0	0	0	0	0	1	0	0	0	1	0	0
<i>Exoclimenella maldivensis</i> Duris & Bruce	0	0	1	0	0	1	0	0	0	0	0	0
<i>Exoclimenella sibogae</i> (Holthuis)	0	0	0	0	1	1	0	0	0	0	0	0
<i>Hamodactyloides incompletus</i> (Holthuis)	1	1	?	?	1	1	0	1	?	0	0	0
<i>Hamodactylus</i> Holthuis	1	1	?	?	1	1	1	1	1	0	0	0
<i>Hamodactylus aqabai</i> Bruce & Svoboda	0	1	0	0	0	0	0	1	0	0	0	0
<i>Hamodactylus boschmai</i> Holthuis	1	?	?	?	1	0	1	1	1	0	0	0
<i>Hamodactylus noumeae</i> Bruce	1	?	?	?	1	1	1	1	1	0	0	0
<i>Hamopontonia</i> Bruce	0	0	0	0	1	1	1	1	0	0	0	0
<i>Hamopontonia corallicola</i> Bruce	0	0	0	0	1	1	1	1	0	0	0	0
<i>Harpiliopsis beaupresii</i> (Audouin)	1	1	1	1	1	1	1	1	?	1	1	0
<i>Harpiliopsis spinigera</i> (Ortmann)	1	?	1	1	1	1	?	1	?	1	0	1
<i>Ischnopontonia lophos</i> (Barnard)	1	?	?	?	1	1	1	1	?	0	0	0
<i>Jocaste</i> Holthuis	1	1	1	1	1	1	?	1	1	1	0	0
<i>Jocaste japonica</i> (Ortmann)	1	1	1	1	1	1	?	1	1	1	0	0
<i>Jocaste lucina</i> (Nobili)	1	1	1	1	1	1	?	1	1	1	0	0
<i>Mesopontonia</i> Bruce	0	0	0	0	1	0	0	1	1	0	0	0

Appendix continued

	A	B	C	D	E	F	G	H	I	J	K	L
<i>Metapontonia fungiicola</i> Bruce	1	?	0	0	1	0	0	0	0	0	0	0
<i>Onycoaridella</i> Bruce	1	?	?	?	1	1	0	1	0	0	0	0
<i>Onycoaridella monodoa</i> (Fujino & Miyake)	1	?	?	?	1	1	0	1	0	0	0	0
<i>Onycoaridella stenolepis</i> (Holthuis)	0	0	0	0	1	1	0	0	0	0	0	0
<i>Onycoaridites anomodactylus</i> Bruce	0	0	0	0	1	0	1	0	0	0	0	0
<i>Onycoaris</i> Nobili	1	?	?	?	1	1	1	1	1	1	1	0
<i>Onycoaris amakusensis</i> Fujino & Miyake	1	?	?	?	1	0	0	1	0	0	0	0
<i>Onycoaris aualitica</i> (Nobili)	1	?	?	?	1	0	0	0	0	0	0	0
<i>Onycoaris callyspongiae</i> Fujino & Miyake	1	?	?	?	1	0	0	0	0	0	0	0
<i>Onycoaris oligodentata</i> Fujino & Miyake	0	0	0	0	1	0	0	1	0	0	0	0
<i>Onycoaris quadratophthalma</i> (Balss)	0	0	0	0	1	1	1	0	0	1	1	0
<i>Onycoaris seychellensis</i> Bruce	1	?	?	?	1	1	0	0	0	0	0	0
<i>Onycoaris spinosa</i> Fujino & Miyake	0	0	0	0	1	0	0	1	0	0	0	0
<i>Orthopontonia ornata</i> (Bruce)	1	?	0	0	0	1	0	1	0	0	0	0
<i>Palaemonella lata</i> Kemp	1	?	0	1	1	0	0	0	0	1	1	0
<i>Palaemonella pottsi</i> (Borradaile)	1	?	?	?	1	1	1	1	0	0	0	0
<i>Palaemonella rotumana</i> (Borradaile)	1	1	1	1	1	1	1	1	1	1	0	0
<i>Palaemonella spinulata</i> Yokoya	1	?	?	?	1	0	1	1	0	0	0	0
<i>Palaemonella tenuipes</i> Dana	1	1	0	0	1	1	0	0	1	1	1	0
<i>Paranchistus</i> Holthuis	1	?	?	?	1	1	0	1	1	1	0	0
<i>Paranchistus armatus</i> (H. Milne Edwards)	0	0	0	0	1	1	0	1	0	0	0	0
<i>Paranchistus pycnodontae</i> Bruce	0	0	0	0	1	1	0	1	0	1	0	0
<i>Parapontonia nudirostris</i> Bruce	0	0	0	0	1	0	0	1	1	0	0	0
<i>Paratypton siebenrocki</i> Balss	1	1	?	?	1	1	0	1	0	0	0	0
<i>Periclimenaeus arabicus</i> (Calman)	1	?	1	1	1	1	1	1	1	0	0	0
<i>Periclimenaeus bidentatus</i> Bruce	1	1	0	0	0	1	1	1	1	0	0	0
<i>Periclimenaeus djiboutensis</i> Bruce	1	1	?	?	1	0	0	1	0	0	0	0
<i>Periclimenaeus gorgonidarum</i> (Balss)	0	0	0	0	1	0	0	1	0	0	0	0
<i>Periclimenaeus hecate</i> (Nobili)	1	1	1	1	1	0	1	1	0	0	0	0
<i>Periclimenaeus leptodactylus</i> Fujino & Miyake	1	?	?	?	1	0	0	0	0	0	0	0
<i>Periclimenaeus minutus</i> Holthuis	1	?	?	?	1	0	0	0	0	0	0	0
<i>Periclimenaeus nobilii</i> Bruce	0	1	0	0	0	1	0	0	1	0	0	0
<i>Periclimenaeus quadridentatus</i> (Rathbun)	0	0	0	0	0	0	0	1	0	0	1	0
<i>Periclimenaeus rastrifer</i> Bruce	0	0	0	0	1	1	0	1	1	0	0	0
<i>Periclimenaeus rhodope</i> (Nobili)	1	1	0	0	1	0	0	1	0	0	0	0
<i>Periclimenaeus stylirostris</i> Bruce	0	0	0	0	0	1	1	0	1	0	0	0
<i>Periclimenaeus tridentatus</i> (Miers)	1	?	?	?	1	0	1	1	0	1	1	0
<i>Periclimenaeus trispinosus</i> Bruce	1	?	0	0	0	0	1	0	0	0	0	0
<i>Periclimenaeus tuamotae</i> Bruce	1	?	0	0	0	0	1	1	0	1	0	0
<i>Periclimenella</i> Bruce	1	1	1	1	1	1	1	1	1	1	0	0
<i>Periclimenella pettithouarsii</i> (Audouin)	1	1	0	0	0	0	0	0	0	0	0	0
<i>Periclimenella spinifera</i> (de Man)	1	?	1	1	1	1	1	1	1	1	0	0
<i>Periclimenes affinis</i> (Zehntner)	0	0	0	?	1	1	1	1	1	0	0	0
<i>Periclimenes agag</i> Kemp	0	1	0	1	0	1	0	1	1	0	0	0
<i>Periclimenes alcocki</i> Kemp	1	?	1	1	1	0	0	1	0	0	0	0
<i>Periclimenes amboinensis</i> (de Man)	0	0	0	0	1	1	0	1	1	0	0	0
<i>Periclimenes anymone</i> De Man	0	0	0	1	1	1	1	1	1	0	0	0
<i>Periclimenes andamanensis</i> Kemp	1	?	1	1	1	0	0	1	0	0	0	0
<i>Periclimenes attenuatus</i> Bruce	0	0	0	0	1	1	0	1	0	0	0	0
<i>Periclimenes batei</i> (Borradaile)	1	?	0	0	1	0	0	0	0	0	0	0
<i>Periclimenes brevicarpalis</i> (Schenkel)	1	1	1	1	1	1	1	1	1	0	0	0
<i>Periclimenes brockettii</i> Borradaile	0	0	1	0	0	0	0	1	0	0	0	0
<i>Periclimenes brucei</i> Duris	1	?	1	0	0	0	0	0	0	0	0	0
<i>Periclimenes calmani</i> Tattersall	0	1	0	1	0	0	0	0	0	0	0	0
<i>Periclimenes ceratophthalmus</i> Borradaile	1	?	1	1	1	1	0	1	0	0	0	0
<i>Periclimenes commensalis</i> Borradaile	1	?	?	?	1	1	1	1	1	0	0	0
<i>Periclimenes consobrinus</i> (de Man)	1	1	0	0	1	0	0	1	0	0	0	0
<i>Periclimenes cornutus</i> Borradaile	0	0	1	0	0	0	0	1	0	0	0	0
<i>Periclimenes cristimanus</i> Bruce	0	0	0	0	1	1	0	1	0	0	0	0
<i>Periclimenes demani</i> Kemp	1	?	0	0	1	0	0	0	0	0	0	0

Appendix continued

	A	B	C	D	E	F	G	H	I	J	K	L
<i>Petchimenes digitalis</i> Kemp	0	0	0	1	1	0	0	0	0	0	0	0
<i>Petchimenes diversipes</i> Kemp	1	1	1	1	1	0	1	1	0	0	0	0
<i>Petchimenes edwardsii</i> (Pauls' on)	1	1	0	0	0	0	0	0	0	0	0	0
<i>Petchimenes elegans</i> (Pauls' on)	1	1	1	0	1	1	1	1	?	1	1	0
<i>Petchimenes ensifrons</i> (Dana)	1	1	?	?	?	1	0	0	1	1	0	0
<i>Petchimenes galathea</i> Holthuis	1	?	0	0	1	0	1	1	0	0	0	0
<i>Petchimenes grandis</i> (Stimpson)	1	1	?	?	?	1	1	0	1	1	0	0
<i>Petchimenes hertwigi</i> Balss	0	0	0	0	1	0	0	1	1	0	0	0
<i>Petchimenes hirsutus</i> Bruce	1	?	0	0	0	1	0	0	1	0	0	0
<i>Petchimenes holthuisi</i> Bruce	1	1	1	1	1	1	1	1	1	0	0	0
<i>Petchimenes imperator</i> Bruce	1	1	?	?	?	1	?	1	1	0	1	0
<i>Petchimenes incertus</i> Borradaile	1	?	1	1	1	1	1	1	1	0	0	0
<i>Petchimenes indicus</i> (Kemp)	0	0	0	1	1	0	1	1	0	0	0	0
<i>Petchimenes inornatus</i> Kemp	1	?	1	1	1	1	0	1	0	0	0	0
<i>Petchimenes investigatoris</i> Kemp	0	0	0	0	1	0	1	1	0	0	0	0
<i>Petchimenes jugalis</i> Holthuis	1	?	?	?	?	0	0	0	0	0	0	0
<i>Petchimenes kempii</i> Bruce	1	1	?	1	1	1	1	1	?	0	0	0
<i>Petchimenes kororensis</i> Bruce	0	0	0	0	1	1	0	1	1	0	0	0
<i>Petchimenes lampes</i> Kemp	1	?	1	1	1	0	1	1	0	0	0	0
<i>Petchimenes lepidus</i> Bruce	1	?	1	0	0	0	0	0	0	0	0	0
<i>Petchimenes longirostris</i> (Borradaile)	1	1	1	1	1	1	?	1	?	0	0	0
<i>Petchimenes lutescens</i> (Dana)	1	1	1	1	1	1	1	1	?	0	0	0
<i>Petchimenes maderporae</i> Bruce	1	?	?	?	?	1	1	1	0	1	0	0
<i>Petchimenes magnificus</i> Bruce	0	0	0	0	0	0	1	1	1	0	0	0
<i>Petchimenes mabei</i> Bruce	1	?	0	0	0	0	1	1	0	1	0	0
<i>Petchimenes nilandensis</i> Borradaile	1	0	1	1	1	0	1	1	1	0	0	0
<i>Petchimenes novaecaledoniae</i> Bruce	0	0	0	0	1	0	1	0	1	0	0	0
<i>Petchimenes obscurus</i> Kemp	1	?	0	0	0	0	1	0	1	0	0	0
<i>Petchimenes ornatus</i> Bruce	0	0	0	0	0	1	0	1	0	0	0	0
<i>Petchimenes ornatus</i> Bruce	1	1	?	?	?	1	0	1	0	0	0	0
<i>Petchimenes perlucidus</i> Bruce	1	?	0	0	0	1	0	0	0	0	0	0
<i>Petchimenes perturbans</i> Bruce	1	?	?	?	?	0	0	0	0	0	0	0
<i>Petchimenes pholeter</i> Holthuis	1	?	?	?	?	1	0	0	0	0	0	0
<i>Petchimenes pilipes</i> Bruce & Zmarzly	0	0	0	0	1	1	0	0	0	0	0	0
<i>Petchimenes platychelus</i> Holthuis	0	0	0	0	1	1	0	1	1	0	0	0
<i>Petchimenes psamthe</i> (de Man)	1	?	1	1	1	1	1	1	1	0	0	0
<i>Petchimenes seychellensis</i> Borradaile	1	1	1	1	1	1	1	1	1	0	0	0
<i>Petchimenes sinensis</i> Bruce	0	0	0	0	1	0	1	0	0	0	0	0
<i>Petchimenes tenuipes</i> Borradaile	1	1	1	1	1	1	1	1	1	0	0	0
<i>Petchimenes tenuis</i> Bruce	1	1	?	?	?	1	1	1	1	0	0	0
<i>Petchimenes toloensis</i> Bruce	1	?	?	?	?	1	0	1	0	0	0	0
<i>Petchimenes tosaensis</i> Kubo	1	?	?	?	?	1	0	0	0	0	0	0
<i>Petchimenes venustus</i> Bruce	0	0	0	0	1	1	1	0	0	0	0	0
<i>Petchimenes watanuae</i> Bruce	1	?	0	0	0	1	0	0	0	0	0	0
<i>Petchimenes zanzibariensis</i> Bruce	1	?	0	0	0	0	1	0	0	0	0	0
<i>Petchimenes zeiniae</i> Duris	1	?	1	0	0	0	0	0	0	0	0	0
<i>Petchimenesoides odontodactylus</i> (Fujino & Miyake)	0	0	0	0	1	0	0	1	0	0	0	0
<i>Philarius</i> Holthuis	1	1	1	1	1	1	1	1	1	1	0	0
<i>Philarius gerlachei</i> (Nobli)	1	1	1	1	1	1	1	1	?	1	0	0
<i>Philarius imperialis</i> (Kubo)	1	1	1	1	1	1	1	1	1	0	0	0
<i>Philarius lifuensis</i> (Borradaile)	0	0	0	0	0	0	0	0	1	0	0	0
<i>Platycauris latirostris</i> Holthuis	1	?	?	?	?	1	1	1	1	0	0	0
<i>Platyponomia</i> Bruce	1	?	?	?	?	1	0	0	0	0	0	0
<i>Platyponomia hvoitis</i> Hipeau-Jaquotte	1	?	?	?	?	1	0	0	0	0	0	0
<i>Pliopontonia furtiva</i> Bruce	1	?	?	?	?	1	0	0	1	0	0	0
<i>Pontonia ascidicola</i> Borradaile	1	?	?	?	?	1	0	0	1	0	0	0
<i>Pontonia katoi</i> Kubo	1	?	?	?	?	1	0	1	1	0	0	0
<i>Pontonia okai</i> Kemp	1	?	1	1	1	0	1	1	0	0	0	0

Appendix continued

	A	B	C	D	E	F	G	H	I	J	K	L
<i>Pontonia sibogae</i> Bruce	1	?	?	?	1	1	0	1	0	0	0	0
<i>Pontonia stylirostris</i> Holthuis	1	?	?	?	1	0	0	1	0	0	0	0
<i>Pontoniopsis comanthi</i> Borradaile	1	1	?	?	1	1	0	1	0	0	0	0
<i>Stegopontonia commensalis</i> Nobili	1	?	?	?	1	1	?	1	1	1	1	0
<i>Thaumastocaris streptopus</i> Kemp	1	1	?	?	1	1	0	1	1	0	0	0
<i>Tuleariocaris</i> Hipeau-Jacquotte	1	?	?	?	1	0	0	1	0	0	1	0
<i>Tuleariocaris holthuisi</i> Hipeau-Jacquotte	1	?	0	0	0	0	0	1	0	0	1	1
<i>Tuleariocaris zanzibarica</i> Bruce	1	?	?	?	1	0	0	0	0	0	0	0
<i>Typton bawii</i> Bruce	1	?	?	?	1	0	0	1	0	0	0	0
<i>Typtonychus</i> Bruce	0	0	0	0	1	0	1	1	1	0	0	0
<i>Typtonychus dentatus</i> (Fujino & Miyake)	0	0	0	0	1	0	1	1	0	0	0	0
<i>Vir</i> Holthuis	1	?	1	1	1	1	?	1	?	0	1	0
<i>Vir orientalis</i> (Dana)	1	?	1	1	1	1	?	1	?	0	1	0
<i>Vir philippinensis</i> Bruce & Svoboda	0	0	0	0	1	1	0	1	0	0	0	0
<i>Zenopontonia noverca</i> (Kemp)	1	?	0	0	0	0	0	1	1	0	0	0